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Vegetation pattern and disturbance effects in the subalpine-alpine interface, Valley of the Ten Peaks, Alberta

Katherine J. Miller
Wilfrid Laurier University

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VEGETATION PATTERN AND DISTURBANCE EFFECTS IN THE SUBALPINE-ALPINE INTERFACE, VALLEY OF THE TEN PEAKS, ALBERTA

by

Katherine J. Miller

A thesis
presented to Wilfrid Laurier University
in partial fulfillment of the
requirements for the degree of

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in
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ABSTRACT

There have been several recent calls in the biogeography and vegetation ecology literature to investigate more thoroughly the role of recurrent disturbance or perturbation in the dynamics of subalpine communities, by assessing persistence and change in the dominant species populations.

In order to study the relationship between conifer regenerative effectiveness, disturbance effects, and the nature of the vegetation pattern, a field study was made of the vegetative cover (composition, abundance, dominance) and its performance (survival, vigour and reproductive mode) in the upper subalpine zone in the Valley of the Ten Peaks, Banff National Park, Alberta. The occurrence of stresses and disturbances is both spatially and temporally sporadic in this zone, and this variable disturbance regime contributes significantly to the 'patchiness' in vegetation cover and performance.

There seems insufficient grounds for labelling this field situation an 'abnormality', or a 'severely-delayed' secondary succession, as no overall replacement community is indicated.

Since it is true in all ecological systems that (A) disturbance effects are spatially and temporally sporadic, and

(F) that just as this environmental change and heterogeneity is ongoing, so will species and populations have ever-readjusting and differential responses, some problems with the strictly developmental scheme of vegetation change emerge. These shortcomings are discussed particularly as they hamper accurate interpretation of a patchy mosaic ecotone.

"This borderland between the upper trees and the barren rocks, where the evergreens scatter and dwindle into a starved and blasted form, is a most interesting region." -- Walter Wilcox (1916) on his first visit (1899) to the upper Valley of the Ten Peaks.

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Chapter I

INTRODUCTION

1.1 THE STUDY OF LANDSCAPE PATTERN

One of the central concerns of geographers, as students of spatial distributions, is the identifying and delineating of landscape patterns, analyzing and interpreting the mechanisms that give rise to them, and developing an understanding of their significance in biological and human terms (Durrenberger, 1971; Haring and Lounsbury, 1971; Fosberg, 1976). In particular, biogeographers, geobotanists and many plant ecologists have chosen to emphasize the patterns and nature of vegetation as a vital, visible landscape feature.

The strategies for seeking spatial and temporal explanations of vegetation patterns are legion. Unfortunately, spatial and temporal explanations are often kept distinct, as are their concomitant assumptions and methods (Mueller-Dombois & Ellenberg, 1974). For example, studies which seek to correlate vegetation gradients with site factors emphasize spatial configurations of species in relation to spatial variations in environment. The interest is in *pattern through space* ; that usually includes only a cursory treatment of historical factors or of future directions in the community. The alternate focus is on *pattern through time* : that embraces the causal-analysis of the origin of plant communities, and "succession" or changes in population structure over time. The biotic and edaphic factors, as well as historic factors such as catastrophic disturbances or climatic changes which initiate plant population dynamics are examined. However, the quality and amount of *spatial* information retained is often sketchy.

Most of the questions posed in plant geography research seem to require the use of both strategies. The challenge of describing plant communities as a key landscape feature *both* as coexistent and successional phenomena is large. It is central for all who would make the interpretation of patterns on the landscape their field of study.

1.2 PROBLEM AREA: THE ROLE OF DISTURBANCE IN SUBALPINE VEGETATION DYNAMICS

Mountainous areas are characterized by sharp and often extreme diversity. The biotic environment displays extreme heterogeneity in time, space and pattern, in direct response to variability in all physical parameters (Webber, 1979). Among these, the position and nature of the subalpine-alpine boundary zone has particularly attracted the attention of ecologists and plant geographers. Moreover this is an ecotone where the complications encountered generally in the causal-analytical research of plant geography are intensified. Close examination of subalpine units in the field reveals marked spatial heterogeneity. Variations in physiographic, edaphic, climatic and biotic conditions are often striking over a short horizontal distance.

Arno and Habeck (1972:420) emphasize the mosaic quality of this zone, "where the dominant vegetation may assume diverse life forms, where homogeneous units of "communities" seem to be absent or tiny, and where unusually prevalent and destructive natural forces (wind, snow, avalanche, fire) seem to defy application of traditional succession-climax concepts". They refer specifically to timberlines which include _Larix lyallii_: "each stand is much more obviously unique in its composition and environment than stands in the forest zones below" (Arno & Habeck:1972, 447).

The existence of a complex pattern in space is also believed to reflect highly variable conditions over time. Thus Major (1979:477) emphasizes that, for example, the sort of "steady state" models used to describe vegetation dynamics over periods of decades or more in other areas, "should not be applied to many problems of timberline plant ecology". This paper shares with a growing body of ecological literature, the view that the conventional succession and climax oriented views are difficult to maintain in many if not all environments. They are especially problematic and appear hardly relevant in the upper subalpine zone.

In approaching our problem we can draw upon the existing wealth of research into the autecology of single tree species, and the physiological ecology of individual trees, attempting to identify the limiting life-factor or factor-complex at timberline (Slatyer, 1976; Baig & Tranquillini, 1976; Tranquillini, 1979; Hansen Bristow, 1979). The performance of individuals or species has been related to particular habitat factors in detail for both alpine and subalpine zones, at several western North American locations (Klikoff, 1965; Fonda & Bliss, 1969; Kuramoto & Bliss, 1970; Sandgren & Noble, 1978). These authors have taken many directions with these vegetation-environment correlations, for example, comparisons with lower elevations, comparison to other treeline zones within one region, or comparisons across several high-altitude regions.

The problem remains, however, that <u>at the community level</u>, the understanding of subalpine vegetation dynamics is poorly developed. That applies to the particular problem which interests this author; the examination of the role of disturbance in vegetation patterns of the upper subalpine. Disturbance 'events' (whether sudden or gradual, direct or indirect) are part of the spectrum of environmental factors that creates and maintains the patchwork units on the landscape. Despite their acknowledged importance, the discussion of disturbances, (except for a small literature on more catastrophic influences) and their timing, nature, and severity, is subsidiary or completely absent from many studies.

For all types of ecosystems, "the role of disturbances—whether natural such as fire, landslides, hurricanes, tornadoes, or floods; or man-created such as forest cutting-- in forest succession is becoming increasingly appreciated" (Oliver and Stephens, 1977:563). Henry and Swan (1974:781) also recognize this need: "There are major gaps in our knowledge of changes in forest vegetation associated with different kinds and intensities of disturbance on different sites".

Mueller-Dombois and Ellenberg (1974:368) seem to encourage the cultivation of this important approach specifically in relation to vegetation pattern:

> A historical analysis of at least the main groups of regional environmental factors and perturbations with regard to their spatial distribution, frequency, and intensity in time. Identification and evaluation of evolutionary stress factors depend on a knowledge of their permanency and pattern of operation.

A discussion of montane ecosystem dynamics (including the role of recent disturbance) by Cole (1977) makes the point that each ecosystem has an 'average' or characteristic type and frequency of disturbance which is 'readable' in the distributions of communities as they are found. Equally visible are <u>changes</u> in these distributions in response to <u>changes</u> in the disturbance regime over time.

Many subalpine-alpine boundary zones are known to experience such changes. Adjustments to them are discernible in both structural and functional parameters of the vegetation communities (Wakefield and Barrett, 1979), such as composition, vigour, and current regenerative capacity. Thus, discussions and field examinations seem to show that a detailed examination of the actual <u>texture</u> of plant patterns as an adjustment to disturbance is a complex but profitable approach. As will be discussed, this can be done in the subalpine zone using the type of small-plot analysis used by Dix and Swan (1971), Henry and Swan (1974), Oliver and Stephens (1977), Reiners and Lang (1979) and Tande (1979). C.L.Smith (1980:1) cites the need for explicit spatial detail: "If stability and stability-related dynamics are to be understood, the spatial complexity must be treated in appropriate detail".

1.3 <u>OBJECTIVES OF THE STUDY</u>

The purpose of the study is to obtain and present evidence relating to the processes responsible for the vegetation mosaic of a particular forest-tundra ecotone. The site chosen lies in the Valley of the Ten Peaks in Banff National Park, Alberta. There is unambiguous evidence in the communities between timberline and the upper treeline of ongoing adjustment to a range of processes or conditions that are diverse both in space and time. Of particular interest for this study is the pattern of conifer regeneration following a catastrophic fire. However, that is taking place in the face of ongoing disturbing agents which include: mass movements, heavy and late snow-lie, unstable soils, climatic change, winter drought and wind-desiccation in years of short growing season. Fundamentally this thesis asks why and to what extent this particular mosaic persists: 1. Where is it changing? What are the signs of change in the vegetation structure? 2. Where are its components persisting? What mechanisms are involved in this?

The form of the analysis is to examine the main groups of controlling environmental factors (including the spatial distribution, frequency, and intensity of perturbations). Life conditions in this area are near the limits of the dominant species' tolerance ranges. Severe chronic stress and periodic disturbance effects are common. Moreover, these have impacts that are often localised in space and/or sporadic in time. The spatial heterogeneity of habitat factors is exaggerated by this 'patchiness' of disturbing agents. Of particular note are the regular avalanching of snow and of debris downhill along linear strips (Reiners & Lang, 1979) and the sudden dramatic increase in wind speed above the closed forest. The latter is out of all proportion to the rise in elevation involved (Pears, 1968).

With respect to a detailed examination of the causal factors underlying a pattern Kershaw (1973) gives the following warning principle. When pattern is slight it is likely that one or few environmental factors control it. When pattern is very marked, it is probable that a complex set of controls is involved whose effects and interactions are hard to separate. A reasonable first step is to examine spatial patterns in the plant cover at a given time, as long as one recognizes its limitations. In fact, this strategy is endorsed for alpine systems by Scott (1974:5):

> The plant cover, as the immediately observable areal expression of the interaction between components... would seem to be the logical starting point for study. A clearer idea can be gained as to possible avenues for further study into other ecosystem components from a description of the vegetation and delimitation into communities, and a visual portrayal of the spatial extent of communities on a map.

Greig-Smith (1964:55) wants to emphasize that "detection and analysis of non-randomness [pattern] is a starting-point for further investigation of the factors responsible and not an end in itself". The larger and incessant problem in vegetation dynamics research is whether vegetation in the main is shaped more by disturbance-free periods of competition and succession, or by repeated disturbance and environmental fluctuation? (White, 1979:260).

Hence, most research analysing the dynamics of a particular vegetation zone is dominated (consciously or unconsciously) by this question: What is the ratio of process controls external to the community in origin (allogenesis) and process controls originating as a result of species or within-community properties (autogenesis)? Some caution is advised however against over-dependence on this dichotomous conceptual split. Allogenesis and autogenesis are always and necessarily present. However, what is central is how they change in their relative effectiveness over time and space. A basic contention of this thesis is that by looking at their spatially varying ratios of effectiveness, we may better understand what is producing the unique community patterns.

The central research question of the thesis is this: What are the relative roles of disturbance and succession in the maintenance and the dynamics of this subalpine mosaic? It is hypothesized that, at the present, repeated disturbance and environmental fluctuation have a stronger influence on the nature of this vegetation zone.

In order to test this hypothesis, we would hope to define and examine indicators in the field that should establish whether present vegetation patterns are linked more closely to the nature and timing of perturbations (allogenic processes), or to progressive, gradual succession (autogenic processes).

Specific objectives within this general aim are:

1. To determine and record the nature of this vegetation mosaic:

   a) at the present, based on stand structure data.

b) in the past, based on direct evidence (e.g., remnant fallen logs and standing snags).

As has been suggested, the distribution, composition and vigour of stands of living trees will be measured, and compared with the extent and growth forms of the dominant species in the past.

2. To devise an inventory of all types of disturbance for which evidence exists in the field, with regard to spatial distribution, frequency in terms of lifespan of the dominants, species selectivity, and severity or duration. It is postulated here that for this particular upper subalpine area, disturbance is one of the major underlying mechanisms responsible for the series of patterns observed.
3. To ascertain the degree to which tree regeneration patterns may be attributed to certain environmental extremes (stresses and disturbances), and to assess their effects on the abundance and development of persistent vegetation features (tree islands, balds, avalanche associations, etc.).
4. To address briefly whether disturbances should be considered part of the definition of the normal environmental setting in all systems, not only in a frequently-disturbed life-zone like the subalpine.

In discussing this particular case, one can hardly ignore the question- to what time-scale and what spatial-scale should statements about vegetation change refer if they are to be valid and useful? The accuracy of such statements changes as one refers to landscape units of different levels. In fact there is an ongoing controversy in secondary succession literature that revolves partly, the author believes, around the failure to take account of such scale-related questions in the interpretation of vegetation status on any given site.

1.4 PREVIOUS WORK

Several investigations have discussed the relative importance of periodic disturbance and regenerational succession as key components in vegetation dynamics. Their perceived relative importance varies in every study. Work in this area stems from the essay of Watt (1947). He proposed a concept of community structure and dynamics significantly different from that widely held at that time. It involves viewing the plant community as a working mechanism whose patches (or phases) are dynamically related to each other. Watt stressed both the developmental, orderly, 'upgrading' phase of biomass accumulation and the destructive, anti-order, 'downgrading' phase when biomass destruction occurs. It is their alternation that results in the units or patches of the community. The patches thus produced account for short-lived or persistent patterns on the landscape. He urged that the "climax" or steady state must include <u>all</u>

phases: the very structure of the community arises from both the tendencies toward and departures from "orderliness".

Watt was working at a time when a more linear notion of vegetation development was dominant. Hence his ideas were recognized and developed only very gradually. Meanwhile, following the early work of Cowles and Clements, the developmental model held that all vegetation progresses through a sequence of successional stages. Each stage has predictable characteristics, but tends to a stable climax, which persists until some interruption occurs (H. Wright, 1974:488).

There is a tendency in this subject (as elsewhere) to see stress or disturbance as 'abnormal', as an interruption or disruption of the 'normal' progress of succession. (That many of the concepts applied to vegetation response seem to be particularly anthropomorphic notions is conspicuous and will be mentioned occasionally through this thesis.) However, as early as 1934, Taylor recognized the 'normality' and significance of extreme environmental conditions in biological communities. "Extremes, and especially intermittent or irregular extremes, must exercise a very potent influence indeed on the composition of many a biotic community" (W.P. Taylor, 1934:376).

In the literature on temporal and spatial explanations of vegetation pattern, it is possible to trace the changing view of the role of disturbance. The authors discussed next have a common aim, namely, to provide a clearer basis for understanding and incorporating the role of disturbance history as a normal process leading to visible landscape patterns (along with a host of edaphic, climatic and biotic site factors). Most of them have drawn on and amplified Watt's dynamic concept of the mechanisms underlying vegetation pattern. However, their conceptual framework is still a 'minority' view.

Orians (1975) and Harrison (1977) call for detailed data-gathering by geographers and field ecologists that allows a fuller understanding of pattern and process in relation to natural disturbance. Orian's point, for instance, is that studies of the traits of organisms that have been exposed to different kinds and frequencies of perturbations will put us in a better position to predict the effects of new (eg. man-made) and unusual perturbations.

Nevertheless, it has recently been reiterated that

> Disturbance phenomena play roles in ecosystems quite independent of human activities ...disturbance at varying scales seems to characterize most environments; this instability often has important impacts upon spatial and temporal features of vegetation. (Vale & Parker, 1980:151)

P.S. White (1979) writes that natural disturbance should be seen as a crucial part of the landscape pattern and not as a disruption or interruption of the 'norm'. His central point is that in studying changes in vegetation communities (whether rapid or very slow) it is important to see disturbances as part of the general phenomenon of dynamics in community structure, and that there are problems with seeing natural disturbances as necessarily independent of endogenous community factors.

Thus a gradual evolution in thought is occurring, from the conception of plant communities as normally fixed, tranquil stages only rarely disrupted by external change (which is thus an 'abnormal' state) to one where 'most environments' are characterized by disturbance. It is now accepted that long, stable steps with gradual species replacement and internal change probably occur in very few or a small portion of all ecosystems. Vale and Parker (1980:151) continue: "The understanding of disturbance in most wild systems is poor, however, and the causes, magnitudes, frequencies, spatial patterns, and effects of various disturbing agents need to be analyzed". Among the types of disturbances, fire has received considerable attention. Surprisingly little work has documented the significant contribution of other disturbance mechanisms (flooding, grazing, windthrow, mass movements) to the character of the vegetation in natural communities.

Dix and Swan (1971) attempted to assess the relative roles of disturbance and biological succession in creating the "patchwork quilt" of largely homogeneous units in northern Saskatchewan's boreal forest. They were interested in whole-stand behaviour and in placing each community within an alternating "pulse" cycle. Periodic severe disturbance by fire and windfall emerged as the main control with the result that most stands were dominated by one species and little succession had occurred. Dix and Swan think it inappropriate to apply a climax concept to communities so frequently disturbed. That agrees with a growing view of the subalpine zone.

Unfortunately, a common technique in many succession studies involves the inclusion in the sample only of homogeneous stands which show no signs of recent disturbance (i.e., in the lifetime of the living trees) (Wirsing & Alexander (1975) , Whipple & Dix (1979) are examples). It is true that the data thus collected can be classified into 'representative' stands, the negative and positive plant associations defined, site factors correlated with the identified community types, and comparisons made for similarity or dissimilarity with other stands. However, this set of techniques introduces some simplicity and possible artificiality into the conclusions on vegetation change. Meanwhile the "messy" aspects of community structure and complexities of overlapping patterns which are lost or ignored in the search for homogeneous units, are potentially very valuable aspects that should not be "sampled out". Deliberate examination of these aspects remains exceptional in the literature.

Hoff (1974:245) advises that spatial heterogeneity and/or instability "must be recognized as fundamental features of a natural situation" and not a drawback of field data to be neglected. It certainly is true for the subalpine-alpine situation that uniform communities are small or hard to discern and difficult to map-- environmental heterogeneity confounds the search for readily classified patterns.

As regards the study of disturbance as a process in subalpine patterns, the research coverage is very thin. Sharpe (1970:32) speaks directly of the lack of information on the importance of disturbance at the subalpine-alpine boundary- "nor has the effective climate for seedling establishment and survival been dealt with satisfactorily at timberline". "The effects of increased environmental stress (on the physiology and morphology of individuals) in determining the upper altitudinal limit of tree growth are now roughly known, but the development and dynamics of actual tree groups and krummholz communities above timberline have only occasionally been recorded (see Franklin et al., 1971; Marr, 1977). Generally, neither the aim nor the practice of botanists or autecologists has been to incorporate historical and disturbance factors into the investigation of vegetation-environmental correlations. However, a few biogeographers (listed above and below) have begun to attend to this need and have appropriate skills to apply to such interpretations of landscape pattern.

This thesis focuses on the role of disturbance (as a central property of environmental change) in producing an ecotonal vegetation pattern: alternative foci could be its effects on biomass production, or on plant phenology. Studies of the former are rare (and nearly non-existent for the Canadian Rocky Mountains), while work on the latter two is copious by comparison. A unique study by Canaday and Fonda (1974) interpreted the effects of a single environmental parameter (the variable accumulation and duration of snowpacks) on all three: pattern, production, and phenology, for an area in the Olympic Mountains, Washington.

The few works investigating the actual texture of vegetation patterns visible as landscape features in the upper subalpine are recent and of areas widely separated geographically. An excellent example for a single peak in New Hampshire (Baldwin, 1977) describes and maps a wide range of features. These include present timberline plant communities, their distribution and condition (growth rates, seed production, age groups); the plant habitats by zone (their soils, local climate, meso- and micro-topography); and a complex disturbance history of fire and human recreation.

For both montane and subalpine forests of a site in western Oregon, Cole (1977) demonstrated the links of both current vegetation and past successional trends to topographical position, slope and the extent and intensity of disturbance (human influences, mass movements, fire recurrence). Here is one of the few cases of a biogeographer analyzing both temporal and spatial variations in the distribution and vigour of tree species and comparing them for adjacent lightly- and heavily-disturbed sites.

Bonnicksen (1975) and Vankat and Major (1978) recorded and interpreted vegetation changes over space and through time in Sequoia National Park, California, using the present age-population structure of the trees and the historical and photographic record as evidence sources. Land use changes and fire suppression emerged as the primary mechanisms of vegetation change. Some of the long-range effects already in evidence and predicted for the future are soil degradation, landsliding, forest to brushfield conversion, and loss of genetic quality.

The parallel impacts of environmental stress and change on vegetation and soils was the focus of two investigations on the Continental Divide: at Boreas Pass in Colorado (Olgeirson, 1974) and at Bow Pass in Banff National Park (King & Brewster, 1978). For the upper subalpine-alpine zone, Olgeirson found the overall pattern of vegetation and soils is a product of historical and geomorphic factors. The major phytoedaphic units thus produced reflect the nature of the historical disturbance regime (forest removal, fire, mining, railroad construction, human trampling, a water diversion program, and grazing since 1922!). The "aggravated ecosystems" are contrasted with adjacent undisturbed sites.

King and Brewster also use the strategy of examining the parallel changes of vegetation and pedogenesis in response to disturbance. "The subalpine at Bow Pass is an ecotone which is highly responsive to changes in the environmental state factors" (1978:295). The soils exhibit a wide range of morphological complexities which are tied directly to volcanic ash deposition, forest fires, vegetational change, and avalanching. Their findings are useful as their study site is only 50 km. north of the author's research site.

Mention should be made of several authors who have stressed the <u>rate</u> of vegetation community replacement after disturbances (Langenheim, 1956; Placcus, 1959; Khapayev, 1978; Zalikhanov, 1978; and Scott, 1979) and after complete destruction by fire (Ives, 1941; Stahelin, 1943; Billings & Mark, 1957; Habeck & Mutch, 1973). The emphasis of these works is on the rate and direction of secondary successions, that is, a stand's position on the <u>linear sequence</u> toward the spruce/alpine fir 'climax'. The temporal analysis is strong, but spatial information slim or absent. Stahelin's useful article outlines the possible successional pathways on high-altitude 'burns' depending on the severity of the original fire, the pre-fire composition and the soil type. Reproduction and conifer restocking are especially slow on sites above the tolerance range of <u>Pinus contorta</u> because once a durable moss, forb or grassland establishes there, it presents stiff competition to tree seedlings. The factors controlling the persistence of various subclimax associations are complex and not well-understood. There will be further discussion of this effect of extant community type on regeneration success in Chapter 4.4.

In any event, these succession studies have revealed that *unpredictability* in recovery patterns (both in rate and direction) characterizes the spruce-fir and timberline zones much more than lower-elevation forests (Habeck and Mutch, 1973:417). This is directly a function of the marked mosaic quality stressed earlier, that is, the sharp differences in substrate, nutrient and moisture availability, wind speed and therefore air temperature, over short distances. Once above the ameliorating effects of the closed forest, the severity and recurrence rate of environmental extremes rise dramatically (Pears, 1968; Tranquillini, 1979). For an alpine tundra site in the Beartooth Range, Wyoming, Johnson and Billings (1962) recorded extreme climatic variability over just two field seasons: their 1959 data shows much higher wind velocity and vapour pressure deficits, and only half the precipitation of 1958.

For this same site *above* the treeline, Johnson and Billings effectively related the alpine vegetation types to patterns of topographic site, snow cover and wind. Smaller patterns within each vegetation type are produced by local disturbances: soil frost action (cryopedogenesis), gopher burrowing, and micro- wind patterns. This introduces the notion of organizing the observed patterns into several scales of pattern. This approach has only very recently been isolated and explored. Vale and Parker (1980:151) encourage biogeographers to explore the potentials of this concept:

> Of particular geographic interest is the question of the spatial scale of disturbance patterns. Though large-scale events generally initiate successional sequences...smaller-scale events...have been shown to be common in most forest ecosystems where they are essential to the maintenance of even a so-called climax-type plant community. Closer examination of this continuum of spatial scale of disturbance may provide insight into such basic concepts as threshold areas necessary to initiate cycles of species replacement.

This particular kind of organization of the variation in vegetation has rarely been attempted. The search for mechanisms and "causes" underlying landscape patterns can benefit from this activity simply of ordering scales of spatial pattern as a clarifying first step. The geographer's training in discerning and delineating patterns first before attempting the causal-analysis of their origins and their biological and human significance can bring insights into areas which seem to display "muddy" vegetation units. Before postulating the history of mechanisms bringing about these heterogeneous units, an organization of 'patches' into several orders of pattern, and a recognition of pieces of terrain with an overlap of several patch sizes and types may help to separate the overlapping and/or cumulative effects of a mix of causal mechanisms.

Only one good study of this type was found. In the White Mountains of New Hampshire, Reiners and Lang (1979) studied pattern-generating processes in the fir zone vegetation. They identified general, or first-order patterns over the landscape that are produced by elevation and wind exposure.

A series of second-order patterns overlying the general pattern are created on the one hand by acute disturbances such as hurricanes and avalanches and on the other hand by more endogenous factors. Some were found to create abrupt changes or marked features and some more subtle textures on the landscape. They conclude (p. 405) that "a conceptualization of vegetation as a hierarchical series of overlapping patterns is an extension of Watt's view of vegetation dynamics and bears important ecological implications". Such a methodology has considerable merit for the subalpine zone and was chosen for this research: to present a series of observed patterns, to discern and describe the extent and nature of actual patches, and to postulate the genesis of these overlapping scales of pattern for a single piece of terrain.

This study was undertaken partly in response to the lack of mesoscale level studies relating species and environmental patterns in the subalpine. This level of examination falls midway between the microscale (the physiological response of the individual tree to site) and the regional or macroscale (where the large-scale response of whole 'associations' and vegetation zones is the focus). There are significant and interesting mesoscale differences in species survival, density and performance on this site. The author hopes not only to report but to explain both the changing and persistent spatial patterns in this subalpine.

There is no doubt that this proposed explanation of the origin of subalpine community structure and pattern can be partial at best. It does not attempt to analyse the complete environmental complex circumscribing the distribution (in a static sense) and development (in a dynamic sense) of vegetation pattern. A comprehensive analysis of the environmental complex, which matches vegetational gradients with clustered environmental gradients, has been accomplished with admirable detail for other regions: see Langenheim (1962), Patten (1963) and Klikoff (1965), for high-altitude belts in Colorado, Montana and California, respectively.

Mueller-Dombois and Ellenberg (1974:410) point to the need to establish a spatial or geographic conceptual framework "within which community dynamics and stability can be studied in detail with regard to the kind and severity of perturbations and the response of biological communities of differing sizes".

> While usually a considerable part of community structure and pattern can be explained from an analysis of current environmental factors and competitive relations among the species, another part cannot be understood without an appreciation of certain significant events (in the form of perturbations) that took place in the past... we are primarily interested in the manifestation of such past events and in the identification of their causes (Mueller-Dombois & Ellenberg, 1974:359-60.

A helpful but perhaps unusual reference to include here are comments by Hewitt (1980:309), who is speaking of hazard and disruption in human systems but which seem applicable to questions of "vulnerability" in plant communities as well.

His concern with response to destructive or distressful phenomena and the details of process and pattern of damage which emerge contains a clue for the biogeographer. "The actual texture of failure and survival- the spatial [organization or] disorganization within damage zones- would tell...much about the specific sources of vulnerability". Like Hewitt, Kellman (1970:194) speaks to the importance of the _actual pattern_ of destruction and recovery across and within the site. The future direction and rate of succession in a stand is linked directly to the 'patchiness' of disturbance: its selectivity, its intensity and its distribution. Greig-Smith (1961:695) advises that it is useful to deal not merely with the presence or absence of species but with more subtle differences in their performance _within_ their ranges of tolerance, if the causal factors of vegetation pattern are to be understood.

It has been seen that a number of studies encourage: (a) the extension of the dynamic (vs. the developmental) concept of vegetation change and (b) the detailed examination of visible vegetation patterns to better distinguish the several processes producing them. This appropriate comment comes from Kellman (1975:116) in _Plant Geography_:

> Enlightened interpretation of the patterns of the earth's plant cover requires an increased familiarity with the complex processes and mechanisms that operate within it. This requires not only an appreciation of the fundamentals of plant biology, but also a familiarity with the developments taking place within plant ecology, population biology and evolutionary theory.

Given that discontinuities in time and space (some abrupt, some gradual) exist as vegetation pattern, it is an incipient challenge to biogeographers, geobotanists and ecologists to identify and interpret the mechanisms giving rise to them and to provide a basis for understanding their significance. To quote Johnson and Billings (1962:195), "much remains to be done before the problems involved in pattern-producing dynamics can be solved".

1.5 ORGANIZATION OF THE RESEARCH

The presentation of material in this thesis follows the steps involved in the research.

Chapter One has given the background to the research, including a review of selected relevant literature.

The next chapter will introduce the general conditions of the study zone as well as the methods employed to meet the objectives as given.

Chapter Three presents the results of the vegetation survey data analysis as an evaluation of the character of community patterns and the performance (successional status) of the dominant species. Changes in the zone along both horizontal and altitudinal gradients will describe the present vegetation and give a cursory reconstruction of the extent of former vegetation. Generally, then, Chapter 3 answers Objective One.

Chapter Four continues the presentation of results by discussing how the complex disturbance regime lends complexity to this patterning of vegetation. A simple hierarchical ordering of the spatial scales of patterns is discussed. Chapter Four, therefore, speaks to Objective Two.

In Chapter Five, the results of Chapters Three and Four are synthesized and discussed. Whether the conventional succession/climax concepts are appropriate in clarifying subalpine vegetation dynamics is evaluated. The importance of *integrating* the 'disruption' phases into an understanding of community development is stressed. This chapter speaks to several questions of additional interest, for example, was the former forest cover a *relict* in some sense from times of prior warmth and therefore when felled (i.e., by fire) will not regenerate? Evidence sources of climatic change for the last several centuries will be looked at. Concluding remarks will summarize both the steps of the research and the interpretation of the field situation. Some possible avenues for future extension of this type of project will be given.

Chapter II

STUDY SITE AND METHODOLOGY

2.1 DESCRIPTION OF STUDY SITE

Location: The site studied is part of the Valley of the Ten Peaks, Alberta, which is located 15 km by road south of Lake Louise townsite in Banff National Park (see Fig.2-1). This area of the Main Ranges of the Rocky Mountains is characterized by rugged, glaciated mountains and wide river valleys with a mix of glacial and postglacial surface deposits. There is great variety of terrain over short distances.

Geology: The geological substrata are composed of nearly horizontal layers of Precambrian to upper Cambrian quartzitic sandstones, limestones, shales, and dolomites (Gardner, 1970; 1972). The strata are thinly-bedded, jointed and of varying resistance to erosion, resulting in a "cliff and bench" type mountain slope (Gardner, 1978:2). Local relief is in the order of 1200m-1800m (3648'-5472').

Topography: The arc of steep, cold north-facing cliffs of the Ten Peaks themselves forms the south and west walls, ranging in elevation from 3045m-3415m (10018'-11235'). The circle of peaks is completed on the north by Eiffel Peak 3071m (10101'), Pinnacle Mt. 3059m (10062'), and Mt. Temple 3534m (11626'), the highest peak in this part of the park.

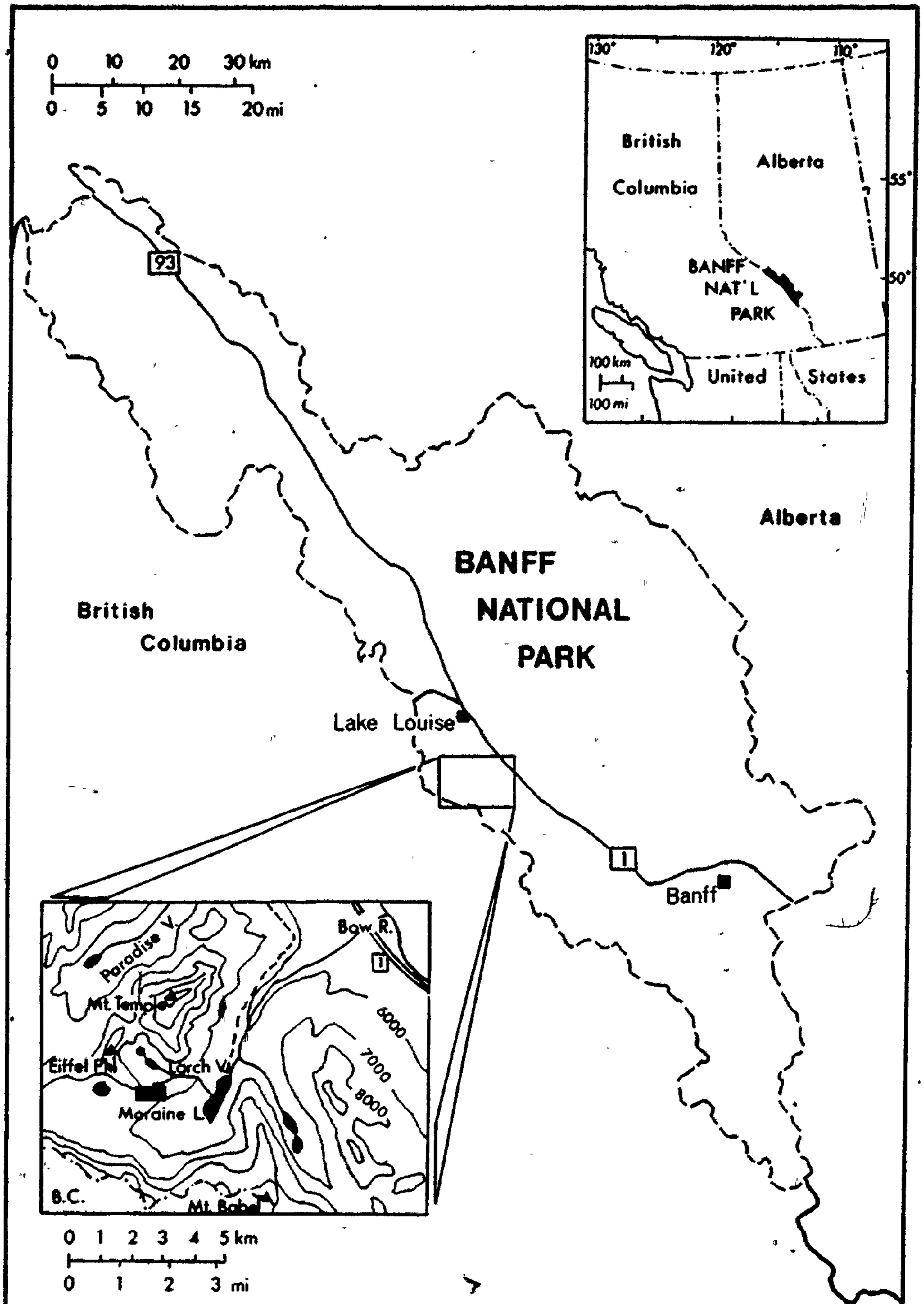

Figure 2-1: Location of the Study

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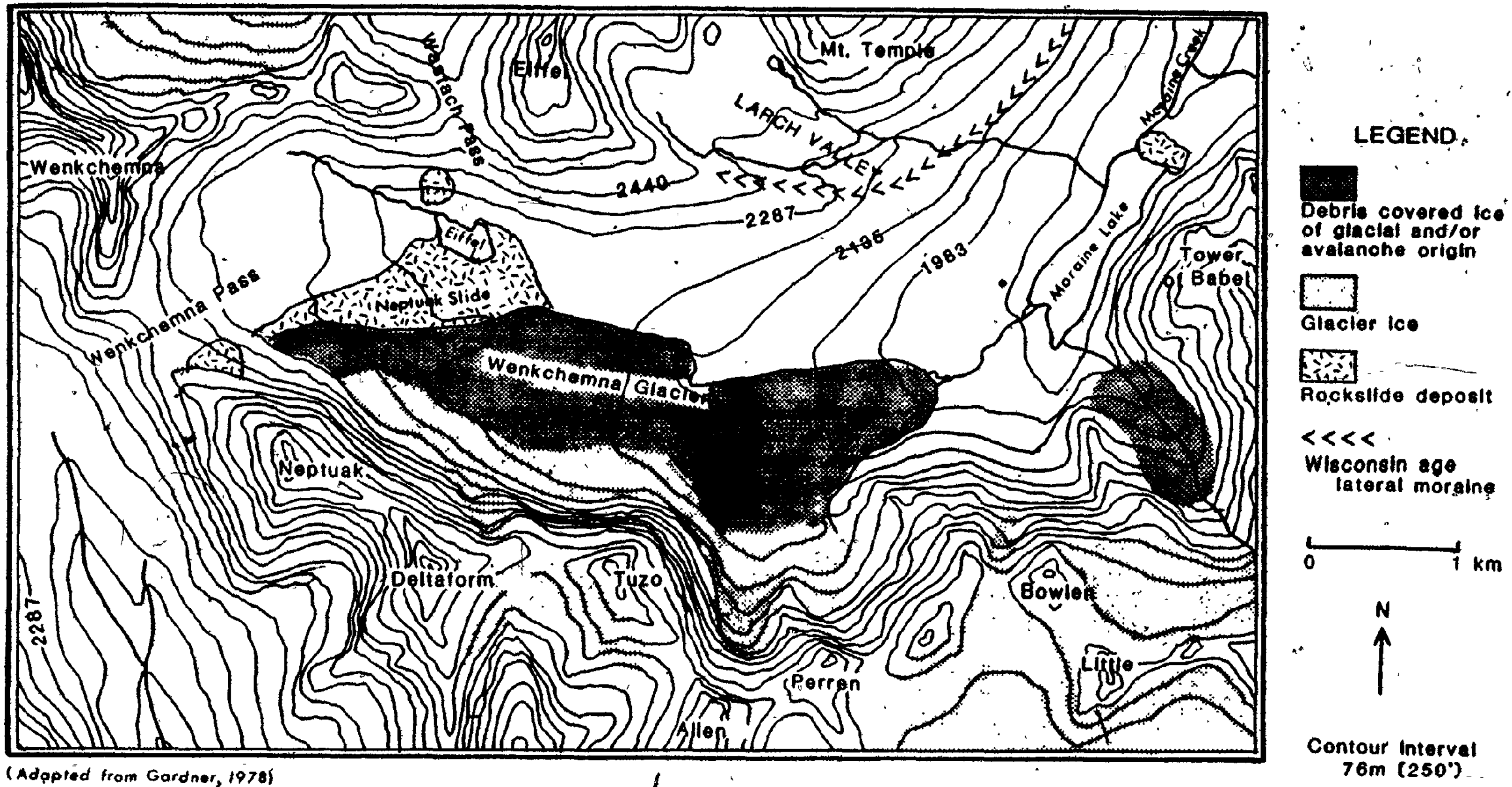
The general morphology of the valley (steep, geomorphically active north-faces and sunnier, vegetated south-facing slopes) is similar to that of Paradise Valley to the north, Consolation Valley to the east, and Boom and Tokumm Creek Valleys to the south. Gardner has identified and mapped the screes and taluses, avalanche debris slopes, landslide deposits and fluvial deposits in the valley's alpine zone.

The valley floor (approximately 11 km long) rises from 1825m (6000') elevation at its junction with the main Bow River valley to 2600m (8550') elevation at Wenkchemna Pass on the Continental Divide. Early visitors noted the great proportion of the valley above treeline in contrast to neighbouring Paradise Valley (Gest, 1970:7).

Drainage: The valley contains two lakes: Moraine Lake, elevation 1881m (6190') from which Moraine Creek flows northeastward to the Bow River; and Eiffel Lake, elevation 2244m (7380'), above treeline, which was formed by a large rockslide from Neptuak Mountain blocking the upper valley (see Fig.2-2). It has no visible outlet but drains downvalley under the rock debris to Moraine Lake.

Wenkchemna Glacier: Nearly five square kilometres (2 mi^2) of the upper valley are covered by Wenkchemna Glacier, elevation 2280m -1950m (7500'-6400') at the foot of the Bow Range (the Ten Peaks). This glacier was advancing into the subalpine throughout the nineteenth century until as recently as 1954, but is now receding and shows numerous slumping



(Adapted from Gardner, 1978)

Figure 2-2: Valley of the Ten Peaks

and stagnation features in the veneer of rock debris on its surface (Kucera, 1974; Gardner, 1977:58). Dead trees can be seen protruding from the toe of the terminal moraine: treeline is depressed to as low as 1950m (6400') by the glacier, the very cold conditions and the little direct sunlight received on this side of the valley. The stream draining Wenkchemna Glacier enters Moraine Lake after dropping 64m (210') in 0.8km (.5mi) (Kucera, 1974:42).

<u>Glacial History and Deposits</u>: Several major Wisconsin glaciations affected the Valley of the Ten Peaks and the most recent, the Eisenhower Junction advance, left the present mantle of debris on the floor and northwest side (Shaw, 1972:41). The prominent lateral moraine runs 7.25km (4.5mi) along the north side dividing the main valley and Larch Valley (see Fig.2-2). It marks the upper limit of Eisenhower Junction ice [a thickness of approximately 320m (1050')] which retreated 9,330 ± 170 yrs. BP (Rutter, 1972:38). Gardner (1978a) located several sites of sorted polygons and gelifluction activity evidence in the upper end of the valley.

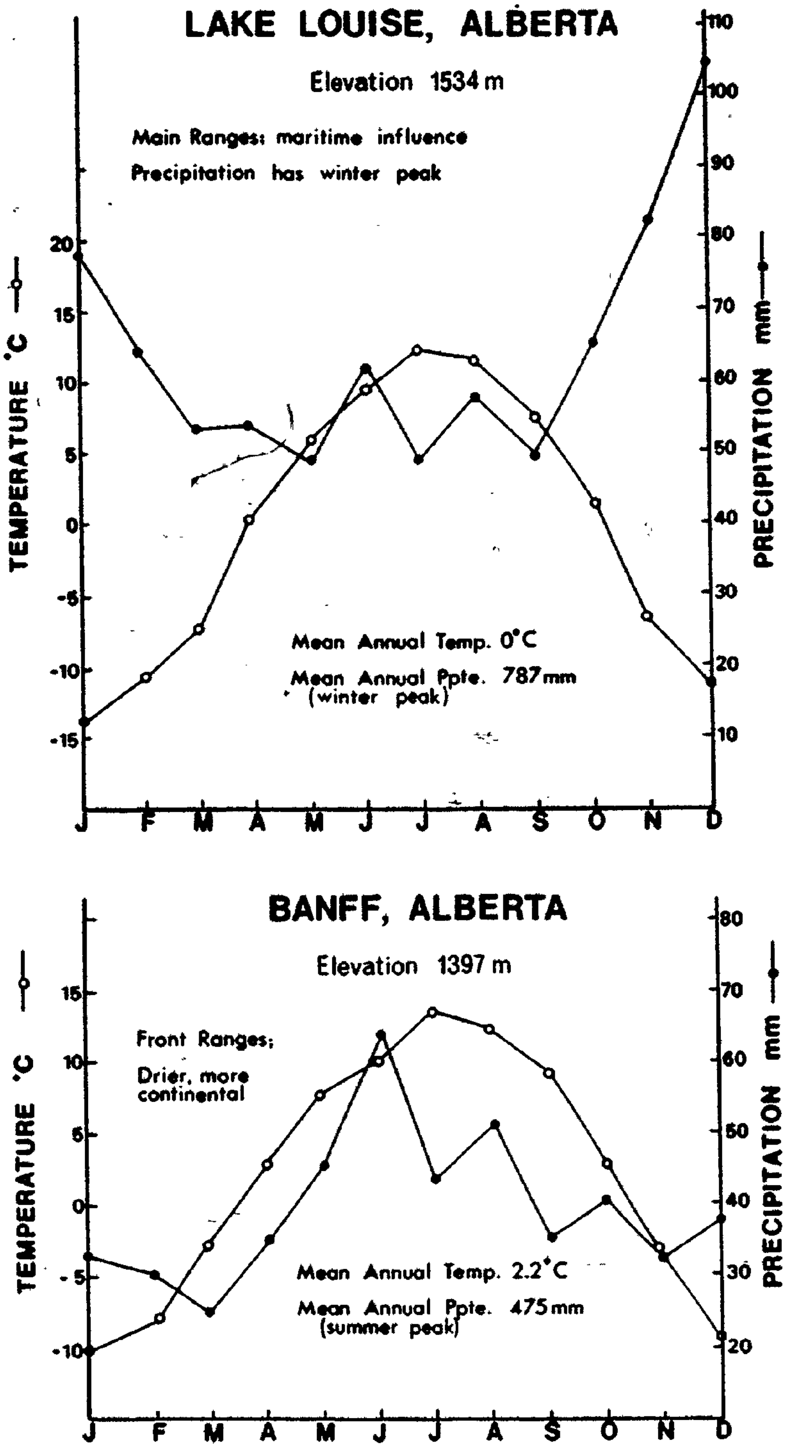
This investigation focusses largely on the high lateral moraine and on the changes in vegetation over its length and altitudinal gradient. Evidence exists in the upper reaches of the valley for Neoglacial ice advances (see Gardner, 1972; 1978), but since none of these recent episodes directly affected the study site, these will not be presented here. However, changes in the climatic regime inferred from these glacial advances and recessions have been important for vegetation change, and these will be discussed in Chapter Five.

The morainal deposit is predominantly calcareous till with a large component of gravel-sized quartzitic sandstone (Rutter, 1972:35). To an elevation of 2195m (7200') slopes are moderate, but above this to at least 2380m (7800'), the moraine is steep and Rutter (1972:Map 1324A-key) classifies its surface as strongly modified by slopewash, with bedrock outcrops common. Slopes in this portion average 28°-35°. "The steep switchback trail from Moraine Lake to Larch Valley crosses small drainage channels that have been cut through the moraine" (Kucera, 1974:19).

Soils: Very generally, the soils of the valley are thin and stoney, but they have not been studied in detail. Investigations at nearby sites in the Main Ranges (Ogilvie, 1969; Knapik et al., 1973; Harris, 1973; Mark, 1974) have described the general formations. Due to the variety of surface parent materials (weathered bedrock and glacial detris) and to highly variable local climatic conditions, the rate and pathways of soil development have been diverse (Rowe, 1972). Where slopes are stable and well-drained, shallow humo-ferric Podzols have formed; Regosols and eutric and dystric Brunisol profiles are frequent; and on the valley bottom, Gleysols and Organic Peats are found on poorly drained sites. On steep portions of the lateral moraine, low organic matter production along with geomorphic processes (the downhill wasting of snow and soil) have prevented the development of a thick or stable soil mantle except in isolated micro-depressions. King and Brewster (1978) link the complex range of pedogenic pathways at Bow Pass (50 km north) to a postglacial history of changing environmental conditions, including forest fire, avalanching, and vcloanic ash deposition. More detailed observations on soils will be presented in conjunction with the vegetation mapping in Chapter Three.

Climatic Regime: The environment of the study site is characterized by long, severe winters and short, cool summers. No exact climatic data are presently available, but general conditions are roughly known, based on metecrological records kept since 1931 at Lake Louise village (15 km north of Moraine Lake and 347m (1158') lower in elevation). Means of over 40 years of data are presented in Fig.2-3. Data for the Banff station are presented for comparison (although it is 46 km southeast of Moraine Lake and 484 m lower in elevation).

The prevailing winds bring maritime airmasses from the west which regularly meet continental systems. "The confrontation of air mass types plus the high mountain situation create complex day-to-day weather in the area" (Gardner, 1978a:2). Daily minimum and maximum temperatures range



(Adapted from Byrne, 1968; Ogilvie, 1969, 1976; Harris, 1973 - based on 40 year means.)

Figure 2-3: Climatic Diagrams - Mean Monthly Temperatures and Precipitation widely, as do seasonal temperatures, for example, a winter low of -40° C to a summer high of 30° C (86° F) (Ogilvie, 1976:34). For Lake Louise, Bowe (1972:144) gives a January average daily minimum of -21.7°C and a July average daily maximum of 21.7°C.

Over half the mean annual precipitation of 78 cm (31") falls as snow. Both the total rainfall and amount of snow increase with altitude, while generally temperatures decline with altitude, on average 0.5 to 0.7°C per 100m in the summer (Gardner, 1970:36). Ecologically, environmental lapse rate is important because of the retarding effect on the growing season and on plant phenology (Ogilvie, 1969:26). The mean annual temperature in Lake Louise is about 0° C, so at the study site it is certainly well below freezing, and thermal extremes are greater. Both freezing and thawing temperatures are experienced in all months of the year. Estimates of mean frost-free days per year vary from 119 in Lake Louise (Gardner, 1978a:2) to under 45 days at Lake Louise (Harris, 1973:A173), to fewer than 7 days in the alpine tundra zone (Ogilvie, 1976:37).

No wind speed measurements are available for the area, but Mark (1974) and Ogilvie (1976:35) affirm that windspeeds are low in valley bottoms and on lee slopes, but increase rapidly with elevation and on exposed ridges or shoulders. Correlations between wind and snow patterns will be presented in Chapter 4.2.

Aspect/Mesotopography: The importance of aspect and microtopography in creating environmental heterogeneity cannot be stressed enough. Gardner (1969) recorded lower temperatures, delayed date of release from snow cover, and a larger number of freeze-thaw cycles on north-facing relative to south-facing slopes. South or west slopes are exposed to drying winds, reduced snow cover, and high light intensities. Ultraviolet radiation increases with elevation and degree of slope. Where these slopes are steep and their soils stoney, runoff of rainfall and snowmelt is accelerated. Under these habitat conditions, drought susceptibility increases toward the end of the growing season.

Soil moisture availability is also linked directly to soil temperature: one of the main inhibitors of plant photosynthetic activity is frozen soil water. Soil temperatures fluctuate over a wide diurnal range in the short summer season but remain below 0 °C for 6 to 11 months of the year. In protected micro-environments (i.e., in the lee of a boulder) or on dark materials, the unusually high radiation inputs can create ground surface temperatures high enough to be lethal to seedlings of conifer species (Day, 1963; Mark, 1974). These localised drought conditions in the growing season, and winter drought due to frozen soil water and desiccating winds occur frequently "despite high annual water surpluses" (Mark, 1974).

The importance of the re-distribution of snow by wind is well-recognized (Klikoff, 1965; Billings, 1969; Marr, 1977; Major, 1979). Where it is not removed by winds, snow accumulates to great depths and may persist throughout the summer in cold shaded situations. In the region generally, a snow cover of 1 to 3m persists in the valleys for up to 6 months a year (Gardner, 1970:136). Kucera (1974:39) roughly estimates a maximum of 6-9m (20-30') snowfall annually in the Wenkchemna Glacier collection area. Harris' (1973:A174) measurement of 2.2m at Vermilion Pass, 14km to the south, elevation 1646m (5416') is likely an accurate average for this study site. Comments will be made in the next chapter on likely snow depths judging from tree morphology evidence. The meteorological data would suggest "an average of two or three months between the last and first heavy snowfalls of any one season" (Mark, 1974). The position of the valley on the Continental Divide testifies to the severity of the climatic regime: a 'winter' blizzard was experienced in the upper third of the valley in mid-July 1979.

Because of the west-east orientation, extremely gusty winds coming through Wenkchemna Pass are a constant feature of the valley head and its northwest wall: drainage of cold air along the valley bottom is common. Nocturnal temperature inversions are very common in the region (Ogilvie, 1969:27) and in winter may persist for several days.

Vegetation: Vegetation zonation reflects the mosaic quality of these habitat conditions. Variety in fixed site factors (eg. substrate, soil texture), and variability in physical factors over time (eg. diurnal, seasonal, and annual climatic fluctutations) contribute to complex vegetation-environment correlations. For instance, the reversed lapse rate that accompanies thermal inversions confounds a simple explanation of plant community distributions.

For introductory purposes, however, the two main vegetation zones are Subalpine Spruce-Fir Forest and Alpine Tundra (terminology: Rowe, 1972). The main conifer species of the forest are *Picea engelmannii* (Engelmann spruce), *Abies lasiocarpa* (Alpine Fir), and *Larix lyallii* (Alpine Larch). Only scattered individuals of *Pinus albicaulis* (Whitebark pine) are found. Deciduous trees are found only in the lower third of the valley on avalanche tracks or fluvial deposits: *Populus tremuloides* Michx. and *Betula occidentalis* Hook. are lacking completely in the upper subalpine.

Continuous coniferous forest cover extends to about 2226m (7300'), but individuals of the three main species are found up to 2501m (8200') (treeline). The great width of the transition between the closed forest and the open alpine vegetation is a striking feature in the Valley of the Ten Peaks. Ogilvie (1976:36) refers to the entire transition zone as the timberline zone: its European term is the Kampfzone. Chapter 3 will contain the results of a detailed reconnaissance of the nature and extent of the community-types making up this transition.

<u>Human Use</u>: It should be noted briefly that considering its relative accessibility, human alterations to Wenkchemna Valley have been minimal, in comparison with the substantial effects upon landscapes elsewhere in the region. The vegetation of the main Bow River Valley is largely a reflection of historical human patterns of environmental modification (Byrne, 1968). In contrast, however, its higher-level tributary is untouched by logging, mining or livestock grazing activities (Byrne, 1968:121). The whole Lake Louise district was designated as reservation in 1892 and incorporated into Rocky Mountains Park which had been formed in 1887 and was re-named Banff National Park in 1930 (Byrne, 1968:143). As a result, on this study site there is no evidence of felling for fuel or construction as elsewhere in the Bow Valley region.

A brief sketch of the human use of Moraine Lake is given in Table 2-1. Today the road and hiking trail lead to Moraine Lake where there is a lodge and cabins that are open one season only. A well-worn foot path leads up and along the lateral moraine to Eiffel Lake and branches into Larch Valley and to Sentinel Pass. No tenting is allowed in either valley. As Gardner (1978:5) notes, "fortunately, (development) has been prudent".

Table 2-1: History of Human Development in The Valley of the Ten Peaks

1893	Wilcox, Allen & Henderson first sight valley from Sentinel Pass while exploring Paradise Valley.
1899	Wilcox first visits Moraine Lake - camped there, wrote of his impressions; photographed the area. Attempted to take pack horses to Eiffel Lake but the way blocked by rockslides. Refers to frequent smoke from distant forest fires in Bow River Valley.
1902	James Outram notes: a broad and easy pack trail almost completed to Moraine Lake.
1908	Accommodations for climbing groups (Alpine Club camps).
1913	Many tenting parties (from Gest, 1970).
1920	A permanent and comfortable mountain camp.
1921	Road from Lake Louise was one-lane, one-way traffic by schedule.
1923	The C.P.R. erected some sleeping huts.
1939	A two-room cabin built.
1946	Opened again after closure during World War II.
1959	Small chalet sold to Brewster Transport Inc.
1968	Road widened and paved; parking lot enlarged.
1970	Public campground (occupying one of the old camping sites) closed due to excessive wear on the vegetation, and waste disposal problems.

2.2 SELECTION OF STUDY SITE

Although a few references have been made to the vegetation divisions found in Wenkchemna Valley (Wilcox, 1916; Gardner, 1978a), no systematic attempt has been made to describe or analyze the community patterns as they are found. The focus of this study is the structure and dynamics of the timberline zone. The aim is to analyse temporal and spatial variations in the distribution of tree species within this forest to tundra transition. In particular, disturbance effects, modes of tree regeneration, and the nature of the vegetation pattern are linked, and the significance of their relationship addressed.

Topographic map and air photo coverage of the area are good. General information on the history, climate and geology was available.

As was suggested in the preceding section, the main focus of the primary and detailed surveys was the southwest-, south-, and southeast-facing slopes of the high lateral moraine that constitutes the north wall of the valley. Primary field survey and air photo work was also done on the valley floor. The coniferous forest on the south side of the valley is truncated by Wenkchemna Glacier (see Fig.2-2).

The interest in this treeline zone was sparked on a visit through the region in July 1979. Part of the general rationale for choosing this study site was the clear distribution of dead standing snags and little-decayed fallen trees that were symmetrical and much larger than any living trees at the same altitude. During the preliminary reconnaissance, it was noted that the south-facing slope of the lateral moraine is generally homogeneous in terms of soil and drainage characteristics and yet vegetation cover (particularly conifer regeneration) is very uneven. Although most of the vegetated area of the upper valley could generally be identified as subalpine forest or semi-open meadow, much heterogeneity in composition, cover, vigour and density is evident.

A return trip in September and October 1980 aimed to study the process controls that are perpetuating this vegetation patchiness. Each of the stands shows differential reproductive success following a mid-nineteenth century fire. With this aim in mind, the detailed field work involved vegetation survey work along a grid of transects through the subalpine-alpine transition. The observations on population structure, vegetation patterns and regeneration success were augmented with comparative air photo analysis and mapping.

2.3 METHODS: EXISTING VEGETATION PATTERN

2.3.1 General Rationale

It has been pointed out that in every vegetation study, the investigator's biases and objectives affect the choice of methods for data collection (i.e., population sampling), and data analysis and interpretation (Kershaw, 1973; Mueller-Dombois & Ellenberg, 1974; Chapman, 1976; Barbour et al., 1980). Since the framework and objectives of this research have been outlined; the purpose of this section is to explain the particular procedures chosen to meet those aims, in light of some of the features or problems peculiar to this timberline zone.

The methods described here and in section 2.4 speak directly to Objective One (page 9). The sources of data and means of obtaining and interpreting them are presented.

Considerable encouragement was found in the literature for combining several methods of documenting vegetation change and succession (Daubenmire, 1968; Henry & Swan, 1974; Mueller-Dombois & Ellenberg, 1974; Barbour et al., 1980). These are summarised in Table 2-2 below. The methods used in this study are marked with an asterisk.

TABLE 2-2: DOCUMENTING VEGETATION CHANGE

METHODS OF STUDYING SUCCESSION

Direct Evidence:

   1. Repeated Observations over Time on Permanent Plots;
*   Studies of Air Photos from Different Times.
* 2. Reference to Historical Records of Vegetation.
   3. Evidence of Change found in the Present Community:
         --Organismic Remains in the Soil (eg. Biogenetic Opal)
*   --The Nature and Occurrence of Relics.

Indirect Evidence:

* 4. Study of Stand Structure-- analysis of species composition
                 of age classes: seedling, sapling, mature.
   5. Inference Based on Studies of Bare Areas, Exclosures, or

Separated Plots of Differing Ages.
6. Fossil Sequences-- preserved in peat or soil.

The use of direct evidence rather than indirect approaches permits unusually detailed reconstruction of past changes in tree form and distribution. It is recognized that interpretations of much longer-term vegetation change on this site would require the addition of palynological techniques (Kearney, 1981); determinations of soil biogenetic opal content (Miles & Singleton, 1975; Vale, 1978); or detailed analysis of soil development sequences (Brewster, 1974; Olgeirson, 1974; King & Brewster, 1978).

At this stage, however, the methods most appropriate to interpreting the site patterns of this vegetation mosaic are: a detailed mapping of the ecotone from air photos and field observations; the location of seedling establishment and its environmental correlates; and a characterization of the current stand structure, as will be described in the next section.

2.3.2 Stand Surveys

Given the several restraints on the scope of the project, some decisions had to be made regarding the most useful community attributes to measure and the most effective methods for gathering this information rapidly. Several features common to the whole zone created problems when choosing the most suitable sampling and descriptive methods. Such characteristics as the highly contagious nature of most conifer distributions, and the prevalent difficulty in defining the limits of an individual tree within clumps meant that most of the techniques developed for closed (lower-elevation) forests with random distributions were inappropriate. Arno and Habeck (1972:421) stress that relatively homogeneous forest units tend to become too small in the upper subalpine to allow use of extensive tree inventory techniques and they suggest a series of 10m squares.

For detailed examination and field sampling, five specific Study Areas were chosen using stratified random sampling, as follows. The entire vegetation segment (the upper subalpine subzone) was subdivided subjectively into seven more or less even-sized segments. Within five of these Study Areas (A,B,C,D,E), random sample plots 10 x 10m were located using coordinates and the random number table (Kershaw, 1973:30; Mueller-Dombois & Ellenberg, 1974:39). These are shown on Fig.2-4 on the upper half of the lateral moraine. Data on both the living and dead trees were collected by means of stand surveying by count-plots and belt transects. In Area A, 4 10x10m regeneration count plots were tallied by species and size (see Table 2-4), and percentage cover types estimated (see Table 2-3).

Also, the widely-accepted Point-centered quarter method was used in Area A, the most densely-covered part of the

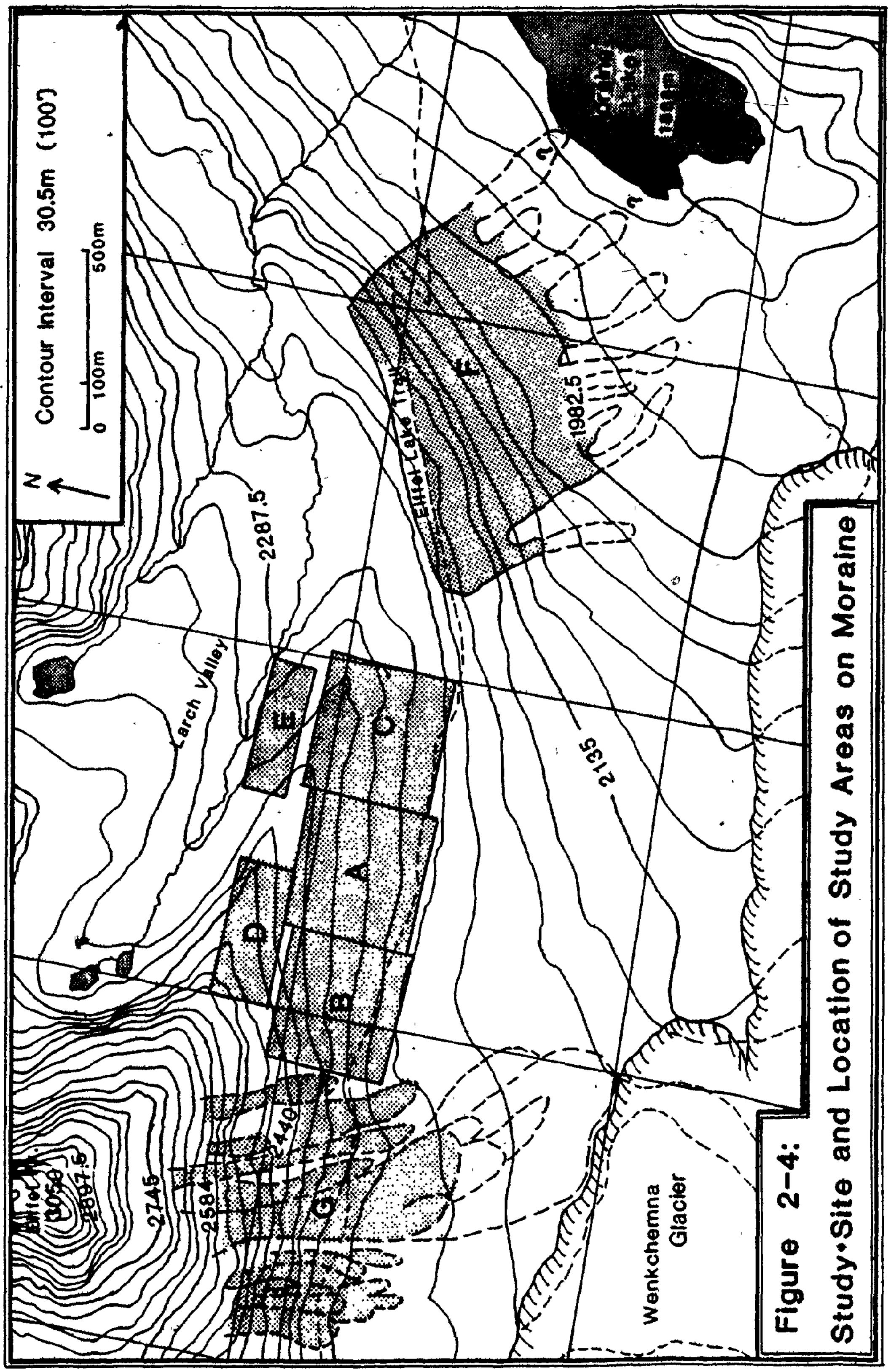


Figure 2-4: Study Site and Location of Study Areas on Moraine

study site. Two transects 15.25m x 213.5m (50' x 700') long were run along a compass bearing across the contours through Area A. In total, 21 points located 15.25m apart along the two transects were sampled according to the Point-Centered Quarter method of Cottam and Curtis (1956). This technique is time-effective as four trees are identified and measured for each sampling point. For each identified tree, circumference, height, and distance from sampling point were measured. In addition, its physical condition or vigour (according to Sprugel, 1976:894), growth form, mode of reproduction (if any), and understory species were recorded.

At each sampling point, site information was also taken: aspect, elevation, slope steepness, concavity or convexity along the contour, and comments on stoniness, bare soil and hummocking.

Basal rather than breast-height circumference was measured because many trees were split or multi-stemmed (Mueller-Dombois & Ellenberg, 1974:96). The circumference values were converted to diameter and to basal area values. The data collected were grouped into size-class distributions, and relative frequency, relative density and relative dominance were calculated for each tree species. These results provide a quantitative characterization of the stand's composition and structure.

Requirements of this sampling technique are that each quadrat must contain one tree, and at least 20 points are needed to sample a stand. It is most suitable for random distributions, and it recognized that in Area A, individuals vary considerably in their spacing. *Abies lasiocarpa* ranges from a random to a clumped habit and as a result may be slightly under-represented in the sample (Mueller-Dombois & Ellenberg, 1974:111-120). However, this technique is information-effective as it gives more data than simple species presence and abundance. One major bonus of the Point-centered quarter method is the derivation of the absolute and relative dominance measure, which indicates areal cover by species (of particular interest in this study).

> Foore (1955) and Dahl (1956) have recommended the use of *dominance* as a major criteria in areas where particular communities may have only few species and particularly where the flora of the general area is not as rich in species as in continental Europe. (from Brooke, Peterson & Krajina, 1970:233)

Areas A, B and C were surveyed by a series of paced transects both parallel and perpendicular to the contours, for the purposes of creating bisect profiles (scale drawings of the vegetation within line strips). Within 4 10x10m random sample plots, surface cover types were recorded according to the classes shown in Table 2-3, and all conifer juveniles counted, according to the height classes in Table 2-4.

In Area D, a chart quadrat 60.8m x 106.5m (200' x 350') at elevation 2455m (8050') was surveyed with 100% sampling coverage. To establish a reference system, each 3.05m (10') grid section was measured and the corners of each double-

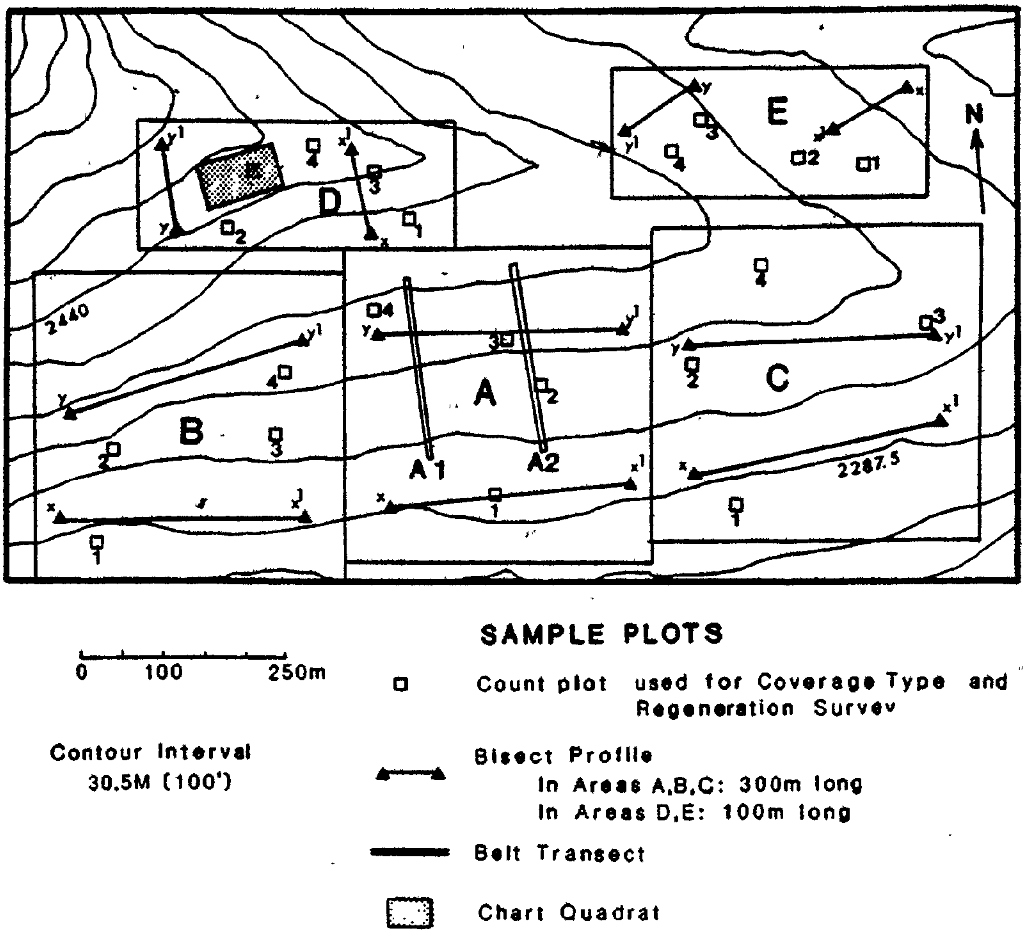


Figure 2-5: Quantitative Sampling Coverage

checked with the Brunton compass. Compass and protractor were used to chart the exact position of trees on the grid-for each shrub its bearing and distance were determined and transferred to the chart (Cain & Castro, 1959:126). The right angles were checked using Pythagorean principle.

Data collection in this tree-island community included tree species, height, vigour and crown condition, and notes on slope exposure, degree of slope, general substrate and understory comments. In four additional 10x10m randomly-located plots, percentage cover types were recorded.

Area E was studied by means of 4-10x10m plots ($400m^2$), air photo study, and repeated field reconnaissance. In these plots, all trees and regeneration size stems (Table 2-4) were tallied by size and species, following the method of Arno and Habeck (1972:421). As well, surface cover types were recorded (see Table 2-3). The stand structure is derived from these population size class distributions.

This section has described the methods of surveying in detail the specific study areas. Fig.2-5 shows the locations of all sample plots, Bisects, and Belt Transects. It emerged that detailed analysis of small plots derived the most suitable (although time-consuming) assessment of the fine-scale mosaic making up this transition zone.

A possible limitation of these methods is the uncertainty about determining successional trends using population size structure rather than actual age structure (i.e., dated ab-

Table 2-3: GROUND COVER CLASSES

(a) Ground Cover Types

- Live vegetation (including vascular plants, moss-selaginella, lichens)
- Dead vegetation, duff, or humus
- Mineral soil (substantially lacking pebbles)
- Gravel (soil surface largely covered with pebbles < 6 cm diameter)
- Bare rock (Bedrock or stones > 6 cm diameter)

(b) Cover Scale

(after Daubenmire, 1959; Klikoff, 1965; Arno & Habeck, 1972)

Cover Class	Range of Cover	Class Midpoints (%)
1	< 5%	2.5
2	5 - 25%	15.0
3	25 - 50%	37.5
4	50 - 75%	62.5
5	75 - 95%	85.0
6	95+%	97.5

Table 2-4: REGENERATION SURVEY

Species	Seedling Height Class 1	 2
Abies lasiocarpa Picea engelmannii	<15 cm	15 cm - 60 cm
Larix lyallii	<30 cm	30 cm - 150 cm

solutely by core-sampling). Buchholz and Pickering (1978) found successional sequences inferred by either method to be equally accurate whereas Vale (1977:33) cautioned that a species' status (i.e., stabilized, increasing, or decreasing in relative importance) could be estimated only generally from size measurements. In a future study, data on absolute dates of origin clearly would increase the accuracy of the conclusions on population dynamics. No increment borings of individuals were taken because of the destruction to both young and mature trees and permission was not granted from Parks Canada. A dozen tree cores taken in Larch Valley and Consolation Valley by J. Gardner in 1966 (1981, pers. comm.) provided a few absolute ages on living larch and fir specimens, but ~~as~~ it turned out these were of limited use to the purposes of this study (see Ch.5.2 below).

2.3.3 Vegetation Mapping

It should be emphasized that in mapping community types in any life-zone, the boundaries are seldom sharp. The gradual change between units (the ecotone), is often drawn at some point midway between the two, unless it is a very broad transition. Ogilvie et al. (1976) agree that a broad forest-tundra ecotone presents problems in its realistic representation on a map: there are difficulties in delineating the upper limit of the forest and the lower limit of the alpine where the two are intricately overlapped. They indicate the usefulness of classifying and mapping the transition as a separate timberline belt, and Barbour et al. (1980:198) agree:

> If the ecotone is unusually large, or if several types coexist in some complex mosaic, then the ecotone or mosaic, may be mapped as a separate unit in its own right.

This is practical only with large-scale mapping, that is, to "map the actual mosaic of tree-islands, krummholz colonies, and scattered trees" (Ogilvie, 1976:171). In his remarks on some interpretation problems of the treeline fluctuation phenomenon, Holtmeier (1979:167) also states "we require detailed mapping of the site patterns which are characteristic for specific timberline areas".

Hence, the large scale of mapping used (1:2,140) in plotting both current and remnant forest cover onto the reference grid allows for the complete inclusion of isolated trees and small groups (eg. clusters of seedling "invasion"). The choice of this detailed recording of distributions was deliberate in order to meet the study's objective to focus on within community dynamics. Sutherland (1974) and Hamet-Ahti (1978:189) point out that it is appropriate to view large superficially homogeneous areas as composed of many smaller patches and that these patches are the local situation of interest: closer examination often reveals a rich mosaic, alternating, for instance, with wetter and drier habitats. The sources of mapping data were aerial photographs, field reconnaissance, primary survey and detailed stand survey. The working base maps (Fig.2-4 & 2-5) were created from an enlargement of part of the Canadian Dept. of Energy, Mines and Resources Topographic Map, Lake Louise Sheet, 1980 edition (contour interval 30.5 m (100')).

Six series of aerial photographs (National Air Photo Library, Ottawa) from over thirty years were obtained for the area: 1947 (1:25,000); 1951 (1:40,000); 1967 (1:15,000); 1973 (1:27,000); 1977 (1:50,000); and 1978 (1:25,000). Fortunately these had been taken in several seasons. The examination of these stereo pairs enabled the location and ages of several features to be determined: landslides and avalanches; the distribution of Larix lyallii (especially on autumn photos); and zones of scant and moderate seedling establishment over the thirty years.

As well, single enlargements were made of the specific study areas for 1951 (brought to scale 1:9,090), 1967 (brought to 1:2,140), and 1977 (brought to 1:5,000). From these, individual trees and krummholz islands could be readily located and their dimensions compared with the 1980 field data (Hansen-Bristow, 1980: pers. comm.). The techniques of analyzing air photos taken at different times corresponds, in essence, to sequential observations of a given vegetation unit (Daubenmire, 1968).

Eight square kilometres were covered by primary survey (the entire zone covered by some combination of forest and tundra), while detailed survey covered a localised area of

2.5 km² For the detection of pattern within this broad zone, the advice of Shimwell was taken, who favours concentrating on the results of vegetation structural analysis: "The detection of stands is then based on difference between external and internal uniformity, that is, when a patch of vegetation shows structural differences with surrounding vegetation which are greater than within the patch, then the patch is considered to be a stand or entity." (Shimwell, 1972:154)

As many different conifer patches (i.e., clusters, tree islands, flag and cushion formations) as possible were distinguished and their boundaries outlined on overlays of the base map. These tentatively mapped patches were examined in the field to check the identity and reliability of the photo interpretation. The boundaries were amended based primarily upon changes in physiognomy and secondarily upon floristic composition (Langenheim, 1962:255; Barbour et al., 1980:198).

To summarize generally then, the data for vegetation mapping was obtained from air photo work and extensive primary and detailed surveys of the upper valley. The next section speaks in more detail to the use of forest remnants evidence in delineating former tree distributions.

2.4 METHODS: FORMER CONIFER VEGETATION PATTERN

The collection of information on former vegetation cover began with research in the Banff Archives of the Canadian Rockies, gleaning historical photographs and descriptions of the landscape by early travellers.

Part of the rationale for focussing on this study zone was the profusion of well-preserved logs, stumps (and charcoal) in Areas A, B, and C well above the present altitudinal limits attained by conifers of corresponding dimension and shape. Pears (1972:33) states that wood remnants and macrofossils provide "the strongest and most direct evidence for past tree-line positions".

The use of direct relic evidence has been advanced by Daubenmire (1968:108) to interpret more accurately ecotonal fluctuations or successions, especially those with irregularities or "peculiar distributions". Various cases of using wood remnants were found in the literature: Molloy et al., (1963) for the New Zealand Alps; LaMarche and Mooney (1972) in the White Mountains of California; Henry and Swan (1974) and Oliver and Stephens (1977) for two New England sites; Bonnicksen (1975) for a Giant Sequoia ecosystem in the Sierra Nevada; Hawk (1979) for a small watershed in the Western Cascades of Oregon; and Elliott (1979) at the northern Canadian tree line in the Keewatin District. The <u>reasons</u> for the contraction of forested area vary and are more clearly understood in some regions than others. It may stem from long-term climatic change, short-term climatic fluctuation, infrequent disturbance by fire, windstorm, or grazing, or some indeterminate combination of the above. Nevertheless, the use of wood remnants above the present upper timber line is well-established as a basis for the reconstruction of past changes in tree form and distribution.

As in the preceding section, the main sources of data were vertical aerial photographs (and enlarged portions), low-angle oblique photographs, and field work. Along the transects described earlier, the presence, distribution, shape and dimensions of fallen logs and dead standing snags were noted. These data were recorded on the plots used for live-stem sampling. Using air photos for confirmation, the relics were compared to the present distributions. Many site photographs were taken.

Chapter 3 will contain the analysis and interpretation of the data on past and present vegetation status. These results include community structure and species performance of the vegetation living in 1980, alongside the rough approximation of the historical forest cover, derived from snag and remnant evidence.

Chapter 4 then relates the differences in structure and performance to differences in the stress and disturbance regime of each study area. The components of the vegetation patterns (especially regenerative success) are related directly to the type, size, and frequency of disturbances.

The methods for detecting these features of the disturbance regime are given next.

2.5 METHODS: SITE CONDITIONS AND DISTURBANCE REGIME

It is an aim of this project to set disturbance regime into its place as part of the total environmental setting. Therefore, the broadly distributed or 'constant' factors of physical site received less treatment in this study than the acute or extreme mechanisms which influence vegetation. But while no instrumentation of broad climatic or edaphic parameters was done, a number of observable environmental variables were recorded during the field work. In the manner of Langenheim (1962) these data were aggregated and overlays of several mappable environmental patterns were made: degree and exposure of slope, mesotopography, heavy snow accumulation, and reproductive success. A general map overlay showing slope aspect and degree (Fig. 4-7) was derived from the topographic map and confirmed with ground truth using a Brunton compass and Suunto clinometer, as well as a general map of slopes in the region from Winterbottom (1974).

The mesotopographical overlay (Fig. 4-3) was developed in the style of Hack and Goodlett (1960), indicating classification of slope segments by their convexity or concavity along the contour. The purpose is to show the tendency of each area to collect or disperse moisture.

A third overlay to indicate probable zones of heavy and late snow accumulation (Fig. 4-6) was made from early winter snow-lie patterns from the 1947 and 1951 photos, which were related to ground observations (1980) regarding microtopography and wind-break effects upon snow patterns.

For use in the discussion of regeneration factors in Chapter 4.4, a fourth map overlay was created of the range of regeneration effectiveness (Fig. 4-12) across the site. In order to produce it, these elements were studied: the location of trees bearing cones, and the location of all tree juveniles, whether sexually produced (individual seedling) or asexually reproduced (by layering) (primarily *Abies lasiocarpa*, and to a lesser extent, *Picea engelmannii*).

As previously described, the quantity and mode of reproduction was recorded along each measured transect and in the surveyed stands. The physical features of areas with abundant seedling establishment were compared against those of areas with little or no regeneration. It is not uncommon for trees under 15cm to be up to 25 years in age: given the very slow growth rate for all species in this zone, they were treated as juveniles regardless of age. The results on stand age structure, layering, and seedling establishment are sufficient to allow a few elementary conclusions on current regenerative capacity across the ecotone. It is a goal of this study to examine the relation between reproductive *effectiveness*, the nature of the vegetation *pattern* in the valley, and *disturbance* effects.

Firstly, regarding disturbance regime, the autecological literature on the general increase in physiological stress with altitude was reviewed, and the differences between 'stresses' and 'disturbances' clarified.

Wherever evidence of the effects of disturbances was encountered in the field, record was made of its nature, extent, degree of localisation, severity, and selectivity (by species). Signs of *chronic* stress conditions and discrete events or *acute* conditions were recorded. There is great variability in the degree of disturbance activity. That is to say, disturbance effects are both spatially and temporally sporadic in each study area and across the study site as a whole.

In effect, this inventory serves as a guide to the frequency and nature of 'hazard events' and is determined by inspecting characteristic patterns (i.e., *known* damage areas) within the vegetation and postulating the causes of these effects. For example, snow avalanche effects are caused directly by mechanical damages or indirectly by late-melting runout or debris deposition.

Sites of recurrent snow avalanche damage were recorded and plant responses described. Locations exhibiting evidence of soil and snow creep and extreme stoniness were noted. The presence of plant species indicative of slope instability was recorded. Some segments of slope were extensively undermined by gopher excavations and showed considerable slumping and a hummocky surface. Several zones of recent rockslide activity into the upper fir flag-krummholz on steep slopes below Eiffel Peak were photographed, measured for extent, and described. All of these mass-movement disturbance effects were confirmed and supplemented with air photo measurements and comparisons from 1947 to 1978.

Plant tissue conditions, especially the presence of winter drought damage, were examined for each identified and measured conifer as well as for many understory species. The severity of desiccation (physiological damage) or ice-blast (mechanical damage) was assessed visually. Damage to needles and cones by snow-fungus was examined where encountered in the stands, as was the related bending and breaking of branches by heavy snow loads.

Reiners and Lang (1979:403) have stated that "fir zone vegetation is subject to a number of processes that lead to a hierarchical set of overlapping patterns", which can be discerned, delineated and analyzed. A 'high-risk' designation ('high-risk' in terms of sexual reproduction, after Stahelin, 1943), is evidently applicable to those sites where an overlap of several of these effects were evident.

The following three chapters will present the results and discussion of the methods and analysis described in this chapter.

Chapter III

VEGETATION STATUS: PAST AND PRESENT

3.1 RESULTS: SURVEY OF LIVING VEGETATION

Generally, the vegetation association dominating the upper valley is Rowe's "Subalpine Forest" (1972:65) or the equivalent "Spruce-Fir Forest" (Ogilvie, 1976:35). This study site is best described by the classification of Walker et al. (1978) as the "Upper Subalpine Subzone", which is transitional between the lower subalpine subzone (closed forest) and the treeless alpine zone. This term denotes an open forest meaning the tree crowns are separated by a distance of 2-5 times crown width. Tree groups and islands are common with heather meadows and grass communities occurring between them. These scattered conifers and ericaceous shrubs form a 'woodland', an area in which trees are present but have less than 50% canopy coverage.

Relatively speaking, the floristic structure of the study area is simple. The tree species are *Picea engelmannii* Parry (Engelmann spruce) occasionally as a hybrid with white spruce; *Abies lasiocarpa* (Hook.) Nutt., (Alpine fir); *Larix lyallii* Parl., (Alpine larch); and rarely, *Pinus albicaulis* Engelm., (Whitebark pine).

Species in the shrub or heath layer (which has high coverage in the area) are: *Juniperus horizontalis*, *Salix arctica*, *S. nivalis*, *Vaccinium scoparium*, *Cassiope tetragona*, and *Phyllodoce glanduliflora*. Common forb species are: *Dryas Hookeriana*, *Fragaria glauca*, *Potentilla ledebouriana*, *Pulsatilla occidentalis*, *Erigeron peregrinus*, *Arnica latifolia*, *Pedicularis bracteosa*, and the main sedges and grasses are: *Carex* spp., *Festuca saximontana*, *Elymus innovatus*, *Koeleria cristata*, and *Poa alpina*. Nomenclature follows Moss (1959) and Porsild (1979).

Ogilvie (1969:35) lists these species in the "abundant bryophyte and lichen layer": *Dicranum fuscescens*, *Lycopodium alpinum*, *Selaginella selaginoides*, leafy liverworts, *Cetraria*, *Tortula*, and *Cladonia* spp.

The second major vegetation type at the upper reaches of the valley is Alpine Tundra (Walker et al., 1978). The shrubs and heaths which dominate the association are: *Phyllodoce* spp., *Cassiope* spp., *Salix* spp., and *Juniperus* spp. These are found in several combinations, and are associated with these grasses and forbs: *Elymus*, *Kobresia*, *Dryas*, *Anemone*, *Carex-Poa*, *Festuca*, *Saxifraga*, *Antennaria*, and *Selaginella*.

The true tundra above the limits of tree growth was not studied, but those heaths and alpine meadows which interdigitate with conifer species were covered in the field survey on foot.

Despite the low number of species and structural simplicity of these two associations, it does not follow that the actual landscape pattern is simple. In this valley, to attempt to 'fix' a timberline (the upper limit of closed forest cover) as a distinct boundary, even a ragged one, would be difficult and of little value. Relatively continuous forest cover exists at 2196m (7200'), but irregular patches of tundra are found below this elevation, and a very broad belt of tree groups, alpine meadows, and isolated trees extends well above it. Actual tree-line (the uppermost limit of living tree individuals, regardless of stature, Löve, 1970) is around 2501m (8200').

The extreme width and complexity of the transition from subalpine to alpine conditions is the most striking feature of the upper end of the valley. Between 2196m (7200') and 2470m (8100') there is a broad zone where tree stands are intermingled with large heaths or meadows (some mesic, some dry and stoney). An early visitor to the valley commented on the great diversity in this "tension belt" above the "forest-line" (Lewis, 1923:133).

In Daubenmire's 1968 terminology, this zone is a "mosaic ecotone", in which peninsulas or island-like areas of each community are mixed in a "large expanse of mixture" (1968:22-24), in contrast to a "simple ecotone" in which the dominants of one ecologic community gradually replace those of a second community along an environmental gradient, such as elevation or soil salinity. The differences between the two are in the nature and extent of the area of 'mixture'.

In this chapter, the results of the field survey and mapping (that is, the data on vegetation structure and performance) are presented and interpreted for each study area.

3.1.1 *Study Area A*

The fairly high density quadrats sampled in Area A are representative of a relatively healthy *Abies* -*Larix* community, marked by the almost constant presence and reproductive success of *A.lasiocarpa* and *L.lyallii*. Only in this Area was recent expansion of tree margins observed, largely because of ameliorated wind conditions, slope concavity, deep snow, (less frost penetration of soil) and therefore less drought damage.

It is recognized that the method used tends to underestimate the number of individuals in contagiously-distributed species. In this stand, *Abies lasiocarpa* shows some clumping, so its distance measures are often very small or very great. Therefore the density values derived for *Abies* may be somewhat inaccurate; on the other hand, the dominance figures were deemed the more meaningful measure here.

Absolute density, frequency and dominance values were calculated from the distance and size measurements at each point. These were transformed to relative values and totalled for the (cumulated) Importance Value for each species. The results are shown in Table 3-1. The size measurements were grouped into classes and tabulated in Fig.3-1.

Table 3-2 presents information on the performance of the main conifer species in terms of tree vigour and growth form. Note that for the three vigour scales, the first column denotes a rating scale for each of the characteristics. Individual trees were ranked by class and the species' mean rating is also given.

These figures can be interpreted as follows. _Abies lasiocarpa_ is high in density, but the stems are small in diameter (Fig.3-1). Therefore, mean basal area per tree and total area for the species are low, as is its dominance (Table 3-1).

The common growth-habit of _Abies_ in this area is an erect flagged leader with "skirt" of lower branches (see Table 3-2). Clumping is common and its incidence increases upslope. Mean height was 2.33m (7.65') and height decreased gradually with elevation. Many individuals with desiccated needles (especially on the windward side) were recorded (43/47 trees) and many others observed.

Although some _Abies_ individuals bore cones, the majority of these cones were 'gummed up' by the snow mould _Herpotrichia_. This fungus damages those branches lying under snowbanks late in spring where water content is high from repeated thawing and freezing (see Fig.4-6). Very few of the cones contained seed.

Table 3-1

Study Area A: Results of Point-Centered Quarter Data Analysis

Species	1 Relative Density	2 Relative Dominance	3 Relative Frequency	(sums cols. 1-3) Importance Value	I.V. Rank
A. lasiocarpa	55.86%	24.39%	46.15%	126.40	2
L. lyallii	34.43%	67.59%	41.02%	143.04	1
P. engelmannii	9.43%	8.01%	12.81%	30.25	3
(Totals	99.72	99.99	99.98)		

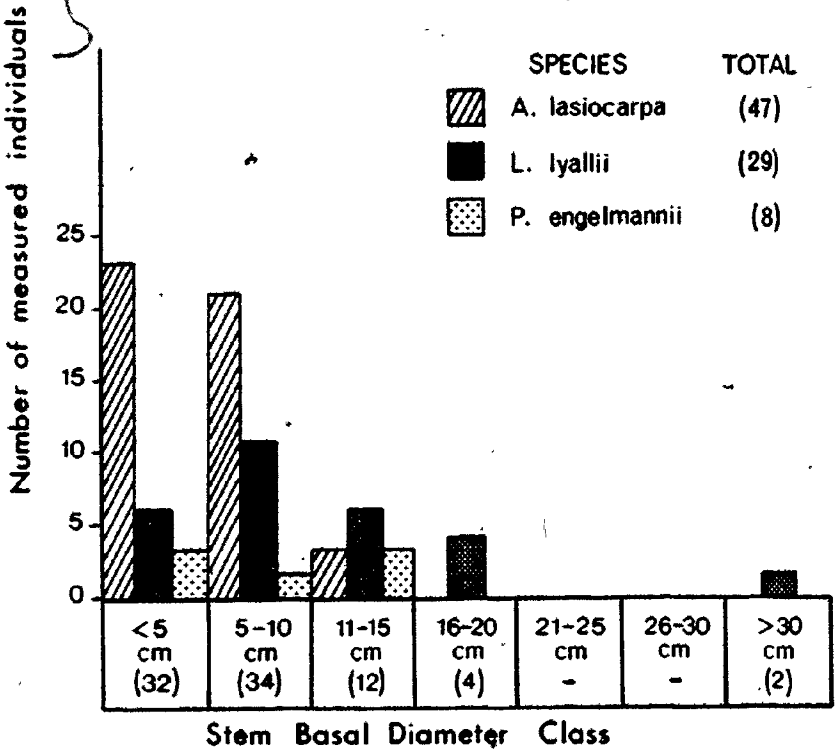


Figure 3-1: Diameter Class Distribution Living Trees Study Area A

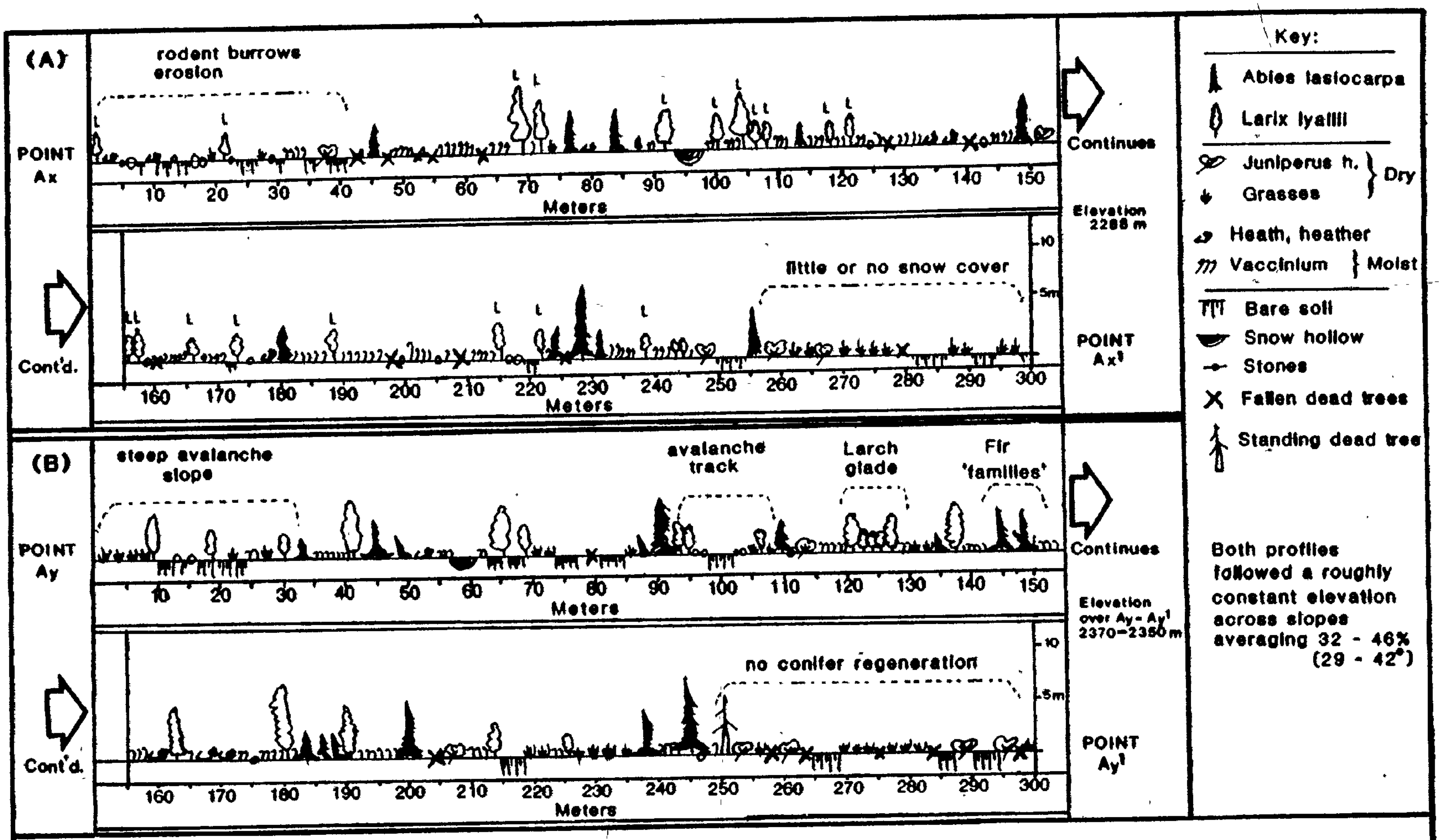


Figure 3-2: Profile of Vegetation in Study Area A. Each bisect shows diagrammatically the vegetation in a 1 meter wide belt. Both bisects have a west-east orientation.

Table 3-2

Study Area A: Observations on Physiognomy and Vigour* of 84 Trees

	Species		
Characteristic	Abies (47)	Larix (29)	Picea (8)
Physiognomy			
1. Symmetrical, erect, single stem	4	10	-
2. Erect, split/double trunk; in clump	11	15	1
3. Flagged; with subnival mat	24	4	3
4. Semi-prostrate mat, no supranival flag	8	-	4
Mean height	2.33 m	5.05 m	2.03 m
General Vigour			
1. Very vigorous; unusually healthy	2	7	-
2. Normal vigour	11	21	1
3. Subnormal vigour; showing signs of ill health	31	1	5
4. Moribund	3	-	2
Mean rating	2.74	1.79	2.13
Tip Vigour (terminal shoot)			
1. Tip vigorous and healthy	5	27	1
2. Tip unhealthy but alive	26	1	2
3. Tip dead	16	1	5
Mean rating	2.19	1.14	2.38
Degree of Browning (Tips red-brown or yellowing)			
1. Little or no foliage brown	4	25	1
2. Less than 30% of foliage brown	30	4	3
3. More than 30% of foliage brown	13	-	4
Mean rating	2.19	1.14	2.38

* (Vigour Scale adapted and expanded from Sprugel, 1976, 894)

No *Abies* seedlings were found within Study Area A; *Abies* is nevertheless very important on the site due to its ability to enlarge original colonies by vegetative reproduction. Layering is linked with areas of maximum snow depth (Whipple, 1975), where the weight of snow holds lateral branches in contact with the earth or humus cover where, over time, they form adventitious roots. In the clonal groups of small stems that result, the 'boundary' of an individual 'tree' may be impossible to discern. Fig.3-2 shows bisect scale drawings of the vegetation along two profiles 300m long (refer to Fig.2-5 for their exact location).

Even though its dominance value (derived from basal area) is low (Table 3-1), *Abies* has important influences on local microclimate. Snow tends to pack into its lower branches early in the winter (Wardle, 1968), and melt slowly in the spring, thereby extending the growing season moisture supply. *L.lyallii* may perhaps extend to higher elevations, "but a single established subalpine fir is capable of colonizing a greater area than any other species in the [timberline or] krummholz region" (Franklin and Mitchell, 1967:12).

In contrast to the status of *Abies*, *Larix lyallii* reproduces by seed almost exclusively, shows largely symmetrical morphology, and reaches the largest diameter and height (5.05m) in Area A. A larger range of size classes is represented (see Fig.3-1), and seedlings and saplings are plentiful. The origin of these areas of regeneration is always traceable to a mature tree westward along the ridge.

Many of the Larix individuals had a healthy cone crop (27/29 trees) and no vegetative reproduction was seen here. Because the needles are shed in the fall, the snow-load on the branches is minimal (compared to that of Abies).

Flagging is much less pronounced in Larix than Abies, but the main trunk is often gnarled, deformed or shows evidence of breaking or splitting in the past (see Table 3-2). It is commonly found in small clumps further upslope and, within these protective groups, retains a largely symmetrical form.

One advantage of the thick bark of Larix is its ability to survive repeated fires, at ground level or from lightning strike. Scattered individuals showed one or more basal or trunk scars and yet appeared vigorous and were fruiting.

Because of its higher mean basal area per tree, the dominance value of Larix is much greater than that of Abies lasiocarpa (Table 3-1). It could be concluded however that the cumulated Importance Value is essentially equal for the two species in this Study Area. Certainly, if sexual reproduction is taken as an arbitrary indicator of species "success" in addition to the measures shown in Table 3-1, Larix dominates slightly in this Area. There are few indicators in the stand age structure that this proportion is likely to change. Because of Abies' minimal seed crop, it is likely that Larix seedlings will continue to expand onto new sites to the lee of Area A, while Abies expands slowly, if at all, at the borders of already established 'families' (see Fig.3-3).

The Importance Value of Picea engelmannii is low in this area (see Table 3-1); it appears only occasionally above the timberline. Few trees are encountered, and these are gnarled and flagged in shape, or clustered in dense groups (Table 3-2). It is found as low cushion krummholz at elevations where Larix and Abies still show erect form. Basal area is low. Generally, Picea prefers a moister, shadier habitat than this site provides, particularly for its initial establishment.

It is postulated, however, that at one time Picea 's role may have been more prominent (i.e., an early 'coloniser'), and has declined in numbers and in vigour. Clues are: its complete lack of juveniles; its frequent position at the western (windward) end of an Abies island; and the existence of upper-slope individual trees now severely deformed which were apparently able to reach considerable height as a symmetrical erect trunk in the past (shown in Fig.3-14a). A few midslope individuals bear cones, but without exception these were blackened by snow-fungus.

Community structure and species performance in Area A can be summarized as follows. Visually, Abies lasiocarpa appears to dominate, but this is explained by its tightly clustered regeneration (Arno & Habeck, 1972:447). Its har-

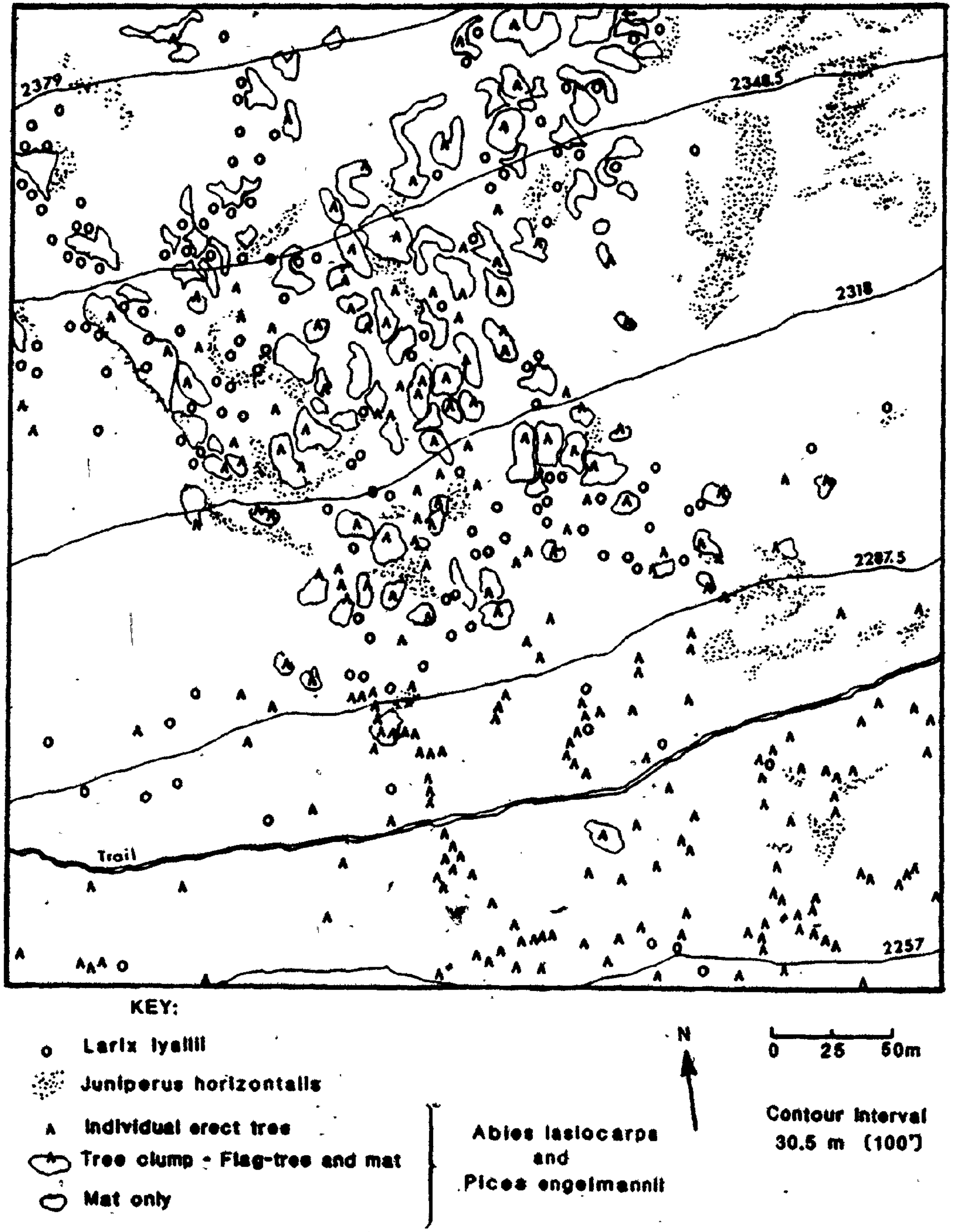


Figure 3-3: Living Conifer Populations -Study Area A

diness is inferior to that of *Larix lyallii* which dominates the site with tall, vigorous individuals and numerous saplings and seedlings. *Picea engelmannii* is infrequent and shows the decreasing population structure (Whipple & Dix, 1979:147).

3.1.2 Past Distribution-A

It is postulated that this area possibly represents what the appearance of much of the morainal ridge was before the 1870 fire. In terms of current conditions, this is a remarkably high elevation for such large symmetrical trees to have established. The amount of fire evidence is low, suggesting less intense burning here (this is further discussed in Chapter 4.3.1.). Signs of long term forest cover are found in stump hummocks and unburied woody remnants (Brink, 1959).

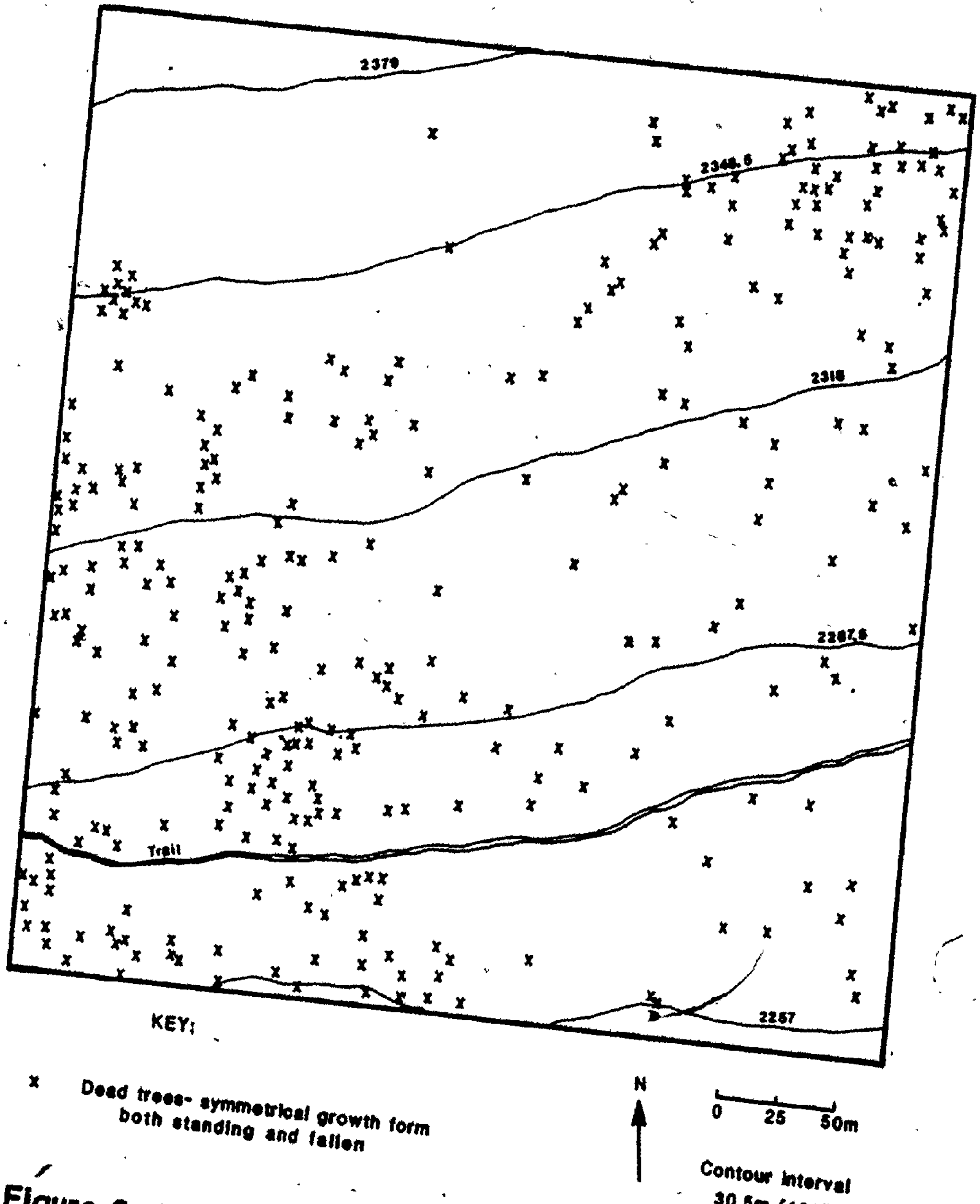


Figure 3-4: Dead Tree Distribution -Study Area A

3.1.3 Study Area B

Contrasting sharply with the vegetation just described is Area B, a very open heath meadow immediately to the west along the ridge (location shown in Fig.2-4). Over the 30 years of airphoto coverage of the site, seedling establishment appears to have been almost nil, and the few small trees found are severely flagged and have desiccated leaders. The entire conifer population is marked in Fig.3-7 by species. All the trees shown are in the reproduction size class regardless of age. Even on the sites of fallen logs and rotting stumps, seedling establishment is very sparse.

The species *Kobresia* and *Dryas* in the herb layer indicate a fairly xeric habitat, and in places the forb and graminoid cover is dense enough to present competition to conifers.

This portion of the moraine has the most westerly aspect of all the study areas, and this, in part, accounts for the xeric conditions. Windiness and solar radiation are high and the surface experiences great extremes of temperature. The amplitude of daily and seasonal temperature regimes is greater than on north or easterly aspects. The soils are generally thin and stony. As much as 55% coverage of 4 sample plots 10mx10m support no vegetation cover at all.

Portions of the study area are convex in configuration, and the prevailing west wind tends to remove snow cover here and redistribute it in hollows farther eastward along the slope. Fig.3-6 presents a schematic diagram of the vegeta-

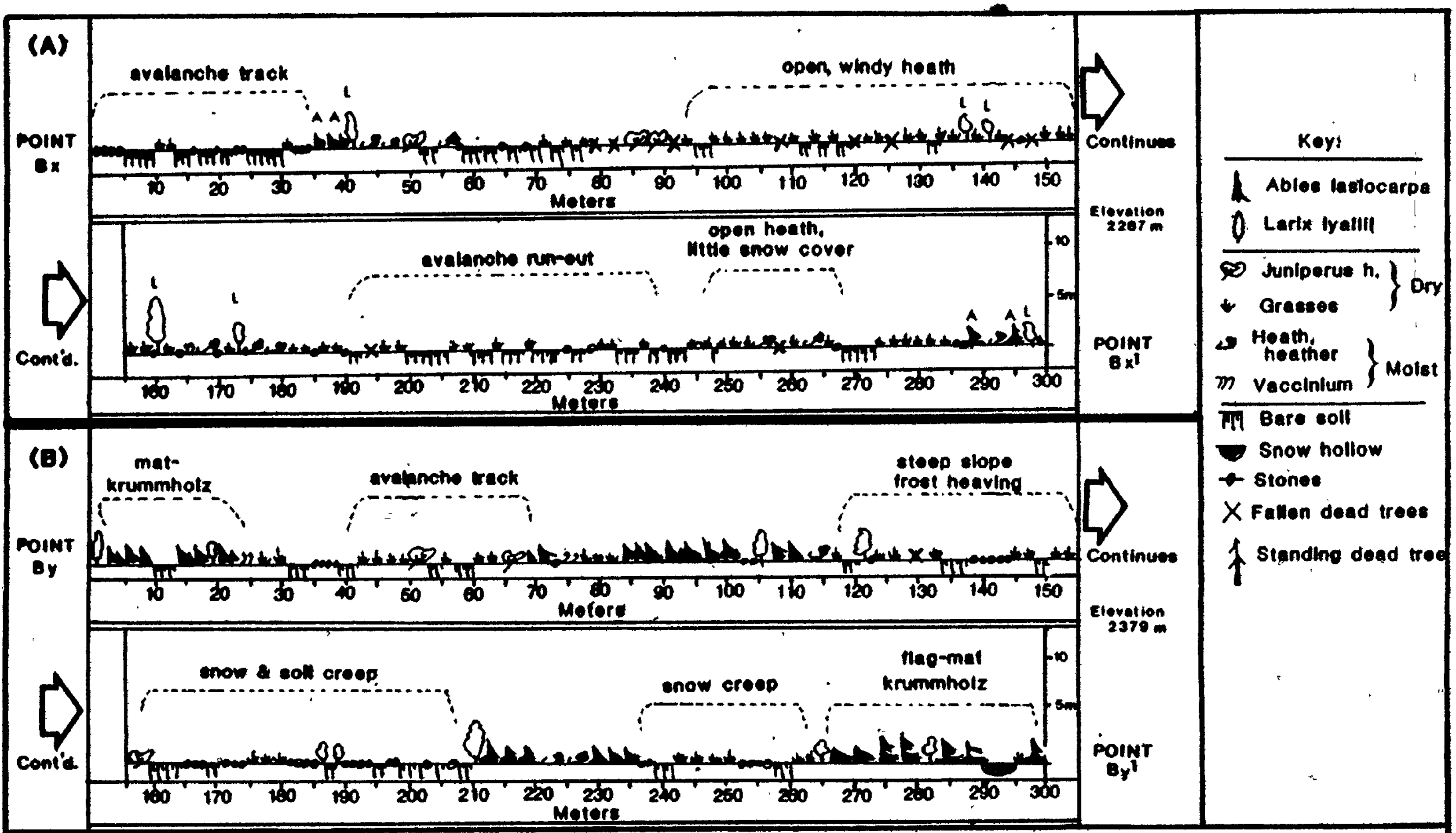


Figure 3-6: Profile of Vegetation in Study Area B. Each bisect shows diagrammatically the vegetation in a 1 meter wide belt. Both bisects run generally west-east.

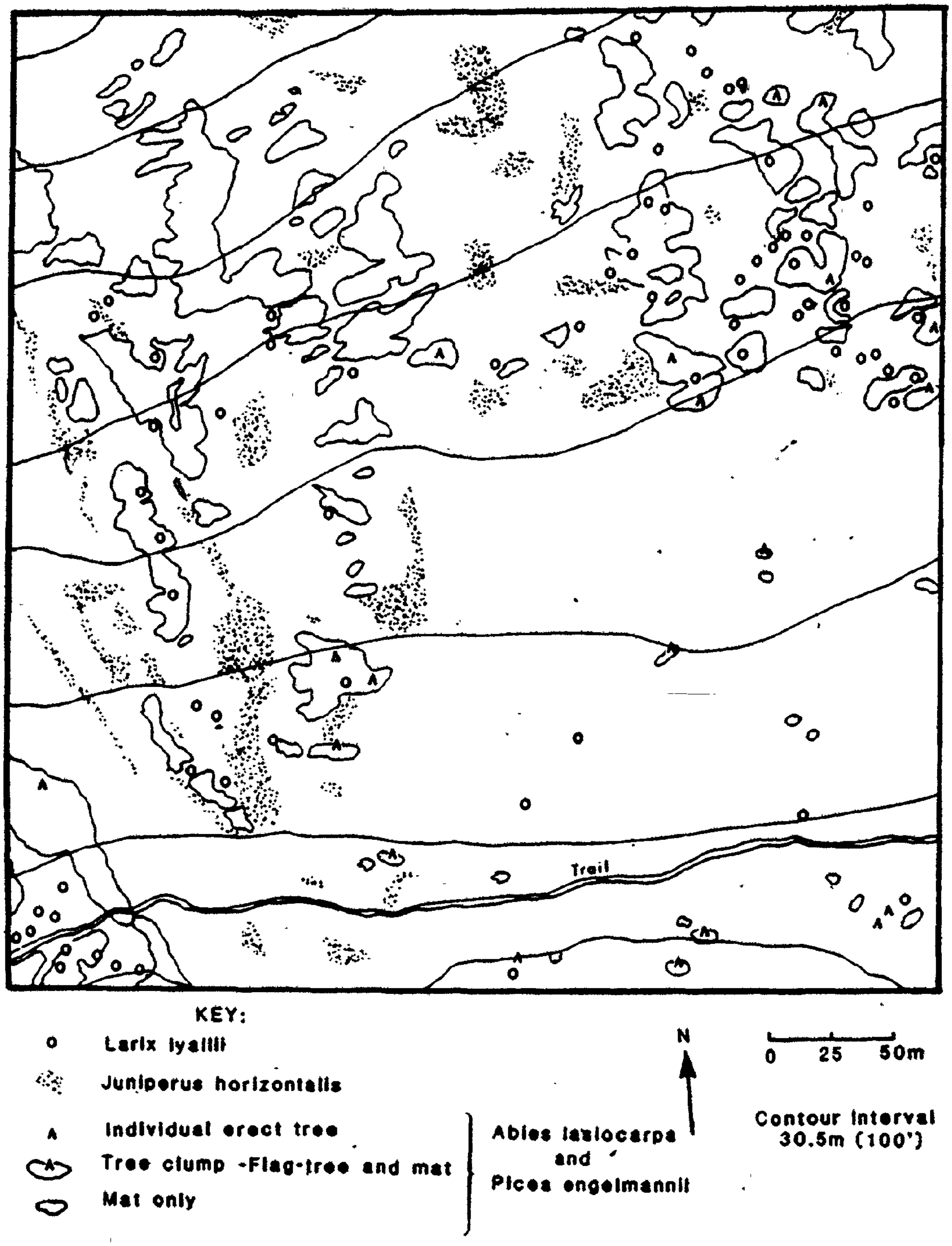


Figure 3-7: Living Conifer Populations -Study Area B

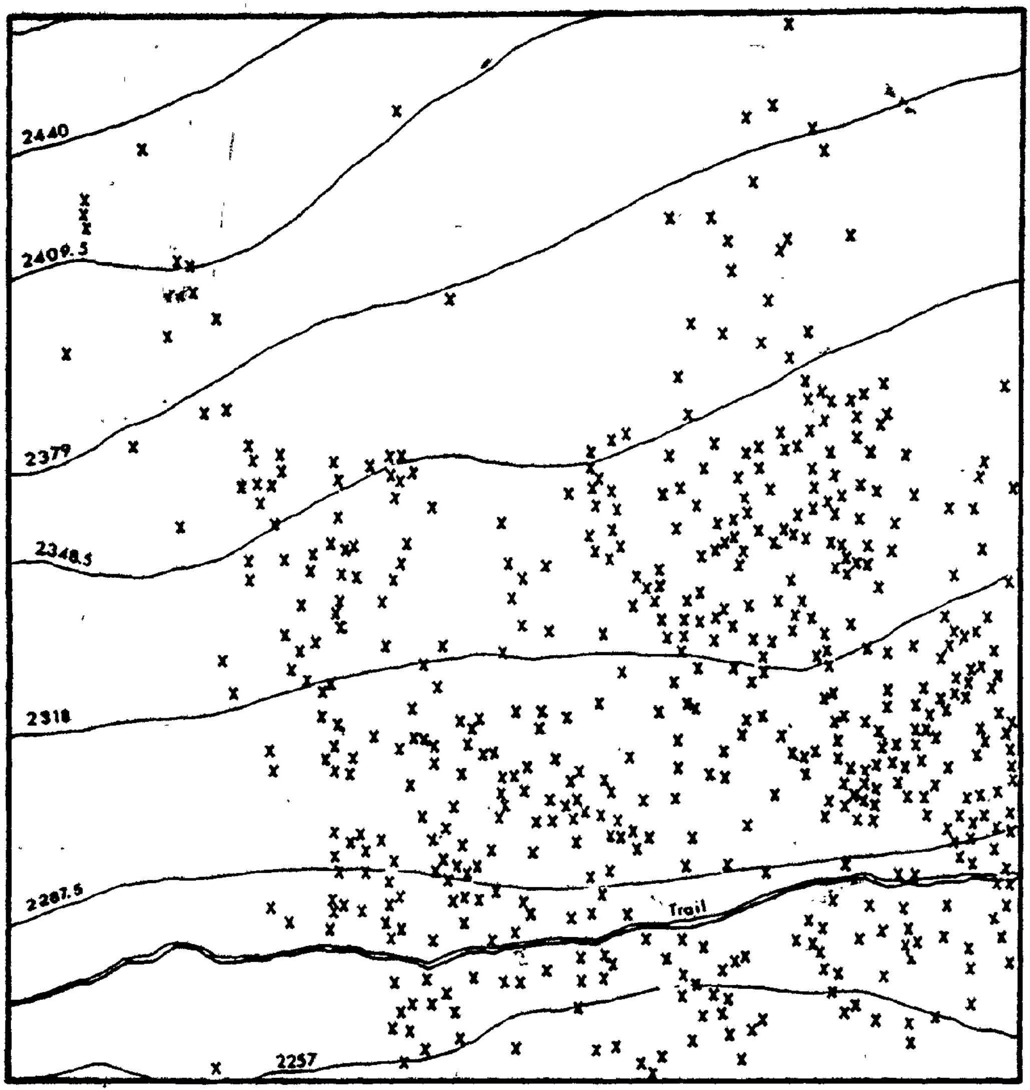
tion in two bisect profiles (Bx-x1 and By-By1) run along contours.

Not all of these conditions (i.e., stony, dry, snow-free) exist in every part of Area B, however: they are intermingled in a finely-textured pattern with more mesic sites ameliorated in some way. Microsites apparently compatible with conifer regeneration exist, for example, in the 'lee' of boulders, stumps, or living trees, in concave slope segments, or in pockets of organic soil or decaying plant matter.

However, almost none of these potential regeneration sites were occupied. Generally the low density of trees or tree islands in this area appears to result from a lack of seed rather than just a paucity of suitable microsites (in contrast to findings in Eastern Colorado, Marr, 1977:1162). Even layering is uncommon.

3.1.4 Past Distribution-B

Area B has a high density of fallen logs and standing snags, all of which show burn evidence. These wood remnants are well-preserved: they have decayed remarkably little in approximately 130 years. Compared to the deformed dwarfs presently found, the fallen trees indicate only very tall and symmetrical individuals, apparently little deformed by wind. Comparison of Figures 3-7 and 3-8 reveals this contrast. Based on the dimensions of 35 sample logs, the aver-



KEY:

x Dead trees of symmetrical growth form both standing and fallen

Contour interval 30.5m (100')

Figure 3-8: Dead Tree Distribution -Study Area B age height of fallen trees was 10.7m (range 8.56m- 12.84m), and the average basal diameter was 13.4cm (range 5.6cm-23.7cm).

3.1.5 Study Area C

A third, and different, situation was found further east along the slope in Area C (see Fig.2-4). Here some regeneration has taken place in the immediate lee of Area A, as found on air photos from 1947 to 1978 and supported by field surveying. More 'potential sites' here are occupied by a juvenile (refer to Fig.4-11). The dense stand of Area A provides the wind-buffering effect and a seed supply. Significantly, most *Abies* reproduction here is not by layering, but by individual seedling. *Larix* and *Abies* reproduction are found on more level microsites than those convex sections showing avalanche or soil creep effects. A fairly significant degree of surface hummocks and undermining caused by ground squirrel activity locally affects conifer regeneration success.

In a series of 4-10m squares (400m²), percentage cover types were recorded, and these contrast with those of Area E. The humus layer is more substantial. Both living and dead heather plants trap snow and provide ameliorated seedling sites. As a rule there is less rock and bare soil except in the ground squirrel colonies (refer to Fig.4-10).

Table 3-3: Cover Type Results

Cover Class in each Sample Plot

GROUND COVER TYPE	A 1 2 3 4	B 1 2 3 4	C 1 2 3 4	D 1 2 3 4	E 1 2 3 4
Vegetation including vascular plants, moss, lichens	5 5 5 4	3 3 3 4	3 3 3 4	3 3 2 2	5 5 6 5
Dead Vegetation, duff, humus	2 2 2 2	2 2 2 3	3 2 3 2	2 2 1 2	2 2 1 2
Mineral Soil	1 1 2 2	2 2 2 2	2 3 2 2	2 1 1 2	1 1 - 2
Gravel	1 1 1 2	3 2 2 1	1 2 2 2	3 3 3 4	- 1 - -
Bare Rock	1 1 1 2	2 2 2 1	2 2 2 2	2 2 4 2	1 - 1 2

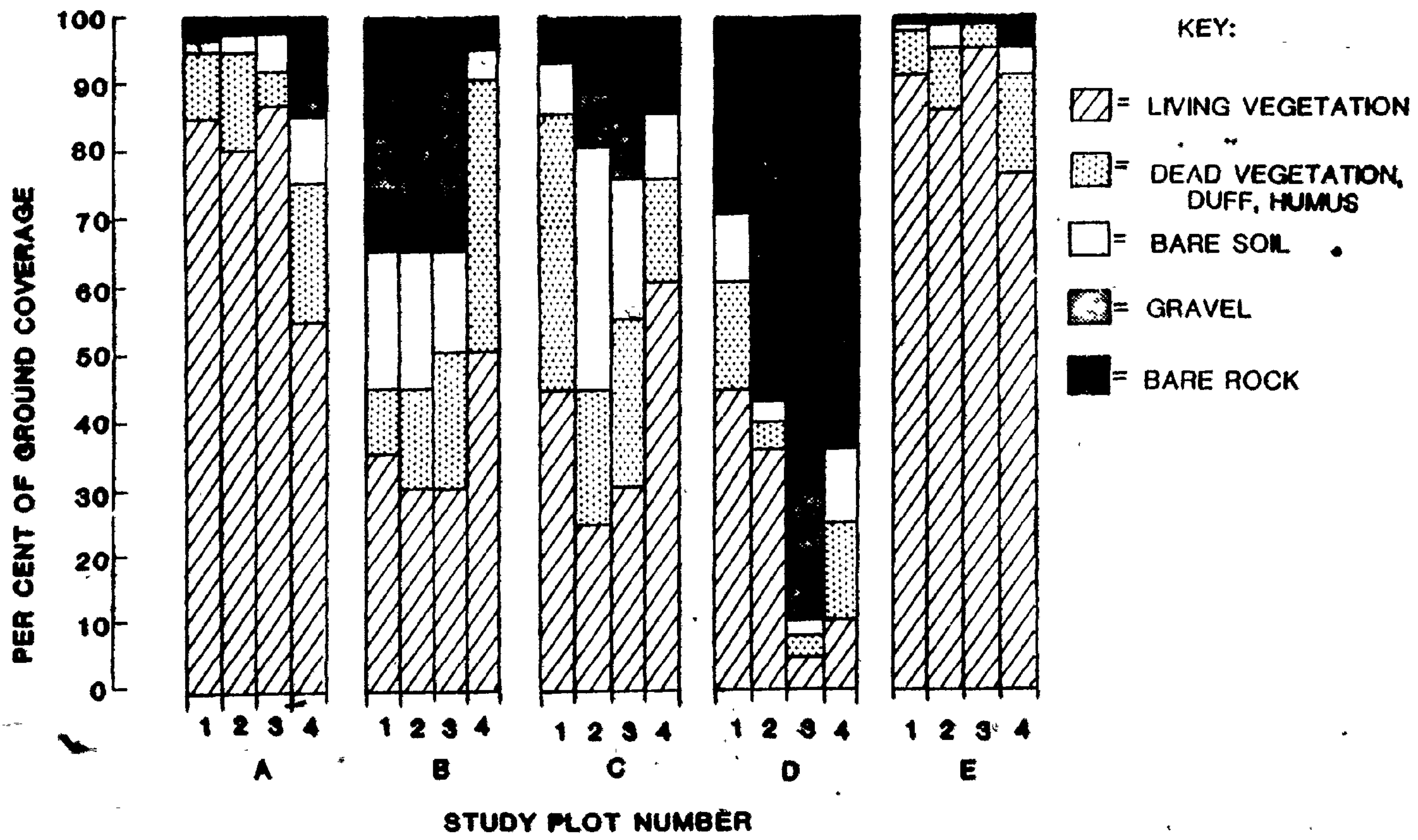


Figure 3-5: Histogram comparing Percentage Cover Type Results in 20 Study Plots

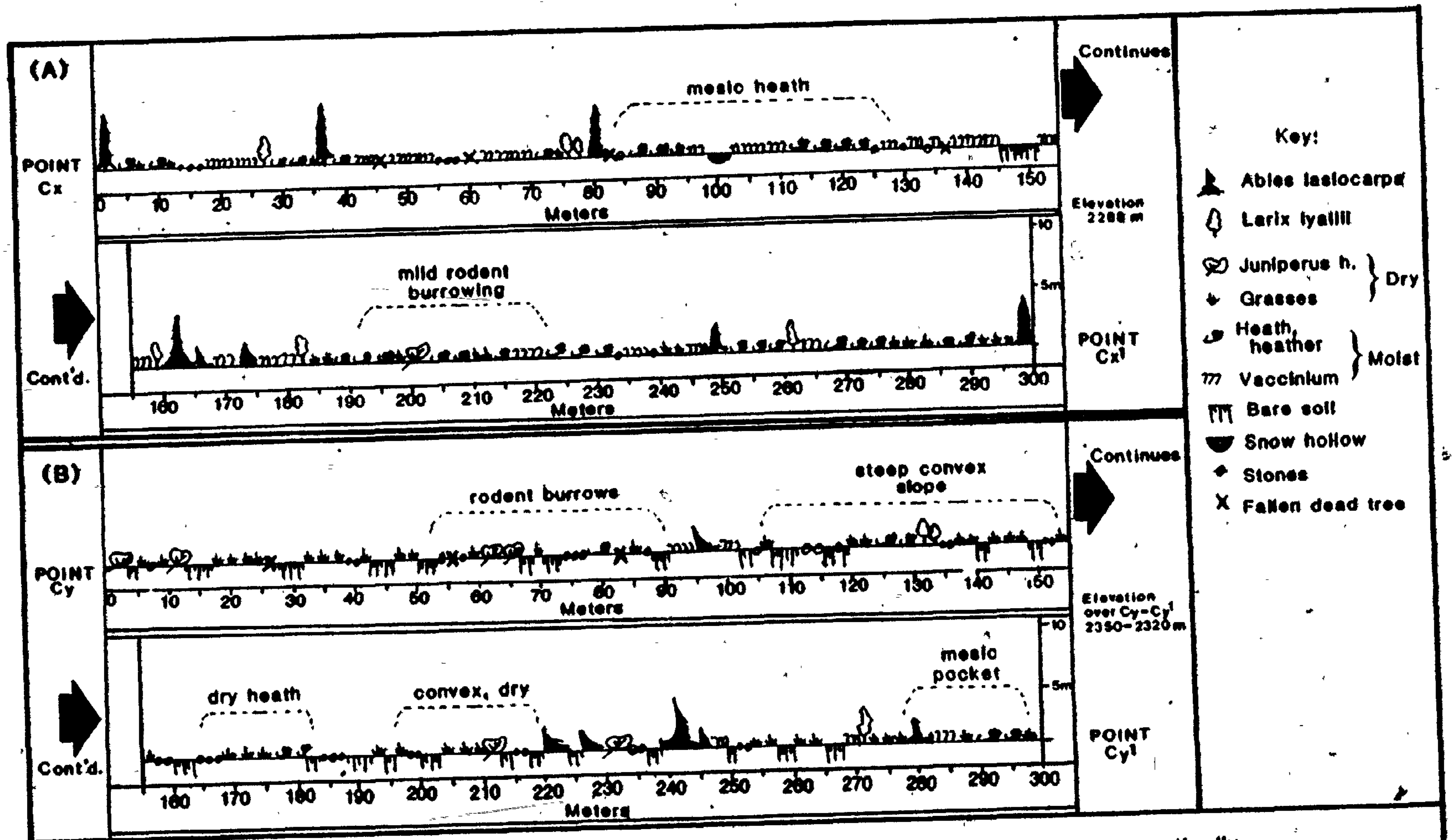
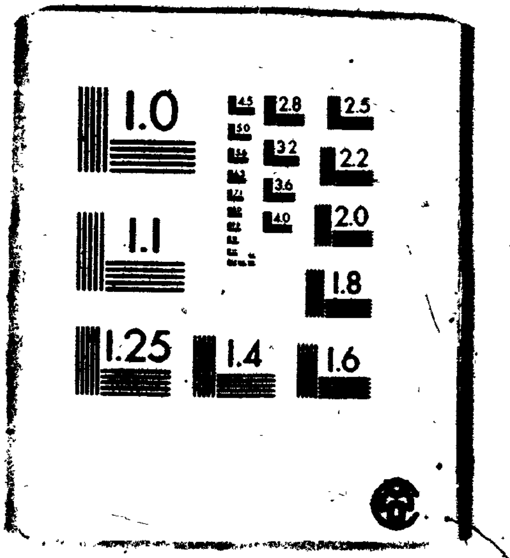


Figure 3-9: Profile of Vegetation in Study Area C. (A) and (B) show diagrammatically the vegetation in two 1 meter wide belts, oriented west-east.

2



The somewhat reduced wind speed means increased snow depth and therefore a longer-lasting soil-moisture supply into the summer. Sharpe (1970) has summarized the research that points to the critical difference made by an additional 10 days to 2 weeks of soil moisture at the end of the growing season, especially on drought-prone southwest exposures. In the understory, Phyllodoce and Cassiope associations indicate the slightly more mesic conditions.

Characteristic across-contour bisect profiles are shown in Fig.3-9. The location of the bisects (1 meter wide belts) was shown in Fig.2-5.

3.1.6 Past Distribution-C

Just as in Area B, there is a profusion of burnt stumps and large logs, all showing symmetrical, erect forms and averaging 11.2m in length (based on 30 sample logs). On steep and convex segments of slope, the logs and stumps have blocked downhill-wasting material and it is only on these small humus- and soil-traps that seedlings are found.

The very centre of Area C is nearly lacking in tree remnants, implying that it has likely always been an alpine heath meadow but of much smaller extent than the "persistent bald" which presently exists (term from Billings and Mark, 1957). It is the most xeric and stony portion of Area C. Larix saplings and the slower-growing Abies are very slowly encroaching on the outer margins of this area, and Fig.3-10 and 3-11 show the contrast between past and present conifer patterns (refer also to Fig.4-11).

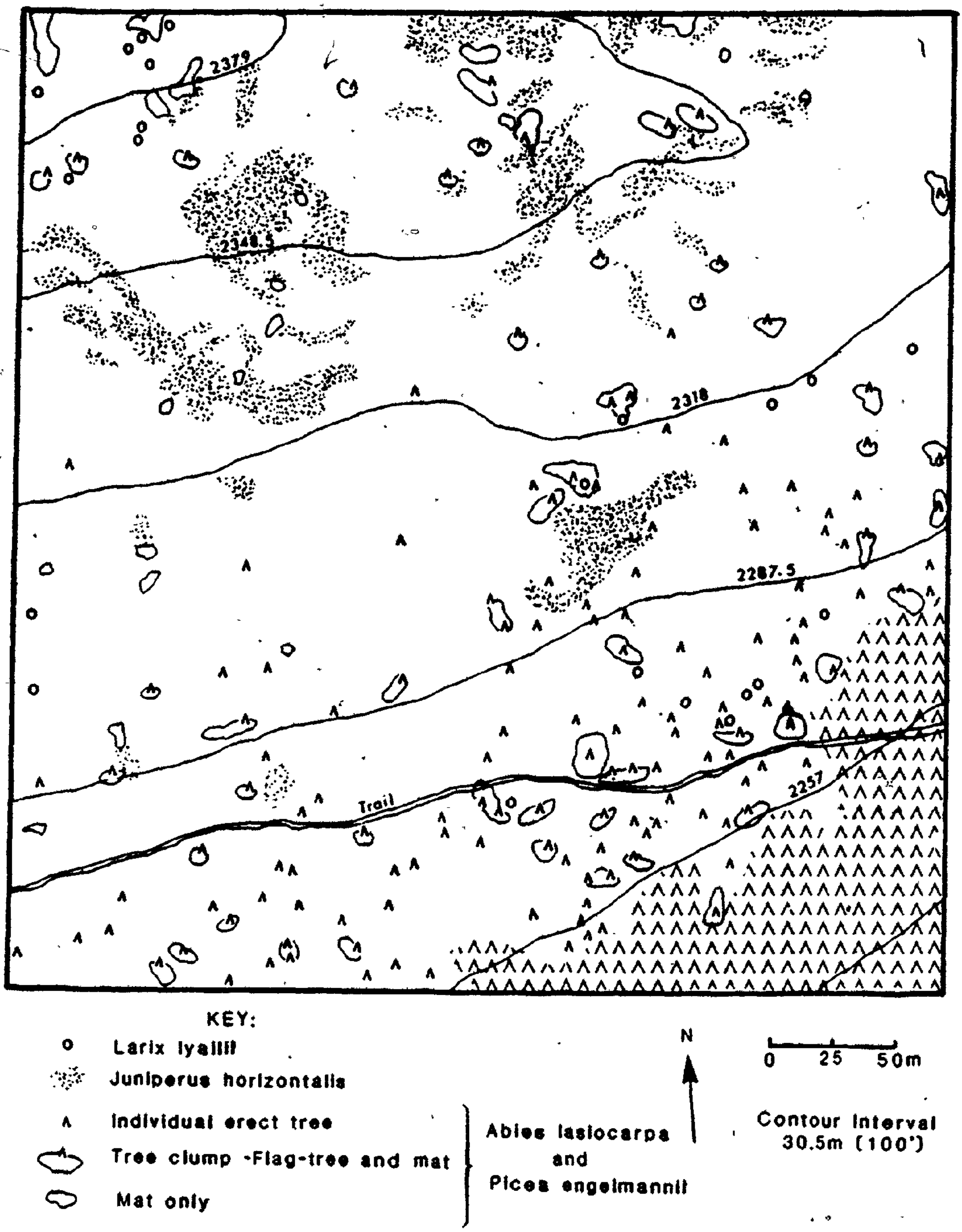


Figure 3-10:
Living Conifer Populations -Study Area C

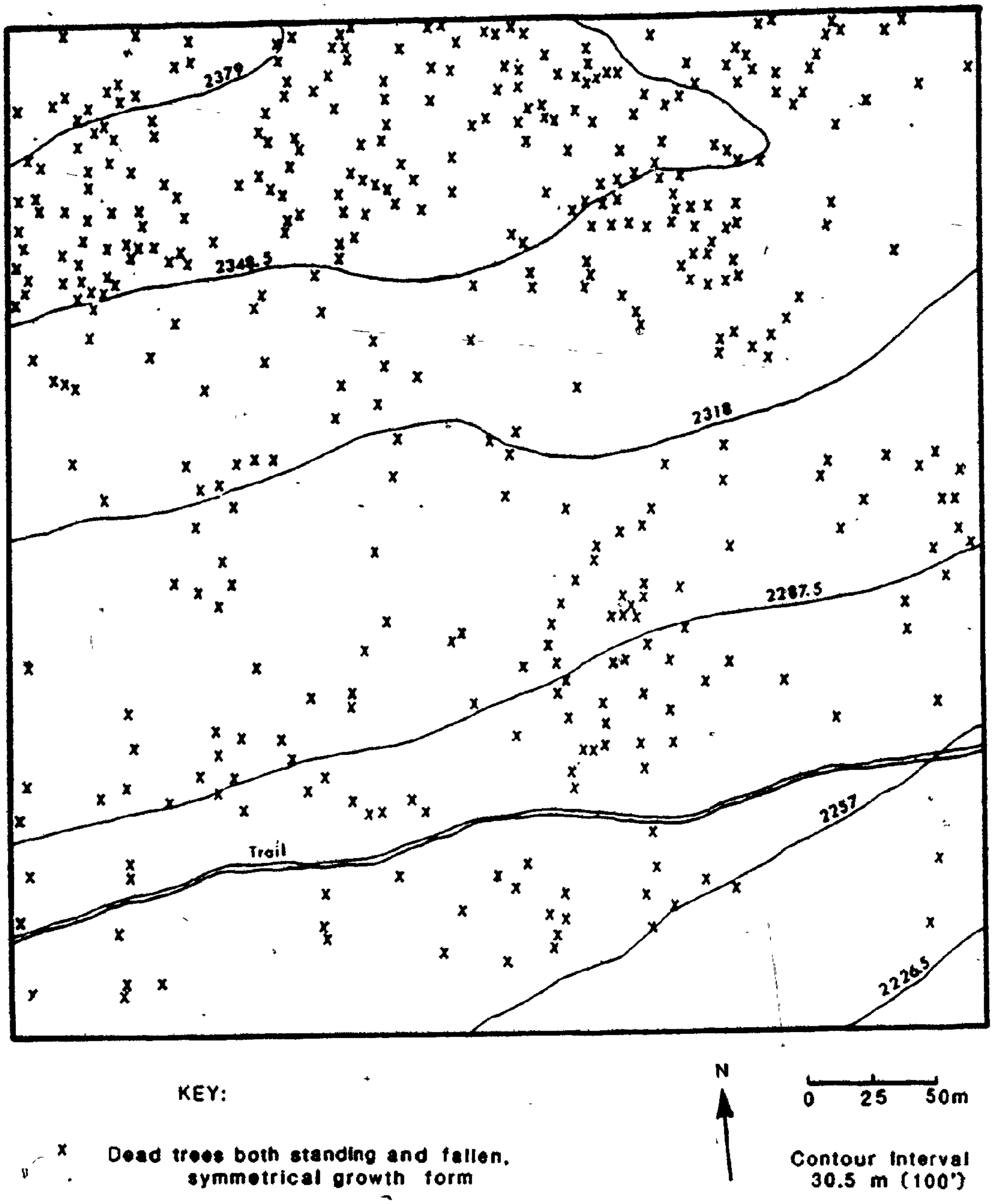


Figure 3-11: Dead Tree Distribution -Study Area C

3.1.7 Study Area D

Area D represents the belt upslope from the erect vegetation of Areas A,B, and C (location shown in Fig.2-5), and is characterized by the same conifer species growing in krummholz or 'elfinwood' forms (Clausen, 1965; Holtmeier, 1981). Individual trees of *Abies*, *Picea* and *Larix* are found but they are flagged or multitrunked (see Fig.3-14a). Both trunk and needles show some degree of mechanical or physiological damage. Tree clumps are much more common.

As Tranquillini (1979) points out, tree groups have decided ecological advantage over isolated individuals, since the group generates its own internal climate where extremes of wind, temperature and humidity are ameliorated. The most common growth form is shrub belts of *Abies* and *Larix* at least 8m in length, which results from death (by winter-desiccation) of plants on the exposed windward side (where snowcover is light and roothold is weak), and lengthwise growth in the slightly more favourable microclimate on the leeward side (Plesnik, 1973; Pontecorvo and Bokhari, 1975). The configuration of the these belts (or oblong circular groups) is NE 60°, trending sideways up and across the slope (which is 180°S).

The maximum height of trees (all species) is 1.52m (5') and the height of the subnival skirt is invariably .5m, a reliable indicator of mean snow-depth in the immediate area.

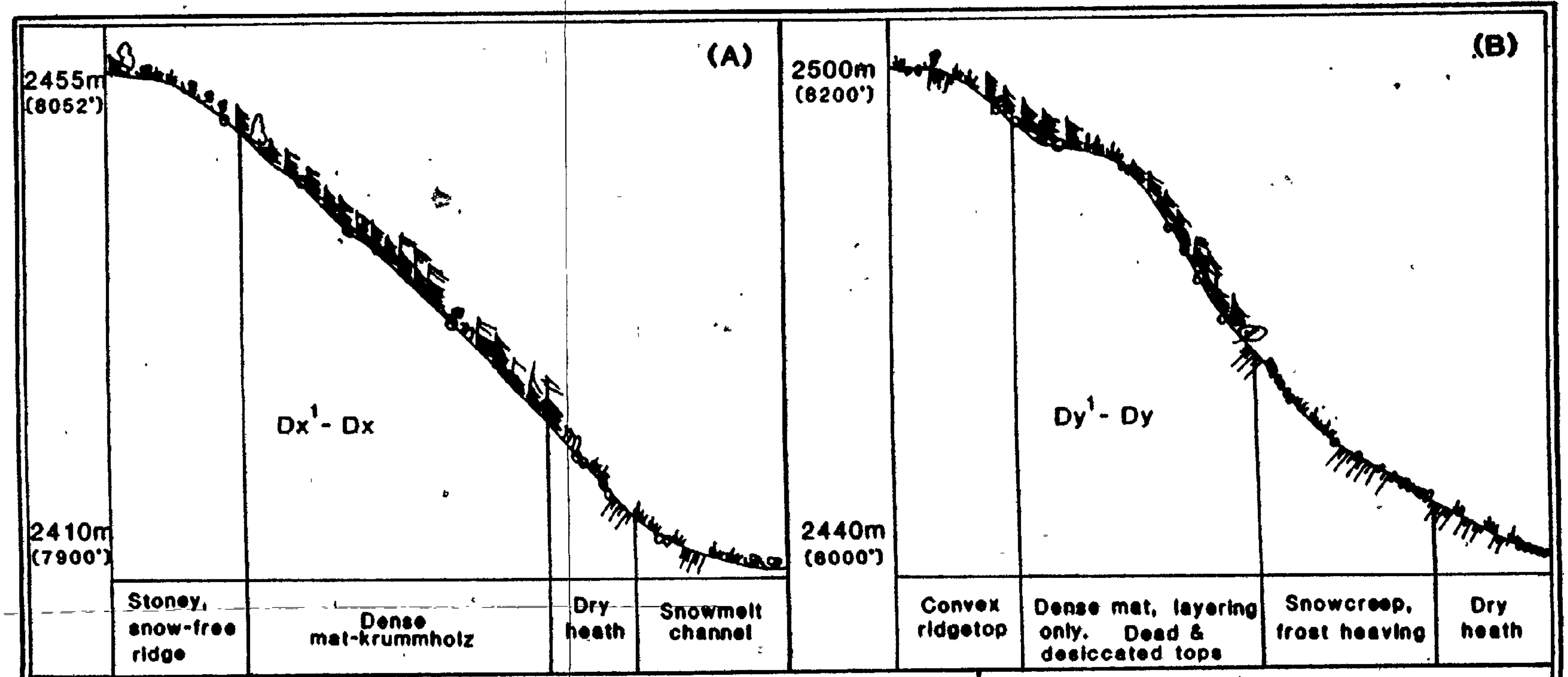


Figure 3-12: Profiles of Vegetation in Area D

(A) and (B) show diagrammatically the cover in two 1 meter wide belts.

Both profiles have a north - south orientation and extend 100m *across* contours. Slope averages 36.6 - 45.5% (33° - 41°)

Key:

Ablies lasiocarpa
Larix lyallii
Juniperus h. } Dry
Grasses } Dry
Heath, heather } Moist
Vacoinium } Moist
Bare soil
Stones

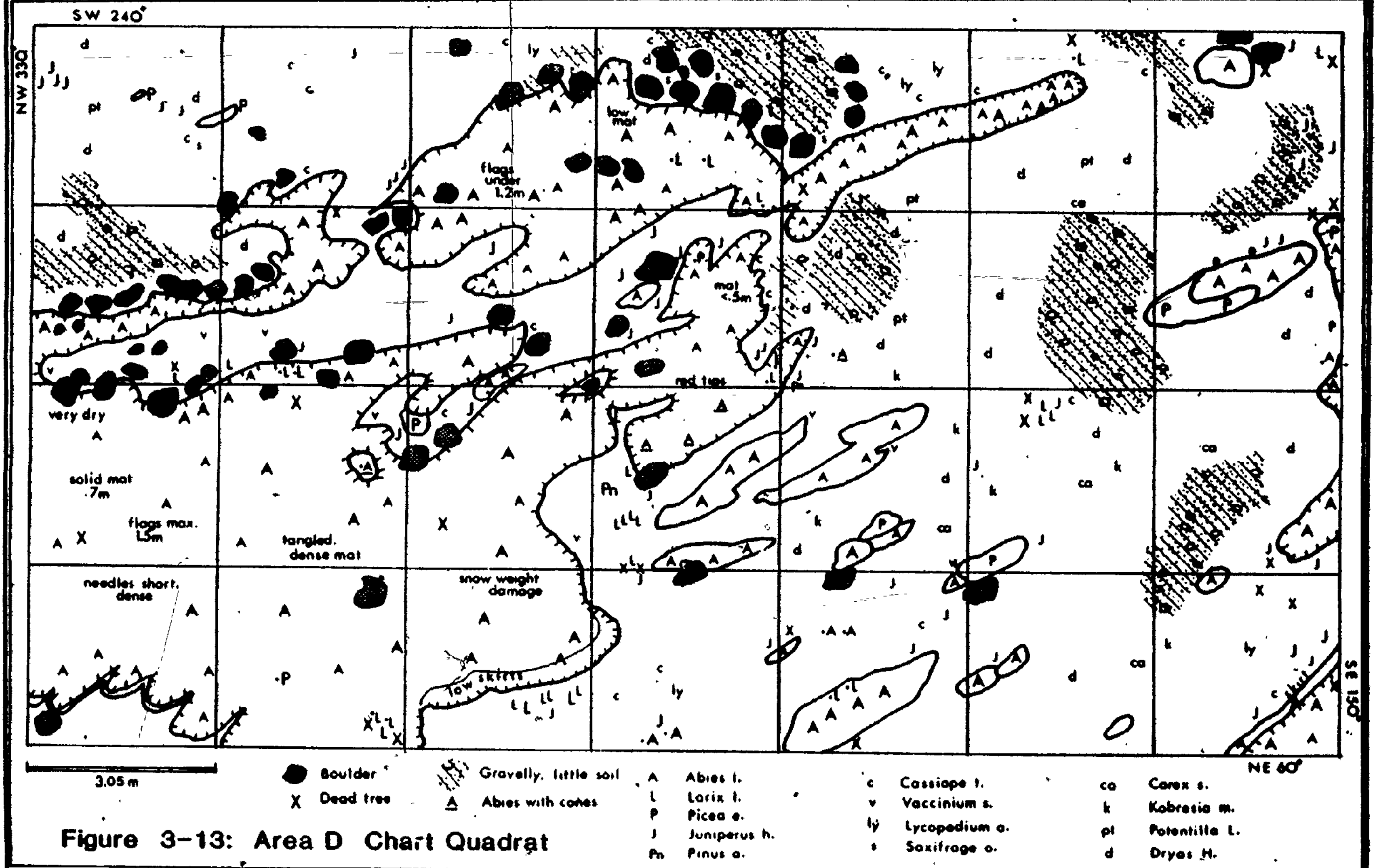


Figure 3-13: Area D Chart Quadrat

With increasing elevation towards the ridge-crest, *Dryas Hookeriana* ground cover and *Juniperus* shrubs indicate those areas which are blown partly clear of snow cover in the winter and therefore suffer some degree of drought by late summer or early fall. In contrast, tree groups and shrubs trap blowing snow in their lower branches and, in their lee, the snowmelt creates localised pockets of slightly more mesic conditions (with *Salix nivalis*, *Luzula* spp. and *Juncus* spp.).

The two slope profiles 100m long (location in Fig.2-5) shown in Fig.3-12 demonstrate the barrenness of steep slope segments subject to frost needle activity. Percentage cover results for 4-10m squares were shown in Fig.3-5 and Table 3-3 above.

A chart quadrat of .65 ha (1.60 acres) total area (location in Fig.2-5) is shown schematically in Fig.3-13. Mueller-Dombois and Ellenberg (1974:112) stress that detailed plot studies are more reliable than distance methods where populations show a strongly clustered distribution, as in this case. Although time-consuming, the measuring and mapping of this 106mx61m grid yielded several definite findings.

New clumps of *Abies* or *Picea* have established *only* in the lee (NE 60°) of boulders at least .5m in height. In this grid, 51% of the plots (each plot $9.3m^2$) contain vegetative *Abies* or *Picea* reproduction, whereas *Larix* reproduces sexually, and individuals or clumps of saplings are found only at the leeward ends of *Abies* shrub belts. (This tends to discount a 'pioneer' role for *Larix*). These *Larix* trees are always at a critical "opportunistic" distance from the tree group: close enough for the wind-shadow effect (4-7m), but wide enough to be beyond the sun-shadow or lee snow-drift. This is consistent with the observations of Gloyne (1955). He found the reduction of wind flow by a medium-density tree barrier to be 80% of the original flow at a horizontal distance 3h-5h (h= tree height) beyond the barrier. By leeward distances of 20h the windspeed is still only 60% of the full force.

Quite substantial differences in moisture availability related to the depth and duration of the snow pack are indicated by sharp changes in species composition of the ground cover over short horizontal distances. Patches of heather meadows between *Abies* krummholz mats would seem to be protected sites, ideal for regeneration, but these are semi-permanent snow glades where snow drifts persist too late into the growing season. *Cassiope tetragona* and *Lycopodium alpinum* indicate a cool, moist snowbed habitat (Ogilvie, 1969; Porsild, 1979).

On a more convex slope segment only 20m away (study plot D4) soils are very shallow and stony (calcareous) and a very dry grass and forb alpine association exists. *Kobresia myosuroides*, *Dryas Hookeriana* and *Potentilla Ledebouriana* indicate a wind-exposed crest blown free of snow early in spring (Ogilvie, 1969; Knapik et al., 1973).

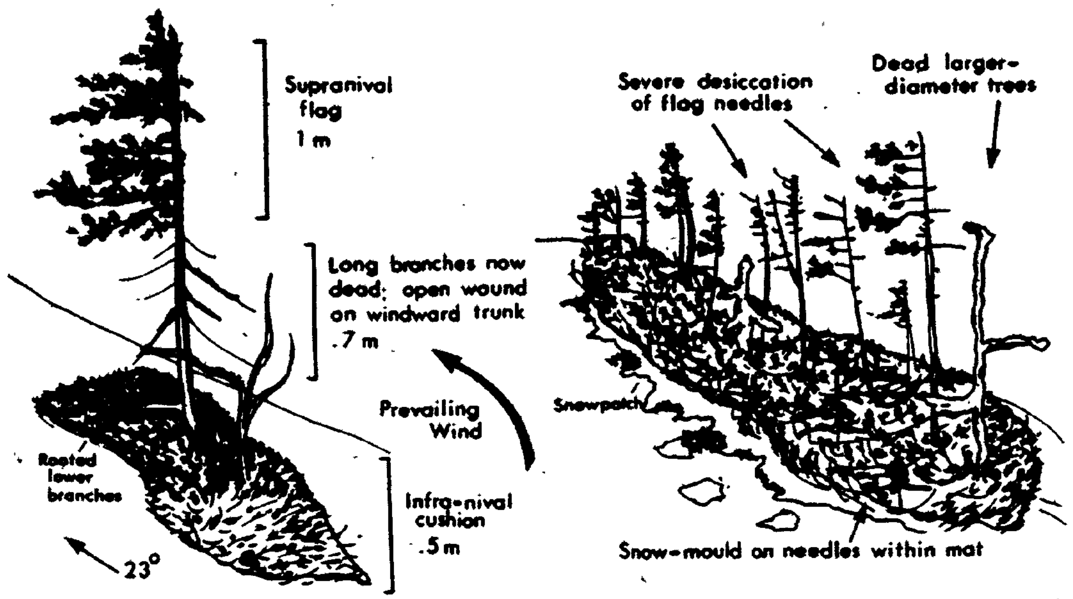
In the western portion of Study Area D (Plot D2 for example), several shrub and graminoid associations indicate continual or infrequent avalanching (*Salix arctica*) or (*Elymus innovatus*), respectively. Both are found with *Bromus*, *Festuca*, *Poa* and *Fragraria* spp. (see Ch.4.3.2).

3.1.8 Past Distribution-D

In Area D, occasional burnt wood remnants are found, but they are similar in size and shape to the conifers now living there (i.e., deformed). No long straight logs or snags were found. So although the *distribution* of conifer growth forms does not appear to have changed substantially over 110 years, there are four features of this area which, taken together, would seem to indicate conditions of increased stress for the current conifer populations.

For instance, the kind of *Abies* and *Picea* formations shown in Fig.3-14b,c indicate that a single isolated tree was able to attain some height as an individual straighter form, and has undergone deformation by wind and desiccation-injury relatively recently, in terms of the total lifespan of the tree. The plant is now 'forced' to its own lee as the windward parts of the plant die (Marr, 1977:1162).

A second feature is the presence of now-dead trunks to the westward end of *Abies* strips that are larger in diameter



a. Picea engelmannii. at 2440 m (8000')

b. Common Abies lasiocarpa morphology from 2320 to 2500 m (7600–8200')

c. Stunted A. lasiocarpa in Study Area D
–at 2420 m (7950') – at 2475 m (8110')

Figure 3-14: Tree Growth-Forms in the Upper Subalpine (Side-views) and of more symmetrical form than any individuals now alive in the group.

A third condition indicating a series of severe years with a shorter or cooler growing season is the widespread desiccation of new annual leaders (see Fig.4-8). Tranquillini (1979) found that the winter drought-resistance of any new growth was sharply reduced in any year in which needle ripening is not completed. All Abies in the mapped grid show some degree of needle discoloration (red or brown) and in 43% of the plots, over half of the foliage shows severe desiccation.

A fourth indicator is the very poor condition of Pinus albicaulis (Whitebark pine), a species which elsewhere fares well in exposed situations. Only a very few individuals were located, and these are sickly and very gnarled, with no signs of reproduction.

The conifers throughout Study Area D show evidence of substandard growth at present, relative to an earlier period in their lifespan. It must be mentioned that no growth-rate data are available to support this statement: physiological stress in the ecotone at present is based on the "clues" of physiognomy and species performance given above. It appears that they pre-date the fire and hence, the visible 'recent' stress is the result of exposure to new open conditions. Important in this regard is the suddenly windier and colder conditions after fire: as long as forest existed below, the prevailing winds moved upslope at a tree-top level rather than at ground level and had less impact on the uppermost trees. However, since the destruction of these tall trees, winds have been unrestricted and move across slope at tundra level, carrying more suspended snow, ice and soil particles. The effect is to severely 'krummholz' and desiccate the uppermost conifer trees (Hansen Bristow, 1979).

3.1.9 Study Area D

This mesic, more sheltered slope is on the northeast-facing lee side of the lateral moraine and appears to have prime habitat conditions for *Larix* growth. Tree density is high, and the maximum sizes attained anywhere in North America by *L. lyallii* are found here (15 -18m height and 40 -60cm diameter). All of these large "patriarchs" carry an abundant cone crop, and based on Arno and Habeck's note that cones are generally not produced in quantity by *Larix lyallii* "until it is two or more centuries of age" (1972:434), these are apparently individuals of great age. Three sample trees aged by J. Gardner (1981:written comm.) became established in 1773, 1785 and 1904 (respectively 209, 197 and 78 years old, at present).

The size class structure of the stand is shown in Fig.3-15. The high density of seedlings and saplings under 1m tall supports the statement that this is a nearly pure *Larix lyallii* stand with an all-aged structure. The frequency and density of *Abies lasiocarpa* are low.

Many of the mature larch trees have a substantial basal fire scar, yet are vigorous and have a straight, symmetrical growth form.

The daily extremes of temperature are less marked than on the windier, drier southwest exposure. The associated understory species (Vaccinium scoparium, Phyllodoce glanduliflora, Erigeron peregrinus, and Anemone occidentalis) indicate a deep snow cover. There is very little exposed soil or rock; a thick duff layer covers boulders and old stump bases.

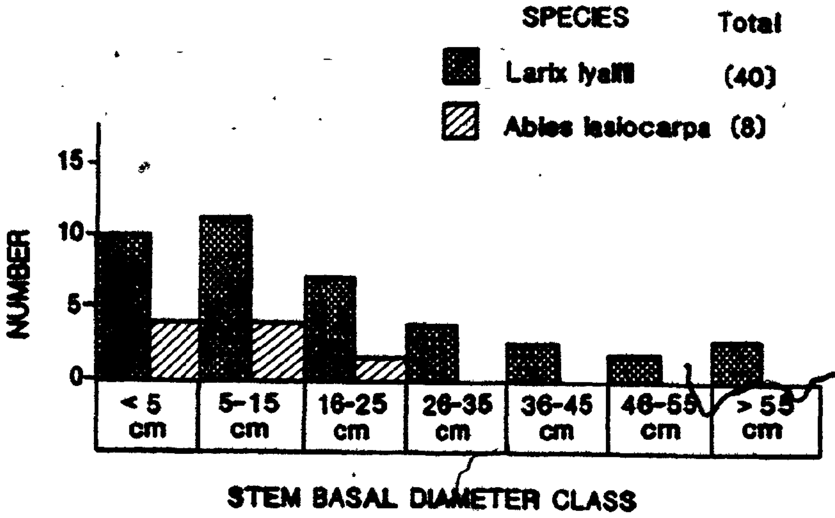


Figure 3-15: Diameter Class Distribution Study Area E Count Plots

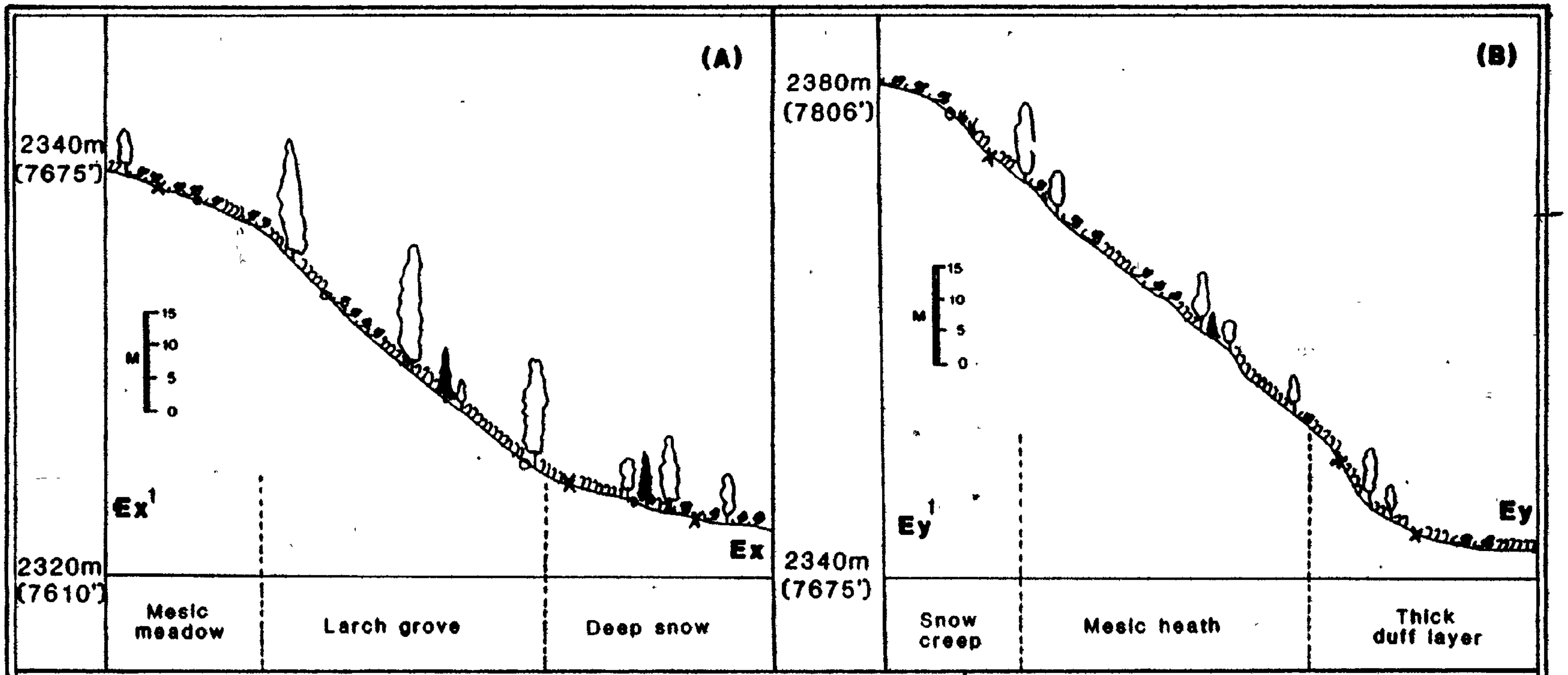


Figure 3–16: Profiles of Vegetation in Area E

(A) and (B) show diagrammatically the cover observed in two 1 meter wide belts.

Both profiles have a southwest-northeast orientation and extend 100m across contours.

Slope ranges from 26.6 - 34.4% (24° - 31°)

3.1.10 Past Distribution-E

There are no signs in the stand's structure or in forest remnants that any significant changes have occurred in this area for at least the lifespan of its giant dominants.

Fallen burnt logs or standing snags are only rarely found. Many *Larix* trees show old fire scars but have survived burning (perhaps repeatedly). Further factors explaining why *A. lasiocarpa* or *P. engelmannii* cannot compete here are presented in Chapters 4.3.4 and 4.4, such as lack of seed, deep snow and steep slopes.

3.1.11 Study Area F

This area was not sampled systematically, but the following observations arose from repeated field reconnaissance and air photo interpretation. This area is further downslope and downvalley than those described so far (see Fig. 2-4), but although temperatures and wind are less severe than upvalley, steepness of slope is extreme (averaging 30-40°).

The most obvious control on vegetation distribution is the influence of rapid snow avalanching and gradual snow creep. The fairly open *Abies lasiocarpa* woodland is distinctively marked by a dozen or more parallel 'ribbons' of avalanche track vegetation. The collection area for this snow-slide zone lacks conifers altogether: on the upper slope segments, only shrubs (*Juniperus* and *Salix* spp.) and herbs with low cushion morphology exist.

The *Abies* and *Picea* populations here are tall, have symmetrical branching, are in good health and produce cone crops. Seedling regeneration is generally restricted to the outer margins of the avalanche tracks, while their centers have been stripped of soil and support only mesophytic herb species.

Considerable deposits of avalanche debris are piled along the base of the break-in-slope. Where late-lying snowslide deposits provide the *optimum* soil moisture, conifer growth is dense and vigorous, but in the runout zones of the largest tracks, too much stagnant snow results in pockets of cold air and saturated soils late into the growing season. These patches are characterized by "alpine" snowbed species associations, with only meagre *P. engelmannii* regeneration.

3.1.12 Past Distribution-F

Some evidence is found that avalanche activity was more frequent and catastrophic in the past, especially following the mid-nineteenth century fire. Olgeirson (1974) and King and Brewster (1978) have documented the sharp increase in snow avalanching immediately after partial or total deforestation by fire on nearby sites within Banff Park.

Below the break-in-slope, very old avalanche paths extend onto the valley floor (their age indicated by the degree of their regeneration). These may have reached the lakeshore (see Fig.2-4). W. Wilcox, writing of his 1899 visit to the valley, believed that the dead trees floating in Moraine Lake at that time had been "stripped" from the slope above by snow-slides (1916:171).

On the upper avalanche zones, little recent snow-impact damage (i.e., breaking) is found. However, both young and mature trees with pronounced butt-sweep attest to the ongoing influence of gradual downhill creeping or slumping of the snowpack.

Several tracks show substantial seedling regeneration, visible on the airphoto series from 1947 to 1978. A dense and uniform lichen cover on the angular rocks in the track's centre also indicates that, if swept by snow, the depth of snow movement has not recently extended to the ground surface. This re-seeding of paths formerly stripped completely suggests that avalanche frequency and/or severity has decreased. Possible explanations are a gradual stabilization of the entire slope over time by increased vegetative cover, or a reduction in the amount of snowfall over time. Munger (1911) pointed out that as forest cover gradually increases, it exerts a preventive influence on avalanche formation at its origin.

3.1.13 Study Area G

Area G refers to a large belt further west (i.e., valley headward) along the moraine (see Fig.2-4). The main characteristic of all vegetation here is the low cushion growth form in response to a high frequency of mass-wasting.

Active rock- and snow-sliding into the dense mat-krummholz colonies forms the upper growth limit. These slopes are extremely unstable and consist of sandstone and slippery shale fragments. At many points below Eiffel Peak, snow avalanche tracks support no conifer vegetation at all. A distinct avalanche and/or ephemeral snowmelt channel marks the eastern boundary of this study area.

Nowhere in this area, which is typified by linear strips of tangled clumps of shrubs on the slight ridges between avalanche tracks, are trees over 1.52m (5') in height found. This marks the average snow depth, and any leaders above this are broken, damaged and the needles severely desiccated.

Only in the lower elevation runout zones are taller *Larix* individuals encountered. Two adaptations of *Larix* that would account for this are: (i) the durable, flexible bole can survive annual flattening by the weight of shifting snow (trunks up to 13cm (5") thick and 6m (20') height); and (ii) its ability to occupy these late snow-lie sites (too damp, too cold, and too short a growing season for the evergreens) (Arno & Habeck, 1972:448).

All *Abies* reproduction is by layering in this area, which results in very high stem densities (approx. 289/100m^2), with very small basal area per tree. On these marginal sites, growth rates are very slow, and destruction of plant matter occurs regularly. Further results on the disturbance regime will be presented in the next chapter.

3.1.14 Past Distribution-G

This Study Area differs from the other six in one important respect: no evidence was found in either the present community structure or in wood remnants that an upright, symmetrical conifer forest cover has ever been supported here. No burn-scars were seen. At several locations, buried trees killed by rockslides were found, but in size and physiognomy they matched the trees now alive around the current margins of the rockslide.

3.2 DISCUSSION: THE POSITION AND NATURE OF THE ECOTONE

The analysis of historical and current vegetation status presented above can be summarized as follows.

The forest-tundra ecotone in the upper end of the valley is extensive and complex. Judging from the distribution of forest remnants the ecotone appears to have been a fairly compact transition belt 110 years ago (about 60m wide), but is now an extensive interdigitating transition covering 335m in elevation. The position of the treeline, or absolute upper limit of tree species, appears to be unchanged, but the nature of the timberline has changed substantially, and is better referred to as a broad, mosaic timberline belt. Scattered deformed trees and island-like clumps of very dense tree growth mix with open heath meadows and persistent balds.

Very generally, conifer juveniles are sparse, while vegetative reproduction (by layering) is common. As Hansen-Bristow (1979) found in the Colorado timberline, production of viable seeds and pollen within the ecotone appears to be rare. More complete results on conifer regeneration capacity follow in Chapter 4.4.

There are several ways in which the situation here does not 'fit' the classic secondary succession paradigm. As it is traditionally defined, succession implies cumulative, _directional_ vegetation change wherein each species modifies the environment in such a way that invading species can then grow more successfully (Drury & Nisbet, 1973:331; Barbour et al. 1980:235). But because there _are_ no species which can 'suppress' or replace them, the same conifers which are the 'pioneers' on this site will continue to be the dominant species. The entire study zone is above the tolerance range of pine (_Pinus contorta_), thus the 'usual' successional sequence after fire in this region in which a pine stage 'prepares' the site for its 'recovery' by spruce and fir, is lacking (Stahelin, 1943; Billings, 1969). Certainly the complete lack of spruce in the reproduction size class in Area A, for instance, indicates that it is not moving 'toward' a spruce-fir association.

While _Larix lyallii_ is usually credited as being the first 'colonizer' of disturbed sites at high altitudes (Arno & Habeck, 1972; Parker, 1982), here its most common location is on microsites somewhat protected by established <u>Abies</u> clumps or krummholz islands.

There is no evidence from the stand structure analysis that any directional species replacement is taking place (i.e., <u>qualitative</u> changes in species composition). Any vegetation changes occurring are simply <u>quantitative</u> differences in the representation of species (for example, differences in coverage, in abundance, or in frequency). There are so few tree species in total that can grow at all in these conditions, that to search for 'seral' or replacement species and 'climax' species that fit a chronological sequence begins to break down. There is no replacement forest community to "anticipate".

The pattern here then is very different from that reported by Brink (1959, 1964) in southern B.C. and Franklin et al. (1971) in Washington and Oregon. They describe a relatively vigorous and rapid invasion of alpine meadows by tree species in recent decades. In contrast, this author's findings suggest a subalpine association not only unable to ascend into 'new territory' but unable even to re-establish in the area formerly forested. This author also suggests that this does not automatically insinuate a situation of 'imbalance'. The particular pattern of persisting and changing conifer patches observed should not be automatically labelled 'normal' in re-establishing areas and 'abnormal' in areas as yet unregenerated. The reasons behind this differential density distribution of conifers must be examined more closely before labelling the whole ecotone as being in a state of 'disequilibrium'.

To interpret the "causal factors" of this timberline pattern correctly (Kershaw, 1973:145), it is necessary to examine the influences both of current site environment and stand history. We have already alluded to some ways in which disturbance effects help to create pattern. [Pattern is defined here as differential density distributions of the dominants.] While this is obvious and intuitively known at a gross pattern level, at finer levels of pattern, our understanding is limited. For example it is clear that a burn site differs from non-burn sites. The question asked here is, within a burn, how does one explain the radically differential cover that makes up the actual texture of the vegetation?

Chapter IV

THE DISTURBANCE COMPONENT

4.1 RESULTS: CONTRIBUTION OF DISTURBANCE EFFECTS TO VEGETATIONAL PATTERN

Having delineated and described the stand structures and the species patterns, we turn to the interpretation of the processes that give rise to them. Faced with an intriguing variation in vegetation cover, the geographer may ask: "Why are (the) spatial distributions structured the way they are?" (Abler et al., 1971:20). To the biogeographer, the pattern of the vegetation poses several problems (Patten, 1963a), including: 1. How did the pattern *originate*? 2. What factors are *maintaining* its apparent stability? and 3. What will the vegetational pattern be in the future? (that is, what *changes* are indicated?)

In this chapter, the factors contributing to the origin and the maintenance of vegetational pattern are discussed. The third question, regarding the future trends of this mosaic (that is, is its stability real or apparent?) is addressed in Chapter Five.

As noted earlier, of particular concern in this context is the role of 'disturbance' in pattern and pattern changes over time. For the purposes of this thesis, *disturbance* is defined as an "extreme" state of any environmental parameter, which means it must be severe enough or of sufficient duration to cause plant tissue destruction. It appears that plant tissue damage involves the extreme end(s) of a continuum of environmental conditions potentially limiting for growth. In the terms of Toleration Ecology these would lie at the latter end of a continuum ranging from optimal through stressful to lethal for any one species.

The definitions used here are a refinement of opinions in Grime (1977:1169), Thompson (1978), and Pielou (1979:229), who concur on working definitions of stress and disturbance as the two classes of external abiotic factors limiting the total plant biomass in any habitat. Stress is defined here as a function of constraints upon the rate of dry matter production. It refers to a lack (or excess) of conditions or substances necessary for plant growth, such as light, warmth, water and nutrients. Where these conditions or substances fluctuate or change in occurrence so as to produce damage in living tissue or to be lethal to some vegetation, 'disturbance' results. Thus, disturbance factors are recognized as events where there is partial or total destruction of the plant biomass. That may be represented by such hazards as wind damage, frosts, desiccation, soil erosion, fire, and human, pathogenic or herbivorous activities.

It is crucial to acknowledge that the factors involved do constitute a continuum of processes, ranging from acute to chronic and from local to widespread. There is a wide vari-

Table 4-1:

Each Disturbance Type has Varying Characteristics:

Ⓐ **In Space:**

resulting in varying Distribution or Areal Extent

Localised ←——→ Widespread

Discrete ←——→ Continuous

Ⓑ **In Time:**

resulting in varying Frequency or Periodicity

Acute event ←——→ Chronic Condition

Intermittent ←——→ Constant

Ⓒ **In Severity:**

resulting in varying Intensity or Impact

Mild ←——→ Severe

- Thus, depending upon where a single disturbance falls along these several continua, its

Effects will range from

Stressful ⟵⟶ Lethal

Vegetation examples are: (Reduced performance; decline in vitality) ←—— (Moribund) ——→ (Death of tree; destruction of tree groups) ety in the nature (type, size) and occurrence (location, frequency) of damaging mechanisms. As shown in Table 4-1 each mechanism can be discussed in terms of these characteristics: time-scale, spatial-scale and severity. Disturbance "events" can be sudden or gradual; they can be direct or indirect in their effects. For example, avalanche effects are both direct (mechanical damage) and indirect (deposition of debris, and late melting of avalanche runout).

In particular, this chapter presents field evidence of the specific ways that disturbance mechanisms (a continuum of historical events and present-day stresses) combine with site conditions to perpetuate the broad transition above timberline.

The distributional characteristics of the vegetation are accounted for by a series of mechanisms, some localized, some widespread in occurrence. Following the suggestion of Reiners and Lang (1979), the variation in vegetation is organized, therefore, at two hierarchical levels: First-order patterns associated with "continuously distributed chronic factors aggregated in elevation and exposure"; and second-order patterns "finer-grained features overlying the broad first-order patterns", caused by either chronic or acute mechanisms (Reiners & Lang, 1979:407, 414). This conceptualization of the vegetated landscape is valuable, especially where patterns are complex or overlapping, in order to recognize when and where the effects of individual mechanisms are occurring.

Reiners and Lang used a hierarchical system of individual processes and patterns to study vegetation structure and dynamics in the upper subalpine fir zone in the White Mountains, New Hampshire, and they recommend its application in areas with little human disturbance, with an essentially continuous vegetation cover (i.e., unbroken by ravines, cliffs, lakes) and with a high frequency of disturbance of external origin (1979:415). All of these criteria are easily met on the Wenkchemna study site.

The discussion that follows, then, has a general division into broad and finer-textured patterns evident on the landscape. The first section (Ch.4.2) summarizes the changes in conifer patterns with elevation and aspect, focussing largely on chronic stress due to the deteriorating energy budget available for conifer growth (both temperature and moisture).

The second section (Ch.4.3) focusses on the impacts of local events and factors (whether physiographic, climatic or historical factors). First, eight types of mechanisms are described according to three categories of their occurrence and effects: frequency/periodicity, distribution /areal extent, and severity/effectiveness. Secondly, their individual and cumulative influences on the maintenance of present vegetation patterns are interpreted (Ch.4.4), particularly as they affect regeneration patterns.

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4.2 GENERAL PATTERNS OF VARIATION

Surveyed very broadly, certain aspects of vegetational cover vary directly with an increase in elevation. These visible patterns are responses to the increasing harshness of conditions for physiological processes and plant growth. Related to the lapse rate in mean temperature, the range of physiological stresses widens: high winds, more extreme moisture and temperature regimes, poorly-developed soils, steeper slopes, and more variability in snow patterns. The physiological ecology literature recognizes that these site factors gain in significance with altitude and eventually become "limiting factors for vital plant processes" (Tranquillini, 1979:viii), but exactly how individual site factors influence phenology and growth are as yet poorly understood (Price, 1971; Webber, 1979).

Moreover, the relation between increasing elevation and increasing severity for plant growth is by no means simple. According to the measurements of Gardner (1968:227), nowhere in this area is the adiabatic lapse rate steady. The temperature conditions are greatly influenced by local effects such as exposure to solar heating and exposure to prevailing winds. He found several slopes in this valley to be somewhat warmer than the expected values under normal lapse rate conditions (1968:227).

Notwithstanding, the following vegetational responses were observed. On an elevational transect 600m (1970') long

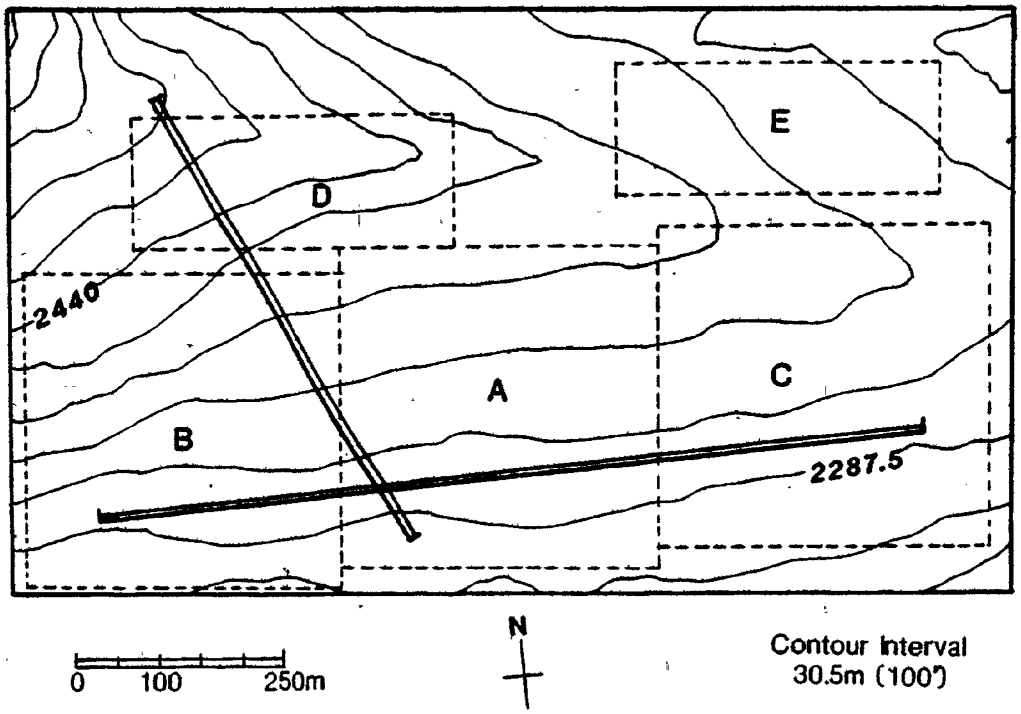


Figure 4-1: Location of Primary Survey Transects

on a southeast aspect (see Fig.4-1), there is a general decrease in mean tree height accompanied by a decline in basal area per tree. Conifers of all species show increased clumping of growth-habit and yet while live tree density within these dense clumps is high, in general the vegetation is more open and there is an increase in the shrub and herb layer coverage. Soil depth tends to decrease and rockiness and substrate instability increase with rise in elevation. Wind exposure increases and with it, variability in snowdrift patterns. As one proceeds upslope, less sexual reproduction is seen in Abies lasiocarpa and vegetative reproduction by layering becomes common (refer to Fig.4-11).

Along a longitudinal transect 1000m (3280') long, run east to west at a constant elevation, 2293m (7520') (see Fig.4-1), patterns are observed that are related more to soil moisture availability. A number of factors especially stressful on west-facing slopes (independent of elevation) are: cooler maximum temperatures than on east-facing slopes due to greater cooling and drying by stronger afternoon winds (Reiners and Lang, 1979:408), and more possibility of physical damage (i.e., breakage and abrasion) by wind. The greater surface temperature maxima and minima lead to a greater incidence of freeze-thaw cycles and particularly on the gravelly soils of convex areas, more vigorous frost-induced soil movement.

As a result, general plant patterns observed are a decrease in tree height with western exposure and greater incidence of pistol-butt or multiple stems. As well, a general reduction in reproductive effectiveness (similar to that associated with elevation rise) is evident. The number of herb and shrub species indicating xeric conditions increases with more western exposure.

Most conspicuous is the increase in number and severity of flag-shaped trees (flag-, hedge- and mat-krummholz) as described in the last chapter. These forms are more a manifestation of localised winter drought conditions than of mechanical impacts of wind directly (their causal mechanism is explained in the next section).

In summary, most of these plant performance indicators seem to merge on an aggregate aspect/exposure gradient that pivots on soil moisture availability as its main mechanism.

The fact that altitudinal zonation exists at all is determined largely by climate. But while climax vegetation zones largely correspond to climatic differences (as controlled by altitude and exposure), there are obviously a great many systems (such as this) in which species other than the 'climax species' dominate due to important local factors such as slope/topography, soils and drainage. As Price (1971:3) stresses, "such situations are natural but are controlled by local conditions within the larger framework of climate".

Veblen (1977, 1978, 1980) makes a similar point throughout his biogeographical work in the Chilean subalpine zone. The regional vegetation can be broken into first-order types representing altitudinal zones modified by topographic position and aspect. Further modifications controlled locally by such factors as slope stability, wind exposure, and disturbances of the vegetation must also be incorporated into our understanding of community dynamics.

While the gross patterns of variation outlined in this section were discerned on the ground, the actual spatial texture is not nearly so simple as a gradient analysis would make it out to be. Because of the nature of this study, a species or plot ordination of this site was considered but then rejected: the degree of spatial information loss was deemed unacceptable for this site, given the objective of the study (which was, in part, to be willing to pay attention to a great deal of confusing but potentially useful vegetation detail). The irregularities of this patchy mosaic are as striking as the broad trends (up and across-slope), and they focus greater attention to the processes that have resulted in this distribution.

Therefore, the *general* configuration of this ecotone is related to the deterioration in effective climate for plant growth with increasing elevation and westerly exposure. To some extent, therefore, it makes sense to group the variation in vegetation cover in this way. But having said this, it must be reiterated that on this site, topographical and disturbance factors have locally influenced vegetation structure and performance to the extent that these expected gradual vegetation/environmental gradients are fragmented. Such simple trends are obfuscated by "finer-grained features overlying the broad first-order patterns" (Reiners & Lang, 1979:414).

4.3 LOCAL PATTERNS OF VARIATION

As described in Chapter 3 above, there is considerable patchiness or local variation in vegetation. These localised or second-level features are caused by a variety of mechanisms, both acute and chronic, both endogenous or exogenous in origin (Reiners & Lang, 1979:414). Direct links between the observed patterns and disturbance regime are postulated where clear, and proposed where several kinds of patterns overlap and the contribution of a single underlying mechanism is difficult to pinpoint. That is, in some cases, this relationship is shown (and supported by other discussions) to be a causal mechanism; in less clear cases, they are known only to be associated mechanisms.

4.3.1 Mechanism 1: Fire

Hawkes (1979:81) stated that "the role of fire in the upper subalpine subzone needs more intensive investigation". Because forest fire rarely extends above timberline (Baig, 1972; Tande, 1979), not a great deal is known of its effects in the upper subalpine. However when it does occur at this elevation, it is typically a medium to high intensity fire that increases in intensity as it burns upslope.

For Banff Park in general, White (1981) gives an estimated fire return interval of 201 years in the Upper Subalpine Spruce-Fir type, and a mean intensity of past fires at 100% crown mortality for upper subalpine plots. The fire return interval is known to vary significantly with elevation and aspect (Hawkes, 1979).

It is generally agreed that at high elevations, stand-destroying fires occur only at long intervals, generally a reflection of relative inaccessibility (in terms of human effects) and greater precipitation (i.e., Mackenzie, 1973:57; Tande, 1979). Fairly mesic conditions due to deep and late snow-lie tend to discourage fires in the subalpine and to make possible large accumulations of organic material. As a result, in periodic severe drought years these heavy fuel loads can burn with catastrophic intensity (Lewis, 1917; Byrne, 1968; White, 1981).

This is almost certainly the case in the upper third of Wenkchemna Valley. There seems little doubt that on this study site, fire is a low-frequency and destructive event having severe effects on vegetation, and subsequently on mass movement. (The latter will be discussed in the next section.)

Frequency: It is believed that the widespread burn evidence visible today dates from a single fire in 1870. This estimated fire date is based on fire-scarred trees sampled at four points by White (1981) as part of a larger fire history project for all Banff Park. These sample points were outside the actual study site, farther east above Moraine Lake.

The lower portions of the valley (Lower Subalpine and Montane Forest types) were also burned c.1760, c.1882 and c.1904. The Banff town newspaper reported the July 1904 fire, commenting on the dry timber, lack of rain, and prevailing hot weather of the previous month. Byrne (1968) postulated that these more frequent fires were a disruption of the natural fire regime in these communities due to the early activities of white men in the Bow Valley. Certainly this is true of the 1882 fire over the entire Bow River Valley, which was reportedly caused by CPR engineers surveying the main rail line (Nelson and Byrne, 1968:48).

Because of its relative inaccessibility, the upper Valley of the Ten Peaks could be treated as a case experiencing a natural fire cycle. Across the study site, all trees observed had only one fire scar, suggesting that overlapping fires have not occurred.

This fire date is roughly confirmed in Wilcox's account of his 1899 visit to Moraine Lake. He describes the upper slopes of the north shore as "burnt over" and some of the fallen trees were very large: "logs three or four feet in diameter". Those dead poles still standing were taller than "the new trees" which in 1899 were "about fifty years old" (Wilcox, 1916:173).

Sporadic lightning-struck conifers are encountered: their locations are indicated on Fig.4-2. It is a simple procedure to discriminate these from the conifers charred by the major fire. Lightning strikes are most commonly identified by a shallow, uniform furl that spirals along the trunk exposing only the outermost layers of sapwood. Occasionally some longitudinal splitting indicates more violent damage, but evidently these are only spot burns with little spreading (Mackenzie, 1973:26). The distribution of this small sample agrees with that of Habeck and Mutch (1973:416) in western Montana, that lightning ignitions most often occur on ridgelines and south-facing aspects.

Fire history information is gleaned directly from fire-scar and remnant analysis, and indirectly from stand age structure and species presence. The stand size-class inventories were presented in the last chapter. More specific focus on the relative severity and intensity of fires involves the combination of several methods (as used in other discussions): the type of stand replacement, the density of regeneration, and the amount of direct fire evidence [presence of fire-scarred stumps or logs; obvious fire scars in neighbouring forest stands; and charcoal in the soil profile or on its surface] (Mackenzie, 1973; Houston, 1973; Lande, 1979; Hawkes, 1979).

Distribution and Intensity: The extent of this fire is believed to have included the area shown in Fig.4-2, based largely on the distribution of fire-scarred remnants: living tree scars, snags, logs, and the common occurrence of charcoal, both buried and unburied.

Infrequent burn fragments on the north-facing lee slope of the moraine and in several moister 'pockets' indicate a reduced fire impact where conditions were more mesic and perhaps cooler. In addition, Wilcox mentioned open groves of *Larix* and *Picea* of great age in Larch Valley which had escaped death by burning.

On the valley floor, Gardner (1978a,b) dated living trees near the terminus of Wenkchemna Glacier as 250 to 300 years of age. Fire scars are seen on the trees of the valley floor, but because no fire-scar dating was done, it is unknown whether this area burned in 1870. If it did, either the impact was milder than on the more xeric lateral moraine, or more substantial regeneration has occurred if it burned severely.

That this was a very intense fire is suggested by the complete lack of smaller fragments, and the very thin soil and humus layers (Douglass, 1954). An intense fire would consume all smaller material turning it to ashes, not charcoal, and this would explain why *all* snags (standing) or logs (lying) are very large.

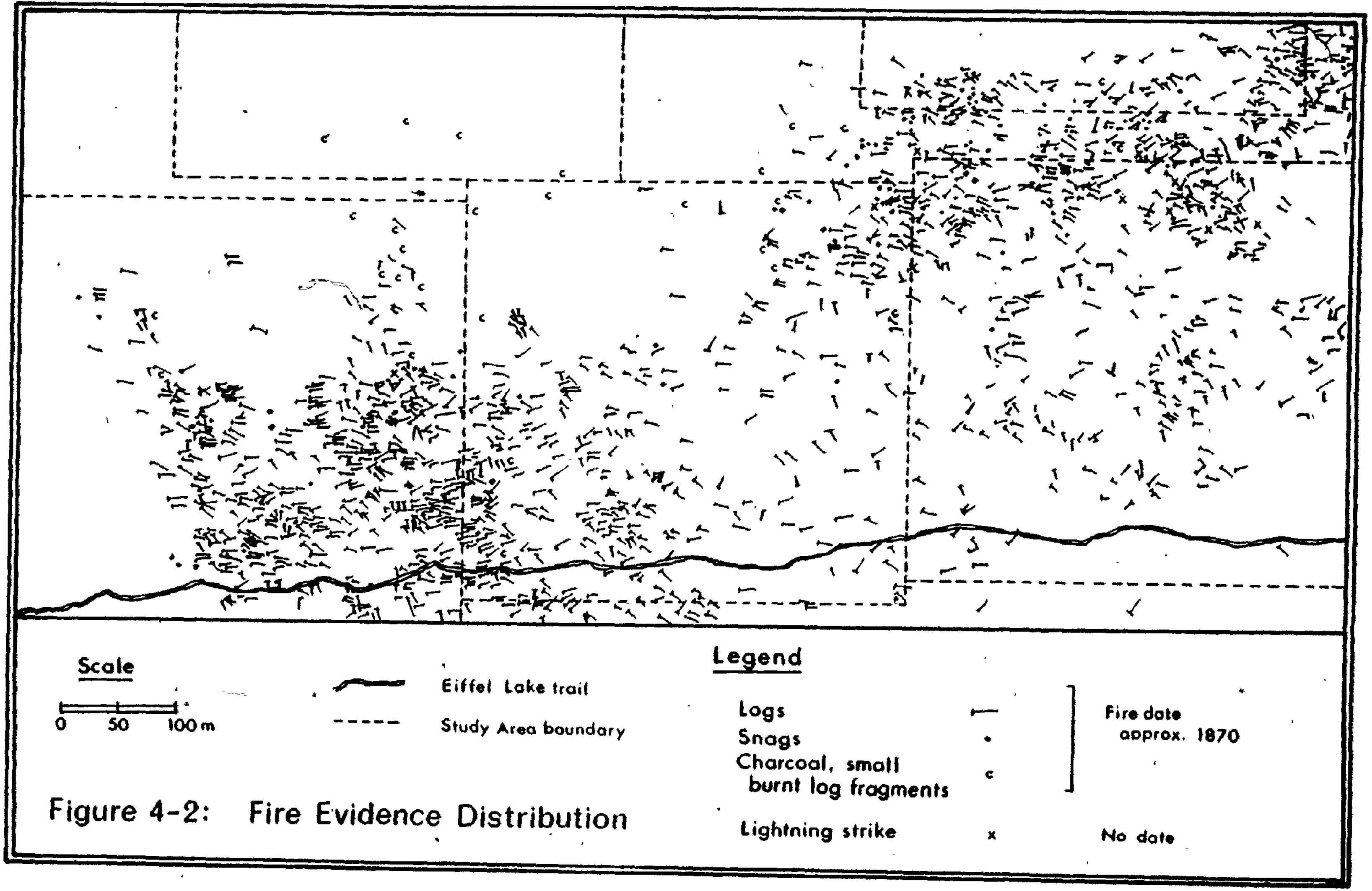


Figure 4-2: Fire Evidence Distribution

However, an equally valid interpretation is that there *was* little or no small sized material *at the time of burning*, meaning that the pre-fire forest was an old-growth one in which the seedling/sapling size classes were poorly represented. Hence, the lack of small fragments on the ground today. (It is a commonplace that over-mature stands are more susceptible to fire (i.e., Barrows, 1951; Mackenzie, 1973; Habeck & Mutch, 1973).

Precisely because of the lack of remaining evidence, however, neither of these interpretations can be conclusive. Meanwhile, it should be stressed that they are not mutually exclusive.

In future, more evidence about the nature of the former vegetation cover could be acquired by analyzing the soil content of biogenetic opal phytoliths across the forest-heath transition. This method was successfully used by Miles and Singleton (1975) and Vale (1978) to date soil and vegetation changes in a Wyoming timberline meadow.

It is unfortunate that firm statements regarding the nature of the pre-fire forest are not possible. Clearly, the reproductive status of the pre-fire forest has important implications for the future regeneration of the site. Significant conifer regeneration depends upon seeds. If the trees in any patch destroyed by fire or cutting are not effectively reproducing *at the time of destruction*, the stand's chances of regenerating are slim (Elliott, 1979; Hansen

Bristow, 1979). In a study of the stability of the species in the Canadian subarctic treeline, Elliott (1979:165) found that:

> buried seed stores are very short-lived, and unless seeds have been produced within the last few years, they are not available for stand regeneration.

More will be said in Ch.4.4 about the conditions conducive to conifer seedling germination and establishment. Regenerative capacity of past trees is important and interesting, but more crucial obviously is the regenerative capacity of trees at present.

In a corresponding ecological subzone in northwestern Montana, Gabriel (1976) found that in higher-elevation forests, larger stand-destroying fires had occurred, but with a sporadic pattern of stand destruction even during relatively high-intensity fires. To be sure, inferences about fire intensity and behaviour are complicated by complex relationships between fuel characteristics, weather and topographical effects.

In this case, the increasing windiness upslope conceivably caused an acceleration in ignition rate (Hawkes, 1979:121). Most fallen logs are oriented SW to NE across the slope which suggests the fire was moving in an easterly direction.

The purpose of Fig.4-3, a slope configuration map, is to show the tendency of each area to collect or disperse moisture. As well, a comparison of this figure with the burn remnants distribution in Fig.4-2 supports Zackrisson's (1977) finding that coniferous forests in Sweden burned more severely on convex features than on concave portions. As suggested earlier, Area A is a slightly concave portion of the moraine now supporting a much denser, more mature cover, which could suggest that it burned less severely than either Areas B or C.

To make further statements about the details of this fire's intensity or behaviour would be unsuitable, as no fire-scar wedges for aging or analysis were taken from either living trees or snags.

Effects: While many of the conclusions about the fire's date, areal extent and severity must be approximate, its long-lasting effects are much more certain.

Fire, particularly high-intensity fire, affects all components of the ecosystem: physical, chemical and biological (including vascular plants, animals, and microorganisms). The primary changes that result immediately after fire are largely self-evident: destruction of forest cover, presence of ash, increased pH value, changes in soil porosity, and greater temperature fluctuations (Widden, 1971).

In the upper subalpine, many secondary environmental changes are just as drastic. The whole energy budget is changed as the forest is opened to the impact of wind, in effect, a switch to virtual tundra conditions. This leads to shifts in the snowdrift patterns both in the new open en-

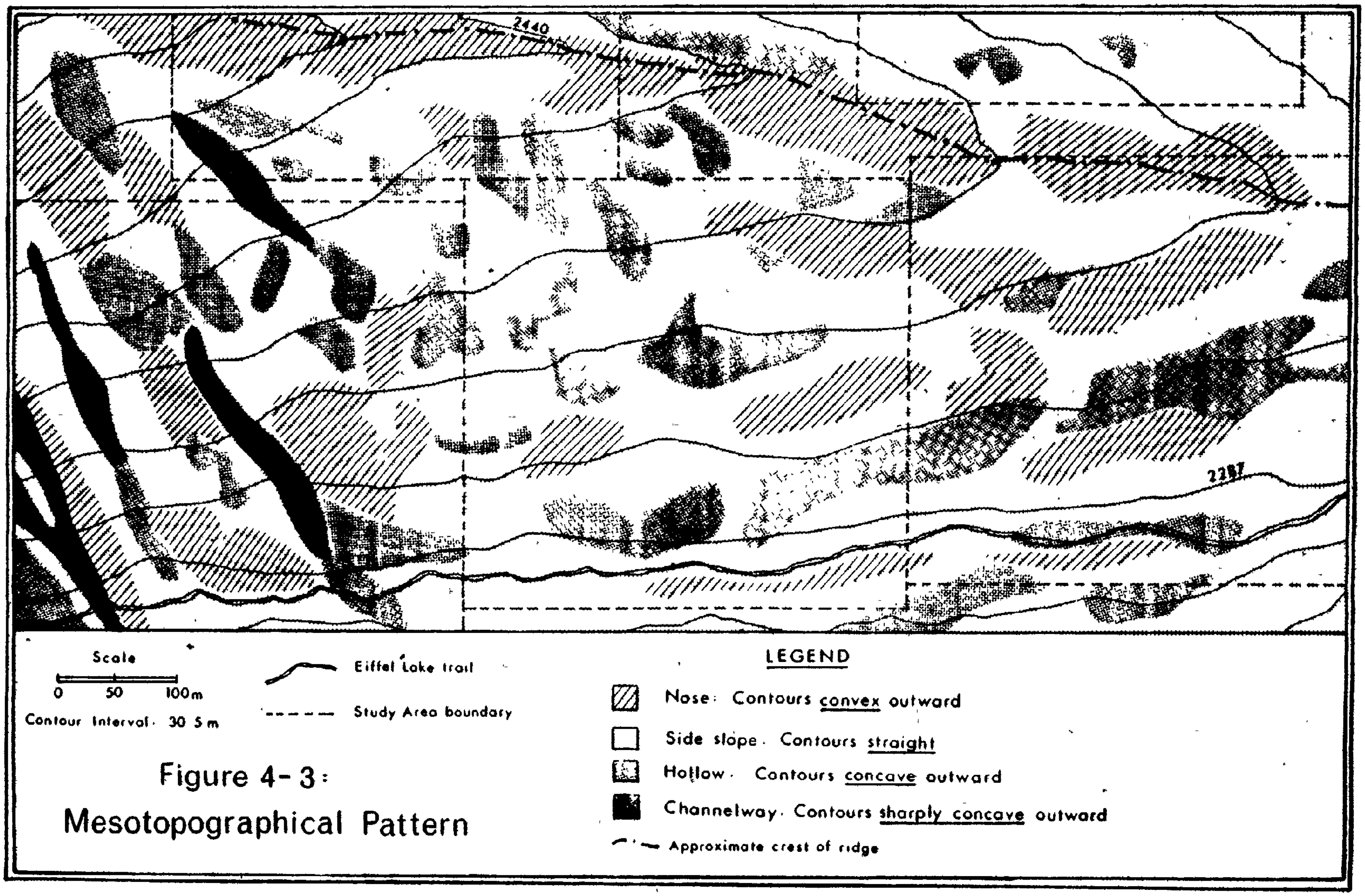


Figure 4-3: Mesotopographical Pattern

vironment and within nearby unburned forest stands. In turn, the local hydrologic balance is affected. Summer drought stress is common in clearings, while snow glades persist within tree stands (Billings, 1969; Alexander, 1974).

That there is minimal snow accumulation on parts of the old burn was already pointed out in Chapter 3, especially in relation to its effects on regeneration. Particularly on southwest- and west-facing aspects, tree establishment is very slow due to the lack of moisture and the extreme range of surface soil temperatures.

Vegetation response after fire in western Montana was studied by Habeck and Mutch who believe that

> some amount of the present-day alpine vegetation in Glacier Park occupies sites that once supported krummholz timber before it was removed by fire. Apparently, the pace at which the forest reestablishes itself above 1850m (6070ft) in Glacier Park has produced a downward extension of alpine species; these remain until the forest succession occurs (Habeck & Mutch, 1973:418).

A further secondary effect is the increased incidence of snow avalanching following fire. This is discussed in the next section.

4.3.2 Mechanism 2: Avalanche

Snowfall estimates for the Ten Peaks area are as high as 20 to 30' (6-9m) annually (Kucera, 1974:39). Whether accumulating in hollows or moving downslope, snow is an important element in this valley

> being present in continuous cover for about 6 months per year, in discontinuous cover for about 9 months, and throughout the year in sheltered locations high on northfacing slopes... (Gardner, 1979:46).

This section concentrates on those mechanical damages caused by downhill wasting of snowloads, whereas the next section will examine physiological effects of deep snow accumulations lying late and stagnant in situ.

The causal factors involved in avalanche formation are vegetational cover, slope angle, and slope orientation. Because it removes stabilizing plant cover, fire causes an increase in avalanche activity. Winterbottom (1974) has shown that avalanche chute enlargement was induced by forest fire in the Field, Lake Louise and Marble Canyon region, and that 38.6% of this region (which includes the present study site), is regularly affected by avalanching. Howell and Harris (1978) concur with Winterbottom (1974) that avalanches occur in this area wherever sufficient snow accumulate on slopes steeper than about 29°.

Specifically on this study site, the characteristics of avalanching as a mechanism are variable. Its distribution is fairly restricted and has likely shrunk in extent over time. Its periodicity ranges from rare or intermittent to a chronic condition. Its severity also ranges widely, depending upon the length of slope over which the snowpack moves and on the depth of the snowpack, which varies from year to year.

Distribution: With few exceptions, the occurrence of avalanching (the rapid downhill wasting of snow) is restricted to slopes steeper than 25°. Fig.4-4 shows the location of avalanche activity evidence: trunk scars, limb breakage, linear tracks, and debris deposits. (The age of scars was evaluated by visual examination only.)

Frequency and Intensity: Ch. 3.1.12 presented the argument that avalanche frequency was high immediately after the fire and has decreased with time (particularly in the more continuous cover of Area F). Regarding these older avalanche strips within the subalpine forest, it is doubtful if the snow wasting now extends to the ground surface as substantial lichen, grass and conifer establishment is found (see p.99).

By contrast, on the basis of a high incidence of recent damage, avalanche frequency is high in Areas A and D. The tracks here are not long but are locally severe (slopes 30-35°), with 'skinned' trees, recent breakage and debris along the chute sides (see Fig.4-4). This is somewhat surprising as the collection area would seem to be too small for sufficient accumulations. The shrub and herb layers include *Phyllodoce glanduliflora* and *Elymus innovatus*, species associated with deep snow cover and avalanching.

In forested terrain, winter and early-spring avalanches are most common, while above timberline, late-spring and early-summer avalanches are "the most frequently occurring slope process" in the area (Gardner, 1970:142). The perennial avalanche slopes of Area G (on the south slopes of Mt. Eiffel, en route to Eiffel Lake) were studied in detail by Gardner. Chaotic unsorted deposits of earth material, turf, branches and bits of vegetation have been transported by snow avalanches. The deeply abraded chutes are typically the work of late-spring avalanches that "invariably make contact with the ground" (Gardner, 1966:176-7).

Effects: Howell and Harris (1978) report that avalanches cause mixing and truncation of soil profiles, and the erosion of material from upper slopes and its deposition in the run-out zone. Jumbled surficial deposits of broken tree sections, stones, and gravel are found in the areas marked on Fig.4-4. In future, more detail on the distribution of the characteristic disrupted soil complexes could be used to delimit the extent of avalanche activity after the burn (Olgeirson, 1974:185; Howell & Harris, 1978:321).

Snow avalanching causes death or damage directly through the breaking or abrasion of plant parts. It also affects vegetation pattern indirectly through the impacts of snow loads in the avalanche track perimeter and run-out zone. Anomalously cold and damp pockets are created in the conifer forest, where proper plant development and reproduction are inhibited. Mesic heath and alpine tundra associations are found in a patchwork fashion in response to the differential soil moisture and temperature conditions.

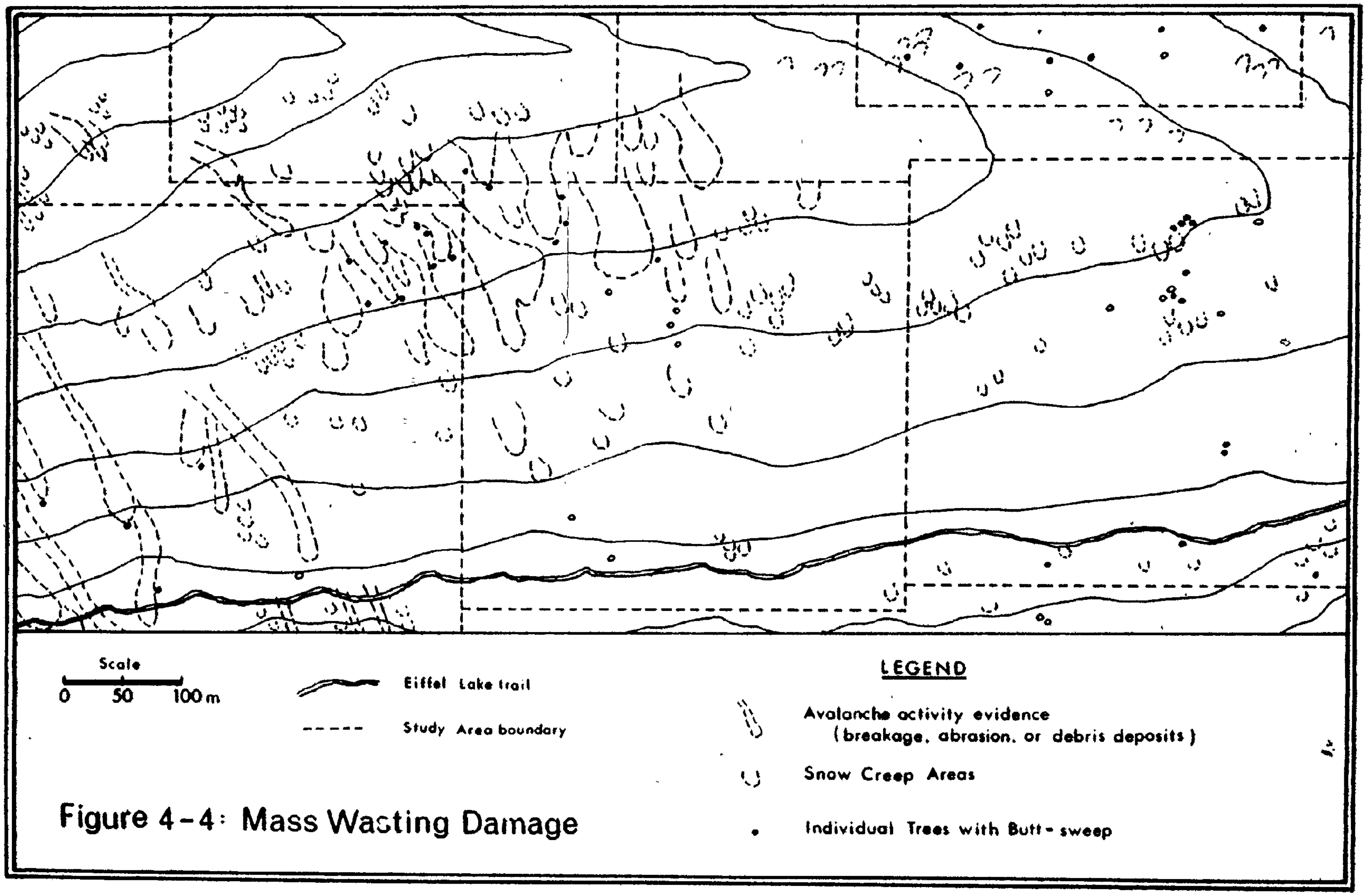
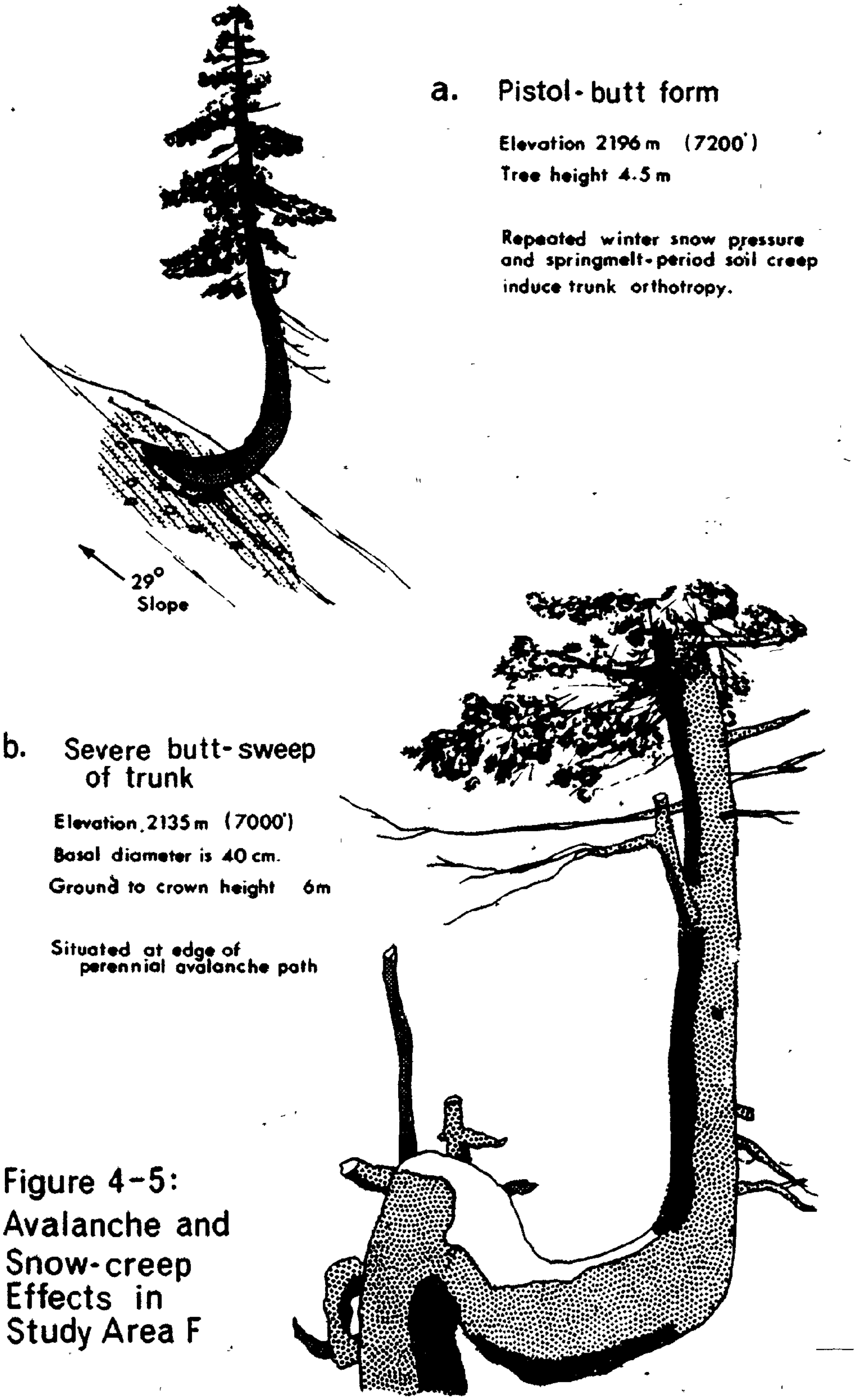


Figure 4-4: Mass Wasting Damage



a. Pistol-butt form

Elevation 2196 m (7200')
Tree height 4.5 m

Repeated winter snow pressure and springmelt-period soil creep induce trunk orthotropy.

b. Severe butt-sweep of trunk

Elevation 2135 m (7000')
Basal diameter is 40 cm.
Ground to crown height 6m

Situated at edge of perennial avalanche path

Figure 4-5: Avalanche and Snow-creep Effects in Study Area F

4.3.3 Mechanism 2A- Snow Creep

More widespread than destructive avalanche activity are the nonlethal or sublethal stresses induced by snow weight. On moderate to steep slopes, slow shifting or slumping of the accumulated snow cover exerts pressure on the conifer stems. Evidently, the response depends upon the mass and periodicity of downward snow creep and the size and species of tree involved. Seedlings and small trees can be uprooted.

Stem deformation is the most visible morphological response to repeated winter snow pressure (Fig.4-5). The characteristic butt-sweep results from tree orthotropy, the growth of reaction-wood on the downslope side of the trunk in an effort to retain a vertical stance (Tranquillini, 1979:100). An occurrence particularly common in *Abies lasiocarpa* is the rooting of the lower branches on the downhill side, forming a substantial snow-skirt.

Tranquillini (1979:101) states that in the Alps these forms of snow damage play no major role in the general distribution of forest. His illustrations show single *L. lyallii* trees with a full cone crop.

On this study site, however, trees with the characteristic butt-sweep are involved in reproduction by layering only; only at much lower elevations do trees so deformed carry cone crops. This lack of sexual reproduction seems to indicate that the pressure of orthotropy may involve enough of the tree's photosynthetic effort in any given year that the reproductive effort is curbed. Clearly wherever this is a chronic situation (see Fig.4-4), no seed crop is produced for dissemination and no new individuals will establish: only expansion at the margins of extant trees will take place. Contrary to Tranquillini's judgment, over the long run, community distributions *will* be affected.

It is a recurring theme of the findings that, in fact, any accumulation of stresses and disturbances, or even a single sublethal stress that inhibits proper plant development and reproduction will patently affect the distribution of forest and tundra. True, snow creep damage is seldom a lethal stress on an individual basis. The point made here is that it does not *have to be* in order to affect vegetation pattern. The next section describes how another mechanism related to deep snow contributes to the nature of plant communities.

4.3.4 Mechanism 3- Pathogenic Fungi

To what extent can snow accumulation and snowmelt patterns be incorporated as an important parameter controlling community patterns? It has been remotely suggested by some and considered primary by others. Shaw (1909:172) was convinced that

> the late lingering beds of wet snow are altogether the most important factor in inhibiting the development of a forest and bringing about the existence of alpine grassland.

Persistent winds and the consequent snow-cover features have been correlated with subalpine vegetation patterns to a more moderate degree by Griggs (1938), Brink (1959), Billings (1969), Kuramoto and Bliss (1970) and Del Moral (1979). There is no doubt that differential snowdrift pattern and timing cause variations in soil moisture and length of growing season. The significance of snowlie in the meadows around and between tree groups is frequently discussed in relation to plant phenology and growth rates.

In this case, the effects of extended meltwater supply will be discussed later in connection to summer drought (Ch. 4.3.8.). This section concentrates on a damaging or stressful condition found within the melting snowpack itself, not during the following snow-free (photosynthetic) period. In areas of deep snow accumulations around the margins of trees or tree groups (Fig.4-6), much of the foliage held under the snow shows damage from pathogenic fungi (a species of *Herpotrichia*). The lower branches are dying, matted and infested with fungus mycelia. Apparently the weight of stagnant wet snow prevents aeration, promoting the fungal growth.

Distribution and Frequency: This snow-fungus damage is found in concave pockets, on lee slopes, on individual trees within snowdrift glades, and on the dense mats of *Abies* and *Picea* clones (see Fig.4-6). The widespread nature of the damage indicates this is a chronic stress over much of this site. Both field observation and airphoto study revealed

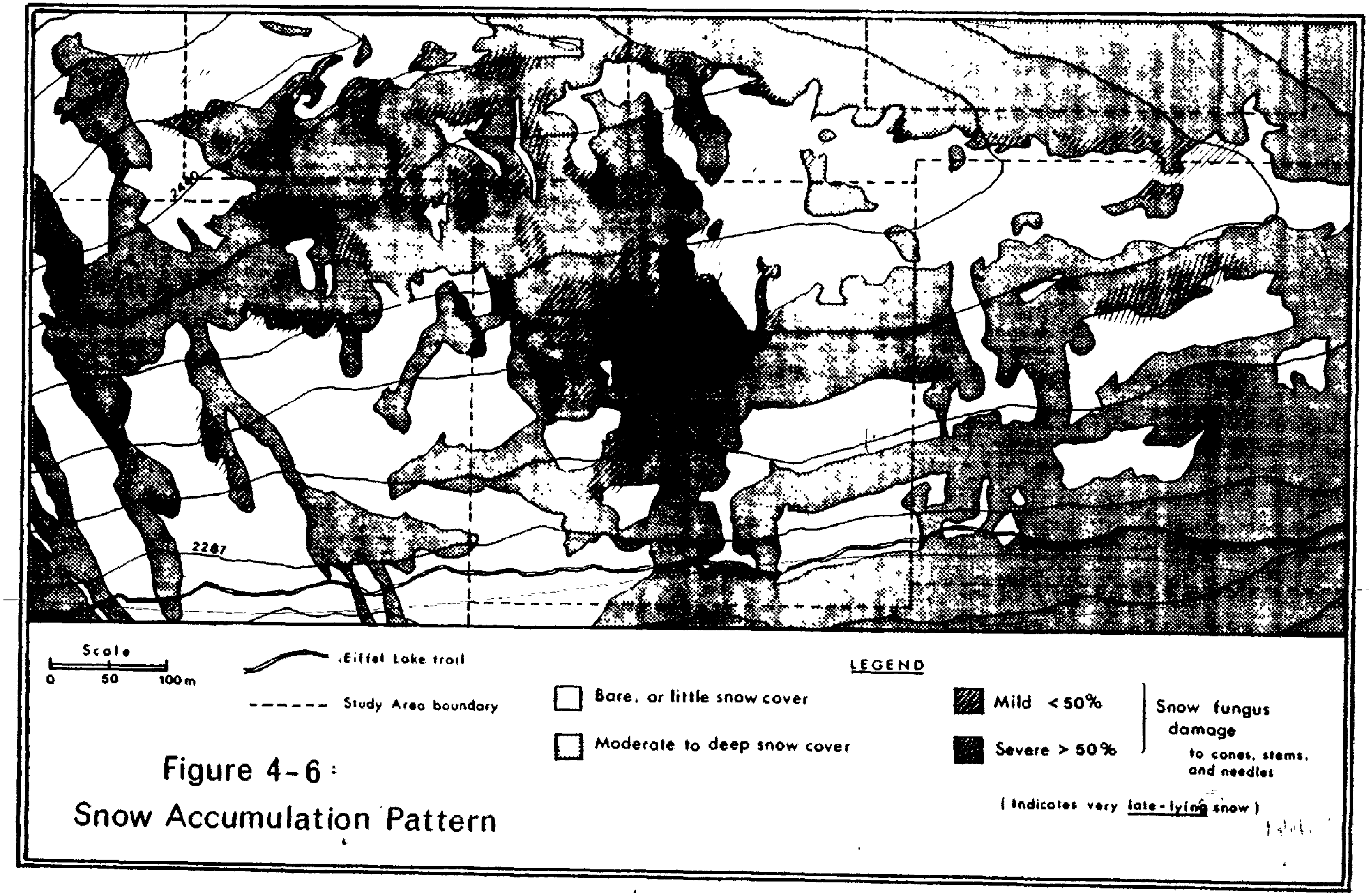


Figure 4-6:
Snow Accumulation Pattern

the annual snowdrift patterns to be fairly consistent, although some variation in amount and re-distribution of snow is expected. Most important to tree vitality is the length of the snowmelt period.

Severity and Effects: In places, complete mortality of lower branches was seen, but generally, injury was found in the needles and cones only on the south- (downslope) and east- (lee) sides of tree islands, where snow is trapped in deeper drifts. Fig.4-6 displays the location of this phenomenon. It was common to see two types of needle damage in close proximity: the blackened, gummy shoots below the snow limit and the red-brown dry tips exposed and desiccated by wind and ice-blast just inches above the snowpack. Clearly too little snow and too much snow each have their accompanying effects.

Reduction of reproduction is one of these effects and is an energy loss these trees can ill-afford. Photosynthetic effort invested either in seed production or adventitious roots in one growing season is "lost" to fungal damage, and tree vitality declines. The effects of pathogenic fungi are not likely to be truly lethal to any one tree. Nevertheless, in keeping with the working definitions employed, fungal effects are considered a disturbance since actual destruction of plant matter is involved.

4.3.5 Mechanism 4- Cold Air Drainage

Heusser (1956:269) mentioned cold air drainage as one of "the more significant factors that may affect the extent to which arboreal vegetation will penetrate the alpine tundra", along with snow cover patterns, slope steepness, soil character, available moisture, and wind. Veblen (1977:293) refers to cold air drainage as one of several forest disturbances which reduces competition below timberline, facilitating "the descent of species characteristic of the zone above timberline to lower altitudes".

Alleys of cold air drainage and the resulting temperature inversions are a common occurrence in Wenkchemna Valley. They move down along the valley floor from the valley head at Wenkchemna Pass (Gardner, 1978a:3). In a sense this is an acute 'event' and yet apparently is very frequent. Separating the intensity of its effects from that of other factors is not easy. In this region, Ogilvie (1976:35) reports that in winter, inversions may be maintained for several days, producing greater and greater cold (down to -40° C) on the valley bottoms, and much warmer air along the valley sides.

The valley floor per se was not part of the detailed study but some observations are of interest. The vegetational pattern is a complex mix of tundra-like heath patches within a subalpine forest. The forest associations themselves vary widely in thriftiness. Pockets of deep snow accumulations were identified on early-spring air photos; these topographical depressions presumably trap cold air.

The moist soils of these snowdrift glades support mesic/hygric heath associations (*Vaccinium scoparium*, *Phyllodoce glanduliflora*, and *Erigeron peregrinus*) with scattered stunted *Abies* or *Larix* trees. Sporadically, actual bogs with water-logged soils form part of the vegetation matrix (*Carex pyrenaica* Wahlenb., *Eriophorum Scheuchzeri* Hoppe, and *Salix barrattiana*). The sub-optimal temperatures, high water-table and black muck soils prevent any conifer growth. These moist heath species also typify the areas of old avalanche deposits at the break-in-slope, where conditions are anomalously cold and wet and the growing season shortened.

One of the straightforward effects of the cold temperatures on the hummocky valley floor and sides is the high proportion of *Larix lyallii* for this elevation. ? Usually scarce in the subalpine forest, *Larix* shows superiour hardiness in habitats combining severe environmental conditions (cold, wind, avalanche sites, boggy sites) (Arno and Habeck, 1972:447). The density of *L. lyallii* is high on the valley floor while 125m (400') further up the moraine slope, tall upright *A. lasiocarpa* form almost pure stands. *Larix* then does not dominate again until 2340m (7700'). This suggests that an inversion of the usual adiabatic lapse rate occurs with great regularity. During these "episodes", the descending cold air tends to push and hold warmer air upslope which is likely to create unusually dry, evaporative conditions. This phenomenon is also discussed on p.37 and p.148. Cold air drainage and nocturnal inversion is also reported by Lindsay (1971:133) in the subalpine of the Medicine Bow Mountains, Wyoming.

4.3.6 Mechanism 5- Rockslide

Weathered shattered bedrock is commonly exposed on the upper and westward portions of the moraine. Scrabbly shale and dolomite boulder fragments make up the rockslides within Areas D and G on slopes averaging 35-45°.

Distribution and Intensity: Rockslides are more restricted in distribution than snow avalanches, and only in the westernmost part of Area G, on the flank of Mt. Eiffel, is rocksliding actively encroaching on colonies of *A. lasiocarpa*. Work by Gardner (1977:232) suggests that high magnitude rockfall-rockslide may have been a more significant geomorphic event and agent in this region than has heretofore been supposed.

Spatially, rocksliding is a discrete event but in terms of frequency it is both an acute disturbance and a chronic stress. Its impacts range from minor abrasion wounds on *Abies* stems (often from individual bounding rocks) to the death of trees completely buried by the entire mass shifting or sliding downward. That plant matter destruction is ongoing and continual is indicated by the presence of scars of all ages. The speed of downward wasting is likely increased during the spring snowmelt or by severe summer rainstorms. Even during very dry conditions the surface of these scree surfaces is very unstable.

Effects on Pattern: Undersized upright trees grow only on the linear ridges between the debris avalanche slopes. Around the margins (the sides and terminus) of each rockslide, the characteristic vegetative response (in both herb and conifer populations) is a cushiony morphology and high stem-density due to layering (in *Abies*).

Other Forms of Rapid Mass Movement: Finer earth materials waste downhill in small-scale, localised events. Where the vegetation cover (especially those plants with fibrous roots near the surface) has been disturbed by avalanche or animal burrowing or feeding, or below persistent snowbanks where soils are saturated, small mudflows and landslips occur. Howell and Harris (1978:315) found that leeward slopes and depressions in this region are very susceptible to mass-wasting if the condition of saturated soils is combined with the effects of frost action and soil creep. Here, in addition, it is combined with coyote digging.

Obviously, seedling establishment is extremely difficult on unstable surfaces where soil development is truncated, or where stones and finer material slide or roll so frequently as to crush small plants (Daubenmire, 1968:156) (refer to Fig.4-4.)

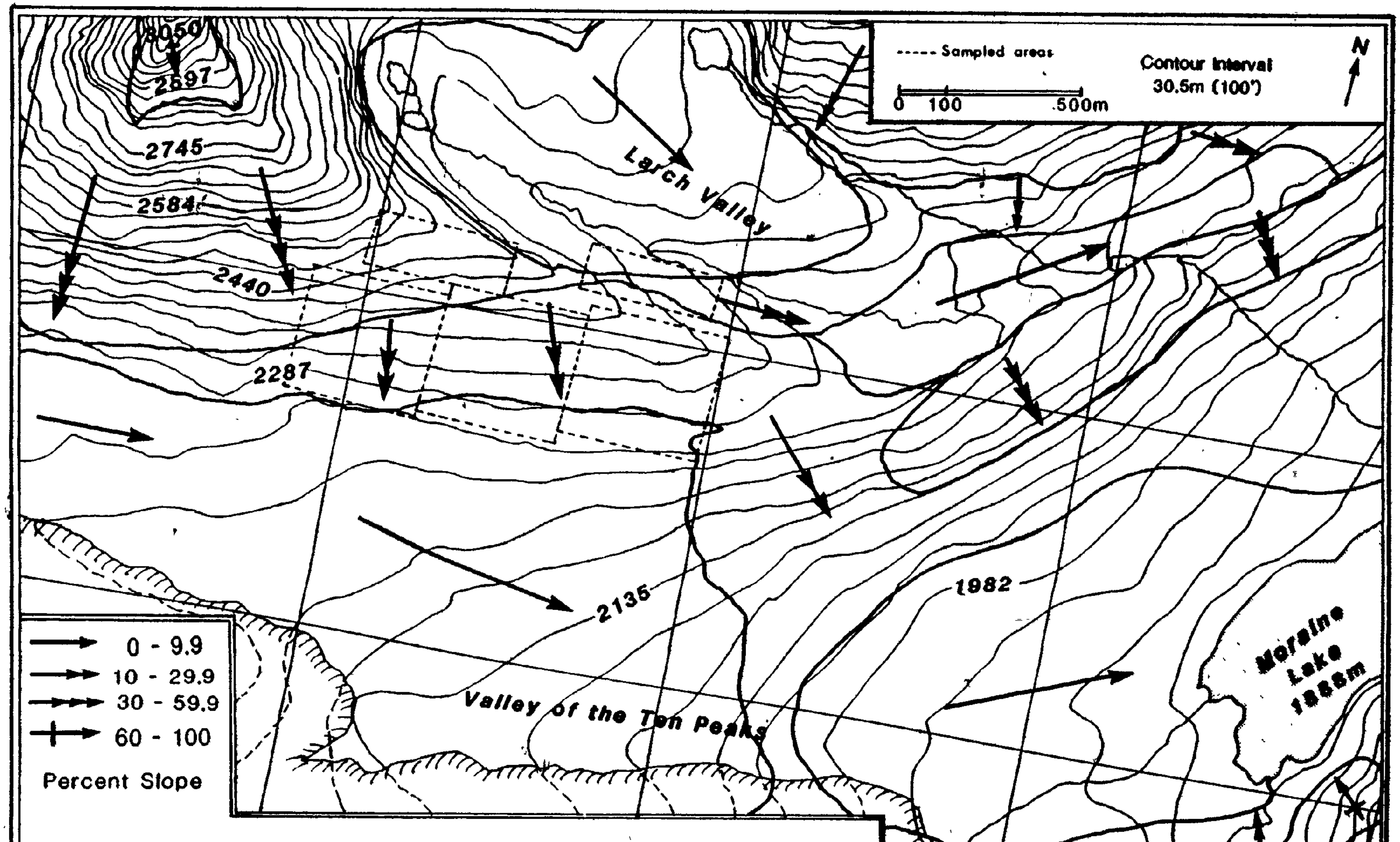


Figure 4-7: Generalized Slope Steepness & Aspect

4.3.7 Mechanism 5i: Soil Creep

Distribution and Frequency: While rocksliding takes place in unmistakable 'fixed' locations, soil creep is less obvious, more subtle in its effects, and very nearly ubiquitous across the study site. Dodge (1975:129) and Howell and Harris (1978) felt that the significance of soil creep and other slow unspectacular forms of mass movement in soil erosion in this region has largely been underestimated.

As reported in Chapter 3, thin calcareous soils and excessive stoniness are common. This is related to the fact that frost-heaving action combines with slope steepness to churn up soil profiles and gradually move material downslope. In Wenkchemna Valley, there are about 133 days per year of frost-alternation (Gardner, 1978a:2), and available moisture is generally high in late spring so the potential is great for freeze-thaw activity in the upper soil layers.

At Vermilion Pass, a site 15 km south of Moraine Lake, Harris (1972) recorded surface movements as rapid as 323mm per year. He confirms that the majority of this movement happens during the early summer when soil moisture contents are high (>40%). As well as varying throughout the year, the rate of soil creep is highly variable from year to year. No instrumentation of the depth or rate of soil creep was done in this study.

Effects: Field evidence for soil creep is somewhat difficult to distinguish from that of snow creep. Damaged, tilted, or uprooted seedlings could be the result of either or both processes. Even this type of microscale disruption of seedling development creates chronic stress and can be lethal during that growing season. A series of growing seasons of sublethal stress will weaken the stem of a small seedling. If it survives, a butt-sweep form compensates for the gravity effects (refer to Fig.4-5).

Particularly on the "balds" of Areas B and C the bare soil areas between heath cushions or graminoid clumps show subtle signs of soil heaving. Soils tend to be hummocky above rocks, stumps and senescent *Juniperus* shrubs and oversteepened below, creating a mesotopographical 'cliff and bench' formation (refer to Fig.4-10). The abundance of stones and boulders suggests that surface erosion of the glacial drift has taken place, probably as a result of the combined effects of fire, avalanching and soil creep.

4.3.8 Mechanism 6- Winter Drought

Earlier opinion that mechanical damage from wind and iceblast was the key factor in determining the forest limit has been clarified by recent physiological ecology research. Death of tree shoots exposed above the snow surface is more the result of winter desiccation or "frost drought" damage (Tranquillini, 1979:100). It is now believed that the absolute upper limit at which tree life can exist is linked closely with the degree of frost-desiccation damage sustained towards the end of each winter (eg. Lindsay, 1971; Wardle, 1971; Noble & Alexander, 1977; Marchand & Chabot, 1978). The degree of physiolcgical damage, therefore, has more to do with a species' drought-resistance than with its frost-resistance. That is, wind is obviously involved, but it affects the moisture more than the temperature of plant organs (Marr, 1977:1162). Tranquillini (1979:102) calls the slow desiccation of shoots "the most common damage to be found in the transition zone above timberline".

During the transition period into winter, timberline trees experience a decline in transpiration. Eventually complete stomatal closure is brought about by increasing water deficits as soil water freezes and groundwater uptake is limited or completely severed (Kozlowski, 1972:70). As winter continues, the high insolation and evaporation rates regularly result in lethal water deficits in plant tissues. Needle temperatures can approach those of summer maxima, especially close to the snow surface.

> High radiation levels amplified by reflection from snow-covered slopes can result in intensities up to twice those pertaining in the valley (Tranquillini, 1979:88).

A relatively high leaf-air water vapour gradient results. These extreme evapcrative conditions commonly occur by March or April (Sharpe, 1970:23). Needle water losses can be alleviated if there are plant parts under a deep snowpack and some meltwater is absorbed. However where the snow cover is sparse or blown free late in winter, no absorption of water ty needles or roots is possible and severe desiccation progresses. Exposed trees and exposed portions of trees are subjected to moisture loss on many winter days (Sharpe, 1970:23). Tranquillini (1979) presents recent research results on the critical damage levels for each species above the Alpine timberline. In severe years, damage can occur even within the upper closed forest as well.

Both winter and summer drought are related to soil water deficiencies. Soil drought is a function of little snow cover, fast runoff, steepness, soil texture/stoniness, amount of organic matter in soil, and wind for surface evaporation. In energy budget terms, winter and summer drought work differently but each has cumulative effects on plant growth. The limitation of summer dry matter production relates directly to failure of needles to mature completely which in turn is linked to the likelihood of winter drought damage.

Drought resistance fluctuates during the course of the year and is greatest in winter. However, Tranquillini (1979:108) found that the uppermost trees in the ecotone possess less evaporative resistance and desiccate more quickly than lower-elevation trees. Apparently this is because the transpiration resistance of new shoots is inadequate if cuticular development was not completed in the previous growing season (Wardle, 1971). Wardle (1968) showed that the water content of immature needles declined more rapidly than that of fully matured foliage during the course of the winter. Hence, any small-scale climatic change that effects a shortened growing season or a decrease in summer heat will have nearly immediate impacts on the winter drought resistance of high altitude trees. Exceptionally severe desiccation damage becomes visible in the timberline ecotone during the following spring (Tranquillini, 1979:108).

Any environmental change (such as climatic fluctuation) which either intensifies the *winter* conditions for desiccation (eg. radiation conditions, changes in snowcover pattern) *or* decreases the length of the *growing* season, retarding needle development (and thereby decreasing cuticular resistance to transpiration) will increase the risk of winter desiccation.

The dry red-brown needles left by severe winter desiccation therefore clearly mark those trees which are at their absolute limit of year-to-year survival (for that species). For this reason, very thorough attention was paid to the nature and location of this form of damage.

Distribution: The extent of desiccation damage is as shown in Fig.4-8. Several contributing factors in this distribution can be isolated and discussed. Firstly, those areas blown free of snow cover permit greater frost penetration of the soil ("the entire root zone is frozen in snow-free areas", Sharpe, 1970:23), and greater exposure of

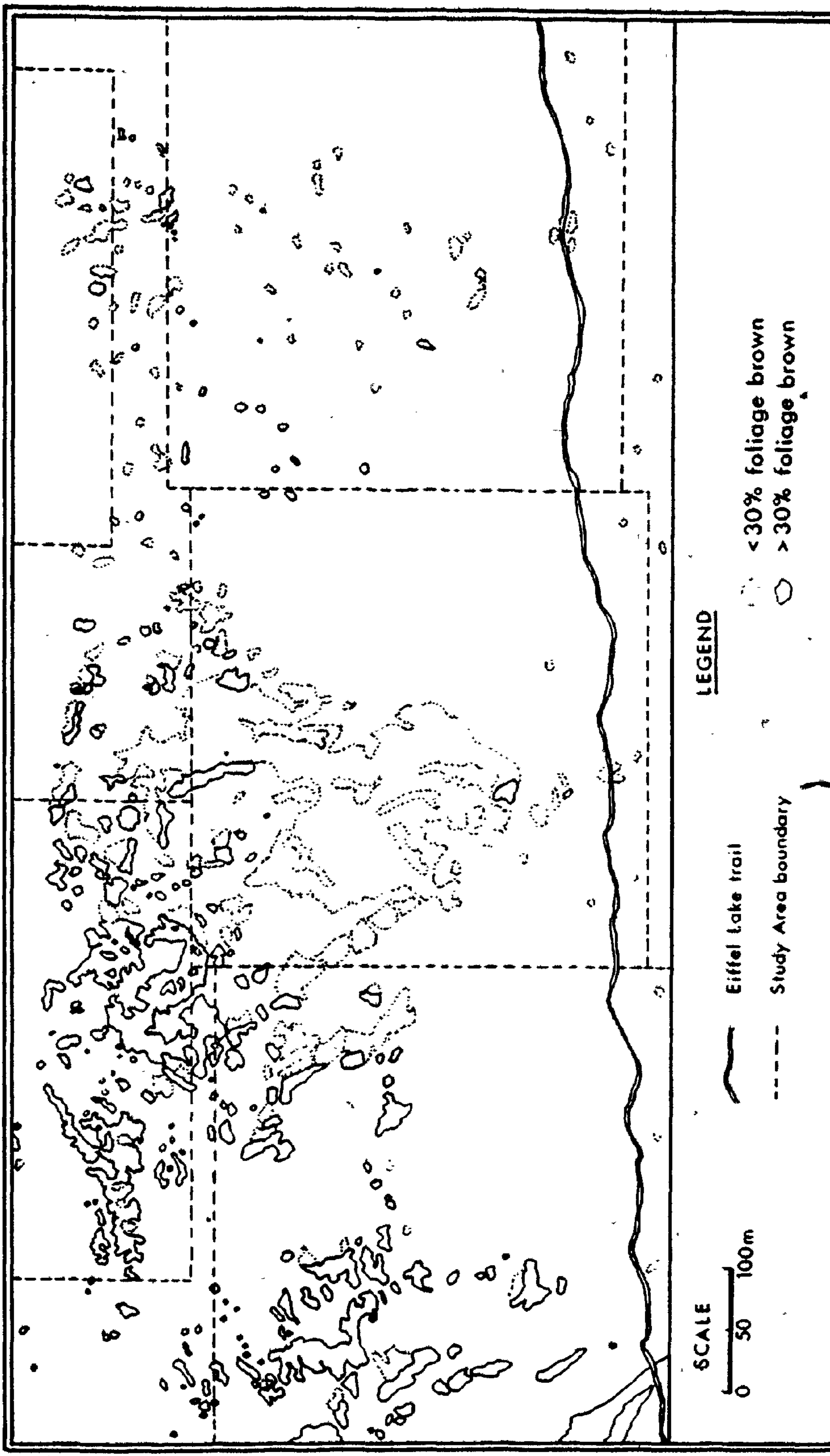


Figure 4-8: Distribution of Desiccation Damage

branches to the drying and cooling action of wind. Secondly, the areas with south and southwest exposure receive the highest insolation values, experience greater extremes in both air and soil surface temperatures, and are exposed to gusty prevailing winds, which, taken together, create an extreme evaporative situation. Thirdly, the upper slope periodically experiences the inversion of the normal temperature distribution with elevation. These warmer, drier episodes may exacerbate needle overheating and the already highly evaporative conditions, in much the same way that Chincok winds may enhance winter desiccation, especially on south slopes (Henson, 1952). At the same time, the actual frost resistance (n.b. not drought resistance) may be lessened, inciting direct freezing injury when temperatures drop to 'normal'.

Species Selectivity: On this site the most severe and widespread desiccation injury is suffered by _A.lasiocarpa_ and _P.engelmannii_. Drought resistance varies by species and is higher in _L.lyallii_. "Winter drought apparently has little effect on the deciduous larch" (Arno & Habeck, 1972:432), and thus it continues to show erect growth forms where evergreen conifers exist only as low and dense krummholz.

However, some reduction in resistance to cuticular transpiration has also been detected in the terminal shoots of larch above timberline (Tranquillini, 1979:108). So while it does suffer an increased rate of water loss, the impact on the tree is not nearly so great as the stress most *Abies* individuals exhibit.

Intensity and Effects: Needles in which the water content fell to lethal limits during late winter turn red-brown in the following summer. The dried needles are shed and the general result is the streamlining or flag-shaping of individual trees (Wardle, 1965:127).

In places, whole tree islands and 'hedges' display desiccation injury to their terminal shoots. Fig.4-8 indicates the location of trees having more than 30% brown foliage (as per Vigour Index, p.68).

Individually, the effect is seldom actually lethal, but it *is* stressful to the plant, as the entire dry matter production of the previous year may be lost ("wasted"). Growth during the following summer may be curtailed seriously especially after terminal buds have been killed (Sharpe, 1970:23-4). Because the expansion of any one tree's branches is limited to its lee side, the overall effect is that dynamic tree island growth is impossible. Wherever desiccation damage is severe, there is a definite limitation on the areal expansion potential for a single established tree or tree group. Only in Study Area A is some expansion of tree margins taking place, as was discussed on pp.72-3.

Frequency: On the basis of the broad distribution of flag-shaped trees and very recent drought damage, it is suspected that this process occurs often. Clearly the severity varies year to year, depending upon the conditions during the preceding summer as well as the energy and moisture exchanges during the dormant season (such as slight changes in snowdrift pattern and duration).

According to Tranquillini's model (1979:110) of how desiccation processes are involved in the location of timberline and treeline, the _risk_ of desiccation damage extends to lower elevations in very harsh years and moves further upslope in milder years. In this valley, trees deformed by desiccation occur as low as 2272m (7450') (see Fig.4-8). This is critical, as it suggests a degree of environmental stress not initially suspected. This situation could be seen as an indicator of lack of synchrony between modern trees and modern climate-- the expediency of this interpretation will be discussed in Chapter 5.2.

4.3.9 _Mechanism 7: Wind (Mechanical Damage)_

Klikoff (1965) cited the importance of abrasion effects from wind-driven ice and snow on timberline trees in the Sierra Nevada (although generally he found the larger contribution of wind was in decreasing temperature). On the Wenkchemna study site, abrasion damage on windward stems and branches was quite localised. Very little superficial evidence of abrasion as a destructive agent was seen on buds which fail to develop (Marr, 1977:1162). _Picea engelmannii_ were observed with a substantial trunk scar or 'polished' and broken branches more frequently than other species.

Few trees are actually snapped off by wind. In contrast to its impact within the lower closed-canopy forest, windthrow has remarkably little effect above timberline. Windthrow is the uprooting or breaking of vegetation by high winds (Barbour et al., 1980:204). Only in the most severe gales does blow-down occur (Mackenzie, 1973:51) and then only of old trees with advanced heart-rot, usually *Larix* snags (Arno & Habeck, 1972:443). Any wind-broken trees observed were on high-"windfall-risk" exposures (Alexander, 1974:12) such as saddles in ridges and upper south- and west-facing slopes not protected to the windward. In Areas C and G, *L. lyallii* was often double- or multistemmed with some bark and foliage battered off the windward side.

Generally, however, direct mechanical stress due to strong wind is of slight consequence. Generally timberline trees appear well-adapted to a variable windiness regime-calm, gusty, persistent, gale and blizzard winds. Wardle (1965:123) observed that in the Rocky Mountains of southern Alberta, trees at timberline are stunted but "deformation by wind is much less evident" than in the Colorado Rockies. It is also much less prevalent than that reported by Pears (1967) for the Cairngorms, Scotland or by Holroyd (1970) for the Adirondacks.

More researchers have shown that the wind exposure effects are linked to the transfer of the snow cover and thus related to desiccation effects. The redistribution of snow to lee slopes or concave pockets, producing local wetter or drier than average areas, has been discussed by Daubenmire (1968), Billings (1969), Howell and Harris (1978) and Reiners and Lang (1979).

It emerges that mechanical damage (abrasion or breakage) caused by wind has surprisingly limited impact in comparison to the considerable influence of physiological damage by winter-drought.

> Physiological damage is a resultant of the interaction of thermal energy and snow interposed as a barrier to energy and moisture exchanges at the plant surface. Mechanical damage results from the interaction of snow or soil particles acting as abrasives, wind as the source of momentum, and snow as a shield for the plants (Sharpe, 1970:26).

Clearly the processes that interact to induce these two forms of damage are significantly different. Yet during the dormant season, both physiologic and mechanical damage may act concurrently on a given plant.

Wind effects (both physiological and mechanical) are responsible for the production of snowmats (*P.engelmannii* and *A.lasiocarpa*) on the upper slopes (Area D). These prostrate forest outposts (under .3m (1') tall) are restricted to depressions and sheltered places, and are a "conspicuous feature wherever the wind blows all snow away except that which is trapped within the foliage" (Sharpe, 1970:24). Griggs

(1938) claimed that this formation is not a regular timberline feature in the Canadian Rockies: on the contrary, at this site, it covers about 65% of Area D.

A second distinctive growth form is linear hedges of *A. lasiocarpa* growing in rows which are one plant wide and are oriented NE 25-45° (parallel to the prevailing winds) for mutual protection from wind. They nearly resemble a planted hedge in appearance. All branches extending beyond this streamlined shape suffer drastic loss of water content and are lost to desiccation.

4.3.10 Mechanism 8- Animal Activities

Damage to plant parts from the feeding and burrowing activities of animals is scattered widely throughout the valley but is severe in a few localities only. Winter girdling damage to the bark of saplings and some trees by porcupines, snowshoe hares and possibly voles was encountered. Red squirrels, ground squirrels and birds (especially the Canada jay) were observed harvesting larch, fir and pine cones. The foliage (buds and needles) of larch and whitebark pine are an important food source for blue and ruffed grouse (and ptarmigan) (Arno & Habeck, 1972:431).

The browsing impact of large mammals (deer, mountain sheep, black bear, grizzly bear) is limited at this elevation. The upper valley is not a regular "route" for grazing ungulates. However all vegetation layers, tree, shrub and herb, are affected by a large variety of rodents and small mammals in addition to those already mentioned: hoary marmots, mice, chipmunks, weasels, and pika or rock rabbits. The seeds and roots of conifers, forbs and graminoids are eaten. Klikoff (1965:201) reports that herbivore consumption is probably insignificant in affecting plant distribution, but is likely of importance in reducing the fund of viable seed. The quantitative loss of seed from animal consumption and other causes is not known. In the absence of data on this relationship, no firm conclusions can be drawn. It is this author's opinion, however, that seed supply reduction is not trivial but probably a significant component.

Direct tissue destruction, however, is generally much less conspicuous than the effects of burrowing. Fig.4-10 indicates the location of certain slope segments where the density of ground squirrel (and pika) tunnelling is very high, to the extent that soils are undermined and mixed, and the surface hummocky. On the steepest and driest slopes, Dryas Hookeriana- Carex scirpoidea communities form tufts above each tunnel entrance. These calcareous sandy heaths are chronically subject to wind erosion, soil creep and frost action, effectively inhibiting any seedling establishment. Patches of exposed soil are mixed with open heath and alpine herbmat species (eg. Anemone Drummondii).

Thorn (1978) documented the "prodigious earth moving capabilities of pocket gophers" in the alpine zone of the Col-

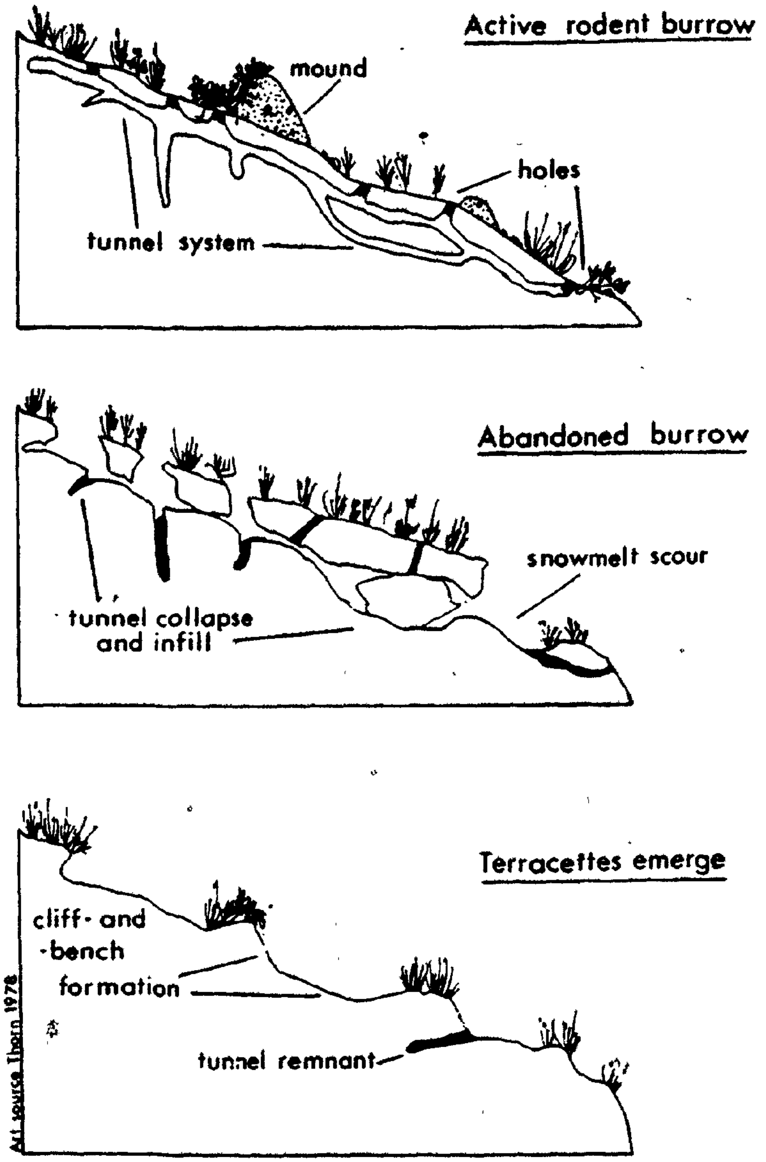


Figure 4- 9: Evolution of Mesoscale Cliff-and-bench Formation.

Once initiated by squirrel burrowing, the normal processes of frost heaving, sheetwash, and deflation ensure the development of a series of risers and bare treads.

orado Front Range, and the production of 'terracettes' at the mesoscale that results. He also noted that pocket gopher populations will readily relocate in response to changes in winter winds and the accompanying snowfield patterns. If a tunnel is 'drowned' by snowmelt, a new drier site will be excavated.

The observations on this site match those of Klikoff (1965) that the distribution of rodent burrows is neither random nor uniform. They tend to be highly concentrated in localized areas in the dry meadows. In the persistent balds of Areas B and C (see pp.79 & 85), the negative influence of this burrowing on conifer regeneration is conspicuous. In addition, the coyote, one of the ground squirrel's predators, has enlarged burrows considerably by digging in several places, as reported for other subalpine sites by Patten (1963:390) and Klikoff (1965:201).

On more moist meadows, the impact of rodent activity is less clear. On more stable sites, *Kobresia myosuroides* and *Cassiope tetragona* are well-rooted and the ~~soil~~ not strongly desiccated. These associations are confirmed by Knapik et al. (1973). In Glacier National Park, Habeck and Choate (1963) found that *Abies* and *Picea* seedling success is actually *enhanced* by frost-heaving and gopher disturbance because of the aeration and mixing of soil and the reduction of competition. Patten (1963:390) also commented that the disturbance of soil by burrowing animals has both beneficial

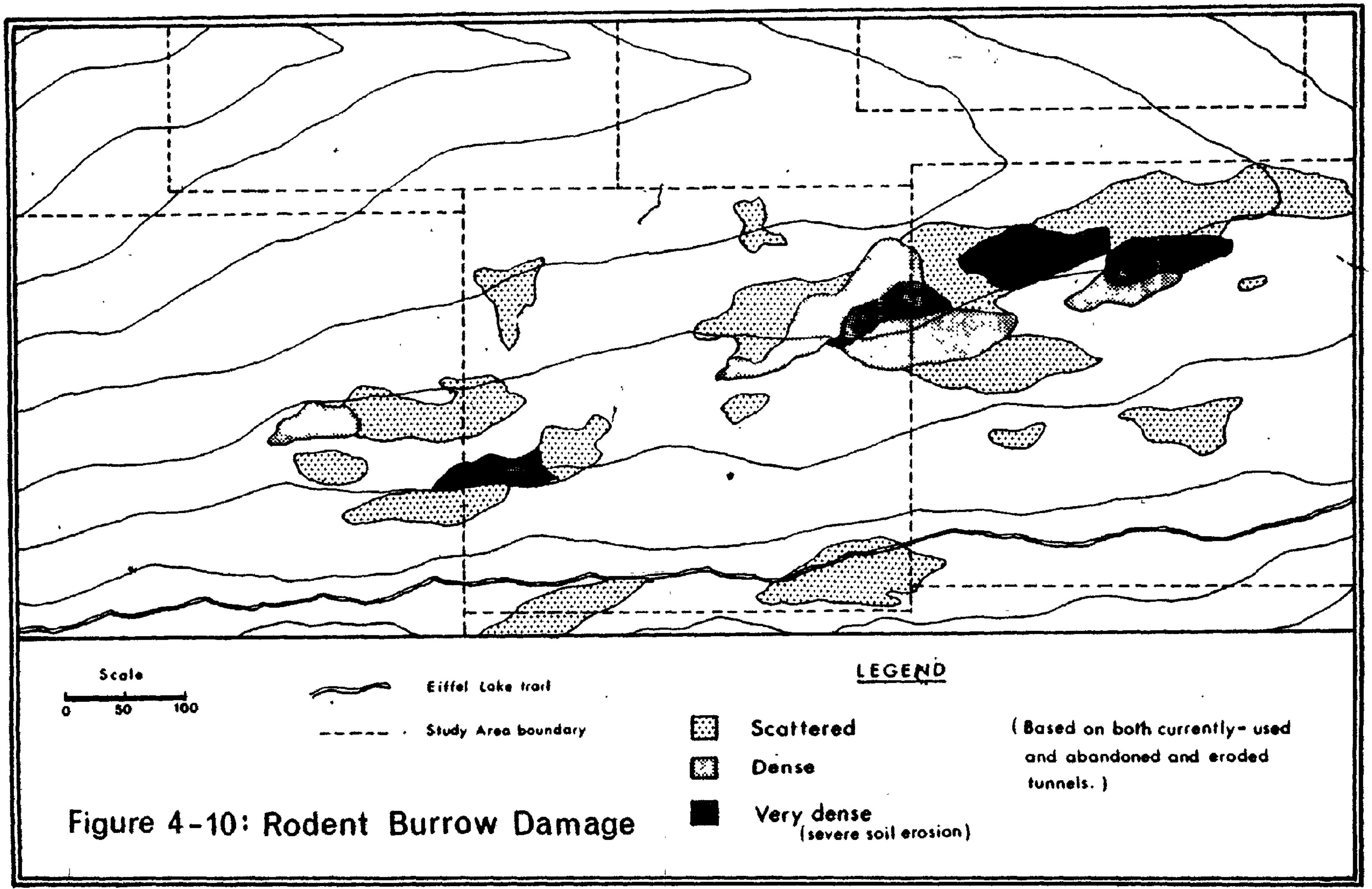


Figure 4-10: Rodent Burrow Damage

and detrimental influence on plant regeneration. Erosion of the loosened surface soil may increase, and yet the looser soil becomes a porous, often moist site for conifer seedling establishment. Olgeirson (1974:196) suggests that the presence of "litter dams" on these terrace sites may in fact provide stable soil surfaces favoring the survival of seedlings (refer to Fig.4-9).

Indeed, on the more mesic areas of burrowing activity, the degree of soil disturbance (hummocks, abandoned tunnels, mounds) is intermediate and yet tree juveniles have established (for example, the slopes immediately below Areas A and C). However, an apparently similar situation at the lower end of Area B supports no conifer regeneration whatsoever. In this case, the lack of seed is the remaining likely explanation.

In wet meadows or on level slopes, rodent activity is almost non-existent.

Thus even in the case where suitable seedbed conditions exist (i.e., plant cover sufficient to trap snow for a summer moisture supply, yet not so dense as to prohibit germination, along with the creation of mineral soil patches by animal burrowing), the availability of seed emerges as the critical factor determining community composition.

In summary, to any individual plant, animal effects occur intermittently and range from stressful to destructive. In terms of overall associations, the effectiveness of this mechanism is generally chronic (in time) but moderate in intensity.

4.3.11 Mechanism 8A: Human Activities

To only a very minor degree, human hiking activity exacerbates some of the effects of other mechanisms already discussed (eg. soil creep). Since no camping is permitted in the valley, the limbing or campfire rings that plague other timberline meadow areas (Bell & Bliss, 1973; Hansen Bristow, 1979:6) are of little consequence here.

The hiking trails are the only unmistakable human impact within the study site but they "remain roughly unchanged in number and configuration" (Gardner, 1978a:5). Weekend foot-traffic is heavy throughout summer and fall, particularly into Larch Valley, but littering and removal of plant parts appear to be negligible. Only slight trampling effects on the heath vegetation (compaction, plant breakage; Willard and Marr, 1971) were found away from this path (presumably 'lunch stops').

The observations here matched those of Cole (1978) in northeastern Oregon who estimated the susceptibility of a variety of vegetation types to trail and trampling effects by comparing changes in plant cover and species composition. Surprisingly, the dense subalpine forest type changed most drastically, open-nature forests changed moderately, while open subalpine meadow was least susceptible, the reverse of what is commonly believed.

This is explained largely by the routing of the path. Where it follows natural drainage lines within the upper forest, as opposed to proceeding across slope, the trail's existence has accelerated erosion processes (very locally). Here soil has been washed from the trail except for pockets between large stones.

Where the trail follows contour lines across avalanche slopes (Area F) or areas of active downslope rock movement (Area G), slope instability is enhanced through oversteepening (on a micro-scale). However the path is very narrow. The total impact of human hiking activity, in terms of area, frequency and severity of effects on vegetation pattern is very limited.

4.3.12 Summary

Barbour et al. (1980) state that by their presence, vigour or abundance, plants tell us a great deal about the past, present, and future course of their habitat. The preceding analysis made use of such stand attributes and performance indicators as presence, cover, vitality, density, and basal area to determine features of the historical and current disturbance regimes. Table 4-2 presents a summary of the major observed vegetation effects and their postulated mechanisms.

In this particular forest-heath transition there can be no mistaking the pervasive influence of disturbance at several scales of frequency and intensity. The inventory of the stress and disturbance regime has shown that the incidence and characteristics of these factors vary widely. Some disturbances are very rare, catastrophic and widespread (fire); others are common, sublethal and widespread (desiccation damage); still others are frequent but confined to particular slope sections (rodent burrowing).

Disturbance effects, therefore, have a spatial organization. This section has presented observations that their causal mechanisms are patchy in occurrence and/or duration: thus, the effects tend to 'accumulate' on specific areas.

The impacts of a single mechanism are often localised or abrupt in space. This patchiness of disturbance effects is important, because it often exaggerates the marked spatial heterogeneity of habitat factors. The converse is also true: the existing heterogeneity of site factors may serve to exaggerate the patchiness of disturbance effects.

No single factor is responsible for the origin, maintenance, or change of the species patterns. Following short-lived or prolonged stress conditions, plant damage or ultimate death seems to result from a synergistic acccumulation of 'causes' (Reiners & Lang, 1979:411). Throughout the results in the preceding section, it emerges that in most cases, two or more mechanisms are or have been involved on the same piece of terrain. Other discussions have also stressed that it is the entire factor-complex which acccunts for the character and distribution of plant populations (Daubenmire,

Table 4-2: Summary Table - Disturbance Mechanisms

Mechanism		Occurrence	Effects on Vegetation Pattern
1.	Fire (approx. 1870)	Widespread across moraine	Fire scarred living trees; Stumps, logs, charcoal remants; Snowdrift glades: herb-dominated openings.
1. a)	Lightning strikes	Ridgetop, upper slope	Sporadic single snags
2.	Snow avalanche	Steep slopes (esp. Area F)	Avalanche tracks: narrow linear strips of vegetation oriented downslope.
2. a)	Snow creep	All aspects (all Areas)	Recumbent trees; stems deflected downhill by snow pressure.
3.	Deep snow accumulation	Lee slopes; Concave pockets; Tree island margins.	Snowdrift glades; snow-fungus damage by pathogenic fungi; Locally enhances conifer seedling survival.
4.	Cold air drainage (temperature inversion)	Valley head Valley floor	Patches of alpine species within subalpine forest; Larch high-density.
		Valley sides	Contributes to frost damage & desiccation in Abies and Picea.

Table 4-2: continued

	Mechanism	Occurrence	Effects on Vegetation Pattern
5.	Rockslide	Steep slopes (below Effel Pk.)	Broken, stunted trees; Cushiony morphology in both herb & conifer populations
5. a)	Soil Creep (Solifluction)	Widespread SW & S-facing slopes	
6.	Winter drought (Physiological damage) - Energy Deficiency	Widespread esp. upper slopes	Desiccation damage to conifer leaders; Krummholz strips.
7.	Wind; Ice-sting (Mechanical damage) - Breakage, Abrasion	Western exposures	Tissue destruction; Individual deformed trees; Tree islands; Clumping.
8.	Animal incl. Human Effects	Localised	Hummocky surface undermined by burrows; Seedling establishment hampered; Trail, old camp-rings.

1954:33; Mooney et al., 1962:272; Patten, 1963:403; Klikoff, 1965:187; Sharpe, 1970:21; and Sprugel, 1976).

> It must be stressed that the external or habitat factors are interactive, and while it is sometimes justifiable to regard one or other as exerting a predominant influence upon distribution, it is seldom that a single factor operates independently of others (Edwards, 1963:89).

The tradition of searching for a single most important environmental factor is still somewhat with us today "but more and more we understand the interdependence of all factors" (Barbour et al., 1980:14). As Knight et al. (1977) have commented, "All factors interact, creating the typical dilemma of trying to clarify the mechanisms whereby environment controls species composition".

It is important to note, however, that the effects of the process controls are not strictly additive. In a hasty effort to quantify the hazardousness of any given site, one might simply sum the total number of stresses evidently at work there. The acquisition of such a simplistic risk 'rating' as this however would entail major problems because of the loss of essential information involved. "High-risk" sites (in terms of sexual reproduction) are high-risk for very different reasons.

By way of illustration, Fig.4-6 showed areas of minimal to maximal snow cover, but would lack of snow cover warrant the same risk ranking to a microsite that excess snow cover would? There is little sense in which they have equal impacts. Both are common contributors to physiological stress but via different mechanisms.

In any case, the incidence and amplitude of environmental rigour affecting any one microsite is complex, and each individual and species responds differentially. Similarly, at the mesosite level each population is responding to the environmental complex in a unique way. The total effect of this is a complex array of plant patterns on the landscape, and

> Any precise explanation of the nature of the environmental control on these plant distributions will have to be made at the specific or population level (Mooney et al., 1962:272).

To better understand the specific patterns across the study site, that is, the variable structure from stand to stand reported in Chapter 3, it useful to consider the interactive and cumulative nature of the effects in Figures 4-2 through 4-10 and summarised in Table 4-2.

Although fire, avalanche and rockslide are obviously large 'events' that are damaging or catastrophic to the plant cover, many of the stresses discussed here are sublethal. It is postulated here that any one stress does not have to be lethal on an individual basis in order to affect vegetation pattern on a community level. This is true because sublethal stresses or small-scale disturbances do affect the regeneration processes of the species population, thereby influencing both stand structure (composition, abundance, dominance) and the spacing patterns of the communities. In this case, that amounts to affecting the very nature and location of the ecotonal boundary.

It has been a recurring theme in this chapter that any single disturbance or combination of sublethal stresses that by their cumulative action limit or restrict a tree's reproductive effort to layering (i.e., expansion only at its own perimeter) will have long-lasting influence on the vegetation pattern of the site.

Disturbances, then, have differential distributions, and work in concert to create environmental patchiness. Clearly a critical influence of this heterogeneity is to create particularly 'high-risk' sites from the point of view of seedling establishment and survival. We have a mosaic of differential conifer reproduction success induced by a mosaic of differential types and frequencies of vegetation disruption. The next section will examine the degree to which the spatial organization of conifer reproduction modes co-varies with the spatial organization of disturbance effects.

4.4 REPRODUCTION PATTERNS

It is evident from the earlier discussion on plant vigour indicators, that it is critical on this site whether the individuals of a population are self-reproducing- where is each species population expanding, self-maintaining or shrinking? Given the marginal environment for plant growth and the large observed variance in tree vitality, the successional pathways possible (if any) will hinge on the type of reproduction possible.

Conifer regeneration capacity provides a readily observed and, in some respects, the most sensitive indication of a species dynamic status both within a given stand and in the wider community. Through his work on population responses to "patchy" environments, Wiens (1976) shows that variable environmental factors have their most important contribution in the dispersal and germination phases of plant life. Extremes in soil and microclimate conditions, as well as competition and consumer effects, are critical insofar as they influence "seedling establishment, screening seeds and dictating germination and survival probabilities" (Wiens, 1976:85).

To understand persistence or change in floristic composition and spatial structure, Veblen and Stewart (1980) believe that examining regeneration modes is very informative because reproductive behaviour is so central to plant spatial structure. It emerges in related subalpine and subarctic research (LaMarche, 1973; Höllermann, 1978; Elliott, 1979; Hansen Bristow, 1979) that the issue of reproductive potential is central in determining the likelihood of persistence or change in the vegetative cover, and yet is poorly-explored. The author agrees with Elliott's (1979) assertion that conifer regenerative capacity is not merely an interesting aspect of ecotonal stability: it is critical.

The question is whether the study area is now experiencing or will undergo (even very slowly) a major change from a mixed meadow to forest cover-- that is, to assess if indeed the ecotone is 'seral' to forest or not. This can be established only by investigating in detail the reproductive success of the dominants. Hansen Bristow (1980) agrees on the significance of ecotone trees that are unsuccessful in reproducing sexually, "as this has great implications in terms of management of the forests and stability of the ecotone".

There are several components of the regeneration process: pollen viability; seed viability; the existence and viability of a buried seed store; regeneration mode (sexual or vegetative); and the existence, location, age and vitality of tree juveniles, whether sexually or asexually produced. Given the several constraints on this project, buried seed store and pollen viability were not determined. Seed viability was not measured but simply assessed qualitatively, noting the production of cones having apparently viable and clearly non-viable propagules.

With these exceptions, the remaining components of the occurrence of coniferous regeneration were studied, particularly in relation to these environmental factors: elevation, aspect, snow-depth and duration, seed source, and destructive events. While it is difficult or impossible to decide which environmental factor or group of factors directly controls a species' distribution (Kershaw, 1973:152), it is clear that those limiting factors are especially significant as they affect the establishment of seedlings and their subsequent performance. Although preceding sections have alluded to several of these relationships, the specific results of this survey are given here.

4.4.1 Results

Reproductive effectiveness varies widely across both the length and width of the ecotone. Some indication of this variability is given in Table 4-3, the results of the survey of tree juveniles in the scattered sample plots. For their exact locations, refer to Fig.2-4. All species show extreme patchiness in their distribution and vitality of juveniles. Within these selected test plots, only about one-twelfth to one-tenth of the total number of individuals were young trees.

Seedling establishment does not coincide with the present upper limit of tree species and this is important. Comparison of the present treeline with a "seedling treeline" by species (Nichols, 1976:42) revealed that not even *Larix lyallii* the hardiest species, is reproducing within its entire present range. However, there are several places over its mature-tree distribution where it has seeded-in vigorously. Generally, in these patches, saplings are numerous while seedlings are nearly or totally absent. Not one *L.lyallii* cotyledon (new seedling) was discovered. A comparison of Figures 4-8 and 4-11 yields some idea of the significance of desiccation damage to the upper trees in terms of curtailing reproductive activity.

Table 4-3: Reproduction Results- Juveniles in 20 Sample Plots

Species		ABIES					LARIX			PICEA				Plot total: All species
Height Class		1		2		Total	1	2	Total	1	1	2	Total	
Regen. Mode#		S	V	S	V		S	S		S	V	V		
Area	Plot													
A	1	1	3	3	-	7	3	9	12	-	-	-	-	19
	2	2	1	3	2	8	2	5	7	-	-	1	1	16
	3	2	4	3	7	16	1	2	3	1	-	-	1	20
	4	-	-	-	1	1	1	8	9	-	-	-	-	10
						32			31				2	
B	1	-	1	-	4	5	-	2	2	-	-	-	-	7
	2	-	3	-	6	9	-	1	1	-	-	-	-	10
	3	-	-	-	-	-	-	3	3	-	-	-	-	3
	4	-	2	-	5	7	1	5	6	-	-	2	2	15
						21			12				2	
C	1	1	-	3	-	4	-	1	1	-	-	-	-	5
	2	2	-	2	2	6	-	1	1	-	-	-	-	7
	3	2	-	1	-	3	-	2	2	-	-	-	-	5
	4	-	2	-	4	6	2	3	5	-	1	-	1	12
						19			9				1	
D	1	-	1	1	3	5	1	5	6	1	-	2	3	14
	2	-	4	-	2	6	-	2	2	-	-	1	1	9
	3	-	-	-	1	1	1	3	4	-	-	-	-	5
	4	-	-	-	1	1	-	1	1	-	-	-	-	2
						13			13				4	
E	1	-	-	2	-	2	2	4	6	-	-	-	-	8
	2	-	-	1	-	1	1	3	4	-	-	-	-	5
	3	-	-	2	-	2	1	7	8	-	-	-	-	10
	4	-	-	2	-	2	4	9	13	-	-	-	-	15
						7			31				-	

Regeneration Mode: S - Sexual V - Vegetative
Height Class: Abies & Picea 1 - <15cm; 2 - 15-60cm
Larix 1 - <30cm; 2 - 30-150cm

No sexual regeneration of *Abies lasiocarpa* is seen above the area indicated in Fig.4-11. Individual seedlings and saplings occur below this. They are widely-spaced, never in dense regeneration clumps as reported by Franklin et al. (1971) in the Cascade Mts. of Washington. Only juveniles produced vegetatively in mat- and hedge-krummholz patches achieve high densities.

Layering is present in all stands examined through the ecotone and appears to be the sole method of propagation for *Picea engelmannii* as well as the dominant reproductive mode for *A.lasiocarpa*. Only three *Picea* seedlings were found over 63ha. The area marked in Fig.4-11 indicates clonal groups of spruce and fir whose reproduction is by layering. This represents juveniles at the perimeters of groups derived originally from sexually-produced individuals. The foliage of these juveniles is extensively damaged by snow mould-- their very formation depends upon the weight of snow, and fungus damage occurs in intermittent years of heavy snow.

These stands have continued to survive in the upper ecotone because of their ability to vegetatively reproduce. They 'migrate' into their own protection, the trees root by layering, and the original part dies out. The spruce and fir stands are apparently maintaining their position, but only barely, based on their declining vigour. They cannot enlarge their area effectively, into the open belts, because

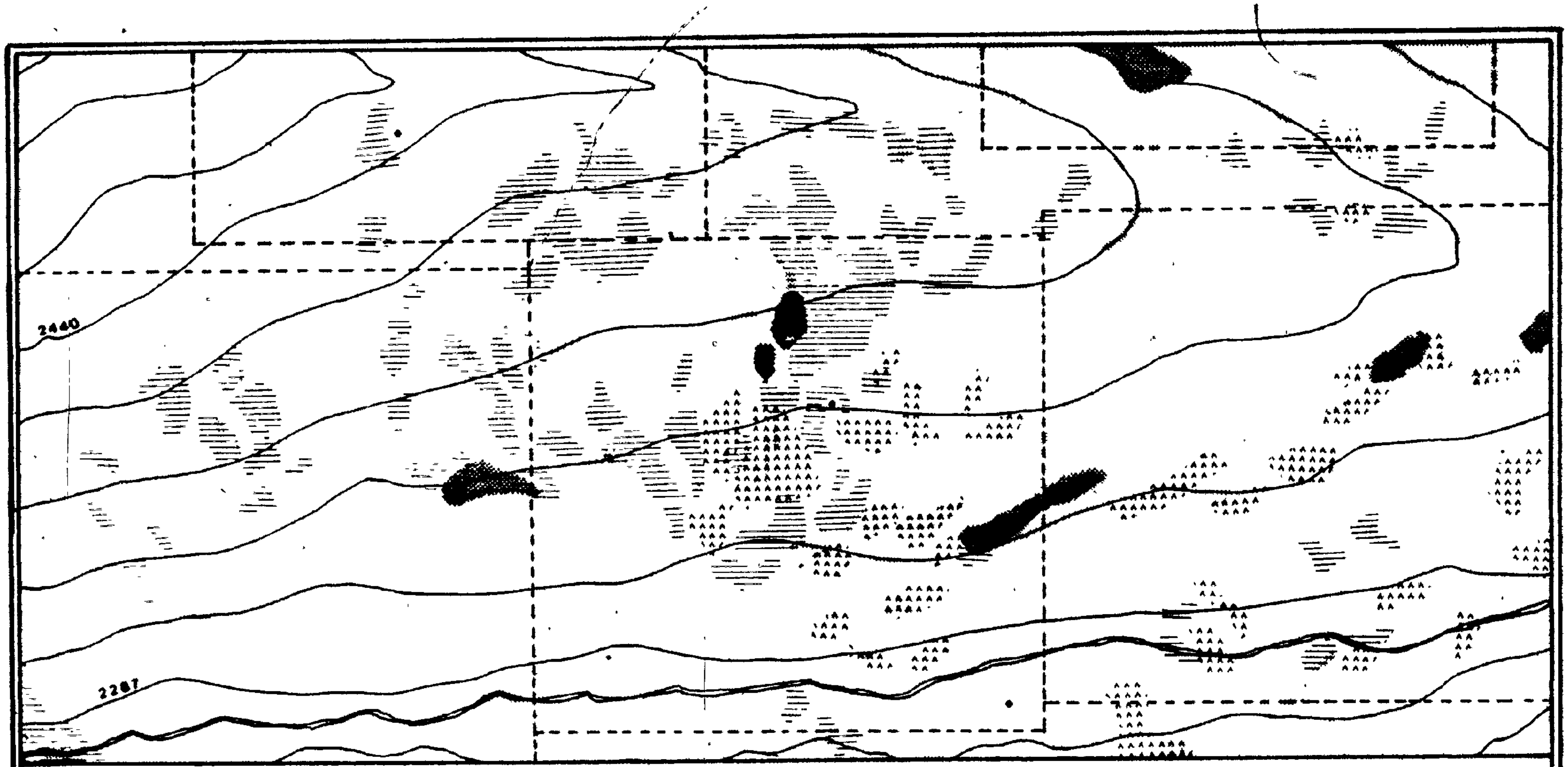


Figure 4-11:
Reproduction Patterns

of the excess snow and insufficient snow conditions in very close proximity about the tree clump. While layering may be an advantageous mode for simply surviving these life conditions, Alexander (1958:9) pointed out that "this method of reproduction is insignificant in the establishment and maintenance of closed forest stands".

The total area of tree stands in the ecotonal belt is insignificant (<15% of ground cover), yet within these patches, the dominance of the flag-trees is absolute. Within tree clusters, the natural regeneration of single forest trees is strongly hampered by low light intensity under the dense krummholz canopies, as shown by the work of Zwinger and Willard (1972), Holtmeier (1981) and the author. Holtmeier (1981:258) states that "therefore the readvance of trees into the krummholz belt should not be expected until after the decay of the krummholz". This inhibition of competition and the extreme slowness of decomposition and detritus recycling contribute to the persistent character of these mats and islands.

There is a striking lack of individual conifer seedlings establishing between these forest outposts, indicating as well a more or less 'stable' situation in the krummholz area. Others have reported that seedling reproduction (i.e., the extension of forest stands) onto the open "balds" between tree clumps proceed very slowly (Billings, 1969; Böllermann, 1978). Here, it is nonexistent except in a few sheltered localities (indicated in Fig.4-11) at relatively low elevations. New reproduction over the 30 years of air photo coverage was detected only in the lee of the lower part of Area A.

The pattern of *cone production* is highly variable over short distances and is likely erratic through time. In the same 10 x 10m plots as Table 4-3, all mature trees bearing cones were counted. These results are shown in Table 4-4. It is stressed that the totals warrant more attention than the subdivisions on seed viability, since this breakdown is subjective and estimated only (no germination tests were performed on the whole and apparently viable seeds).

Only *L.lyallii* trees bear cones anywhere near the present limit of living trees. *A.lasiocarpa* bears cones in scattered patches only and a large fraction of these are mould-damaged or contain no seed. It is unknown if these cones ever bear viable seed, and if so, at what interval.

Nowhere within the study plots were cones observed on *Picea engelmannii*.

Table 4-4: Reproduction Results- Cone-bearing Trees in 20 Sample Plots

		Species					
		ABIES		LARIX		PICEA	
Area	Plot	Viable	Non viable	Viable	Non viable	Viable	Non viable
A	1	1	-	1	-	-	-
	2	-	-	1	-	-	2
	3	2	2	-	-	-	3
	4	-	-	1	-	-	-
B	1	-	-	1	-	-	-
	2	-	-	-	-	-	-
	3	-	-	-	-	-	-
	4	-	1	1	-	-	2
C	1	1	-	-	-	-	-
	2	1	1	-	-	-	-
	3	-	-	-	-	-	-
	4	-	1	-	-	-	-
D	1	-	1	1	-	-	-
	2	-	2	-	-	-	1
	3	-	1	1	-	-	1
	4	-	-	-	-	-	-
E	1	-	3	3	-	-	-
	2	-	2	4	1	-	-
	3	-	2	2	-	-	-
	4	1	-	6	-	-	-

Table 4-5: Reproduction Modes in Study Area A (84 trees)*

	Species		
Reproduction Mode	ABIES	LARIX	PICEA
1. None seen	1	6	2
2. Cones only	4	23	-
a) Apparently viable	(3)	(20)	
b) Clearly non-viable	(1)	(3)	
3. Cone-bearing and Layering	16	-	1
a) Cones viable	(2)		(-)
b) Cones non-viable	(14)		(1)
4. Vegetative - by layering only	26	-	5
Total trees tallied	47	29	8

*These observations refer to the same trees reported in Table 3-2.

4.4.2 Discussion

What gain is there in asserting whether a single *Picea* or *Abies* is reproducing itself by seed, by layering or not at all? In fact, the future composition and dynamics of both forest communities below and tundra communities above will hinge on this. We can determine whether a replacement community is indicated for the ecotone, that is, whether or not the ecotone is 'seral' to forest cover.

A considerable amount of information was gained by studying the density, size and health of juveniles (be they seedlings or asexually produced). Here this spatial variation in regeneration mode and success is related to the spatial variation in site conditions and disturbing agents. This interpretation will attempt to suggest the processes accounting for the variable effectiveness of the reproductive effort.

Lack of Seed: In the upper subalpine, there is only enough energy to meet the tree's yearly requirements for respiration and new tissue production (needle renewal and production of a small band of wood). There is almost no energy remaining for expansion, and little for the maintenance of a large root and stem system as in lowland trees (Zwinger & Willard, 1972). With increasing altitude, trees become progressively smaller, more compact, and they set seed or have cones only rarely. There are real limits on the amount of photosynthetic effort taken up by the reproduction effort. Low temperatures and short growing season contribute as well to very rare seed years (Barbour et al., 1980:72). For example the female strobili on Larix lyallii are sometimes killed by hard frost in early summer (Arno & Habeck, 1972:434).

Even under ideal conditions, Abies lasiocarpa produces a crop only one in every 3 years, with only 38% seed viability (Alexander, 1958b:9). With increasing elevation, phenological events are accelerated in adaptation to the shortened growing season, but there are limits to this condensation, usually to the detriment of seed development. At high elevations, especially on sites where snow persists longer, A. lasiocarpa matures its seed very rarely, being dependent on seed blown up from below (and on layering of its own branches).

The rate of seedling success might be very different in a valley of different configuration and therefore different wind patterns- the upper valley here is long and narrow and oriented with the prevailing and constant westerly winds. It is doubtful that seed transport from downvalley occurs other than sporadically.

In this valley, the influence of Wenkchemna Glacier covering half the valley floor is very important in this regard: the seed source for Picea and Abies (the simple number of mature trees at lower elevations) is unusually limited. In addition, because of the cold air drainage and

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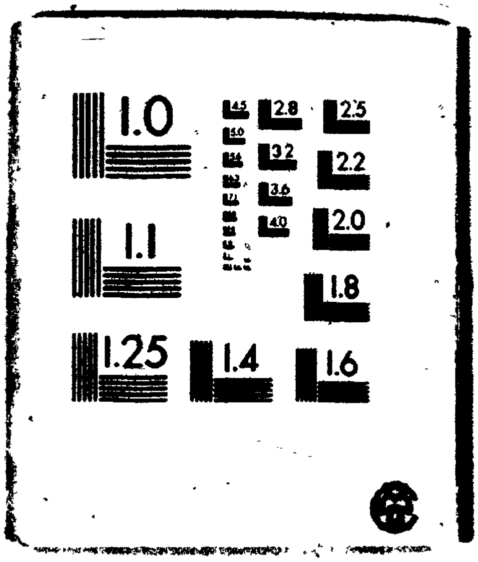

seepage conditions it is doubtful if the valley floor trees are prolific or regular seed producers. Germination micro-sites actually tend to be more suitable (warmer, better-drained) upslope on the moraine. Hence, the relative lack of seed to "get to" the study site is particularly disadvantageous.

Plesnik (1973) reports that seed years are rare in the Carpathians and the Tatras and that when they do occur, many seeds do not germinate anyway. He cites this inability of the upper-altitude trees to supply sufficient replacement individuals as the main explanation for the 'disintegration' of forest cover into groups and scattered trees.

Certainly the relative success of L. lyallii relates to its more dependable seed source. Only larch trees bear cones anywhere near the present maximum of treeline. Scattered seed trees which survived the fire serve as an important fund of seed, even though it be a supply sparse and irregular in its production (Arno & Habeck, 1972:447). Small pure stands of regeneration are undoubtedly linked to these few 'mother' trees. Shearer (1961) notes that this species generally germinates very poorly or not at all. The species generally does not bear seed until after reaching 100 years of age.

Thus, although the number of trees bearing cones is higher than other species (Tables 4-4,4-5) its actual germination and establishment success is highly variable. This accounts in part for the near-absence of new juveniles (Table 4-3). As well, the consumption of seeds by birds and small mammals works to some extent against tree establishment in the meadow areas.

A supply of viable seed is only one of several requirements for natural regeneration (Alexander, 1974:15). Also critical factors are a suitable seedbed and an environment compatible with germination and seedling growth.

To understand better the relative success of each species in the upper third of this valley it is necessary to compare other details of their regeneration requirements.

Species Requirements for Energy and Water: The seeds of P.engelmannii are small and light. While they are easily transported, their germination and survival probabilities on arriving in this timberline zone are slight. It is absolutely essential that Picea have shade and moisture to survive on a south aspect (Noble & Alexander, 1977). Due to the high radiation levels and limited shade on this south and southwest aspect, it has been difficult for P.engelmannii to 'pioneer' new individuals. Its seedlings are more sensitive to microslope aspect than A.lasiocarpa (Day, 1964:19); and are generally more exacting in their seedbed requirements than are A.lasiocarpa or L.lyallii.

The distances which A.lasiocarpa seed can be wind-carried are much shorter- it is much larger and 4 times as heavy as that of Picea (Douglass, 1954:91). It can germinate at much lower temperatures and can readily survive on a duff layer. The larger endosperm confers an advantage to *Abies* : this food reserve may enable the roots to reach mineral soil before the seedling dies of desiccation. *A.lasiocarpa* seedlings are commonly found on sites of litter accumulation such as elevated parts of the microrelief as provided by fallen logs, the upslope side of boulders and gopher mounds. The moisture-retaining capability of microsites with a duff layer becomes more advantageous as the growing season progresses. Throughout the subalpine, many *Abies* seedlings are observed on duff such as dead exposed *Vaccinium* or *Juniperus* root-mats, or on piles of cone scales thrown down by squirrels. Douglass (1954:96) also observed the latter in the Colorado subalpine.

The small amounts of shade and slight snow-trapping tendency provided by such microsites are important. The slightly lowered temperatures and decreased evaporation during peak radiation input hours help to create a habitable microenvironment. Juveniles of both *Abies* and *Picea* are nearly absent on open ground exposed to direct solar radiation. For both species, both initial establishment and growth are inhibited by direct sunlight. High surface and air temperatures on the south- and southwest aspect (i.e.,all Areas except E) increase evapotranspiration rates and create a drier environment, resulting in poor germination and high seedling mortality from drought. Stems and foliage that are not killed but damaged by light injury and desiccation are then vulnerable to mechanical damage by snow creep and wind in subsequent seasons. Whipple and Dix (1979:154) believe that the long delay in the establishment of P.engelmannii and A.lasiocarpa seedlings in the Colorado subalpine following disturbance is probably caused by elevated soil temperature and lowered soil moisture due to direct sunlight. Even under favourable conditions (a shaded, cool, moist habitat) both species grow very slowly in the seedling stage.

In contrast, Larix is shade-intolerant and prefers an open grassy slope. It can inhabit very rocky, gravelly and cold sites, but it must have abundant soil moisture.

Rapid temperature changes and drought are important inhibitors of seedling growth to all species, and are strongly aspect -related. This is confirmed by the work of Noble and Alexander (1977). They recognized nine factors causing the mortality of P.engelmannii and A.lasiocarpa seedlings in the Colorado subalpine zone: drought, clipping of cotyledons by birds and animals, frost heaving, heat girdle, light injury, freezing, washing, damping-off, and snow mould. On a north aspect, drought (30%), frost heaving (23) and clipping (22) accounted for most mortality. On a south aspect, drought (53%), clipping (25) and heat girdle (14) accounted for >90% of all mortality. Certainly the main controls on seedling survival on the Wenkchemna site are coldness and dryness.

Heat and drought are also negatively correlated with snow depth, and more specifically, to the variation in moisture availability related to winter snow deposition and spring melt patterns.

Snow Accumulation Patterns and Moisture Availability: Tranquillini (1979) stated that tree *form* is largely dependent on winter snow-cover. While interesting, this is less informative than examining to what extent the spatial variation in *regenerative success* is dependent on the patterns of winter snow cover.

There is no doubt that persistent snowbanks shorten an already short growing season and possibly saturate soils well into the growing season. Other mechanisms whereby an excess of snow from drifts, creep or avalanching might affect growth and species composition are by affecting nutrient availability as a result of changes in decomposition rates or leaching, or by improving the environment for pathogens such as snow moulds (Knight et al., 1977:318).

On the lower southwest or protected northeast slopes, and in the lee of dense tree clumps on the upper slopes (shown in Fig.4-6), *intermediate* to *late*-snow-lie sites show signs of snow mould and frost heaving. Shaw (1909) discussed the chronic problem of mould damage in persistent snow hollows: fungus mycelia enwrap the lower foliage and in order to exist the tree must expand its foliage above the late melting beds of wet snow. Noble and Alexander (1977:427) found frost heaving to be a serious cause of *P. engelmannii* seedling mortality.

> This phenomenon occurred when soil moisture was at or near field capacity, there was no vegetative or snow cover, and day-night temperatures were alternately above and below 0 C...Frost heaving is most likely to occur during the 2-3 weeks following spring snowmelt, and again just prior to permanent snow cover in the fall.

These excess-moisture related stresses in the first half of the growing season counter-balance with the advantage of cooler, moister conditions through the late summer and early fall.

On the upper south and southwest slopes, growing season length is determined as much by late summer water stress as by the initial snow-free date. Late snowmelt could delay late-summer water deficits and therefore increase annual productivity by prolonging the growing season. Any process which enhances the chances of tissue maturation (both seeds and needles) during the photosynthetic period will also reduce the likelihood and severity of desiccation damage during the dormant period. The combined effects of intermediate snow-lie in concavities (which protects foliage through the winter) and extended meltwater supply (which reduces summer drought) is one of these processes. The location of new conifer growth in such concavities reflects this factor.

Seedlings of both *A. lasiocarpa* and *L. lyallii* are found from the middle to the outermost limit of the influence of accumulated winter snow, not in the deepest portion of drifts, nor on the snow-free convex areas. Microsites with little snow cover and early snowmelt rapidly change from too cold and wet to too hot and dry for germination and survival, particularly if no rain falls in the critical first weeks. Drought is especially damaging to *Picea* regeneration during the 6 weeks following spring snowmelt (Noble & Alexander, 1977:427).

These same sites with little snow cover also suffer 'winter aridity' and the desiccation processes discussed in Chapter 4.3.8. In order to exist, the developing tree's 'concern' is to develop sufficient foliage in its own lee (Shaw, 1909), that is, to adapt to the highly evaporative situation in late winter and survive within the limitations set by both the mechanical and physiological effects of wind. *Vaccinium scoparium* and mesic grasses dominate the areas of light winter snowpack. This matches the findings ~~of Canaday and Fonda (1974:344).~~

Areas which receive no snow or are blown completely free of their snow cover by strong winds support a dry species association: *Dryas Hookeriana*, *Kobresia myosuroides*, *Carex nardina*, *C. scirpoidea*, *Fragraria glauca*) and no trees. On these steep slopes, where it is coupled with strong erosive forces, rodent disturbance is causing the enlargement of dry gravel areas through degradation of the already patchy *Carex* and forb sod. Lowdermilk (1925:996) also concluded from his post-burn reproduction study in western Montana that

> the thin vegetative cover on the upper southwest slope and the presence of the more drought-resistant species indicate the severity of the site.

By affecting both conifer success and understory composition, uneven snow distribution and the ensuing differential snow duration is an important factor regulating species distribution. It is held by some researchers that at high elevations above the range of *Pinus contorta*, *P. engelmannii* is generally pioneer (Stahelin, 1943; Langenheim, 1962; Patten, 1963). More accurately, *Picea* will dominate (both pioneer and climax) on the sites of longest snow lie (the most mesic sites near timberline) but on intermediate to low moisture and snow lie sites, *Abies* (Whipple, 1975) and *Larix* (Arno & Habeck, 1972; this study) perform better.

Others have commented on the increasing prevalence of *A. lasiocarpa* at higher altitudes within the subalpine where growing conditions are rigorous (especially seasonal desiccation; Douglass, 1954:91) or where the seed source for *P. engelmannii* has been destroyed (eg. devastating insect epidemics; LeBarron & Jemison, 1953).

The extensive distribution of *layering* in both *Abies* and *Picea* is striking and serves as reasonable grounds for inferring that a large portion of these species populations are in a static situation. The maintenance of the krummholz belt is strictly by the very slow expansion of the perimeters of the existing krummholz islands through vegetative reproduction, as windward parts of the patches die out.

This process is occurring as low as 2272m (7450'). There are no new islands beginning: the role of sexual reproduction in the maintenance or expansion of krummholz is nil. Especially on the upper and westernmost slopes, many trees are maturing but not reproducing adequately to replace themselves.

All patches with layering are likely to persist. The sprawling shrub form survives the periodic slumping or sliding of snow much better than do erect stems. Compared to long, 'open' branches, the dense tangle of foliage tends to create an ameliorated microenvironment in terms of air temperature, wind speed and relative humidity. Even though snow mould damage is rife in the lower foliage, from an individual survival point of view, layering confers some advantages. In general, sexual reproduction or seed years are very episodic while layering is more likely to be continual.

From a community dynamics viewpoint, however any 'advantage' is rather dubious. As discussed earlier, the dense lower branches effectively block out any chance 'invading' species. Understory species are sparse, even mosses and lichens. While the interior patterns of the mats and islands may slowly change (Zwinger & Willard, 1972:61), the general configuration of tree patches is remarkably fixed. Wind funnels between the ribbon strips, and the pattern of snow glades and wind-swept "blowouts" is quite similar year to year (Billings, 1969).

Downslope below the persistent 'balds', wherever some seedling establishment has occurred on the more moist meadows, it is plausible to predict somewhat more dynamic possibilities for community change. But within the flag-krummholz belt, there are few species composition changes and hence little community change. The patterns are to some extent self-perpetuating, as Whittaker and Levin (1977:126) explained:

> Frequency and intensity of disturbance may affect the reproductive pattern, survival of dominant species, and growth-form structure of a community. Composition and structure of the community may in turn affect its susceptibility to, and the frequency of, disturbance.

If one takes persistence to mean "stability", the krummholz belt is more or less stable. However, the expediency of this assumption will be discussed in the next chapter and its accuracy challenged. Stability is a more complex concept than the simple persistence of mosaic components.

In any event, extremely persistent species patterns (decades, centuries) are indicated over a large portion of the ecotone, even though much of the environmental flux here is short-periodic variation (hourly, daily, monthly).

Sporadically-Recurring Extremes: The regeneration survey results directly reflect the fact that the different regeneration requirements of each conifer species are not being met (at all) or else not consistently enough for juvenile establishment to occur. Temperature and moisture conditions necessary for germination to take place in a given year mean little if a series of years with conditions compatible with successful survival and growth do not follow. This issue of the recurrence interval of suitable years needs further research, and deserves much more attention than is possible here.

However, it seems a reasonable assumption that each conifer individual carries a record of how, *in its own past*, it successively solved the formal problems of survival and adaptation. Slobodkin and Rapoport (1974:191), in refining their efficiency model of stress response noted that "organisms must not make excessive or unnecessary commitment in responding to perturbation", and that flexibility must be maintained since environmental stresses are constantly changing. Under these very difficult sexual regeneration conditions, for instance, the tree which has produced cones and set seed in an unfavourable year, only to lose them to cold or drought, has made an inappropriate energy expenditure from both self-regeneration and adaptation points of view. Again, to the individual, layering confers some advantages; at the same time, in some ways it is limiting to the species. The colonization of completely new sites is not possible for the evergreens as it is for *Larix*.

[An important point to make here is that the issue of regeneration in this timberline situation is very different from 'gap-phase' dynamics and regeneration within a full forest cover type. In the latter, typically, all the prerequisites are 'in place'- seed source availability, an ameliorated habitat- in a sense, the surrounding species are just 'waiting' for gap-creation to occur (and competition is fierce for the new space). In the former, by contrast, the availability of 'gaps' is no problem- 'gap-creation' has occured and continues to occur. We have plenty of 'gaps' and competition is a minor issue- it is all the other prerequisites that are lacking: reliable seed source, and meso- and microenvironments compatible with plant establishment and development.]

A fairly simple example of a short-periodic variation in environmental parameters is the erratic daily cycle of temperature and relative humidity. Extremely rapid weather changes are common all along the study ridge. Within a half-hour of sunny, dry and calm weather, the wind can be suddenly chill, sharp and damp, and *graupel* falls, a kind of half-snow, half-hail. It stings plant tissue "with the force of hurled gravel", whitens the ground, and "bounces off rocks like popcorn" (Zwinger & Willard, 1972:16). The cloudiness passes in another half-hour and soon a hot sun rapidly dries all surfaces. The author witnessed these episodes on the Wenkchemna study site in three months, July, September and October. These unusually cold temperatures in midsummer caused minor frost damage, but "their potential for serious damage...should not be overlooked" (Noble & Alexander, 1977:426). A single intense rainstorm can wash seeds and new seedlings away, especially on steep or convex slope areas. The kinds of temperature and precipitation interactions that cause drought and frost-induced soil movements (which are locally serious factors) were discussed earlier. Certainly both new and established seedlings and recently-formed tissues on older plants are vulnerable to damage or mortality from this type of short-periodic variation. It is beyond the scope of the present paper to document the full range of environmental stresses to which these ecotone trees are subject (stress meant here as those environmental extremes which inhibit or curtail biomass production). Field research which monitors meso-climatic parameters and conifer physiological responses throughout the year is being conducted at the present time by Hansen-Bristow in the Colorado Front Range to determine what combinations of climate and inadequate physiological "preparedness" result in the limitation of tree growth in the upper subalpine.

An example of a longer-period variation as indicated by vegetation performance is an apparent increase in the environmental conditions contributing to the desiccation process. As currently understood in the physiological ecology literature (Tranquillini, Wardle,...), the combined effects of little snow cover and highly evaporative late-winter conditions account for the bulk of desiccation damage and the subsequent flag-shaping of trees. This author submits that the extremely broad distribution of foliage desiccation damage is field evidence of a substantial year-to-year variation in one or several of the factors contributing to the desiccation process. In the absence of direct data on this relationship we can only conjecture if this has been: a reduction in snow cover; a reduction in winter cloudiness and enhanced radiative conditions; a series of drier late summers and autumns (prematurely reduced soil moisture); or several consecutive cooler growing seasons (tree needles are immature going into the winter season) or a combination of some or all of these factors.

Unfortunately it cannot be known if this is the end of an 'extreme' cycle, the middle of such a trend, or if this swing toward an increasing winter-drought situation has just begun and will worsen still further. In any case, there is widespread <u>recent</u> damage, and it is hard to believe that this degree of damage and biomass loss can occur very frequently. This statement is made on the grounds that great numbers of trees exhibit <u>major</u> desiccation damage across a wide elevational belt. In effect, this denotes that this degree of desiccation was 'not anticipated'. Relative to the previous experience in the life of these trees, it seems that neither the extent nor severity of the change was 'predictable'. All three conifers (and <u>Juniperus</u>, as well) had expanded plant parts into positions that are now (suddenly?) incompatible with life, whether related to an intensified water-loss situation about the needles themselves (due to increased radiation, windiness) or to an increased level of water deficit in the whole tree (due to lighter snow cover, deeper frozen layer, reduced root uptake of replacement moisture, and upper and outer foliage lost to drought).

Although firm conclusions are not possible on this disturbance 'event' (its duration, relative and absolute severity), the general point made here is that the capacity of the organisms to deal with some annual degree of winter drought has been surpassed by an unprecedented degree of variation. That is to say, previous responses made to enhance predictability (i.e., growth strategies to 'know' the possible range of winter-drought stress) were inadequate for this recent set of changes.

Again from a community dynamics viewpoint, all trees exhibiting major desiccation damage (shown in Fig.4-8) are not 'going anywhere'. The distribution of foliage desiccation damage correlates closely with that of vegetative reproduction. Within this broad belt all species lack young juveniles. All areas where plants 'choose' or are forced to flagging above and to layering in the lower branches indicate a growth environment that is roughly marginal for the two evergreen conifers. It is the narrow fluctuations about that margin that show up as visible vegetation effects.

Much of the field evidence seems to support the idea that it is environmental extremes that are controlling this ecosystem boundary rather than the mean climatic values. For each of the conifer dominants, we are at the margins of its tolerance range of several critical environmental factors. Evidently, 'unpredictable' recurrence intervals for environmental variations are a major problem for all plants at the margins of their tolerance limits. It is suspected (though not substantiated) that, on this site, it is the *sporadic* nature of many environmental extremes that accounts for much of the regeneration failure and its spatial variation.

Role of Shrubs and Grasses: Douglass (1954) reported that on southern exposures on a Colorado ridge, *Juniperus horizontalis* "often forms very dense patches of considerable extent and excludes all other ground cover". On this site, however this shrub poses much less competition as it is only found singly. Others have reported substantial competition to conifers in heath meadows from dense sedge and grass mats (Stahelin, 1943; Langenheim, 1962; Dye & Moir, 1977). *Salix arctica*, *S. nivalis*, and the heaths are common elements in the mosaic of this site. The literature suggests that they do not inhibit seedling establishment to the degree a dense herbaceous (graminoid and forb) cover does.

In fact conifer seedling density can be strongly related to a high density of *Vaccinium scoparium* and *Phyllodoce glanduliflora* (Franklin et al., 1971:220). Saplings of *A. lasiocarpa* and *L. lyallii* coexist with clumps of heath and heather throughout the ecotone. Where graminoids have high coverage (*Festuca saximontana*, *Elymus innovatus*, *Koeleria* *cristata*, *Poa alpina* and *Carex* spp.), these community types show a negative correlation with seedlings of any conifer.

Minimal Role of Pine: A very distinctive feature of all plots is the nearly total absence of *Pinus* spp. There is no *P.contorta*, the site being well above its altitudinal range. Stahelin (1943) commented on the very slow process of coniferous "restoration" in Colorado and southern Wyoming wherever the 'pioneering role' of pine or aspen is absent.

P.albicaulis is so rare as to be almost negligible. It certainly has no functional role here as a 'pioneer' species as has been reported elsewhere. Several authors believe this species to be fire successional above the range of *P.contorta*: it is reported as a significant timberline tree in the Oregon Cascades (Price, 1971:23); Glacier Nat. Park, Montana (Habeck, 1969); Kananaskis Prov. Park, Alberta (Hawkes, 1979); and Waterton Lakes Nat. Park, Alberta (Mackenzie, 1973). Habeck suspects that *P.albicaulis* originates after fire, citing its position as the nucleus around which *Abies lasiocarpa* seedlings develop, leading eventually to "islands" of *Abies* krummholz surrounding old pine trees.

Hypothetically it seems possible that the conditions following the fire (and existing today) on this study site would have favoured *Pinus albicaulis*, had its disseminules been available. However it is rare in this region, yet elsewhere outside this region it fares well on ridges and exposed situations. (Wilcox (1916) observed: whitebark pine is "rather scarce in these mountains".) The species cannot migrate by itself since its seeds are wingless, and its seed dissemination depends on birds and abandoned squirrel caches (Price, 1971:22).

To summarize this section, these are the major factors identified which influence the establishment and performance of seedlings and layering:

1. seed source availability; cone crop limitations (viability, periodicity);
2. southwesterly exposure (wind and cold air convergence);
3. major inhibitors of seedling growth: heat, drought, excess snow depth, frost heaving, growing season length changes;
4. the varying periodicities of major environmental extremes or disturbances;
5. some degree of resistance offered by graminoids and shrubs;
6. the absence of the 'pioneering role' of pine.

By and large, combinations of these factors create the processes that are involved in reducing the effectiveness of the conifer reproductive effort in some areas and enhancing it in others.

4.4.3 Summary

Given the highly variable stress and disturbance regime on the study site, and the reproductive ecology relationships discussed above, we can summarize the field situation as a whole, and the main points of each species' status.

The upper Wenkchemna Valley contains an example of a timberline zone of marked individuality. The ecotone between subalpine forest and alpine tundra is a complex interdigitating mosaic, the components of which vary from changing rapidly to remarkably persistent and unchanging to barely maintaining their position.

The Upper Subalpine Subzone is described by Walker et al.(1978) as occurring in Banff Park from 2000-3000m (6560-9840'). However, in this valley, this subzone is lower, extending from 1930-2440m (6350-8000'), an elevation difference of 70m (230') at the lower border and 560m (1836') at the upper limit. Meanwhile, the downvalley extension of Upper Subalpine conditions is conspicuous here. Gardner (1978a:3) pointed out that although continuous forest cover exists at 2300m (7544') this is "a rather meaningless figure", as timberline is extremely variable and is found as low as 1900m (6232').

Larix lyallii is found on cool, moist sites where competition from other conifers appears to be reduced due to low temperature and snow accumulation. In other upper subalpine situations, such conditions are limited to a very narrow belt above extensive *Abies* and *Picea* -dominated forest. Usually the downward extension of *Larix* is more sharply limited by high maximum temperatures (Arno & Habeck, 1972:447).

However, in upper Wenkchemna Valley, conditions amenable to *L.lyallii* extend to lower elevations. The main factors involved are: the funnelling of winds down the valley from the western pass, the presence of Wenkchemna Glacier at a low elevation, the influence of avalanche run-out debris at the base of the lateral moraine, and seepage areas on much of the valley floor.

Thus, for this portion of the Continental Divide (51° 04' to 51° 27'), it has been stated that "the species (*L.lyallii*) is normally found in a narrow belt between 2130 and 2340m (7000 -7700')" (Arno & Habeck, 1972:425). However, *L.lyallii* and *A.lasiocarpa* were found to be co-dominate as low as 1980m (6500'). *Larix* can tolerate better than *Abies* the bogginess across a large part of the valley floor.

Within the actual study site, *L.lyallii* is capable of growth in habitats too cold and moist for *A.lasiocarpa*. An example is the lee side of the dense clump in Area A, where saplings of the former are vigorous while the latter commonly suffers fungal damage to its lower branches (compare Figs.4-6 & 4-11). A second case is the western portion of the lateral moraine (Areas B and G) where slopes are steep and avalanche-prone. Especially below the break-in-slope, *Larix* dominates and in places forms pure stands or 'parks'.

The flexible boles of *L. lyallii* show minimal damage while *A. lasiocarpa* is rare, and where present, unthrifty.

The previous sections describe, in effect, a "geography of risk" for regeneration by species. Saplings are nearly absent and small seedlings totally absent or rare over much of the site. In the main, all three conifer species are clearly not at present regenerating through seedling establishment.

The initial visual impression is that *Larix lyallii* has obvious signs of a species maintaining itself (saplings and mature trees with cones). However, although erect healthy *Larix* saplings are found at higher elevations than arborescent *Abies lasiocarpa*, *nowhere do seedlings* of *Larix* dominate over *Abies* juveniles, whether sexually or asexually reproduced. (The only exception is in Area E, east of the main ridge site.) That is to say, on this study site, regeneration of *both* species is both spatially and temporally sporadic. The two tend to be found together (though not exclusively), reflecting the greater similarities between *Abies* and *Larix* germination site requirements than between *Abies* and *Picea*.

Both *A. lasiocarpa* and *L. lyallii* show a lower number of young seedlings than saplings. *Abies* saplings are found only in Area A plots. Elsewhere the nearly total lack of seedling sized stems and a very low number of 15-60cm stems indicates that in all stands studied, *Abies* has not been regenerating recently other than by layering.

There are small patches of advanced *Larix* reproduction with abundant stems over 2.5m, smaller numbers in the 30-250cm height class, but seedling stems (<30cm) only rarely. Arno and Habeck (1972:434) report that successful *Larix* reproduction occurs at long, irregular intervals, creating small even-aged clumps or 'reproduction glades'.

If this situation were reversed; if *Abies* showed an *increasing* number of seedlings and *only* *Larix* had older stems only, then it might be inferred that 'pioneer' *Larix* has 'prepared' the site for the later invading *Abies*. However a completely different situation is demonstrated by the data. In fact, both co-dominants are establishing fewer seedlings over time. Individuals of both species seem stressed relative to an earlier point in their lifespans, and both species show declining reproductive success.

In addition, *Larix* individuals (both saplings and large trees) are commonly located to the east or leeward end of a hedge or island of *Abies*. This reflects *Larix'* need for both *light* and *moisture*, and strongly suggests it established more recently. There seem insufficient grounds on this site to ascribe a 'pioneer' status to *Larix lyallii* (contrary to its generally-assumed role, eg. Franklin and Dyrness, 1973:281). If the performance of both of these hardy species is deteriorating, there seems no reasonable basis for anticipating their *successional* replacement by other species or sets of species.

Picea engelmannii is frequently to occasionally present. Yet everywhere it has fair to poor reproductive success, and only by layering. Its juveniles and adult trees are only a minor component in these stands. *A.lasiocarpa* and *L.lyallii* remain the dominant conifers of course because there *are* no more tolerant (i.e., replacement or 'climax') tree species. It would appear that the mesoclimate at present is severe enough to effectively curtail reproduction by seedling of *any* species, even *Larix*. As long as current climatic conditions exist, it is reasonable that the present associations will persist. Certainly no *less hardy* species will inhabit sites where the hardiest tree species are faring only marginally well.

A recapitulation of germination and growth requirements will serve to spell out the largely unfavourable conditions of this south slope: all three major species do best on a cool and moist habitat. *Picea* and *Abies* prefer quite heavy shade (*Picea* 40-60%) and suffer under excessive sunlight. The germination of *Larix* increases with increasing light, but is impaired if on a dry substrate (Tranquillini, 1979:16). None of these species can withstand drought (whether summer or winter) in the seedling stage. As Höllermann (1978:381) points out, seedlings and young trees are extremely sensitive to the critical ecological factors, while mature trees are able to maintain themselves "much better".

The mean densities of these timberline species seem unlikely to change much, given the low rate of recruitment, and the mortality and poor vigour of individuals. All three conifers are experiencing poor performance and high seedling mortality due to desiccation, frost heaving and snow- and soil-wasting on this fine-grained mosaic of severe environments.

Chapter V

DISCUSSION AND CONCLUDING REMARKS

5.1 PERSISTENCE AND CHANGE IN THE ECOTONE

Based on the evidence of regeneration patterns and stand structure, no replacement community is indicated for the sampled areas. The living tree populations seem to be relatively static, indicated by variable but generally poor performance. In the upper two-thirds of the ecotone, this includes a widespread lack of reproductive success and dead or moribund trees equalling healthy ones in number.

On a few favourable regeneration sites, advanced L.lyallii glades or dense A.lasiocarpa layering clusters have established, apparently prior to 1947. Almost no juveniles have been established recently, and many apparently favourable sites are vacant. In addition, a considerable proportion of the sites range from unfavourable to very severe for regeneration.

The situation contrasts with that of the high-elevation forests in the southern Rocky Mts. in New Mexico where Dye and Moir (1977) say spruce-fir forest is 'aggressively displacing' the herb-dominated fescue community. Others have also documented a recent 'invasion' of upper subalpine meadows by conifer seedlings. On the Continental Divide in Glacier Nat. Park, Montana, 350 km or 210 mi south of this site, Habeck and Choate (1963) and Habeck (1969) suspected that treeless alpine areas at Logan Pass were "in the process of being invaded by krummholz vegetation". They think this 'may well have been' secondary succession following destruction by fire. They cited a *positive* correlation between disturbed earth (from frost heaving and/or burrowing mammals) and the natural occurrence of alpine fir and Engelmann spruce seedlings, as well as rapid expansion around the perimeters of krummholz islands. Habeck (1969:72) states that 'environmental factors seem to be well within the range for tree development', and that in the absence of fire disturbance, "*there is no reason to doubt* that a continuous forest cover, dominated by *Abies lasiocarpa*, could develop *throughout the 5,500 to 7,000 foot zone*" (1675 -2130m) (author's emphasis). On the Wenkchemna site the key question is whether the belt from 7,000' to 8,000' (2130-2440m) will regenerate, a much less likely circumstance. Trees survive in a variety of flag, flag mat, and mat krummholz forms across this wide elevational distance, but the upper limit of sexual reproduction is tellingly low.

A great deal of this ridge experiences very severe regeneration conditions. Juveniles are rarely established due to locally severe slope steepness, mass movements and rockiness, rapidly varying temperature and moisture availability regimes, and animal disturbance.

These site findings are consistent with those of Hansen Bristow (1979) for the Colorado Front Range. Within that forest-tundra ecotone no seedlings less than 15 years old were found. Hansen (1940:44) made comparable statements about a high-elevation site in the Medicine Bow range, southeast Wyoming that was burned over in 1860. *No seedlings* were found. Reforestation was progressing by the gradual enlargement of tree groups, each with an old specimen at its center. At another site in the Medicine Bow Mts., Billings (1957) reported *P. engelmannii* and *A. lasiocarpa* having extreme difficulty invading fire-origin tundra areas where once well-developed forest stood (and of which some stands remain). Due to the post-fire changes in mesoenvironment, especially unrestricted wind movement and extensive changes in snowdrift patterns, the grass and heath associations persist "indefinitely".

> Ridges are almost bare during the bitter winters, and late-melting drifts invade remaining forest patches causing death of trees and lack of reproduction. This mosaic of severe environments, coupled with inability of lodgepole pine to invade at high elevations, allows tundra species to invade downward and *to control potential forest land*. (my emphasis) Billings (1957:70).

This situation is remarkably similar to the Wenkchemna site. The author's only argument with Billings' interpretation is that it therefore seems unreasonable to see the area as being "potential forest land". This is discussed further in section 5.3.

The situation in Wenkchemna valley also appears similar to that reported by Baldwin (1977) on Mt. Monadnock, N.H. In the 150 years since fire removed the subalpine vegetation, re-invasion of vegetation had proceeded well at first, and portions of the slopes were "regained". Now, however, the lack of new seedlings, diminished growth as well as the mortality and deteriorating condition of spruce suggest that "succession" has slowed to a halt and "spruce may even be retreating from its former outpost" (1977:324).

Baldwin's interpretation shares with that of Griggs (1937, 1938) the problematic assumptions that vegetation change is somehow taking place over a uniformly- colonizable surface and under a climate uniform through time. Throughout the literature, these enticingly simple assumptions are extended to vegetation change of all kinds, not only 'recovery' following an obvious disruption. Certainly it is simplest to understand the latter case as a temporary fluctuation about some mean position of the ecosystem boundary, with the succession locally 'delayed' by topographic complexities, edaphic limitations, etc.

The problem is that such assumptions lead one always to anticipate and seek a single reference point or ground state by which to define and classify any given landscape situation. In cases where we lump together areas as part of a single vegetation zone, that may lead us to 'miss' cases in which a sufficient degree of environmental change has occurred that the system is now responding to a new ground state (Horn, 1974). Thus we may have to recognise, for instance, vegetative covers that are moving toward equilibrium with a new harsher climate. From the point of view of degree of success in regenerating to its former position, this particular timberline zone in Wenkchemna Valley is largely failing. Meanwhile, the evidence we do have suggests that in fact the whole mosaic may be in phase with the present environmental situation, involving both climatic and surface conditions.

Interesting corroboration for this hypothesis is found in Hansen Bristow's assessment of the stability of the Colorado timberline zone. Present physiological stress in the ecotone requires the trees to survive under harsher conditions than in the past when they first established at treeline. They are highly stressed and extremely unstable under present day climatic conditions (Hansen Bristow, 1981). The status of the trees in the upper two-thirds of the ecotone is perilous: if they were destroyed by fire, felling or recreational stress, the ecotone would be very unlikely to recover in its present location. It is postulated here that the Wenkchemna site upper forest was in just such a marginal situation at the time of its removal by fire.

Ergo in Hansen Bristow's terms it is now experiencing the same regeneration difficulties as the Colorado subalpine. A similar point has been made by Elliott (1979) about the Canadian subarctic treeline. Another way of putting it has been explored here, however; namely, that rather than 're-generation' of the old ecotonal situation, we have a new or different ecotonal 'equilibrium' in place or developing.

Even under consistently favourable climate, the uppermost forest is easily susceptible to some replacement by shrub-tundra (Stahelin, 1943). A widespread climatic deterioration can exacerbate these on-the-ground difficulties resulting in a more 'permanent' eradication.

At this point, however, the author would stress again that the changes in vegetation zonation are taking place in a complex context of both long and short oscillations in climate, as well as over a surface that is varied and far from uniform.

5.2 THE QUESTION OF CLIMATIC FLUCTUATION

At the same time that frost heaving and desiccation have been _selectively_ lowering the survival altitude of the subalpine species it is possible that the elevational distance between treeline and timberline has increased in response to a general climatic deterioration. Other researchers have roughly concurred on a chronology of macro-scale oscillations in climate in recent centuries.

The size and position of snags and logs lying on the surface suggests that _timberline_ was higher than the present for some time before 1870 (evidently, long enough for sexually-reproduced seedlings to grow to tall, symmetrical trees). These trees had very large diameter bases, and as annual biomass production is very slow in this environment, they are assumed to have been quite old when they fell. The lowering of timberline was initially induced by fire, but is now maintained by localised mass movements, severe variability in meso- and microclimate, and lack of seed.

Nichols (1976:42) has proposed that such failure of tree regeneration after historically-dated fires may be the result of the alpine treeline being in disequilbrium with modern climate. While it cannot be answered conclusively, the question of whether the living trees are in or out of phase with contemporary climate in the valley is raised here for discussion. Though the author lacks firm evidence of a receding treeline (i.e., an actual retraction of range), the field data seem consistent enough with comments by others on the question of regional climatic fluctuation to support this hypothesis.

For instance, the krummholz clones at the upper end of the ecotone are very old and appear to be the farthest outposts ever reached by these species. This treeline position has been maintained by vegetative reproduction through climatic changes in recent time. The preceding discussion shows it is highly unlikely that subalpine trees will seed-in the extensive balds to reach these upper trees again. In addition, many of the deformed and clustered trees on the mid- and upper slopes of this ridge appear to be relicts of a more extensive and more densely populated subalpine forest area in the past (Figure 5-1). While treeline appears to have been quite stable, it is the timberline, and most precisely, the upper limit of sexual reproduction that has fluctuated markedly with changing climatic conditions.

If in fact the inherent ability of the larch-spruce-fir forest to replace itself following natural disturbance has not been maintained or has declined, the explanation would turn upon how much climatic conditions have changed. In fact, relative to other current timberlines in the region, this pre-fire forest was remarkably high-altitude. Anywhere in the region *at present*, it is illogical to find a failure of these species to re-stock over 2200 to 2380m (7,200-7,800') as 'disappointing'. Modern authorities list the usual range of *Larix lyallii* as 1830-2130m (6,000-7,000'), *Abies lasiocarpa* from 610-2285m (2,000-7,500'), and *Picea engelmannii* as ascending to 1830m (6,000') only (Hosie, 1979; Porsild, 1979:36). How then was it possible (climatically) for upright trees to be growing at 2380m (7,800') in Wenkchemna Valley? Specifically, more than 500 years previously when these large trees established, there is widespread evidence of a period of more amenable conditions.

This is borne out by the generally-held chronologies for climatic change in this part of the Rocky Mountains. In the

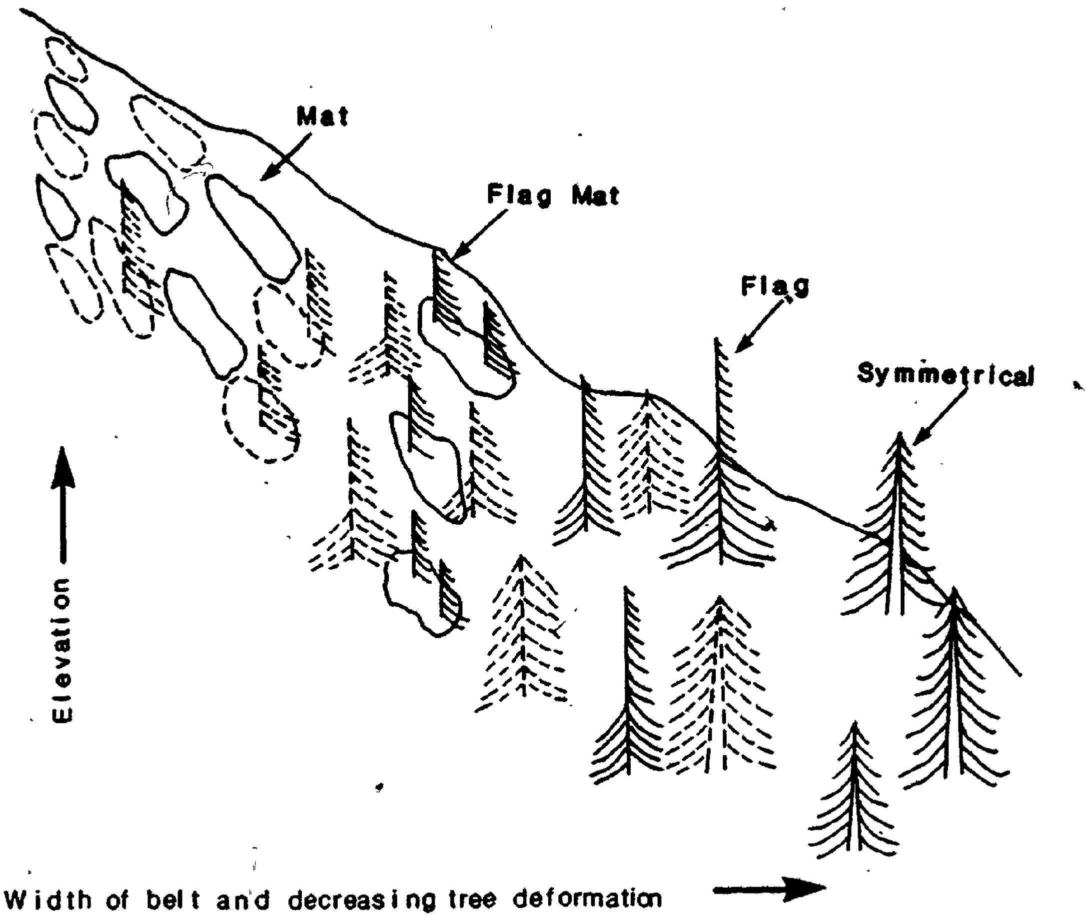

Figure 5-1: Interpretation of Remnant Tree Forms

Solid line tree forms represent present situation and broken lines represent hypothetical former situation within the forest-tundra ecotone. (Adapted from Hansen Bristow, 1981) timberline zone along Dolomite Ridge, east of Bow Lake, Heusser (1956:297) also recorded the presence of dead remnants of an early more thrifty forest where presently only smaller living trees exist. Moreover, this had occurred <u>in the absence of fire</u>. He postulated that these are remnants of an earlier period of climatic amelioration. Kearney's (1981) thesis used the increasing representation in the pollen record of arctic-alpine taxa in upper elevation sites (in Jasper Nat. Park) as evidence that

> the last c.500 years, characterized by the lowest timberlines in the record, have witnessed particularly severe climates (1981:iii).

Using glacial terminus fluctuations, tree-ring evidence and peat deposit dating, Heusser (1956) and Schulman (1953) concurred on general regional postglacial climatic changes as well as more recent trends. In general, the 15th, 16th and 17th centuries saw the onset of cooler conditions (first dry then more humid), and glacial advances continued well into the 1600's (Byrne, 1968). In the early 1700's, a lack of snowfall and higher summer temperatures initiated glacier recession. The climate has generally been dry and warm from 1775 to the 1940's, except for glacier re-advances in 1830-40 and high rainfall around 1890-1900.

Relatively dry and warm conditions from 1850 to 1940 are cited by Schulman (1953), Heusser (1956), Byrne (1968), and Gardner (1972). In this century, in general they report a general increase in mean annual temperature and a decrease in precipitation slowly and regularly until about 1920, and more rapidly until the early 1940's. Schulman's tree growth rates attest to a late 1930's drought and Luckman (1982:11) cites "the warm decades of 1930-49". In the 1940's and 50's, temperatures declined, both winter and summer, and precipitation increased. In this valley, Gardner (1977) reports that Wenkchemna Glacier was still advancing into the valley floor forest until as recently as 1954, but is now receding.

At the central Keewatin and Labrador treelines, the general absence of new juvenile trees in the forest-tundra ecotone corresponds to the gradual cooling since the 1940's (Elliott, 1979:249). Schulman's growth rate curves of trees near Banff also reflect this general cooling. The Lake Louise townsite records indicate a 1-2°C decline in mean annual temperatures from 1945 to 1955, followed by a 1-2°C rise in temperature from 1955 to the mid-1960's and a decrease in precipitation (Gardner, 1972, 1978a; Luckman, 1982:4). Another decline in temperature has occurred from the mid-1960's to 1980.

From a vegetation stability point of view, the <u>duration</u> of fluctuations is important. Slow-growing subalpine vegetation "accommodates" to climatic fluctuation as does vegetation everywhere but its response has a lengthy lag period (Brink, 1959:15). To some extent, one would not be surprised that this valley exhibits vegetational inertia in the face of these environmental changes. To support this statement, growth-rate changes in 60 trees over Wenkchemna and Consolation Valleys failed to show significant correlations with climatic change (Gardner, 1981:pers. comm.).

The record given above of variations in modern temperatures and precipitation suggests that both 10-20 year fluctuations as well as single extreme years have occurred. As discussed earlier, conifer seed germination and seedling establishment requires consistently warm summers. Kearney (1981:iii) demonstrated that seedling establishment at timberline is significantly correlated with higher than average mean minimum summer temperatures. Some of the post-fire reproduction was probably established in the mild period prior to 1945. Perhaps some occurred in the late 50's and early 60's, but it is not detected on air photos from 1947 to 1978. In the absence of dendrochronological data, these statements cannot be verified, only inferred.

Elliott (1979:166) reports that for all Canada, temperatures in the 1970's have been even more variable than in the previous two to three decades. The consistently warm summers needed haven't occurred in that period. As suggested in the earlier reproductive ecology discussion, the probabilities for conifer establishment depend not just on temperature but on moisture availability and perhaps snow depth changes. A reduction in seedling years is more complicated than just increased cold.

An illustration of this is the widely-reported tree invasion of subalpine meadows that occurred approximately 1925 to 1940 in the Washington and Oregon Cascades (Franklin & Mitchell, 1967), the Olympic Mts. (Fonda & Bliss, 1969; Kuramoto & Bliss, 1970), and the B.C. Coastal Mountains (Brink, 1959, 1964). These are high snowfall areas, and the seedling establishment generally took place in years of decreased snowload and therefore a longer than average growing period. The directional change occurred on sites both with and without fire evidence, but basically ceased after 1945 (Franklin et al., 1971). Although the latter date corresponds to the cessation of juvenile establishment on the Wenkchemna site, the exact mechanism for this enhancement of regeneration was likely different. Because further inland on the Continental Divide, more extreme temperature and dryness factors prevail, therefore, a host of factors such as protection from radiation (eg., increased cloudiness) and extended water supply would come into play.

The question of climatic fluctuation, both long and short-term, is complex and beyond the scope of this paper to answer thoroughly. Wardle (1974) believes that the kind of anomalous population structure recorded here (i.e., with the numbers of old and moribund trees exceeding the young and healthy) can indicate significant climatic change if considered along with ineffective regeneration and fluctuations within the lifespan of existing trees. Without doubt, the uppermost living trees, which pre-date the fire, were established well above what is currently possible. However, the more powerful tools available in palynology, dendrochronology and macrofossil analyses are required to characterize this climatic change in more detail. A future study is planned to examine more precisely this issue of synchrony between modern vegetation and modern climate.

5.3 PROBLEMS WITH THE CLASSICAL SUCCESSION INTERPRETATION

In this field situation, the conventional secondary succession paradigm would 'expect' a general revegetation sequence, eventually returning to a full forest cover, albeit over very long time periods if necessary. However, none of the criteria for such a directional sequence are being met at present. Under that scheme, a mixed meadow-parkland that is seral to full forest cover would show widespread and abundant seedling establishment. There would be occupation of all available regeneration sites by juveniles, and an upslope migration of subalpine understory species.

In fact, nearly the opposite situation is indicated by the field evidence. We have a downward extension of alpine indicator species and scarce and localised juvenile establishment, none of it recent. There is no convincing evidence that heath meadows are retreating before forest encroachment. Forest recovery was not to be found. Therefore in a sense, it is misleading to *look* for it, anticipating a directional advance.

As a whole, the ecotone is not "succeeding". The evidence implies more a mosaic persisting in such a way that its present structure and appearance *are* the new equilibrium state. It has been shown that a complex of many factors contribute to the origin and maintenance of the fragmented mosaic pattern: it is not so simple a matter of 'not enough time having elapsed'. *In toto* the site conditions and disturbance relations contribute to an "inertia" in the configuration (and elevation) of the ecotone (term: Davis, 1977:213). The communities examined do not show evidence of passing through a sequence of successional states that converge on a single climax community. If anything, further fragmentation of the mosaic into an even finer-grained pattern is indicated as plants and plant groups continue to respond differentially to site conditions.

It must be underscored that the present 'steady-state' condition of the ecotone is more a property of the entire mosaic than of any single constituent vegetation unit. For example, in any one patch the amount of biomass or cover may increase, while on a patch immediately adjoining, fungal or desiccation damage inhibits biomass production or actually destroys existing biomass. Significantly, most changes in vegetation seem only to involve phases where the species' *performance* fluctuates *as* "*distinct from* cycles in which the actual species change in a recognizable sequence" (Kershaw, 1973:162) (author's emphasis). Little compositional change is indicated by the data and thus a main criterion of succession is not met.

Del Moral (1979:1124) interpreted a subalpine basin in the Wenatchee Mts., Washington as a severe environment in which 'succession' consists of little compositional change and the 'pioneers' may persist in stable vegetation. In a similar way, the Wenkchemna site could be labelled a mosaic of 'seral' and 'climax' stands or stages and that the whole thing is in "a gradual process of development" (Del Moral (1979:1113). But the question recurs: is our understanding of these features actually aided much by such explanations? (Wiens, 1976:91). We can continue to speak of vegetation's status in these traditional terms, but we should query the usefulness of referring as 'pioneer' to vegetation that shows signs of being well- adapted to regional and site conditions, that is apparently in balance with the environmental mosaic that is presently found.

Franklin and Dyrness (1973:264) have pointed out that many subalpine ecologists, foresters and range managers work with the presupposition that subalpine parkland is potentially forested habitat, i.e., the climatic climax vegetation is (spruce-fir) forest. "Consequently, most hypothesized successional sequences lead toward forest, and in the Clementsian sense, all meadows are seral to forest".

This "thinking scheme" (Mueller-Dombois & Ellenberg, 1974:410) is extremely pervasive-- this author believes, too much so (see Billings, 1957; Klikoff, 1965; Price, 1971; et al.) Under situations of regional climatic change, it may no longer be 'inevitable' that heath meadows are *potential* sites for forest. Upper krummholz trees and even high-altitude *erect* trees below them may be, to some degree, historical outliers or relicts that are now *out* of equilibrium with regional climate. Thinking in timberline ecology and its fluctuations should be flexible enough to concede that this is just as possible on burn as non-burn sites.

This serves to illustrate a very central problem with the classical paradigm: its assumption of a constant climate and a stable physical environment. Franklin and Dyrness (1973:280) for instance propose a general successional sequence in tree clump development (at Oregon and Washington timberlines) as the pattern expanding tree groups "should follow", "given sufficient time for tree clump development and a constant climate". The point is the system hasn't got these: it does *not* have long time periods with a uniform climate. The upper subalpine is a highly variable environment that not only varies widely and frequently, but both the rate and amplitude of these variabilities *vary*. Similarly, Hansen (1940:446) aims to predict what the future conifer cover in a southern Wyoming subalpine belt will be "if the normal forest succession is not interrupted".

This underlying assumption of normality in an unchanging climate and the 'desirability' of an uninterrupted developmental sequence has long been criticized. Field reports from various ecosystems show these assumptions to be largely untenable (Drury & Nisbet, 1973; White, 1979). There is considerable case evidence that many vegetation aggregations are surviving and responding to environments that are <u>characteristically</u> unstable such that the basic assumption of stable physical environments is usually of no use. Therefore expectations of succession and climax are going to be thwarted (Raup, 1957). Raup maintains that such aspects of classical succession theory have actually hindered accurate understanding of how plant communities are created, and how they persist by <u>adjusting</u> to the instability of site. The entrenched viewpoint focussed on identifying to what degree plant associations matched (or failed to match) 'known' steps in a theoretical replacement sequence. Meanwhile, except for individual plant physiology, remarkably little is known about vegetational responses to environmental <u>fluctuation</u> -for example, the adaptive traits exhibited by species or communities which successfully adjust and persist through <u>changing</u> disturbance periodicities.

This is by no means the first report to register some complaint with the conventional succession paradigm and the Clementsian school of vegetation interpretation. Those using it with insight early recognised its limitation. Yet its usefulness as a place to begin, to begin to handle the complexity in the field, was treated as the best available (see Cooper, 1926). Its main terms were avidly adopted, and not all researchers remembered to hold its main concepts 'at arm's length' as simply a guide. They yielded too easily and uncritically to the scientific need to classify and thereby "control" the multiplicity of the vegetated landscape.

If one examines the original meanings of these terms carefully (Clements, 1916, 1936, 1949) one would label the Wenkchemna ecotone a polyclimax landscape, with immediately adjacent portions of the ecotone as disclimax, subclimax, preclimax and postclimax at the same time! There is no intrinsic error in the scheme [Clements explains that these units or consociations are necessarily fragmentary, each on the "proper situation" (1949:149)], but it quickly becomes unwieldy and can be misleading. There are very valid reasons why each of these ('inferior') patches doesn't support full spruce-fir forest. One must then ask why, if they are never going to support the climatic climax because of other environmental 'limiting factors' they must be tenaciously referenced to that hypothetical climax? Assurances to the effect of 'If undisturbed, the climax will be attained in n hundred years' may be an interesting academic exercise. They are extremely limited in interpreting ecologically the actual situation on the ground. At a time-scale comprehensible and useful to humans, as well as a level of spatial detail that is informative, useful, but most of all, responsive to the evidence on the ground, such assurances are highly artificial.

A widely-adopted approach in the secondary succession literature has been to use spatial variations in vegetation of different ages to infer a time sequence. But how valid is this historical tendency to interpret all spatial distributions of plant populations automatically as chronosequences? From a biogeographer's viewpoint it creates another major problem in the 'developmental' scheme of vegetation dynamics- that it tends to interpret the 'patches' of a spatial pattern necessarily as stages of temporal change. In this, of course, it is identical to the Davisian and other schemes for landform evolution which have caused similar problems in Geomorphology.

Most successional schemes have been intuitively determined from observations on adjacent plots of different successional ages, zoned in obvious bands such as the concentric rings of vegetation around the edges of an infilling bog (Barbour et al., 1980:214). In many other cases, however, the sites of apparently different ages are randomly scattered throughout a region, and their age sequence is assumed. It is assumed that the 'older' vegetation plots had all progressed through seral stages still present on the 'younger' plots.

Clearly, problems arise with this strategy because there will always be some degree of spatial variation unrelated to time (Kellman, 1970:193). More specifically, adjacent components in the complex timberline mosaic may not be related to each other temporally or sequentially in any way. To assume that all patches will pass through similar stages at all, or even slowly may be faulty, for it infers rather than documents precisely responses to site at the specific or population level. The strictly time-sequence interpretation assumes that established conifers are found on some units or patches, therefore will eventually be found on neighbouring patches (mesic forb and heath meadows), and given enough time, on all microsites (the balds, fellfields and dry *Carex* heaths). Perhaps this scenario is more aesthetically pleasing than the patchiness which is likely to persist- but it is remarkably inaccurate.

More accurately, the mosaic reflects periodic, local disturbance, such as fire severity and mass wasting and very specific topographic differences in soil quality or moisture-retaining capacity. For this reason, the "thinking scheme" must be expanded. To some extent, these patches represent different stages of recovery from disturbances to the matrix, and the mosaic expresses some successional relationships between meadow and conifer cover. However, communities must also be seen as responding to a localized environment that fluctuates randomly (for example, a south vs. north microslope aspect). In this sense, the patches or stands do not bear any successional or sequential relationship to each other.

Drury and Nisbet (1971:60) have warned against the use of even a "weaker" sense of <u>succession</u> because succession is still linked (necessarily) to the <u>climax</u> concept-- "each is unintelligible without the assumption of the other". Because of the unusual variety of disturbance and the intricate and persistent mosaic quality characterizing the <u>Larix</u> timberline zones which they studied, Arno and Habeck (1972:420) concluded that the upper subalpine "seem(s) to defy application of traditional succession-climax concepts".

Whittaker and Levin (1977:117-8) point out that

> Time has dealt unkindly with generalizations about succession...Drury and Nisbet (1973) show how, under further observation, the generalities of succession become raveled into increasing numbers of exceptions and divergent complications.

It is by no means the intent of this discussion to deny that succession (a cumulative, temporal sequence of species replacements) is a very real form of vegetation change. On the other hand, as Barbour et al. (1980:211) have commented, in interpreting complex mosaic patterns in vegetation,

> some ecologists have attempted to fit toposequences into successional schemes, but the results stretch the definition of succession too far and can be misleading.

The essential problem with conventional succession and climax ideas is that they <u>conceptually</u> limit the investigation of vegetation dynamics to the delineating of developmental stages and focus on the future 'attainment' of the 'normal' 'mature' formation. As Wiens (1976:90) states:

> We must thus exercise some restraint in embracing optimality based theories... and should not con-

> sider Nature to be remiss if the theoretical optimum is not the normal state of affairs.

It seems reasonable and beneficial to heed the counsel of P.S. White (1979:283):

> If the climax concept is used it must be referenced to specific environmental situations, including natural disturbance regime and other dynamic properties.

A recent review by O.L. Smith (1980:1) sums up this problem well:

> While much can be learned from the relative simplicity of purely temporal models, the spatial variable is often important, if not critical, to realistic assessment of system stability.

It is very difficult to look closely at succession and climax concepts as they apply in subalpine dynamics (and elsewhere) without at some point addressing the very notion of stability.

Stability is a much-investigated dimension or descriptor in community ecology, but considerable confusion arises from the differing conceptual and semantic uses of the term. "Stability" is used variously as a latent or potential characteristic of a system *as yet undisturbed*, and as a descriptor of a system *which has been disturbed* and is 'recovering'. Thus, some uses of *stability* do not include the system's actual resistance to disturbance (i.e., its 'propensity' to be seriously perturbed), but focus on various 'recuperating' stages as being unstable. For instance, LaRoi, Lee & Tande's interpretation (1975) is unsatisfactory: they simply equate *stability* with *rapidity of successional* change. That is to say, stability is seen more as a measure of the amount of change (i.e., repair-response) the communities are presently experiencing, with no mention of their vulnerability to disruption initially.

The stability-diversity controversy is a long-standing and complex one and cannot be addressed here. The problems with defining and assessing vegetation stability have been treated in detail elsewhere (see Whittaker, 1979; Barbour et al.,1980). The concept is raised simply to show that understanding of many community properties such as stability is still quite primitive and demands further inquiry.

Of direct interest to this site is empirical support from evolutionary ecology and theoretical population biology suggesting that fine-grained spatial heterogeneity in environment and vegetation may in fact enhance stability (Holling, 1973; May, 1973; Steele, 1974; Wiens, 1976). Niche availability is enhanced in patchy environments, creating greater diversity which in turn can reduce the 'fragility' of the system. The resiliency of vegetation is one aspect of stability that deserves more consideration in the geographic literature on ecotone fluctuations.

Specifically in relation to the upper subalpine, many useful questions remain to be asked and solved. For example, exactly how do some species respond more successfully than others to integrate change and major disruptions? Is the notion of 'success' or 'optimization' by populations and communities simply our judgment of what would be 'optimal'? We may come to understand that judgments such as environmental "severity" and "unstable zones" have less validity than traditionally assumed. We may come to understand that compared to adjoining habitats, ecotones are in some ways more stable ecosystems that can better tolerate stress factors. Clearly a more detailed inquiry into this problem area is beyond the scope of the present paper.

5.4 ALTERNATIVE PARADIGMS

Because of these important problems in the very basis of the conventional "engine of analysis" (Raup, 1964:22), alternative interpretive schemes have arisen. Several authors are questioning the utility of the Clementsian concept of climax under severe recurrent fire and disturbance conditions (Heinselman, 1973; Denslow, 1980). Others are extending this inquiry to systems across the whole range of disturbance frequencies and severities (Drury & Nisbet, 1973; Cattelino et al., 1979; Bormann & Likens, 1979; White, 1979). These authors found the strictly developmenal scheme of limited use and state the pressing need to formulate a more "kinetic" scheme of vegetation dynamics, one in which fluctuation and disturbance are recognized and incorporated as a major influence on community composition, structure and spacing (Vitousek & Reiners, 1975; Sprugel, 1976; Reiners & Lang, 1979; and Veblen et al., 1980).

It is important to stress that this line of thought is concerned with enhancing the value of dynamic ecology research and with advancing our understanding, not with discarding the entire extant system. Early on, Cooper (1926:412) was cautioning against the unquestioning use of "concepts and terms which clearly tend toward rigidity", and urged carefulness and some 'fluency' in their use.

The very foundations of dynamic vegetation ecology recognized the universality of change (Warming, 1896, 1909)-- the perennial problems have centered on the more subjective and arbitrary classifications that were erected over this foundation (Cooper, 1926; Gleason, 1926; Whittaker, 1953). Like P.S.White, this author quarrels with the basic artificiality introduced into our perceptions by the dichotomous classification of such concepts as seral or pioneer and climax; regressive and progressive successions; autogenesis and allogenesis. For instance, concerning this latter, the simple procedure of attributing certain phenomena solely to "internal" and others to "external" causes is inaccurate (Cooper, 1926:397) for events concerned with the organism or its environment necessarily involve both.

Even with Watt's (1947) terminology the split between regenerative and degenerative phases can be deceptively simple. However, because it stressed the equal importance of both types of 'phases', his pattern and process thesis began to lay the groundwork for understanding dimensions of vegetation change with less rigid concepts than the Cowles-Clements school of thought. As the field matures, others agree that the classical model deals incompletely with many aspects of vegetation change. There has been increasing concern that the classificatory 'mind-set' and methods does damage to the facts of ecological complexity. [As Slobodkin (1974) reminds us, "the ecological world is a sloppy place".]

Whittaker and Levin (1977:136) urge researchers to recognize the nearly universal occurrence of "internal patterns, mosaics and related phenomena in natural communities". They stress that

> Ecological theory is not precluded by, but should make realistic allowance for, the intrinsic diversity of ecological phenomena.

In a similar vein, Wiens (1976:81) comments:

> The maturation of both theory and practice in population biology... demands broader consideration of the sources of environmental heterogeneity and the dimensions of population responses to this patchiness.

Hence, there is a concerted voice in the literature relevant to biogeography that is demonstrating that the longstanding utter dependence on the Clementsian model of succession and climax (and its variations) should be examined, relaxed, and its unrealistic aspects abandoned.

As Wreford Watson (1982:395) points out, geographers' work is involved not only in the explanation of earth-surface phenomena, but "in explanation itself". The geographer [redacted] [redacted] [redacted]

who is investigating the manifestations of ecosystemic changes on the landscape cannot but delve into these ongoing issues in theoretical community and population ecology. In this study as in others, geographical or spatial considerations in the analysis of environment and plant community seem to show up the limitation of the Clementsian scheme, or to be greatly weakened by its application.

According to the classical secondary succession paradigm, the ecotone of the Wenkchemna site (given its history, its nature and its configuration) would be interpreted as a subclimax, a seral stage that exhibits 'extremely slow succession'. It is 'stalled' indefinitely in many places, 'on its way' to the eventual recloaking of the moraine with a spruce-fir climax (the climatic climax of the region for this altitude).

The several problems with this explanation of the vegetation mosaic have been alluded to in preceding chapters (eg., the 'seral' species are the climax dominants as well; the high proportion of larch not spruce as dominant; and a recurrence interval of many stresses and disturbances shorter than the time 'required' for a 'unit succession' to reach its 'end-goal').

Rather than label it easily as a subclimax, or a 'failed' secondary succession, this thesis has attempted an alternative interpretation of the field situation on this site. It is based in the broadest sense on the premise that vegetational change is due to the interaction of changing organisms and changing environment. The type of Kinetic Scheme referred to by Veblen and others is not drastic in its important changes, but subtly improves the accuracy of landscape interpretation.

We have a patchy distribution of individuals and of species, and this patchiness is revealed in a wide spectrum of spatial scales. To a large extent, this patchiness persists. The bulk of the preceding discussion has suggested the processes (both major and minor) affecting this environmental and vegetational patchiness. "We have, in fact, habitat variations in space as in time" (Watts, 1947:17).

Particularly in understanding how and why the components of the mosaic exist, regeneration effects are the pivotal link between disturbances and vegetation pattern. The kinds of disturbance vectors examined in detail in Chapters 4.2 and 4.3, and the differential responses of young and mature conifers to them, reveal that, in fact, the vegetative cover is likely not 'out of synch' with environment at all. Indeed it lacks homogeneity, but there is nothing 'improper' (Clements, 1949) about this pattern. When the actual texture of the vegetation cover is examined, it makes sense with both regional and mesosite conditions. (There is no evidence that it is 'on its way' to something else (i.e., more 'mature').)

It was hypothesized at the outset that the combination of site conditions and disturbance relations limit the rate and direction of the revegetation sequence. In fact, they limit revegetation so effectively that the notion of a 'sequence' proceeding in a 'direction' becomes inappropriate.

It was a basic objective of this research to examine the nature of a particular forest-tundra ecotone and the factors responsible for its position and varied character. It emerged that it is desirable to interpret the fragmented timberline pattern more accurately than is possible within the developmental scheme of vegetation change.

In general, the results support the conclusion that individuals of the conifer populations are maturing, but in the main are not reproducing adequately to be considered significant evidence of a directional change. Recurrent disturbance (i.e., plant tissue destruction caused by environmental extremes) and its related effects on reproductive behaviour is significantly responsible for both the dominance structure and the patterns of the vegetation complex on this site.

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