Forest Dynamics In A Forest-Tundra Ecotone, Medicine Bow Mountains, Wyoming

by

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A dissertation submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy

University of Washington

1993

Approved by ____
(Chairperson of Supervisory Committee)

Program authorized to offer degree: .
College of Forest Resources, Division of Ecosystem Science and Conservation

Date____

Signature________________________

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University of Washington

Abstract

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The alpine timberline in much of western North America is characterized by a structurally complex transition from subalpine forest to alpine tundra, the forest-tundra ecotone. Trees within the ecotone are typically arrayed across the landscape within clumps or "ribbon forests," elongated strips oriented perpendicular to the prevailing winds. This study describes the structure and reconstructs the development of two study plots, one containing ribbon forest and the other, tree clumps. These data are used to develop a theory of ribbon forest origin and development. The plots are located within a forest-tundra area dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*).

At the clump plot, most trees have established by layering. Consequently, clumps typically contain one species (spruce or fir). All clumps contain trees that consist of a flagged leader growing above a krummholz mat. Evidence from a regional tree-ring database suggests that an episode of new clump establishment and leader release between 1850 and 1925 occurred in response to a period of relatively warm summers. Presently, patterns of snow accumulation and seedling establishment suggest that microsites covered by < 1 m of snow are too dry, and microsites with > 1.5 m of snow are too wet, for successful seedling establishment.

The ribbon plot is dominated by spruce, most of which established from seed. The forest also contains clumps of fir, which established primarily by layering. Before 1750, the forest apparently consisted of discrete tree clumps. Many of the oldest trees display relict krummholz growth form features suggesting that they experienced an environment similar to that now found at the clump plot. These trees show an abrupt increase in radial growth beginning ca. 1750 and from this time until about 1830 widespread seedling establishment occurred, with many trees establishing several meters from their nearest neighbor. This

process did not coincide with any recorded amelioration of climate, but probably was a period when the ribbon trees had grown sufficiently large and numerous to trap snowdrifts at least 1 m deep, providing optimum soil moisture conditions for seedling establishment. Since 1830 seedling establishment has been biased towards the windward edge of the ribbon, indicating that when snow depths were too deep for seedling establishment within the forest, establishment was still possible at the drier and sunnier windward edge of the forest. Presently, deep snows both within and adjoining the forest largely preclude seedling establishment.

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ACKNOWLEDGEMENTS

I have received considerable guidance and assistance in what has become a rather epic voyage through the field and theory of the timberline. Interviews with Drs. Jim Agee, Steve Arno, Estella Leopold, Jerry Franklin, Jan Henderson, Tom Hinckley, Mark Huff, and Will Moir introduced me to much of the relevant literature and guided me to memorable field sites scattered across western North America. Conversations with Will Moir and W.D. Billings greatly enriched my understanding of the Medicine Bow Mountains in general and aspects of seedling establishment and ribbon forest development in particular. I received logistic support and much friendly encouragement in this work from many personnel associated with the Glacier Lakes Ecosystem Experiments Site, most notably Doug Fox, Frank Vertucci and Mark Conrad. Erin Moore provided invaluable assistance with the fieldwork. Both the statistical analyses and the quality of the writing were improved greatly by the advice of Dr. David Ford. Finally and most notably I must thank my major advisor, Dr. Linda Brubaker. Linda helped me with every aspect of this project from formulation of the problem to finalizing the dissertation and kept me employed in various engaging paleoecological studies through most of the endeavor. She has taught me things about the practice of science that I will never forget.

Transitions from one sort of vegetation to another -- tension zones they have been called -- are places of unusual interest to botanists. For along these lines, if they be in fact under tension from the struggles of diverse plants for ascendancy, are afforded our best opportunities for unravelling the complex of factors which condition the success of the types concerned. Sometimes such vegetation lines... are evidently due to transitions in physical or climatic conditions, each type of vegetation being clearly restricted to the habitat suitable to its own growth. In other cases the cause of the change in vegetation is not so readily apparent. Some of these obscure transitions are due to less obvious physical factors which may be made out by study or experiment. Others, conceivably at least, might represent actually moving migration fronts in no way related to physical factors. It was an attempt to gain an understanding of one of these more obscure boundaries that led to the present paper.

Robert F. Griggs (1934)

Chapter 1. INTRODUCTION

The cold timberline, marking the limit of forest growth at high altitudes or latitudes, has long been recognized as a distinctively harsh physical environment (Griggs 1937; Mills 1920; Muir 1894). It is widely supposed that timberline constitutes a relatively simple ecotone where a single limiting factor, temperature, is of paramount importance (Tranquillini 1979; Wardle 1974). In practice, timberline is often far more complex than this simple description suggests. Seldom a “line,” it typically represents a transition zone across which forests grade into tundra ecosystems. In mountain ranges this transition may happen within the space of a few hundred meters, but at some alpine and most arctic timberlines the transition occurs across a span of kilometers, often called the forest-tundra ecotone (Ives and Hansen-Bristow 1983). Within this ecotone, a variety of physical factors besides low temperature may constrain the precise location and structure of timberline. These include topography, substrate, the quantity and distribution of snow, and wind. Trees within the forest-tundra ecotone show a species-specific or autecological response to these physical factors. The individual tree may display growth form adaptations (*e.g.*, krummholz), reproductive adaptations (*e.g.*, reproduction by layering rather than seed), and ecophysiological adaptations (*e.g.*, tolerance of low temperatures). Tree populations are affected by the physical environment in ways that are both demographic (changes in establishment and mortality rates) and structural (*e.g.*, the formation of tree clumps). Besides this autecological response, both the tree populations and the forest community are affected by disturbance, which may vary in type, frequency, and intensity across the forest-tundra ecotone. Finally, the structure of a timberline forest may in turn afftect physical conditions on the site by altering patterns of wind and snow deposition. This association between physical factors, autecological responses, forest structure, and disturbance is diagrammed in Figure 1.1.

Many authors have described the importance of snow in the forest-tundra ecotone (*e.g.*, Arno and Hammerly 1984; Brooke *et al.* 1970; Franklin and Dyrness 1988; Peet 1988). In areas with especially heavy snowfall, such as the Pacific Northwest, the trees near timberline typically grow in clumps scattered across the landscape. Tree establishment between the clumps is hindered by deep snowdrifts that persist into the brief growing season, while earlier melt-out adjacent to the clumps permits occasional seedling establishment in these marginal sites (Brooke *et al.* 1970). One of the most dramatic examples of this kind of forest-snow interaction was described from the spruce-fir forests of the Medicine Bow Mountains of Wyoming by W.D. Billings (1969). The Medicine Bows have many square kilometers of nearly flat terrain supporting forest-tundra vegetation in which narrow stringers of trees, typically 25 to 50 m wide and 150 to 300 m long, are aligned perpendicular to the strong prevailing westerly winds (Figure 1.2). From the air, these stringers resemble the snow fences that dot the Wyoming plains, and in fact, they have very similar effects. As with the snow fences, deep snowdrifts 50 to 100 m wide accumulate in the meadows between the ribbon forests. These snowdrifts typically persist well into the growing season, effectively preventing seedling establishment in the underlying meadow (Billings 1969). In front of the windward edge of the ribbon, or where the winter winds scour snow away from each end of the ribbon, seedlings establish successfully, perpetuating or extending the ribbon (Billings 1969).

Billings' pioneer study described the existence of these unusual forests and proposed a theory about their initiation and growth. He suggested that ribbons would "spread laterally by seedlings and also vegetatively" and that persistent snowdrifts would "provide ideal moisture conditions for seedling establishment" in areas that melted free by early July, while "the part of the drift melting later than mid-July favors the moist or wet meadow vegetation of a snow glade." Billings did not confirm these hypotheses, and although later work has helped to clarify our understanding of the distribution and

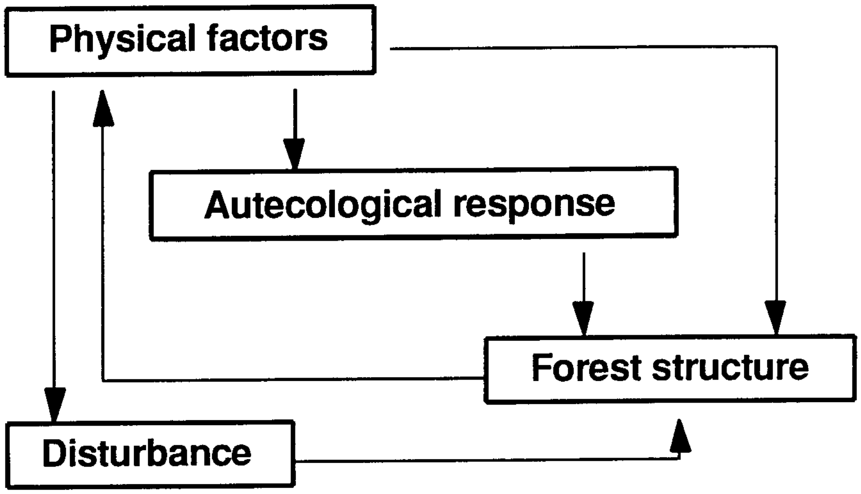

Figure 1.1. Diagram of causal relationships between major elements of the timberline environment at a given site. Arrows point in the direction of a presumed causal relationship. Note that forest structure can cause a change in the physical environment at a site.

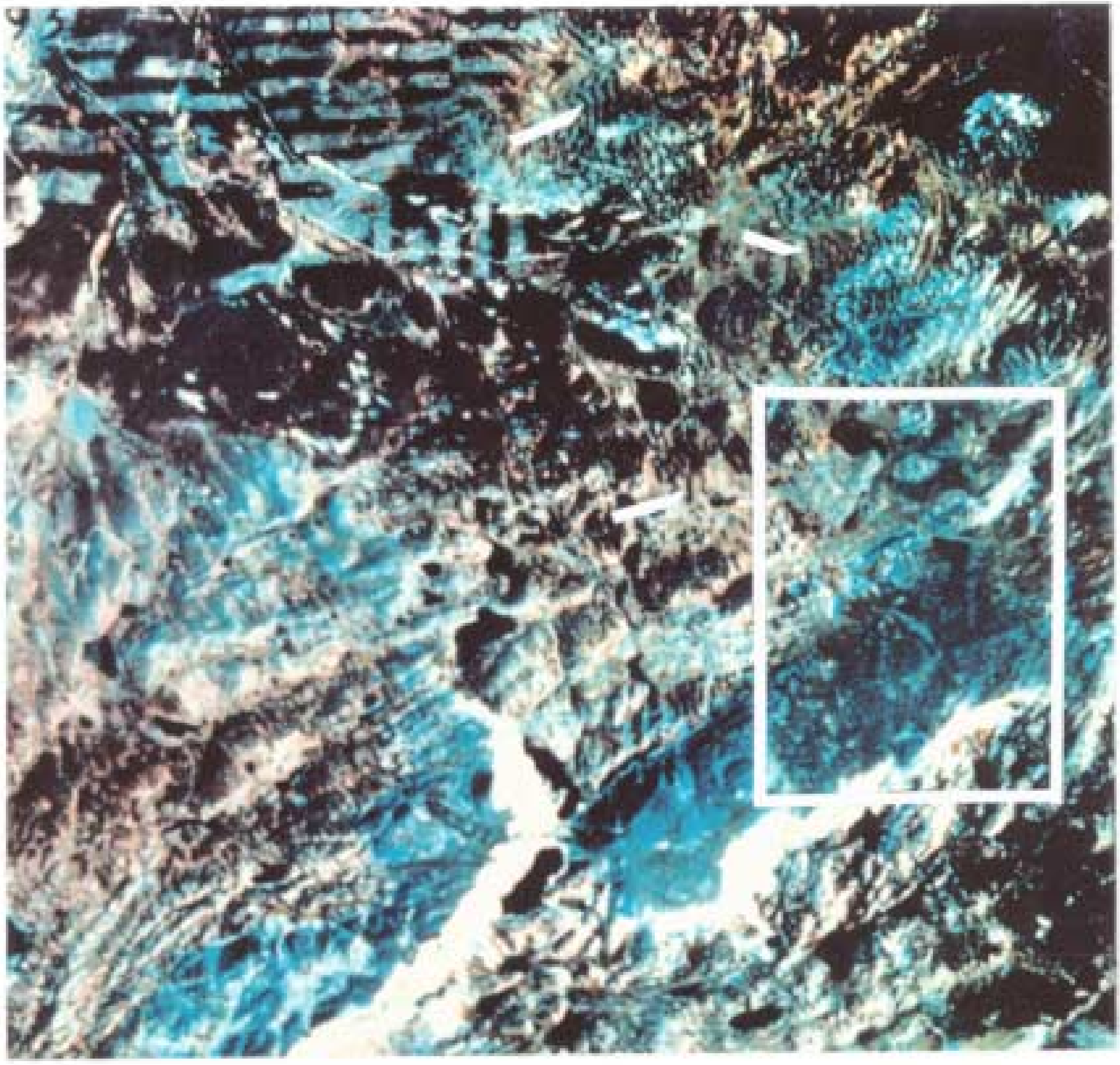

Figure 1.2. Satellite image of the Medicine Bow Mountains, 17 September 1981. White rectangle encloses the study area. White pointers indicate selected ribbon forests, which appear as dark lines ca. 0.5 to 1 mm wide and 3 to 5 mm long north and west of the study area and in the lower left portion of the image (the rectilinear bands at upper left are clearcuts). The Snowy Range cuts across the lower third of the image.

structure of ribbon forests (Buckner 1977; Holtmeier 1987), little is known of their initiation and growth. Many ribbon forests occur near areas of tree clumps. Small ribbon forests resemble tree clumps in the asymmetry of growth and establishment between windward and leeward edges of the clump/ribbon. These observations apply both in the Medicine Bows and at the sites studied by Buckner; indeed, many "ribbons" on Buckner's site are no longer than they are wide, and could fairly be called clumps (Buckner 1977, Figure 1). Tree clumps and ribbon forests may then represent successive stages of forest development. The idea that ribbon forests may develop from tree clumps has not previously been proposed, nor has it been tested by a study of the similarities and differences in seedling establishment near clumps and ribbons. No published ribbon forest study presents an attempt to trace the actual changes within a single ribbon forest across the period of its development. In this study, I present evidence that tree clumps developed into a ribbon forests at a site in the Medicine Bow Mountains. I also offer a mechanism for this development, derived largely by observing how tree clumps and ribbons affect local patterns of snow accumulation and by reconstructing the development of the modern forest at representative clump and ribbon forest plots.

The study focuses on the interactions of physical factors and ecological processes in the development of tree clumps and ribbon forest. This is done by describing the present forest-tundra environment and reconstructing past changes in the extent and structure of the forest. This reconstruction is achieved with four different methodological approaches, each of which answers specific questions and contributes to an overall description of ribbon forest development:

1. *Modern environment.* Surveys of nonarboreal vegetation and snow accumulation patterns are used to infer variations in soil moisture, an important determinant of seedling survival. Winter and summer photography of trees partly buried by winter snow are used to demonstrate how snow accumulation pattern controls tree growth form. In this way, modern snow and vegetation patterns are causally linked to phenomena that can be reconstructed: patterns of tree establishment and tree growth form.

2. *Forest development.* Changes in forest structure over time are reconstructed by mapping tree locations and determining the date of establishment of nearly every tree present in a section of ribbon forest and an area of tree clumps. This tree census also

permits me to estimate whether each tree established from seed or by layering. This distinction is important to an understanding of the factors influencing tree establishment and also explains much variation in the spatial pattern of establishment.

3. *Growth form.* Transitions from a krummholz to an erect growth form were dated by dendrochronological methods. These dates were used to determine whether growth form changes coincided with changes in rate or spatial pattern of tree establishment, changes in forest structure, or changes in climate or disturbance regime.

4. *Climate and disturbance history.* The study plots were chosen to exclude disturbance by fire, but have been subject to climate change and to varying levels of livestock grazing. The influence of grazing was assessed by comparing tree establishment records with historical records of livestock grazing in the study area. The influence of climate variation was assessed by examining the statistical associations between dates of tree establishment, instrumental records of climate variation, and tree-ring widths. Variations in past climate and grazing history were examined to assess the effect of such changes on clump and ribbon development.

The results of these investigations are integrated to provide a conceptual model of the inception and development of both tree clump and ribbon forest areas in the Medicine Bow Mountains. The interaction between snow accumulation and forest structure is shown to constrain the growth form of mature trees and the spatial pattern of seedling establishment. These constraints substantially limit the development of both tree clumps and forest ribbons. However, other factors in the physical environment can strongly affect the rate of this development and the timing of developmental stages. These factors include climate variation and disturbance events. Clump and ribbon development is also controlled in part by an autecological property, variation in the mode of establishment (by layering or from seed). Such variation causes the two dominant tree species to show differing responses to environmental variation. In this way, the development of tree clumps and ribbons can be shown to be driven both by external forcing factors such as climate and disturbance and by internal factors reflecting autecological and structural constraints.

Chapter 2. OBJECTIVES

This study was undertaken to better understand the development of tree clumps and ribbon forests on a site with minimal variation in topography. On such a site, the ongoing establishment of trees is likely to be controlled by microclimatic variations that are due to the presence of previously-established trees, by the autecological properties of the establishing trees, and by environmental changes due to climate variation or disturbance. Therefore I undertook to assess the relative roles of forest structure, autecological factors, climate change, and disturbance in the development of these forests. Specific objectives included:

1. To determine how contemporary forest structure determines meter-scale variations in snow distribution and soil moisture. This was achieved by mapping the locations and sizes of all trees, the distribution of understory vegetation types, and the maximum depth of snow accumulation on the study plots.

2. To determine the timing, spatial pattern, and mode of tree establishment on the study plots during the period of plot development. This reconstruction of forest development was achieved by mapping (above) and by determining the ages of all trees, snags, and logs on the plots.

3. To assess the influence of climate variation, a major source of variation in the physical environment, by:
    a) Examining the statistical association between tree establishment and instrumental climate records, for the period of climate data. This indicated climate conditions that might lead to successful seedling establishment.
    b) Examining the statistical association between tree establishment and tree-ring widths, a proxy indicator of climate variation, for the period of the tree-ring record. This might indicate periods during the tree-ring record that experienced a climate suitable for seedling establishment.
    c) Comparing tree establishment with a published reconstruction of long-term climate variation derived from an extensive tree-ring sample network. This,

again, might indicate periods that experienced a climate suitable for seedling establishment.

4. To determine how physical and structural factors affect the two autecological properties, mode of establishment and tree growth form. This was assessed by examining the spatial distribution of specific growth form anomalies or modes of establishment, relative to mapped variations in snow accumulation and understory vegetation.

5. To determine the role of disturbance (specifically, grazing) on the study plots. This was achieved by comparing the published chronology of grazing with the reconstructed times of seedling establishment.

6. To integrate the results of the foregoing Objectives into a conceptual model of clump and ribbon initiation and development. This model assumes that forest development is driven by variation in physical factors, and uses conclusions about the effect of those factors on autecological properties of the trees to explain the observed structural development of the forest. Because the study found little evidence of significant disturbance, disturbance plays a minor role in the model. Nonetheless, the model allows me to describe the relative importance of physical factors and forest response (changes in establishment mode, growth form and forest structure) as controls of ribbon and clump growth.

Chapter 3. LITERATURE REVIEW

In this chapter I review some of the large body of literature describing the physical factors, autecological responses, and forms of disturbance that combine to determine the position and structure of arctic and alpine timberlines. I examine these factors in some detail as they apply to the initiation and development of tree clumps and ribbon forests in the Rocky Mountains, and conclude with an examination of how these factors influence timberline dynamics, defined as long-term changes in the form and position of a timberline.

PHYSICAL CONTROLS OF TIMBERLINE

Comprehensive recent reviews of the timberline literature have been presented by Tranquillini (1979) and Arno (Arno and Hammerly 1984); Innes (1991) provides a brief but useful review of studies examining climate change at timberline, while Walter (1979) describes timberlines in the context of the global diversity of ecosystems. The present review is restricted to studies deemed relevant to timberline forests of the Medicine Bow Mountains.

In the Pacific Northwest, snowy ranges of the central and northern Rockies, and northern Québec, tree establishment in the forest-tundra is limited by the accumulation of a thick winter snowpack that persists well into the growing season (Billings 1969; Buckner 1977; Franklin and Dyrness 1988; Lavoie and Payette 1992). Because local topography can strongly affect the depth of the snowpack, the resulting timberline is poorly defined, covering a broad elevational or latitudinal range. The thick winter snowpack melts slowly, causing saturation of soils and a shortened growing season, which may impede or prevent tree establishment (Ballard 1972; Brooke *et al*. 1970). Seedling establishment may also be prohibited when seeds germinate on the surface of the snowpack (Franklin and Mitchell 1967), when soil temperatures are too low to permit survival of germinants (Patten 1963), or when seedlings are uprooted by a sliding snowpack (Lowery 1972).

Regardless of snowfall, all cold timberlines have a brief growing season. This can cause incomplete maturation of foliage and poor development of needle cuticle, with subsequent foliage death due to desiccation by winter winds (Tranquillini 1979). In areas where uniform topography permits little variation in wind and snow cover, or where snowfall is low, timberline is clearly defined and may be constrained mainly by temperature

(Tranquillini 1979; Wardle 1968). Studies in the Medicine Bow Mountains have augmented the foliar desiccation theory by showing that snow crystals blown across the snowpack can actively abrade cuticle, leading to desiccation and death even of foliage that has experienced normal maturation and cuticle development (Hadley and Smith 1989). Foliage that is shielded from abrasion by concealment beneath the snowpack remains unharmed. Such shielding from windblown ice and snow is the primary cause of the krummholz growth form, which is best displayed at sites where only shielded foliage can survive through the winter (Holtmeier 1980; Wardle 1968). At some sites in the Rocky Mountains the growth of individual trees may be constrained by any of several distinct processes. For example, a single krummholz tree may be subject to incomplete needle maturation due to a short growing season, cuticle abrasion due to exposure at its windward edge, and needle death due to snow fungus at its leeward edge (Holtmeier 1980; Marr 1977; Wardle 1968). A few meters away, deep and persistent snowdrifts may entirely preclude seedling establishment, or permit sporadic establishment leading to development of a forest-tundra parkland, where clumps or ribbons of trees remain separated by expanses of subalpine meadow (Holtmeier 1980, 1987).

AUTECOLOGICAL CONTROLS OF TIMBERLINE

Although physical factors generally constrain the position of a local timberline, the interaction of physical factors with autecological characteristics of the affected trees can strongly influence the structure of a timberline. The most important of these characteristics are growth form and mode of reproduction. These characteristics influence structural features of the forest such as the presence of dead wood and the pattern of trees on the landscape. Two landscape patterns of special interest are tree clumps and ribbon forests.

Growth forms

Within the spruce-fir forests of the Rocky Mountains, most trees are described as having a spire-shaped crown (Oosting and Reed 1952). In closed-canopy forests shaded lower branches may be dead or absent, but the exposed crown typically retains this spire shape. The spire form changes gradually with increasing elevation and exposure to stronger winds and the abrasion of needle cuticle by wind-blown ice crystals. First, the mature trees become shorter, have fewer and thicker branches and a more strongly tapered trunk

(Löve *et al.* 1970). Next, the trees show wind-flagging, that is, the dieback of branches on the windward side of the tree and the wind-training of lateral and leeward branches (Holtmeier 1980; Wardle 1968). The dieback of windward branches is most pronounced near the snow surface, where scarification by saltating ice crystals is most severe (Hadley and Smith 1989). At such sites the trees may develop a two-part growth form in which much of the tree is low and bushy and remains covered with snow throughout the winter months, while slender wind-flagged leaders rise several meters above the snowpack and often display some dead foliage. The lower, bushy part of the tree has a krummholz form; it often does not have a well-defined central stem, and the bushy branches may emerge from a large, knotty bole (Holtmeier 1982), hereafter called a "krummholz base". At the highest elevations, no portion of the tree can survive above the winter snowpack and all trees are low, bushy krummholz (Holtmeier 1980; Wardle 1968).

Mode of reproduction

A tree species dominant mode of reproduction may strongly affect its spatial distribution on the timberline landscape. Layering, or adventitious rooting, may occur where a branch touches the ground, establishes roots, and subsequently gains apical dominance, growing as a separate tree. Presumably a physical link to the parent tree provides layered shoots with food and nutrients beyond what they could attain if they grew from seed. The prevalence of layering in conifers is often taken to indicate a severe environment. In areas where trees have a krummholz form, most trees expand solely by layering (Holtmeier 1980; Wardle 1968). Black spruce (*Picea mariana* (Mill) B.S.P.) in northern Canada shows a transition from seedling establishment to layered establishment as the timberline is approached (Black and Bliss 1980; Payette and Gagnon 1979), and a similar pattern occurs in Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) growing near temperate alpine timberlines (Arno and Hammerly 1984; Holtmeier 1980, 1987; Oosting and Reed 1952). The layering habit, while permitting reproduction in a harsh environment, severely restricts population growth. An estimate of the potential rate of range expansion by layering is available for the spruce-fir timberline. "Islands" of spruce krummholz in Colorado layer downwind while being killed by winter desiccation upwind, traveling no more than a few meters per century (Benedict 1984; Marr 1977). Range expansion due to establishment from seed can be much more rapid; Shankman (1984), studying a burn at timberline in Colorado, found extensive seedling establishment by Engelmann spruce, subalpine fir, and limber pine (*Pinus flexilis*) 75 yr after the stand-destroying fire.

Structural consequences of autecological controls

Woody structures (trees and dead wood), although produced in response to physical factors, can later influence physical factors by altering microenvironments of seedling establishment and tree growth. This constitutes a feedback mechanism: the mere presence of a tree in a timberline environment may significantly alter that environment so as to increase the chances of further tree establishment. This kind of structural control over tree establishment and growth may lead to the formation of structures much larger than the individual tree; two examples are tree clumps and ribbon forests.

<u>Tree clumps</u>

Tree clumps are widespread in forest-tundra environments near both the arctic and temperate alpine timberlines (Arno and Hammerly 1984; Elliott-Fisk 1988). They may be loci of relatively deep, or relatively shallow, snow accumulation relative to the surrounding meadows. In the Pacific Northwest, clumps develop shallow snow accumulations relative to the surrounding meadows (Brooke *et al.* 1970). In these areas infrared radiation emitted from the clump edge promotes early snowmelt in adjacent meadows, lengthening the growing season and increasing the likelihood of seedling establishment (Brooke *et al*. 1970). This tends to restrict seedling establishment to the clump perimeter, while seedlings in the wetter and colder environment of the surrounding meadow do not survive (Lowery 1972). The clumps are found well below the local upper elevational limit of tree growth and they occur in areas which experience low wind velocities, suggesting that their growth is not significantly limited by winter desiccation. Elsewhere, such as in northern Québec or the Rocky Mountains (Holtmeier 1987; Lavoie and Payette 1992, Légère and Payette 1981), tree clumps are points of relatively deep snow accumulation relative to the surrounding meadows. Such tree clumps trap and retain windblown snow; in consequence, foliage is protected from cuticle abrasion and winter desiccation (Hadley and Smith 1989; Holtmeier 1980; Wardle 1968). Such clumps still display evidence of winter desiccation such as flagged leaders which project above the snow and the presence of a krummholz mat which conforms to the shape of the enclosing snowdrift. Little is known of the long-term development and stability of these clumps, but several studies in northern Canada (Payette and Gagnon 1979; Payette *et al.* 1989b; Sirois and Payette 1991) suggest that catastrophic fires can destroy large areas of clumps, causing treeline retreat, while a long period of relatively benign climate is generally required for a significant timberline advance. In the Medicine Bow Mountains, tree clumps are typically large clones produced almost wholly by layering (Oosting and Reed 1952). Fire is the principal disturbance in this area, and postfire recovery of clump areas is very slow (Billings 1969).

Ribbon forests

One of the most profound examples of the feedback between physical factors (snow and wind) and forest structure is found in forest-tundra areas where strong winds blow from a single direction during the winter. Ribbon forests can form in these environments (Billings 1969; Buckner 1977; Holtmeier 1980, 1982, 1987). Buckner (1977) observed that in these environments, wind scours snow away from the ground immediately in front and to both sides of scattered tree clumps in open meadows while thick snowdrifts pile up in the lee of the clumps. In the springtime, the meadow in front and to both sides of the clumps is free of snow relatively early in the season, promoting seedling establishment, while thick leeward snowdrifts persist long into the season and effectively preclude seedling establishment. Buckner suggested that seedling establishment continues upwind and laterally until the tree clump starts to enter the leeward snowdrift of the next upwind clump. Thereafter establishment prevails at the sides of the clump, causing it to elongate in a direction perpendicular to the prevailing wind, forming a forest ribbon. Aerial photographs of the Medicine Bow Mountains, where ribbon forests reach perhaps their greatest extent, reveal patches of several square kilometers where scores of ribbon forests are arrayed in ranks across the landscape, roughly uniform in the width of the ribbons and in the spacing between ribbons (Figure 1.2). Ribbon forests have been reported from many sites in the Rocky Mountains (Arno and Hammerly 1984; Billings 1969; Buckner 1977; Daubenmire 1981; Holtmeier 1982, 1987), and this writer has observed unreported examples in the Okanogan Mountains and Oregon Cascades. In a survey of ribbon forests in the Rocky Mountains, Buckner (1977) found that ribbons generally develop in areas where four conditions are met: (1) location within the forest-tundra ecotone, (2) strong and consistent winds, (3) relatively flat, so that topographic effects do not disrupt the development of a ribbon pattern, and (4) heavy snowfall.

Billings (1969) suggested that the ribbons would slowly migrate into the wind as new seedlings established on the windward edge and old trees died on the leeward edge of the ribbon. However, he presented no data relevant to this problem. In view of the uncertainties in Billings' and Buckner's theories of ribbon forest development, it is reasonable to ask some specific questions about the ribbon forests of the Rocky Mountains: (a) how are they initiated, (b) do they grow by seedling establishment at microsites determined by soil moisture,and (c) do they move across the landscape? Subsequent research has provided only partial answers:

(a) Initiation of the ribbons: The evidence on this point is scanty and largely conjectural. Billings (pers. comm., 1990) thinks that ribbons can sometimes form in areas of continuous forest, and reports having visited sites in the Medicine Bows supporting this proposition. However, field evidence reported for ribbon forest sites on Mt. Audubon (Holtmeier 1987) and the Park Range (Buckner 1977) in Colorado, as well as for the Medicine Bow Mountains (Billings 1969), suggests that ribbons do form in previously treeless landscapes. Of these studies, Buckner's (1977) theory of ribbon forest development (above) has been best supported by observational data. At Buckner's study site, ribbons are developed on elongate rocky ridges and presumably were initiated on those sites. Seedling establishment occurs at the ends of some ribbons, and snowpack measurements accord with the distribution of windward and leeward snowdrifts described by Billings (1969). However, it is worth noting that elongate rocky ridges do not occur on many ribbon forest sites, including those studied by Billings (1969). This is why, in this study, I present an alternative suggestion: ribbons may develop from tree clumps.

(b) Seedling establishment: Brooke *et al.* (1970) found that early snowmelt around the perimeter of tree clumps in British Columbia contributed to the successful establishment of mountain hemlock (*Tsuga mertensiana*) seedlings; they attributed this success to the longer growing season (as much as 6 weeks longer than in adjacent meadows) and higher soil temperatures found in these microsites. Both Billings (1969) and Buckner (1977) found a similar zone of early snowmelt in the windward edge and at the ends of ribbon forests, and found established seedlings growing in some such microsites. However, few studies have examined seedling survival in the timberline environment of the Rocky Mountains, and none have documented the ecophysiological limits to seedling establishment in the vicinity of ribbon forests or tree clumps. A variety of studies have examined seedling establishment in spruce-fir forests and have generally found soil

moisture to be a very, although not exclusively, important factor. For example, in first- and second-year subalpine fir seedlings water use efficiency is substantially lower than in older seedlings, causing extensive mortality due to drought and/or high temperatures. This mortality is particularly high among seedlings growing in sunny, rather than shaded, sites (Cui and Smith 1991). Drought is also a major cause of seedling mortality in Engelmann spruce (Knapp and Smith 1982), and Alexander (1987, p.33) emphasizes that "[t]he moisture provided by precipitation during the growing season is particularly critical to the survival of [Engelmann spruce] seedlings during the first year." Some studies have compared seedling survival in shaded and sunlit microsites at elevations of more than 3048 m (10000 feet). Ronco (1970) found that the extremely high light intensities encountered in the open at high altitude could inhibit photosynthesis in planted spruce seedlings, causing seedling death. Paradoxically, seedlings may be killed by high temperatures near timberline; ground surface temperatures as high as 66°C have been recorded on unshaded sites at 3200 m elevation in Colorado in June, whereas a surface temperature of 54°C is sufficient to kill a first-year spruce seedling (Alexander 1987). A moderate amount of shade was found to reduce light intensity, lower maximum temperatures and conserve soil moisture, contributing to seedling establishment and survival (Alexander 1987). Frost can also kill seedlings at any time from germination (usually in June or July) until early fall, and shading tends to reduce this mortality by reducing radiative cooling (Alexander 1987). These studies suggest that the observed seedling establishment in meadows adjacent to ribbon forests may be due to: (1) reduced light, temperature and moisture stress associated with microsite shading, (2) a prolonged growing season due to relatively early snowmelt, and (3) increased soil moisture due to the prolonged period of snowdrift melting.

(c) Forest movement: Buckner (1977) examined phytoliths and charcoal fragments in soil transects across ribbon forests. He found large numbers of conifer phytoliths and charcoal fragments in ribbon forest soils. Soils of the adjoining meadows contained abundant grass and herb phytoliths, but little charcoal. There was a clear demarcation between these two groups, indicating the forest/meadow boundary had remained relatively stationary across the long soil residence time of charcoal and phytoliths. A study of ribbon forest and adjacent meadow soils in Cinnabar Park of the Medicine Bow Mountains (Doering and Reider 1992) also found a clear demarcation in soil morphology and stratigraphy between forest and meadow soils, and concluded that the ribbon/meadow boundary has been stable for *ca.* 2000 yr. Both of these studies indicate that ribbon forests do not move across the

landscape, but instead remain stationary for a period of centuries or more. This conclusion poses a new question, though: if (as Billings observed) establishment occurs primarily on the windward edge of a ribbon, why does the ribbon fail to migrate upwind? Although this problem has not previously been addressed in the literature, I offer a hypothesis: The windward edge of the ribbon does expand to the windward until the ribbon has grown to its full width, *i.e.* the point at which further windward expansion is precluded by the snowdrift formed in the lee of the next ribbon to windward. The time required for the ribbon to achieve this full width may be long compared to the interval between episodes of stand-destroying disturbance (discussed below); if so, then the ribbon does not exist long enough to develop a uniform age structure from its windward to its leeward edge.

DISTURBANCE

Population changes at timberline may be driven by such nonclimatic factors as disturbance or structural changes in the forest. Disturbances are particularly important to timberline populations because recovery may be extremely slow in comparison with neighboring closed-canopy forests (Ives and Hansen-Bristow 1983; Sirois and Payette 1991). However, apart from avalanches (Arno and Hammerly 1984; Johnson 1987), the primary disturbances encountered at arctic and temperate timberlines are the same as those that affect adjacent boreal and subalpine forests: fire, wind, insect infestation, disease, and human impact.

Globally, fire is the most prevalent of these disturbances. It is widespread in the boreal forest (Elliott-Fisk 1988; Payette 1992) and affects most other conifer-dominated timberlines in North America (Franklin and Dyrness 1988; Huff *et al.* 1989; Peet 1988). Fire destroyed several square kilometers of tree clumps and ribbon forest at Libby Flats in the Medicine Bows in 1809 (Billings 1969), indicating that the open structure of the forest-tundra does not necessarily protect the trees from catastrophic fire. Tree re-establishment at Libby Flats has been slow and extremely patchy.

Although wind is an important disturbance in subalpine forests of the Rockies (Veblen *et al.* 1989), there is little evidence for windfall of healthy trees in the forest-tundra. Spruce and fir in these forests are most susceptible to windthrow when in open stands or when anchored by a shallow root system. When trees are in dense stands (such as ribbon forests or tree clumps) or when developed on deep, well-drained soils, windfall risk is relatively low (Alexander 1987).

Insect infestation at timberline is not well documented. In the central Rockies, insect disturbance is chiefly characterized by bark beetle (*Dendroctonus rufipennis* Kirby) outbreaks (Veblen *et al.* 1991), although it is not clear whether bark beetles are active at the elevation of the forest-tundra. Fungal pathogens are more important and include the root rots and butt rots that affect lower subalpine forests (Alexander 1987). In the author's experience, root and butt rots are encountered much less frequently in the forest-tundra than in nearby closed-canopy subalpine forest. Late-melting snows may encourage the growth of snow fungus (*Herpotrichia* spp.), which grows on and may kill foliage (Simms 1967; Wardle 1968) and seedlings (Buckner 1977; Holtmeier 1987).

Anthropogenic disturbances, including logging, firewood gathering, grazing, clearing of land, construction, mining, aboriginal burning, and a host of other activities, are widespread at temperate timberlines throughout the world (such disturbances comprise the focus of the journal, *Mountain Research and Development*). The primary anthropogenic disturbances in the Medicine Bow Mountains are logging and grazing, which have only been important since the late 1800's (Thybony *et al.* 1985). Individual trees have been cut for fencing, shelters or firewood in areas where domestic animals are grazed, near mines, or near hunting camps. I observed clearcut logging of ribbon forests in the Medicine Bows in 1989.

It has long been known that grazing is an important and continuing disturbance in many forest-tundra habitats (Griggs 1937, 1938; Muir 1911; Shaw 1909). Active grazing may effectively preclude seedling establishment (Vankat and Major 1978), and the cessation of grazing may permit seedling establishment due to reduced competion from meadow herbs. For example, Dunwiddie (1977) argued that subalpine meadow invasion of a forest-tundra site in Wyoming was probably due to grazing of meadow herbs and grasses, which permitted seedling invasion by opening patches of bare mineral soil and otherwise reducing herbaceous competition. Seedling invasion of montane and subalpine meadows has also been linked to the cessation or reduction of grazing for sites in California (Vankat and Major 1978), Oregon (Vale 1981), Idaho (Butler 1986) and New Mexico (Allen 1989). Grazing, principally by domestic sheep, continues to be an important disturbance near timberline in Wyoming (Stephen Arno, pers. comm. 1989). It has affected near-timberline habitats in the Medicine Bow Mountains since the late 1870's (Bruce 1959; Thybony *et al.* 1985) and has probably influenced meadow invasion by seedlings in some areas (Will Moir, pers. comm. 1989, 1990). Finally, in a study of ribbon forests in the Park Range of Colorado, Buckner (1977) found that grazing by pocket gophers could kill seedlings.

TIMBERLINE DYNAMICS

The physical and autecological factors controlling timberline can be expected to change through time, causing changes in the position and form of timberline. Excepting geological changes, which mainly occur at very long time scales, the physical environment changes largely in response to climate change. Growth form, mode of establishment, and forest structure can change in response to climate change, or because of disturbance such as fire, grazing, or disease. The role of disturbance has been discussed, but there may also be changes in the frequency and type of disturbance due to climate change or changes in land management policy. Although changes in the position of timberline are commonly attributed to climate changes (Innes 1991), such an inference can only be valid if climate change is the primary control of tree establishment or death at timberline. Therefore it is essential to assess changes in disturbance and forest structure in order to determine whether forest change at any given timberline is driven by climate change.

Responses to climate change

Timberline dynamics are expressed on the landscape by the establishment and death of individual trees. Accordingly, many studies of timberline change have taken a demographic approach, examining changes in establishment and/or mortality rates. Most such studies have focused on establishment rather than mortality and most have concluded that timberline has been advancing during the 1900's. A study of seedling establishment in the subalpine parkland of Mount Rainier National Park found that increased establishment was associated with a period of relatively warm, dry climate (Franklin *et al.* 1971). Similar findings have been reported for other sites in the Pacific Northwest (Brink 1959; Kuramoto and Bliss 1970; Lowery 1972). Seedling invasion at timberline has also been attributed to climate change in Fennoscandia (Kullman 1981, 1988, 1991b; Kullman and Engelmark 1991), Québec (Payette and Filion 1985; Payette and Gagnon 1979, 1985; Payette *et al.* 1985), and many other sites around the world (reviewed by Holtmeier

[1979] and Innes [1991]). Although studies of seedling establishment near timberline in the Rocky Mountains have largely focused on forest response to disturbance by grazing (Dunwiddie 1977) or fire (Daly and Shankman 1985), a study from the Canadian Rockies documented two episodes of seedling establishment at a spruce-fir timberline during the 1900's and found that these episodes were associated with above-average mean minimum summer temperatures (Kearney 1982). Other studies have used tree ring data to describe the association between climate and tree-ring width in Engelmann spruce (Hansen-Bristow *et al.* 1988; Kienast and Schweingruber 1986; Yamaguchi 1990). These studies provide background that permits exploration of the association between establishment success, tree growth, and climate variability at the study plots.

Due to problems with dating and interpreting the causes of tree death, fewer studies have found a clear association between climate and tree mortality at timberline. Studies of past tree mortality tend to be problematic because dead trees decay, making it difficult to determine death dates. It is also often difficult to show specific climatic causes of tree death. Since mature trees are generally less vulnerable to harsh climate than are seedlings, a larger climate change is necessary to kill a tree than to prevent the establishment of one (Kullman 1989). Because of these problems, most studies describing timberline recession due to tree death have addressed changes at time scales of centuries or more and have detected the effects of relatively large climate departures such as the early Holocene thermal maximum or the Little Ice Age (Bryson *et al.* 1965; LaMarche 1973; LaMarche and Mooney 1967; Payette and Gagnon 1979; Scuderi 1987; Sirois and Payette 1991). A few studies, notably by Kullman (1979, 1981, 1988, 1989, 1991a, 1991c; Kullman and Engelmark 1991), have succeeded in using tree death to reconstruct relatively small climate changes at decadal or even annual time scales by detailed recensusing of tree populations. Kullman's studies have addressed mortality in trees occurring on the open tundra, where competitive interactions were negligible. In tree clumps and ribbons, where closely-spaced trees interact, mortality may be a more important indicator of ecological interactions than of climate change.

The mode of tree establishment may also be expected to vary in response to changing climate. Tree populations will tend to reproduce by layering during periods of harsh climate and by seed during periods of benign climate. For example, Payette and Gagnon (1979, 1985) found that eastern larch (*Larix laricina* (Du Roi) K. Koch), which establishes solely from seed, experienced population expansion only during periods of benign climate. Black spruce, which establishes mainly by layering, continued to establish through periods of both benign and harsh climate. Establishment of layered shoots, which have access to moisture, food and nutrients from the mother plant, should generally show a weaker association with climate than does establishment of seedlings, a situation previously described for black spruce near the arctic treeline (Légère and Payette 1981). The problem of changing establishment mode has apparently not previously been examined for a site at a temperate timberline.

Structural changes

Structural changes are an important control on the spatial pattern of forest-tundra development. Since tree establishment in the forest-tundra is strongly influenced by the presence of pre-existing trees, the presence of forest structure affects the trajectory of forest development, and changes in structure must also affect that trajectory. This concept has received little attention in the literature. Griggs (1938) may have been the first to examine the process of clump growth when he noted that reproduction by layering can produce circular tree clumps of subalpine fir. Studies of clump development in the Pacific Northwest found that successional transitions between different tree species may alter the structure of tree clumps (Franklin and Mitchell 1967; Lowery 1972), and a similar process operates in the Little Belt Mountains of Montana (Stephen Arno, pers. comm. 1989). In the forest-tundra of the Medicine Bows, structural effects are likely to be important in the process of ribbon forest formation. As trees establish, grow, and die, they will alter patterns of snow accumulation and of further tree establishment (Billings 1969; Buckner 1977). Tree death can also alter the forest structure by changing microscale patterns of light and nutrient availability, which may then affect seedling establishment. In regard to the present study, structural changes are clearly important because of the ways that they guide the inception and development of tree clumps and ribbon forests, as described above. However, the process of tree death also poses significant problems to any effort to reconstruct forest development, because trees that were formerly structurally important to the forest may have since died and decayed.

Chapter 4. STUDY AREA

SITE SELECTION

The study site was selected after extensive literature review, interviews (see Acknowledgements), and field reconnaissance of sites along a transect ranging from the wet coastal mountains of the Pacific Northwest to the easternmost ranges of the central and northern Rocky Mountains. The principal purpose of this reconnaissance was to visit examples of forest-tundra parkland representing the full range of alpine climates found within this region, in order to select a study site where patterns of tree distribution primarily reflect the influence of regional climate rather than of local variations in topography, soils, vegetation, or disturbance. A secondary purpose was to visit and photograph sites described by previously published studies, including those of Billings (1969), Buckner (1977), and Lowery (1972). In the course of this reconnaissance, the following site selection criteria were developed:

1. The study site had to be as nearly as possible free of microtopographic variation, *i.e.*, flat or uniformly sloping. At all reconnaissance sites, seedling establishment appeared to be (or was reported in the literature as being) determined largely by patterns of snow accumulation. The great majority of sites contained considerable microtopographic variation, which appeared to be the principal factor controlling local variation in snow depth. Consequently, the distribution of tree clumps or ribbons was probably controlled more by topographic variations than by any effect the trees had on snow accumulation pattern, rendering such sites unsuitable.
2. Maximum snowpack depths should be in the range of 2 to 3 m. Across the subcontinental region surveyed, snow accumulation was found to vary widely, with maximum snowpack depths ranging from >10 m in parts of the Olympic and Cascade Mountains to <1 m in some of the intermountain ranges, such as the Independence Range of Nevada. I sought a location with snowpack depths representative of most regions from the eastern Cascade Mountains through the middle and northern Rocky Mountains, so that the results of the study would be relevant to an understanding of snowpack effects on timberline forests over a large area.
3. The site should be dominated by Engelmann spruce and subalpine fir. Within the reconnaissance area, many tree species may be encountered as dominants at the alpine

timberline. Whitebark pine (*Pinus albicaulis*) occurred as tree clumps with a roughly spherical form, occupied by several trunks that sprouted from a single seed cache (according to the model presented by Hutchins and Lanner [1982]). Subalpine larch (*Larix lyallii*), lodgepole pine (*Pinus contorta*), bristlecone pine (*Pinus aristata* and *P. longaeva*) and limber pine seldom formed tree clumps of more than a few individuals. In one area (the Little Belt Mountains) I found clumps that displayed a characteristic succession from pine to fir to spruce, but this succession arose in response to edaphic factors (a limestone substrate) and thus posed a relatively isolated problem (interested readers may wish to consult Bamberg and Major [1968]). By far the most common clumps were comprised of two or three species that reproduced sometimes by layering and sometimes from seed. In mountains near the Pacific coast these species were mountain hemlock, Pacific silver fir (*Abies amabilis*), and subalpine fir; but over most of the area these species were Engelmann spruce and subalpine fir. Thus, the study site represents an especially widespread timberline community.

4. Site variation due to soils must be minimal, so the study site had to be in an area of siliceous (as opposed to calcareous or other) soils, preferably underlain by a single uniform rock type such as sandstone or granite. Calcareous soils were undesirable because they are considerably less common than siliceous soils in the reconnaissance area and because, on these glaciated sites, it would be very difficult to find a site with soils of uniform carbonate content. Other soil types, such as serpentine-derived soils, saline soils, or clay-rich soils, are relatively rare in the reconnaissance area. Soil uniformity was important because heterogeneous soils might affect the spatial pattern of tree establishment.
5. The study site had to be on land where I could get permission for sampling by cutting seedlings and removing increment cores from larger trees. This sampling was needed to determine dates of tree and seedling establishment and/or death.

A suitable region for the study was located in the Medicine Bow Mountains of southeast Wyoming. Parts of the area meet the first four criteria cited above. It is also the site of Billings' (1969) pioneer work on ribbon forests and is the study site for many relevant publications on the ecology, climate, and ecophysiology of the spruce-fir forest and adjacent alpine tundra. Moreover, it is the site of the Glacier Lakes Ecosystem Experiments Site, operated by the U.S. Forest Service Rocky Mountain Forest and Range Experiment Station. Personnel associated with the Station agreed to make logistic support, library facilities and climate data available for this study, and intervened with the Medicine Bow National Forest to get permission for sampling, thereby meeting criterion (5). After several days of field reconnaissance, I selected a study site conforming to the above criteria. The site was selected to include plots representative of both tree clump parkland and ribbon forest.

STUDY SITE

The Medicine Bow Mountains are a north-south trending anticlinal range with a broad, nearly level summit region lying at an elevation between 3000 and 3600 meters, encompassing the entire forest-tundra ecotone. Most of the forest-tundra ecotone lies north or south of the Snowy Range, an east-west ridge that includes the highest peaks of the range. The local bedrock is an early Proterozoic quartzite (Houston and Karlstrom 1992) that is also the principal component of overlying soils derived from glacial till, principally of Pinedale age (Sansom and Reider 1974). Timberline tree species include Engelmann spruce and subalpine fir on most sites, with some limber pine and lodgepole pine on drier sites or as seral species on disturbed sites (Alexander *et al.* 1986; Oosting and Reed 1952). The closed-canopy subalpine forest is represented by spruce-fir and lodgepole pine associations, the latter reflecting drier sites and higher fire frequencies (Romme and Knight 1981). Trees occur as krummholz patches, scattered tree clumps, or ribbon forests across extensive (kilometer-scale) areas.

Data from weather stations at the Glacier Lakes Ecosystem Experiments Site, *ca.* 3 km south of the study site at 3290 m elevation, indicate a continental climate with June-September average daily temperatures near 10° C and midwinter low temperatures of about -30° C. Precipitation, which averages 1076 mm yr^{-1}, is quite variable. Summers are relatively dry (mean June to October precipitation 52 mm), but summer thunderstorms are an important source of growing season precipitation. Winters are wet, with most precipitation from November to May (monthly mean 112 mm) falling as snow and accumulating to depths of one to three meters on the study plots. Most snowmelt occurs during June (Knight 1975); in 1989 and 1990, when most fieldwork was done, the study plots were snow-free by July 10. The region is extremely windy, with prevailing winds measured atop the Snowy Range (elev. 3475 m) blowing from due west in all months. Average hourly wind speeds of 2 to 3 ms^{-1} in the summer and 7 ms^{-1} in the winter are typical (Glacier Lakes Ecosystem Experiments Site meteorological records, unpublished).

STUDY PLOTS

Two study plots were sited on the long, gently inclined north slope of the Snowy Range (Figure 4.1). Study plot boundaries were designated so that both plots were oriented with respect to the local prevailing winds. These winds blow from due west (azimuth 270°) at the "clump" plot. Due to topographic redirection of the wind, this angle is rotated at the "ribbon" plot to 212°. In reference to the study plots, this azimuth will hereafter be described as "windward".

Both plots are dominated by a mixture of Engelmann spruce and subalpine fir; no other tree species are present. Both plots are currently subject to moderate sheep grazing during the summer. Historical records indicate that the extensive subalpine meadows on the north and south slopes of the Snowy Range, including the study area, have experienced higher grazing intensities in the past (Bruce 1959; Thybony *et al.* 1985). The absence of charcoal fragments in the soil or fire scars on any trees, logs or snags indicates that neither plot has experienced wildfire within the last several centuries. It is possible that some large spruces were killed by bark beetles in the latter 1800's, a time of widespread regional bark beetle mortality (Baker and Veblen 1990). However, the large spruce logs on the site have a wide range of death dates, suggesting that there has been no major episode of tree mortality on the site.

The "clump" plot, covering 1.0 ha at an elevation of 3310 m, is located within a large grassy meadow about 1 km wide and 3 km long, containing many tree clumps (parts of the plot are shown in Figures 4.2, 4.3 and 4.4). Although this meadow is virtually flat, most tree clumps are developed on slight topographic convexities which often have a relief of only a few decimeters. This plot includes 352 trees in 14 tree clumps of various sizes. The tallest trees are 5 to 7 m tall, and many are less than 2 m tall. Many trees consist of erect, wind-flagged leaders rising above a krummholz mat. The krummholz mat rises to a height of 1.4 m to 2.0 m, corresponding to the depth of winter snow (examples in Figures 4.2, 4.3 and 4.4). The largest trees usually have a "krummholz base," defined as a large,

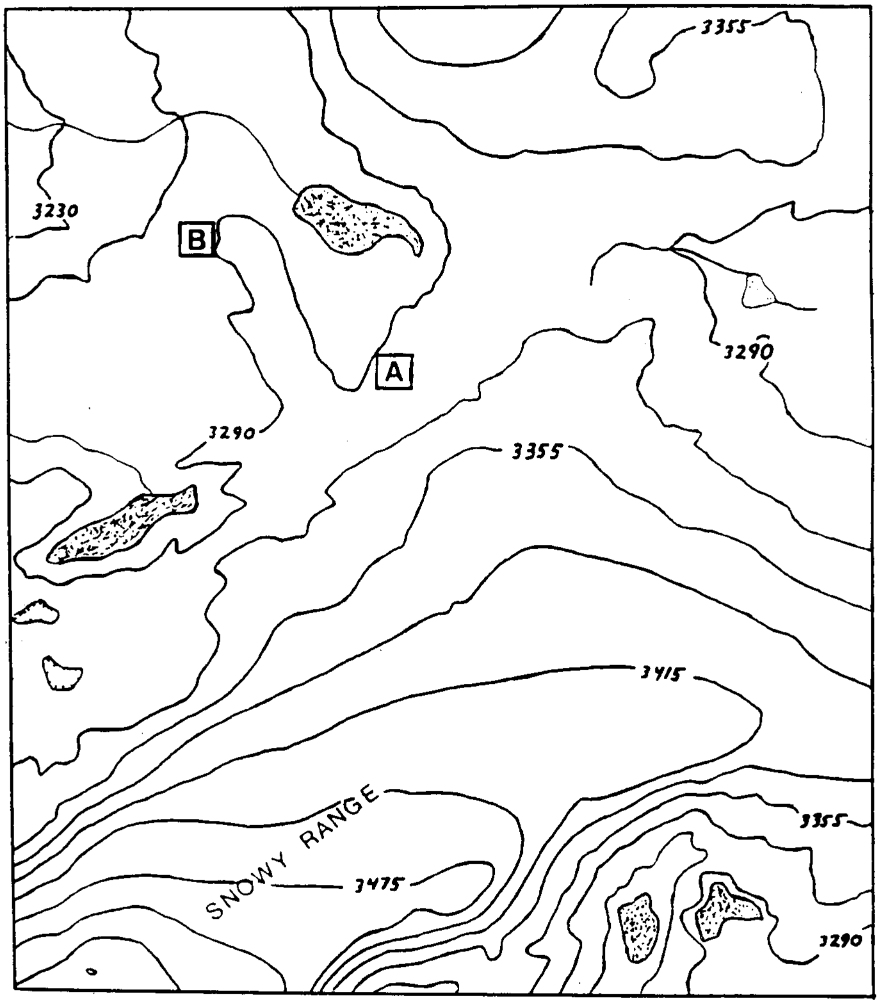

Figure 4.1. Map showing the study area and locations of the study plots. "A" marks the location of the clump plot, and "B" the ribbon plot. Elevations in meters. Contour interval 30 m (100 ft). Map width is 2.50 km (scale 1:22 500).

Figure 4.2. Rephotography of a small spruce clump (#10 in Figure 6.2), 27 April and 20 August 1990. The krummholz mat is buried by winter snows on this clump and on background clumps. Branches are absent on the windward side of the main stem, particularly near the snow surface, due to abrasion by ice crystals. This abrasion has also killed foliage on shoots projecting above the snow surface, indicated by their brown color.

Figure 4.3. Clump 2 at the clump plot, seen from the north. Prevailing winds blow from the right. The foreground tree has a wide krummholz base largely enclosed by vegetation of the krummholz mat and surmounted by two prominent leaders. Leaders rise 3-4 m above the krummholz mat, are prominently wind-flagged, and display pruning of branches on the windward side. This pruning diminishes with distance above the krummholz mat, showing the diminished effect of scarification by saltating ice crytals with increasing distance above the snowpack. Background trees share this appearance.

Figure 4.4 (above). Clumps 3, 4, and 5 (of Figure 6.2) at the clump plot, seen from the north. Prevailing winds blow from the right. All clumps display a prominent krummholz mat surmounted by numerous wind-flagged leaders that rise to heights of as much as 7 m above the ground.

Figure 4.5 (below). View looking north along the windward edge of the ribbon forest. Stakes at left mark the windward edge of the plot. Trees have spire-shaped crowns and show little evidence of windforming.

knotty stem (up to 50 cm in diameter) with branches emerging at various angles, layered stems, and at least one leader projecting above the krummholz mat (example in Figure 4.3). Subalpine fir dominates this plot, representing 65% of the trees.

The "ribbon" plot covers 0.4 ha at an elevation of 3290 m and includes 660 standing trees or snags (part of the plot is shown in Figure 4.5). Spruce represents 58% of the trees. The plot comprises a 50 m wide transect across a section of ribbon forest. This plot is bounded on the windward and leeward sides by grassy meadows about 70 m wide, which are bounded in turn by parallel ribbon forests. These ribbons occur on slight topographic convexities or on short slopes, often with a total local relief of less than one meter. Trees in the ribbon plot are taller (up to 16 m) than at the clump plot. Mature trees are spire-shaped and do not have flagged leaders or a basal krummholz mat. However, most trees have thickened branches and strongly tapered trunks. Reproduction by layering is common and accounts for the majority of fir stems. Many older, larger trees at the ribbon plot display relict growth form features (*e.g.*, the trunk is divided into multiple leaders at about the same height as in trees on the clump plot, or a krummholz base appears on a tree that otherwise has a regular spire shape and is presently growing in the forest interior, as shown in Figure 4.6). These relict features suggest that the ribbon plot formerly experienced an environment similar to that now found at the clump plot. Trees at the ribbon plot also display some growth form features that are not found at the clump plot. For example, suppression of understory seedlings and saplings has produced an "umbrella" growth form typical of advance regeneration. Some trees show crown damage due to heavy snowfall or browsing, and some trees have been damaged by falling trees or snags.

Figure 4.6. A krummholz-base spruce near the leeward edge of the ribbon forest. The understory shrub is *Ribes montigenum*.

Chapter 5. METHODS

FIELD MAPPING

Tree and dead wood locations

The clump plot measures 100 m × 100 m and the ribbon plot measures 80 m × 50 m, with the long axis oriented windward-leeward. The boundaries of each plot were surveyed by transit and corners were marked with wooden stakes. Each plot was divided into 25 m × 25 m squares and within each of these squares, 5 m × 5 m grid squares were delimited by lines of string. The location of each tree was measured within each grid square with a precision of 5 cm. Each tree is located with respect to its neighbors with a probable accuracy of ± 10 cm. All trees were sampled, measured and their growth form noted (as described below) at the time of mapping. Several prominent trees on each plot were labeled with numbered aluminum tags to facilitate plot relocation. Dead trees and down logs were mapped and described by species (fir, spruce, or unknown), approximate diameter at breast height, and decay class. Five decay classes were defined (Sollins 1982). Decay class 1 (DC-1) wood is solid with intact bark, DC-2 has solid wood but bark beginning to slough, DC-3 indicates the loss of bark and softening of sapwood, and DC-4 indicates softening of the heartwood. DC-5 wood can be crumbled in the hand.

Vegetation composition

Vegetation was also mapped at this time. For each 5 m × 5 m grid square, the percentage area falling within each of several different ground cover types was estimated. These types included: 1. Bare ground. 2. Dead wood. 3. Needle litter. 4. Live conifer foliage (<1 m above the ground). 5. Bare rock. 6. *Ribes montigenum*. 7. *Vaccinium scoparium*. 8. *Deschampsia cespitosa*. 9. Cyperaceae/Juncaceae. 10. *Sibbaldia procumbens*. 11. Other moist meadow herbs. Taxonomic nomenclature follows Dorn (1977).

Snow Survey

A snow survey was performed on April 26 and 27, 1990, near the time of maximum snow accumulation as determined in that year by Forest Service personnel who performed the snow survey at Glacier Lakes. On each plot I located the corners by resurveying from tagged trees and ran snow survey lines on a 10 m × 10 m grid. Therefore the survey grid for the clump plot includes 11 × 11 = 121 points and that for the ribbon plot includes 6 × 9 = 54 points. Accuracy of the grid location is ± 1 m within the forest and near tree clumps and ± 2 m in the open meadow areas. Snow depth was measured by inserting a graduated probe vertically until the ground was encountered. Snow density was not measured, but did not appear to be greatly variable, judging from resistance to the probe.

Contour plots of snow depth were produced using the SURFER program package (Golden Software 1987). This package interpolates and contours values using an inverse-square algorithm according to user-defined parameters. Plots were created from the matrix of snow depths on each plot. Contours were defined using each grid point value and the values for the four contingent grid points.

STRUCTURE AND COMPOSITION OF TREE CLUMPS AND RIBBON FOREST

Stem density and basal area

Contour plots of tree stem density and basal area were produced with the SURFER program package (Golden Software 1987) using a procedure similar to that described for snow depth maps. Plots were created by generating a matrix showing either the number of trees or the total basal area within contiguous 5 × 5 m grid squares across the plot. Contours were defined using each grid square value and the values for the four contingent grid squares.

Spatial pattern in tree clumps

Each of the 14 clumps at the clump plot comprised a clearly distinct group of trees, separated from other groups of trees by at least several meters of meadow. The presence of an aggregated, random or dispersed spatial pattern of tree clumps was determined by a simple Monte Carlo procedure. Such tests (as described by Diggle [1983]) are commonly used to detect pattern in spatial point data because there is no *a priori* probability distribution that can be applied to the data. Therefore a test statistic is defined and its distribution determined empirically by repeatedly calculating the statistic for different arrays of synthetic "random" (*i.e.*, defined by a Normal distribution) data. The measured experimental data may then be compared to the calculated empirical distribution.

The test statistic, **S**, was created by calculating the distance from the center of a clump to the center of every other clump on the plot, for each of the 14 clumps (thus, 13+12+...+1 = 91 distances). The 14 smallest distances so calculated were saved as the test statistic, so that **S** is a 1×14 vector. **S** was calculated 100 times: once for the coordinates of the observed clump centroids, and for 99 simulations each consisting of 14 points randomly located within the plot area (these points were generated by random number generator RANO1 in Press (1989), using the program provided by Sprott (1991)). The 14 distances in each value of **S** were ranked from lowest to highest for each of the 100 trials, so that the rank of the observed data indicates the probability that it represents a random spatial pattern. For instance, if the observed smallest clump-to-clump distance was 10 meters, and the modeled smallest distance was greater in 49 of the random simulations, then the rank of the observed datum would be 50, indicating spatial randomness. A rank >50 indicates that the observed distance is larger than expected in the random model, so that the observed data display a dispersed pattern. Conversely, a rank <50 indicates an aggregated pattern.

Tree clones

As used herein, the term "clone" does not necessarily indicate a member of a group of genetically identical individuals, although this is generally the case. Timberline ecologists have long used the term to describe any tree that appears to have derived from a parent tree by adventitious rooting (layering). Only recently has this usage been investigated by genetic studies of apparently clonal spruce and fir individuals (Shea and Grant 1986). This work, performed in a Colorado spruce-fir forest very similar to the closed-canopy subalpine forest of the Medicine Bows, found that in most cases of apparent regeneration by layering, trees were genetically identical. However, the stems of multiple-stem trees were often not genetically identical and presumably established from seed clusters.

For the purposes of this study, trees were described and mapped as "clonal" if they: (1) displayed a direct physical linkage with a parent tree, or (2) shared stems with immediate neighbors that radiated from a central point that was occupied either by a large old tree (of the same species) or the stump of such a tree. Previous studies of timberline conifers that reproduce by layering have used similar criteria (Knowles 1991; Légère and Payette 1981). Clonal and nonclonal trees were only distinguished at the ribbon plot. At the clump plot nearly all trees appeared to have established by layering. The principal exceptions were trees that initiated the growth of clumps and occasional seedlings in the youngest spruce clumps.

Tree growth form

Tree growth form was recorded only when anomalous. Normal growth form was considered to be the spire form typical of subalpine fir and Engelmann spruce in high elevation forests (Oosting and Reed 1952). At the clump plot, the following aspects of growth form were recorded: (1) The association between snow accumulation and tree form, by photographic comparison of snow depth and the height of the krummholz mat (one such comparison is shown in Figure 4.3). (2) The azimuth of flagging for the tallest tree in each clump (such flagging is visible in Figures 4.2 and 4.3). (3) The number of leaders on a tree, and the height(s) at which the trunk divided to produce those leaders (example, Figure 4.3). (4) The presence of a krummholz base (example, Figure 4.3). (5) For trees with a krummholz base, the number of upright leaders. (6) For trees with a krummholz base and upright leaders, the age of the base and the age of the leaders. (7) One small, young spruce clump in which most trees had established from seed was cored for age determination and also for determination of the time when trees began to grow above the level of the krummholz mat. Trees were cut at the base for age determination and were cut at the top of the krummholz mat at a height of about 0.9 m to determine the date of leader growth above the mat.

At the ribbon plot, "release height" was recorded. This is defined as the height at which a trunk changed from a knotty and crooked form (*i.e.*, a krummholz base) to a straight form with fairly regular branch whorls (example, the top of the krummholz-base branches in Figure 4.6). The analysis of growth form at the ribbon plot also includes assessment of evidence that krummholz base trees established beyond the edge of the extant forest. This was done by defining the location of the forest edge at the date of establishment of every tree. All trees located within 5 m of each other at a given date were defined to constitute a forest patch. The polygons delimiting these patches were then defined as the forest edge. The distance that a tree established from the forest edge was defined as the shortest distance between the tree and a point on a polygon.

DEMOGRAPHIC ANALYSES

Tree establishment dates

All live trees >20 cm tall and all snags or stumps on each plot were sampled to determine dates of establishment and/or death. Trees <3 cm in basal diameter and most dead trees were cut and disks removed. Larger live trees and the largest dead trees were cored with an increment borer. Samples were taken as close to the base of the tree as possible. Species, sampling height, diameter at sampling height, tree height and diameter at breast height (DBH, measured at 1.4 m above the ground) were recorded. Samples were prepared according to standard methods (Stokes and Smiley 1968) and counted under a stereo microscope. Visual crossdating was done, based on ring width variation and the presence of occasional frost rings. These methods permitted exact dating of establishment year (*i.e.,* a pith date at ground level) for about one-third of the trees. The remaining trees required age corrections for: (1) sampling above the base of the tree, (2) sampling that did not recover the pith of the tree, or (3) sampling that recovered very little wood because of advanced decay, mainly a problem in dead trees. Type (1) corrections were made from a height-age calibration curve. This curve was developed by cutting 25 seedlings of each species growing near the windward edge of a nearby forest ribbon. Five seedlings were cut in each 20 cm height class from 20 cm to 100 cm tall, the rings were counted in sections taken at 10 cm height increments, and a linear regression line was fitted to the resulting age-height relationship. A separate regression was developed for each species. Type (2) corrections were made by measuring the curvature of the innermost ring sampled, estimating the radial distance to the center of the tree, and extrapolating according to the growth rate observed in the innermost few rings. Type (3) corrections, representing fewer than 5% of all sampled trees, involved dating by analogy with neighboring trees of the same species and comparable appearance, growth rate, and diameter. The age estimation procedure is further detailed in the Appendix.

Age structures and spatial patterns of tree establishment

Age structures were developed as histograms with decade age classes (*e.g.*, 1901-1910). Spatial trends in tree establishment at the ribbon plot were portrayed by maps indicating the establishment of trees in sequential 50 yr time intervals (*e.g.*, 1831-1880). For the ribbon plot, tree locations and establishment dates were used to calculate the distance that each tree established from its nearest previously-established neighbor (the NPN distance). This was determined by a computer program written by the author which calculated the distance from a given tree to every previously-established tree, assigning the NPN distance to the nearest calculated neighbor. The NPN distance showed an exponential decrease through time, which was approximated by fitting a negative exponential regression line to the NPN data. The departures from this line were calculated for sequential 50 yr intervals and a t-test was used to test for significant differences between the sequential means.

Dating dead wood

Establishment and death dates for dead wood at the ribbon plot were determined by measuring the ring widths on samples taken by saw or increment borer and crossdating with a spruce tree-ring chronology (below) using program COFECHA (Holmes *et al.* 1986). Because the entire tree does not decay uniformly, on most dead trees it was possible to find a sampling spot with intact bark and sapwood. However, a few death dates may be slightly too old due to loss of outer rings from sapwood decay. Mast (1991) reports that only a few years of sapwood are generally missing when determining the death dates of bleached spruce and fir snags in the Colorado Rockies. About 1/3 of the snags, and about 2/3 of the stumps and logs, could not be dated because not enough wood could be recovered to reliably crossdate with living tree samples.

Death dates were not determined for trees at the clump plot. Datable samples could not be recovered from most dead trees on the clump plot because: (1) most dead wood was badly decayed and so could not be sampled, and (2) when samples could be recovered, tree-ring sequences did not crossdate well with the tree-ring chronology for the ribbon site.

Rates of population change

Rates of establishment, mortality and net population change are expressed as the change in population during one decade divided by the total population at the beginning of the decade. For example, if the population in 1901 is 100 trees and 2 trees die between 1901 and 1910, the mortality rate for that decade would be 2 ÷ 100 = 2%.

CLIMATE AND ESTABLISHMENT

Tree-ring chronologies

Two tree-ring collections were made to assess the association between climate and ring width and to develop proxy time series of tree establishment. Since it is generally thought (Kienast *et al*. 1987; LaMarche 1974) that tree growth near the upper timberline is primarily limited by temperature, and tree growth near the lower timberline is primarily limited by available moisture, collections were made at both these locations. The lower collection was taken from Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco.) growing on steep, south-facing slopes near the lower timberline on the east slope of the Medicine Bow Mountains, about 30 km from the forest-tundra study plots. This collection has been archived with the International Tree-Ring Data Bank as site SHEIND, latitude 41° 8' N, longitude 106° 3' W, elevation 2375 m. The upper collection was taken from spruce growing within the ribbon forest plot. This collection has been archived as site MB4IND, latitude 41° 24' N, longitude 106° 17' W, elevation 3290 m. At each site, 40 cores were extracted from trees with a Haglofs increment borer. For the lower collection two cores were taken from each tree, while the collection for the upper site relied on one core from each tree. The cores used at the upper site were selected from the full range of samples taken to determine tree ages, and were chosen for their length and continuity. Sampling and sample preparation were done in accordance with standard dendrochronological procedures (Fritts 1976; Stokes and Smiley 1968). Samples were measured with a Henson-Bannister Incremental Measuring Machine. Samples were crossdated visually and final crossdating was done using program COFECHA (Holmes *et al*. 1986). The measured series were standardized to remove growth trend (Cook *et al.* 1990; Fritts 1976) with the help of program INDEX (Graybill 1979, 1982). In most cases this simply required fitting a negative exponential curve; about a quarter of the samples were fitted with a cubic spline curve (typically, the spline removed >50% of variance at periods of >128 yr). Comparison of ring-width plots for all of the samples suggested that the low-frequency trend removed by this process was not concurrent between the samples, indicating that the trend was related to tree-specific factors such as competition rather than to climatic variation. The standardized ring width series were averaged for each site to produce site chronologies, each of which consists of a dimensionless ring-width index time series.

Climate data

Climate data were acquired for both local stations and divisional averages (Wyoming Division 10). The local station data for high elevations in the Medicine Bow Range are incomplete and cover a relatively short period, and so are unsuitable for investigating statistical associations with annual ring width or seedling establishment. Climate data for stations at Centennial (elev. 2462 m) and Foxpark (elev. 2760 m) cover a longer period (1948 to the present) than the high elevation station data, but data are missing for several intervals within this period. The Centennial and Foxpark records are very highly correlated ($r > 0.9$) with the Division 10 averages, which cover a longer period and contain no periods with missing data. Thus, the Wyoming Division 10 averages were selected for use in all analyses. These data include monthly total precipitation and average temperature for 1895 to 1987.

Climate-growth association

Due to biological processes such as long needle retention and a large year-to-year carryover in stored carbon, tree-ring indices for trees growing near the alpine timberline tend to show high serial autocorrelation (Schweingruber 1988). To accurately assess the significance of correlations between the tree-ring and climate data, this autocorrelation was removed by autoregressive (AR) modeling of the tree-ring chronologies (Box and Jenkins 1976). The spruce chronology was best fit by an AR(2) model, while the Douglas-fir chronology required an AR(3) model. Although most monthly climate variables did not show significant autocorrelation, July and August average temperature required an AR(1) model. Model residuals were stationary, free of autocorrelation, and normally distributed, indicating that these simple AR models yielded data fitting the Ordinary Least Squares assumptions used in correlation and regression coefficient estimation (Draper and Smith 1981).

The association between tree growth and climate was assessed by calculating simple Pearson product-moment correlation coefficients between each tree-ring chronology and each monthly climate variable for an 16-month period, from the June preceding the year of ring formation to September of the year of ring formation. This interval encompasses a period in which many phenomena thought to influence ring width occur. These include the growth of new foliage, accumulation of excess food, synthesis of various growth hormones, formation of buds, fall hardening, and growth processes concurrent with actual ring formation (Fritts 1976; Kienast *et al.* 1987). Due to collinearity between some climate variables, these correlation coefficients cannot be regarded as mutually independent.

Climate-establishment and growth-establishment associations

The association between tree establishment and climate or ring width was investigated using a subset of the establishment data consisting of trees that required total dating corrections (corrections for coring height plus corrections for distance to pith) of 10 yr or less. The climate-establishment analysis period began in 1895 (the beginning of the instrumental climate data) and the ringwidth-establishment analysis period began in 1850 (before which time relatively few trees required dating corrections of <10 yr). In addition, some ringwidth-establishment analyses were conducted using a data set including all trees established since 1600.

Because few trees established in any single year and no trees established in many years, the dates of tree establishment follow a Poisson distribution with mean and variance near 1.0. However, the time series of tree establishment at both study plots have nonstationary mean and variance due to long-term trends related to gradual changes in tree establishment rates. This nonstationarity was reduced by applying a square-root transform to the establishment time series. The transformation removed low-frequency variance from the establishment series, but increased series stationarity to achieve compliance with regression model assumptions. The association between monthly climate variables and the transformed establishment series was tested by fitting a separate Poisson single linear regression model for each monthly climate variable, using the Glim program package (Aitkin *et al.* 1989; Healy 1988). As with the correlation coefficients, these regression coefficients are not independent due to collinearity between the climate variables. The strength of the association between establishment and a monthly climate variable is expressed as the coefficient of the predictor (climate) in the model, divided by its standard error (*i.e.*, the t-value).

The divisional climate data cover the period 1895-1987. Establishment at the clump plot largely ceased in 1980, but this cessation was probably not due to climate change, since years since 1980 display climate variation well within the limits of the 1895-1980 data.

Therefore, the association between climate and establishment was tested for the period 1895-1980. Because establishment at the ribbon plot largely ceased in 1963, the climate-establishment analysis for that plot was similarly truncated to the period 1895-1963. Climate-establishment associations were tested for climate variables from March to October of the year of seedling germination, a period covering one entire growing season and the period of heaviest snowfall during the preceding winter. Testing for an association between monthly climate and tree establishment implies that the year of seedling establishment could be determined with complete precision. This assumption was explored by lagging the time series of estimated establishment dates both forward and backward relative to the climate data. If this procedure produced higher correlation coefficients, it would indicate a consistent bias in estimation of establishment dates of more than 1 year.

Associations between tree establishment series and tree-ring chronologies were also tested by fitting linear regression models, again applying a square-root transform to the establishment data and assuming a Poisson distribution. For these models, either or both tree-ring chronologies were used as predictors of the establishment series. Predictors were tested at lags of from -3 to +3 yr because tree-ring widths can be affected by climate for several years before formation of a ring, while seedling establishment can be affected by climate either before establishment (*e.g.*, by affecting the timing and size of seed crops) or after establishment (*e.g.*, by affecting survivorship in young seedlings).

Tree-ring chronologies and establishment data were also compared graphically with plots including all establishment data (rather than a best-dated subset), covering the period 1600 to 1990 (during which >90% of all trees now present at each plot were established). The series were transformed with a digital filter passing variance with frequencies longer than 8 years (Fritts 1976, p.270). This facilitates visual comparison of the data, but removes degrees of freedom and thereby prevents testing the significance of any similarity between the transformed data series.

Chapter 6. RESULTS

SNOW ACCUMULATION AND MELT-OUT

Snow is perhaps the most important single variable in the physical environment at the study site. At a scale of tens of meters, as recorded by the snow survey, the depth of snowdrifts and their persistence into the growing season chiefly influence soil moisture and length of growing season, important determinants of vegetation composition and seedling establishment success.

Clump plot

Snow depths at the clump plot were quite variable, with deep snow accumulations within tree clumps and shallow accumulations in open meadow areas (Figure 6.1). The deepest drifts were >2.5 m deep in the two largest clumps, while a uniform snow depth of about 0.5 m prevailed in portions of the meadow far from any clumps. Prominent snowdrifts extended approximately 20 m to leeward of tree clumps 3, 4 and 5 (see Figure 6.2 for clump numbers). At the beginning of the growing season, these areas were occupied by late-melting snowdrifts. The steepest gradients in snow depth were developed on the windward and northern edges of these clumps, while a relatively shallow depth gradient extended southward. Clumps 1 and 12 developed minor leeward snowdrifts and contained few trees that projected above the snow surface, compared with clumps 3, 4 and 5. The other tree clumps did not display prominent leeward snowdrifts and exposed very little foliage above the snow surface. This suggests that clumps affect snow deposition in proportion to the number and size of trees exposed above the snow surface, presumably by affecting surface windflows.

Ribbon plot

Snow depths at the ribbon plot were as variable as at the clump plot, but the patterns of snow accumulation were markedly different (Figure 6.3). Snows were uniformly deep in the meadows, with an average depth of 1.8 m. The wind had blown out a trough along the windward forest edge, along which the snow was ≈1 m deep over a band 1-3 m wide. In the spring the snow melts early along this trough, but the deeper snow immediately to the windward persists much later in the growing season. Most of the ribbon forest interior contains winter snow depths of about 1.4 m, but snow depth within the ribbon is more

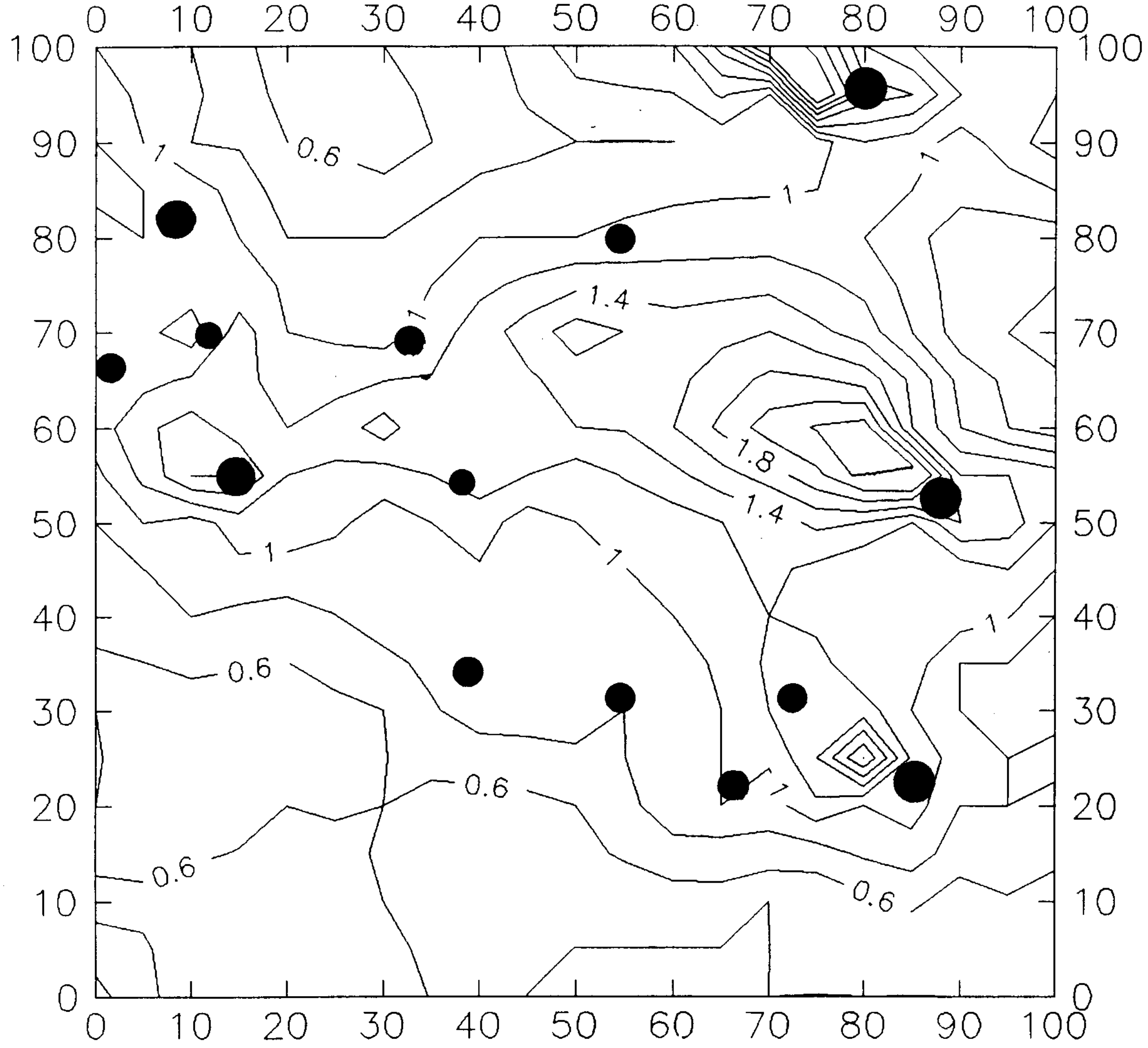

Figure 6.1. Map of snow depths at the clump plot. Large and small dots represent centers of the 5 large and 9 small clumps, respectively. Scale in meters; contour interval 0.2 m.

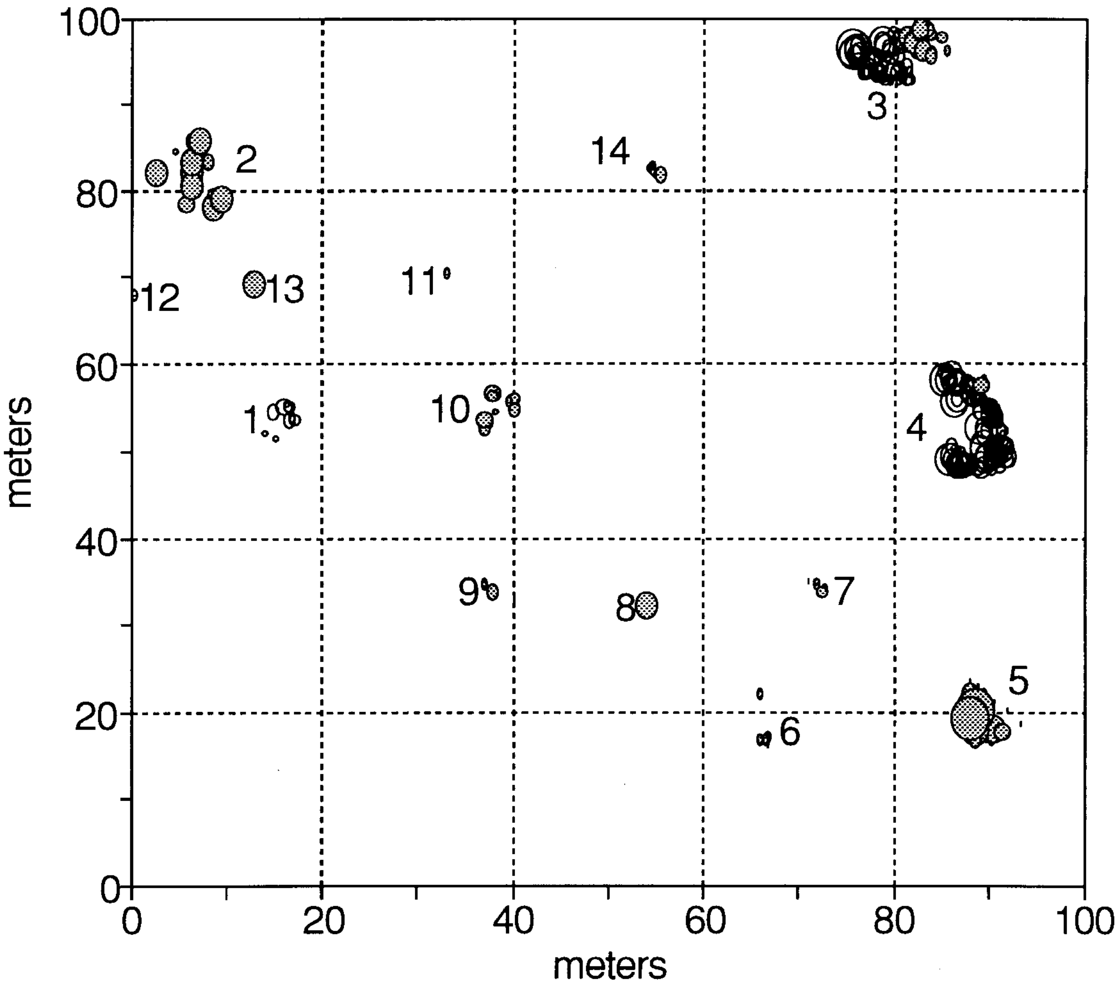

Figure 6.2. Stem map for the clump plot. Windward edge of plot is at right. Circle diameter is proportional to DBH but has been exaggerated by 15×. Clumps are numbered for identification in the text.

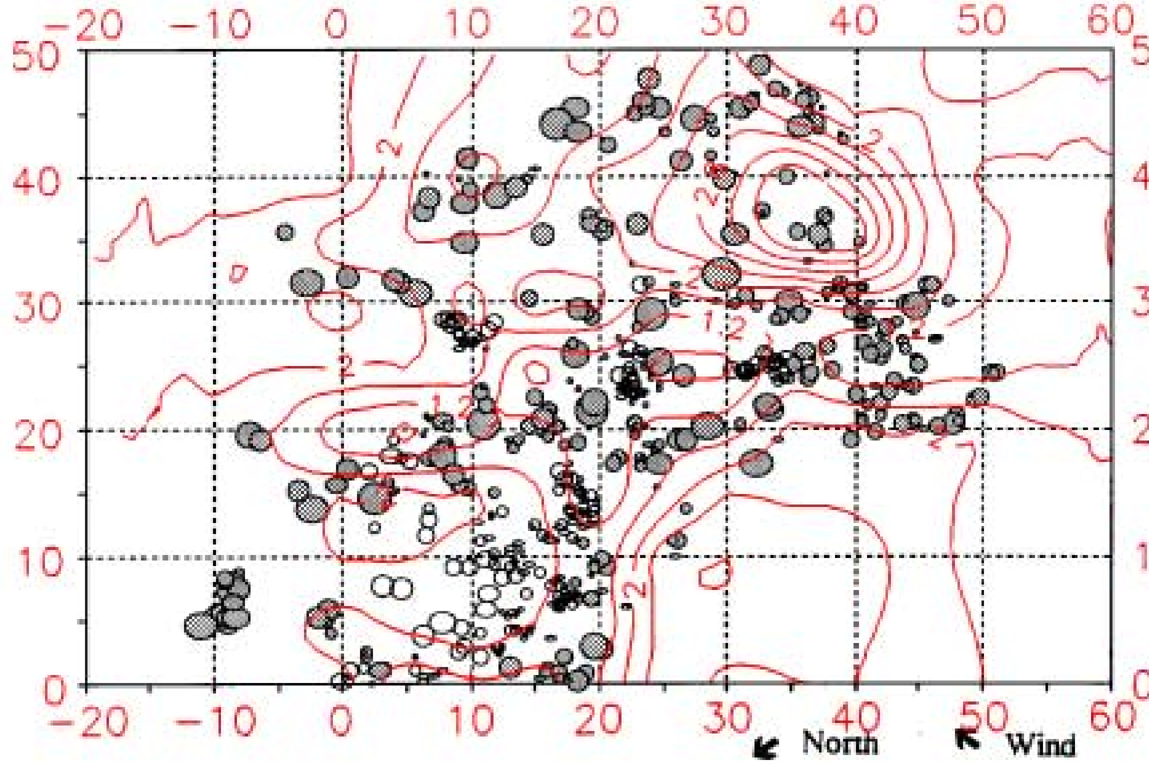

Figure 6.3. Map of snow depths at the ribbon plot, overlaid on a stem plot. Scale in meters; contour interval 0.4 m. Windward edge of plot is at right. In the stem map, circle diameter is proportional to DBH but has been exaggerated by 4x.

variable than in the adjacent meadow, ranging from 0.6 m to >3.0 m. Generally, snow depths are less in areas with a high density of small stems, and greater in areas with scattered large stems. At the leeward edge of the forest and in the adjacent meadow snows are generally 2.0-2.5 m deep. This deep snowdrift extends across the leeward meadow for *ca.* 70 m, reaching the edge of the next ribbon to the east.

VEGETATION

The meadows at both plots are dominated by grasses, chiefly *Deschampsia cespitosa*, and sedges, chiefly *Carex haydeniana*, with an associated forb community dominated by *Sibbaldia procumbens*. These species are characteristic of the Dry Meadow and Wet Meadow associations of Thilenius (1970), who noted that "a great deal of floristic gradation is present between communities... due mainly to gradations in available moisture which appears to be a major environmental factor in the alpine zone."

Clump plot

Two clearly distinct meadow communities exist on the tree clump plot, one dominated by grasses and sedges and the other by forbs (Table 6.1; Figure 6.4). A grassy meadow dominated by *Deschampsia cespitosa* covers most of the plot (see Figure 4.4). In this meadow *Deschampsia* typically accounts for >35% of the ground cover in each 5 m × 5 m grid square. The sedges, *Carex haydeniana* and *C. aquatilis*, are secondary dominants varying in cover from 5% on relatively xeric to 35% on relatively mesic grid squares. The most xeric microsites are typically found near the windward and lateral edges of each clump. Conversely, the forb-rich, very mesic community is only found immediately leeward (*i.e.*, over a distance not longer than the height of the clump) of the three largest tree clumps (clumps 3, 4 and 5 in Figure 6.2). *Sibbaldia procumbens* and *Juncus drummondii* account for 30% to 94% of cover in these areas. Small tufts of *Deschampsia* and *Antennaria rosea* are also present with 6% to 70% cover. This community coincides with the location of the latest-melting snowdrifts and is underlain by wet soils through most of the summer. Finally, an understory community occurs within the tree clumps. The dominant cover in this relatively dark, cool environment is conifer needle litter, accompanied by locally abundant *Ribes montigenum* and very low cover of a few forbs; *Deschampsia* occurs here as well.

Table 6.1. Plant species found on the clump and ribbon plots.

1: Clump plot, grassy meadow.
2: Clump plot, forb meadow.
3: Clump plot, forest understory
4: Ribbon plot, meadow.
5: Ribbon plot, forest understory.

	1	2	3	4	5
Deschampsia cespitosa	X	X	X	X	
Senecio dimorphophyllus	X	X	X	X	
Artemisia scopulorum	X	X		X	
Juncus drummondii	X	X		X	
Vaccinium cespitosum	X	X		X	
Potentilla diversifolia	X			X	X
Polygonum bistortoides	X			X	
Erigeron simplex	X			X	
Carex haydeniana	X			X	
Phleum alpinum	X			X	
Salix brachycarpa	X				
Trifolium parryi	X				
Geum rossii	X				
Carex aquatilis	X				
Carex atrata	X				
Danthonia intermedia	X				
Trifolium dasyphyllum	X				
Gentiana algida	X				
Pedicularis groenlandica	X				
Salix planifolia	X				
Mertensia ciliata			X		
Thlaspi montanum			X		
Abies lasiocarpa			X		X
Picea engelmannii			X		X
Ribes montigenum			X		X
Lewisia pygmaea		X		X	
Antennaria rosea		X		X	
Sibbaldia procumbens		X		X	
Erigeron melanocephalus		X		X	
Erigeron peregrinus				X	
Festuca brachyphylla				X	
Carex nigricans				X	
Pedicularis bracteosa					X
Poa cusickii					X
Vaccinium scoparium					X
Arnica latifolia					X

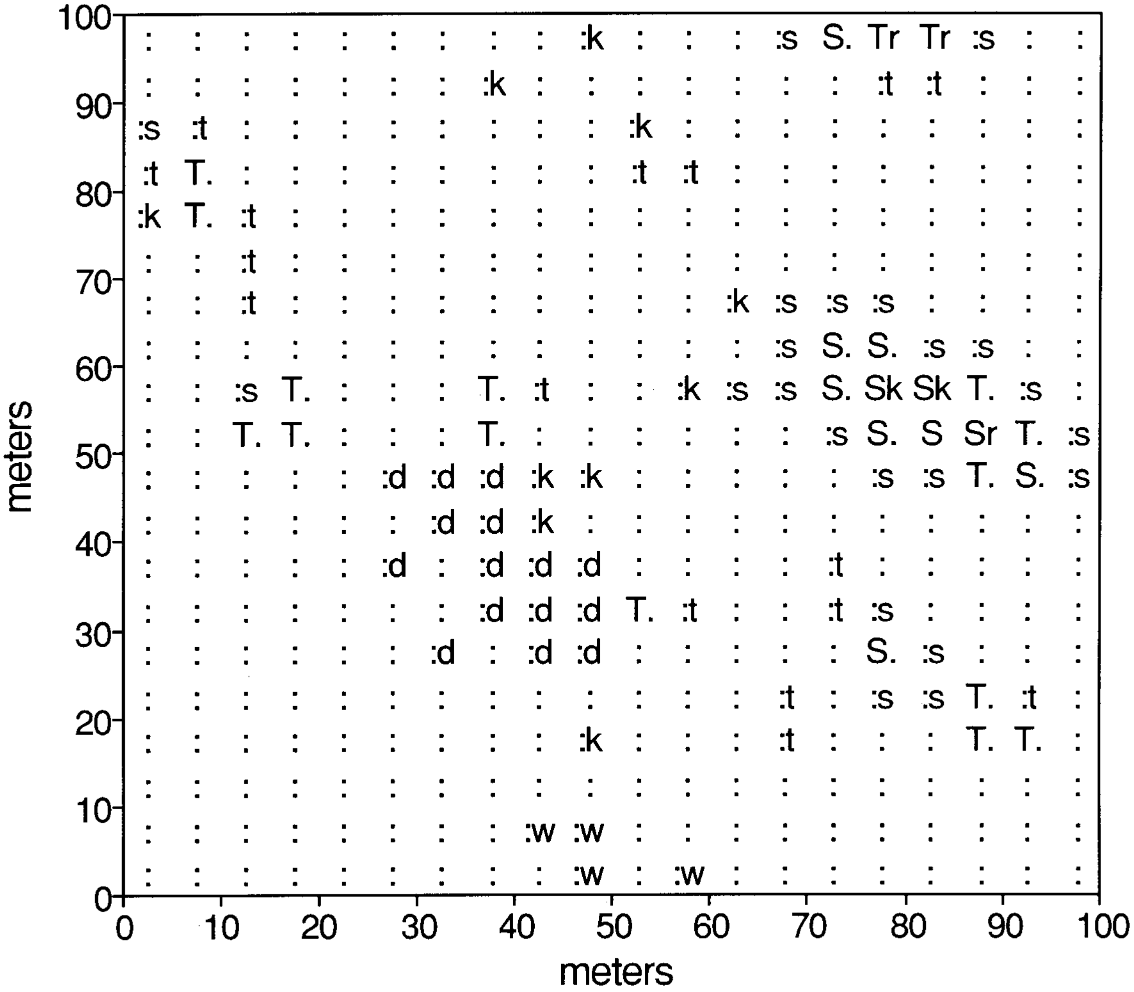

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Figure 6.4. Map of vegetation on the clump plot. For each 5 by 5 m cell, the first symbol indicates the dominant cover type and the second symbol indicates the secondary cover type, if the dominant type covers less than 90% of the cell, as follows:

Cover type	Dominant	Secondary
Spruce and fir	T	t
Ribes		r
Sibbaldia	S	s
Grass	:	.
Sedge		d
Salix		x
Rock		k

Note that "T" cover type indicates locations of clumps.

Ribbon plot

The meadow at the ribbon plot is clearly more mesic than at the clump plot, containing vegetation matching the Wet Meadow association of Thilenius (1970). For example, the herbs *Sibbaldia procumbens* and *Antennaria rosea*, which are largely restricted to the wet, clump-leeward meadows at the clump plot, are widespread in meadows at the ribbon plot. Parts of the meadow located far from the ribbon are relatively dry, dominated by *Deschampsia cespitosa* (Figure 6.5). *Sibbaldia*-dominated meadow forms a nearly unbroken band along both windward and leeward margins of the ribbon and patches of *Sibbaldia* occur in light gaps within the ribbon. In these areas *Sibbaldia* apparently indicates wet, cold soils that coincide with the location of late-melting snowdrifts.

The *Sibbaldia* meadow along the leeward edge of the ribbon has 30% to 65% bare ground in each 5 m × 5 m grid square. Many lines of bare soil and vegetation clippings are present, indicating that the herbs in this area are heavily grazed by rodents during the winter months. Although the ribbon plot is subject to sheep grazing, the sheep were seen to avoid areas dominated by *Sibbaldia* in preference for *Deschampsia* meadows. The presence of sheep is reflected in the vegetation by abundant *Erigeron melanocephalus*, an indicator of disturbed sites, along a faint sheep trail passing through the windward meadow.

The understory of the ribbon forest is depauperate. Bare ground, dead wood or needle litter typically account for 50% to 80% of the cover, and the woody shrubs *Ribes montigenum* and *Vaccinium scoparium* are dominant. *Vaccinium* here, as in neighboring closed-canopy subalpine forest, occurs primarily in small light gaps. *Ribes* is most prevalent near the leeward edge of the ribbon (Figure 6.5), but nearly absent near the windward edge. At the leeward edge, *Ribes* extends 1 m to 2 m into the meadow from the forest edge. It may grow farther to leeward along the edges of spruce logs that have fallen into the meadow. This distribution suggests that dead wood, forest litter, shade and persistent snowpack on the leeward edge create conditions suitable for the growth of *Ribes*.

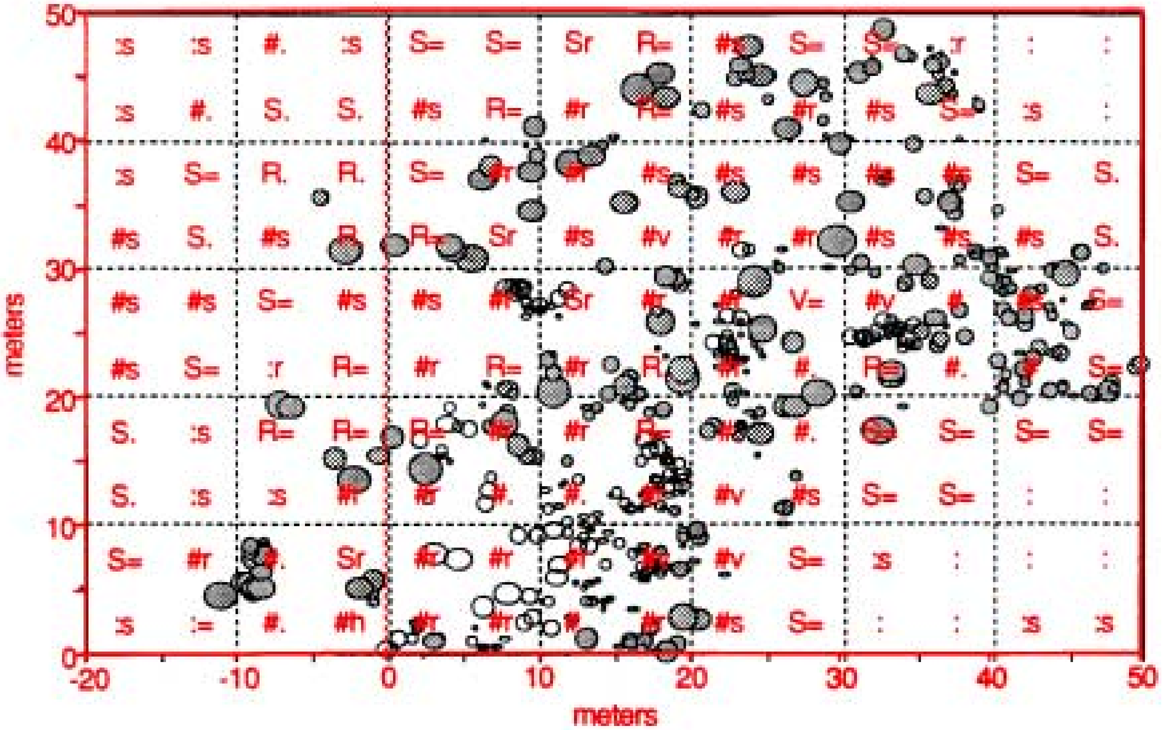


Figure 6.5. Map of vegetation on the ribbon plot, overlaid on a stem plot. For each 5 by 5 m cell, the first symbol indicates the dominant cover type and the second symbol indicates the secondary cover type, if the dominant type covers less than 90% of the cell, as follows:

Cover type	Dominant	Secondary
Ribes	R	r
Sibbaldia	S	s
Grass	:	.
Bare ground	#	=
Vaccinium	V	v

DESCRIPTION OF TREE POPULATIONS

Clump plot

The clump plot contains 352 trees in 14 clumps, with a total basal area of 2.04 m^2 on a 1 ha plot. Fir accounts for 69% of the stems and 65% of the basal area; the remainder is spruce (Table 6.2, Figures 6.2 and 6.6). Tree diameters ranged from 0 (90 stems < 1.4 m tall) to >25 cm (3 stems). For both spruce and fir, most stems are in the 0-5 cm size class (Figure 6.7), with exponentially decreasing numbers of stems in larger size classes. Fir is more numerous than spruce in all but the largest size class.

The five oldest clumps (clumps 1 to 5 in Figure 6.2) contain 84% of the stems and 96% of the basal area on the plot. Clumps 1 and 4 are fir clumps, clumps 2 and 5 spruce clumps, and clump 3 contains both species. All five clumps contain snags, logs, and live trees. The remaining nine clumps, numbered 6 to 14, contain only spruce, with 1 to 14 stems per clump. The stems in these clumps are uniformly small, with an average DBH of 2.7 cm; 42% of the stems are shorter than 1.4 m and thus, have a DBH of zero. The small clumps consist of a krummholz mat approximately 1.0 m tall, surmounted by one to several released, wind-flagged leaders. These clumps are nearly devoid of dead wood.

At short distances, the spatial pattern of the clumps is strongly dispersed (Table 6.3). For instance, the random pattern model indicates that the smallest clump-to-nearest-clump distance should be 5.2 m while the smallest observed distance is 11.9 m. At this scale, the observed spatial pattern of clumps differs from randomness with 99% confidence. This confidence level drops steadily at larger scales up to the clump-to-seventh-nearest-clump distance, which in a random model is 12.0 m and in the observed data is 17.3 m. This differs from a random point pattern with only 63% confidence. At larger spatial scales, the observed data differ from a random point pattern with less than 65% confidence. Since the clumps vary in diameter from 2 to 13 meters, the clumps generally do not occur within a distance of several clump diameters of each other. This finding suggests that some process may be inhibiting the juxtaposition of clumps. However, the spatial pattern of the clumps does not either confirm the existence of such a process or demonstrate a possible mechanism.

Table 6.2. Summary of tree numbers and basal areas for the clump plot

Basal area is calculated as stem cross-sectional area at breast height; trees shorter than breast height were assigned a DBH of 0.5 cm (area = 0.79 cm^2). Percentages are given relative to the total number of all trees and the total basal area for the plot.

Species	Alive or Dead	Number of trees	%	Basal area (m^2ha^{-1})	%
fir	alive	209	59.4%	1.15	56.5%
fir	dead	34	9.7%	0.17	8.1%
spruce	alive	99	28.1%	0.55	27.0%
spruce	dead	10	2.8%	0.17	8.4%
fir+spruce	alive	308	87.5%	1.71	83.5%
fir+spruce	dead	44	12.5%	0.34	16.5%
fir	alive+dead	243	69.0%	1.32	64.6%
spruce	alive+dead	109	31.0%	0.72	35.4%
fir+spruce	alive+dead	352	100.0%	2.04	100.0%

Table 6.3. Results of clump location modeling.

Note: "Order" is clump to n-th nearest clump distance, from smallest (1) to fourteenth-smallest (14). "Observed" is the observed clump to n-th nearest clump distance, and "Expected" is the mean of these distances for the 99 model realizations. "Rank" is the rank of the observed tree clump data relative to 99 realizations of a spatially random point array model and corresponds to the significance level of the departure from the random model.

Order	Observed (m)	Expected (m)	Rank
1	11.9	5.2	99
2	13.7	7.9	97
3	15.2	10.2	95
4	15.6	12.0	89
5	16.1	13.5	82
6	16.8	14.7	73
7	17.3	16.0	63
8	18.1	17.0	64
9	18.8	18.2	61
10	20.5	19.5	65
11	20.8	20.6	55
12	21.2	21.7	56
13	22.3	22.8	44
14	22.8	23.9	40

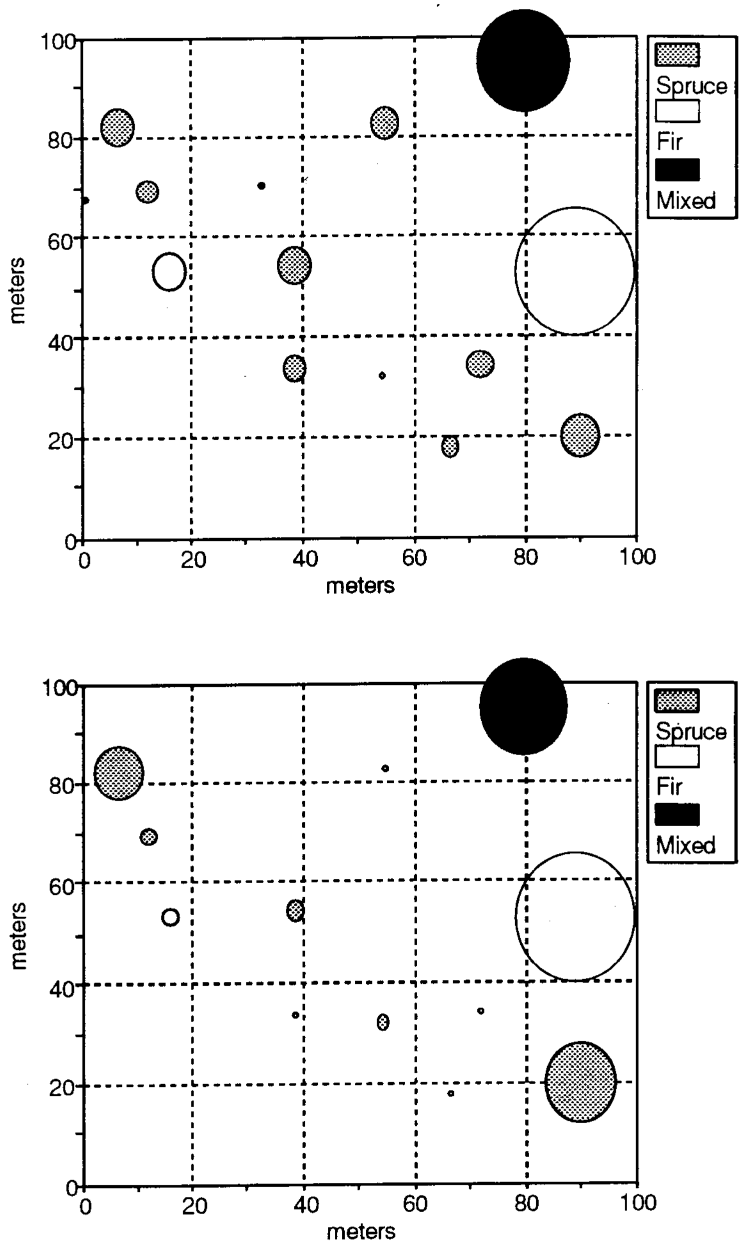


Figure 6.6. Map showing stem number (above) and basal area (below) for the clump site. Diameter of each circle is proportional to the number of stems or total basal area of the clump. Data have been normalized so that clump 4 is the same size in both maps.

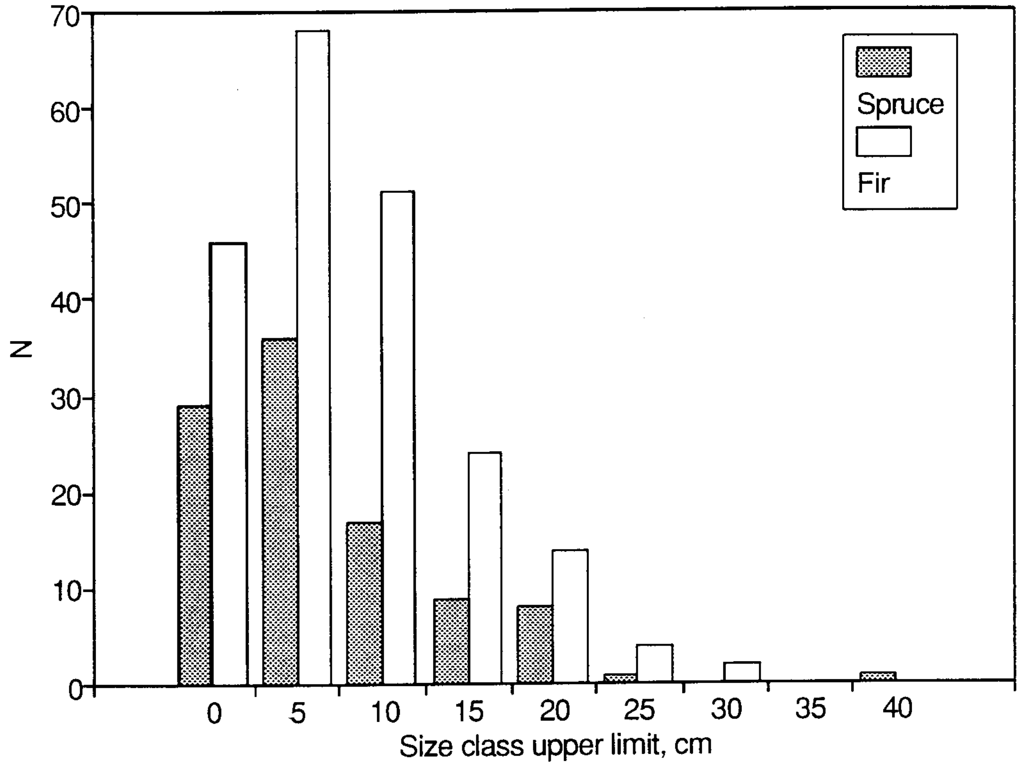


Figure 6.7. Diameter class histogram for trees at the clump plot.

Ribbon plot

The ribbon plot contains 660 trees. Spruce predominates, accounting for 57% of the trees and 81% of the stem basal area (Table 6.4). Total basal area is 18.6 m^2, 46.6 m^2ha^{-1}. This is 4.85 times the average basal area per tree and 22.5 times the basal area per hectare at the clump plot. Snags contribute 9% of stems and 9% of basal area. They represent decay classes 1 to 3 (predominantly 2) and proportionally represent the living tree population according to species, establishment mode, and size class.

Tree diameters are much larger than at the clump plot, ranging up to 83 cm. The size structure of fir at the ribbon plot resembles that seen at the clump plot, with a peak in the 0-5 cm size class and exponentially decreasing numbers of larger stems (Figure 6.8a). The smaller fir stems are predominantly clonal, and clonal stems account for most of the variation between size classes. Similar numbers of nonclonal stems occurred in each size class up to 26-30 cm. Conversely, spruce shows similar numbers of trees in all size classes up to 16-20 cm (Figure 6.8b), with exponentially decreasing numbers of stems in the larger size classes. Clonal trees are more prevalent in the smaller than the larger size classes, but the proportion of clonal trees is much smaller for spruce than for fir.

The ribbon has a heterogeneous structure (Figure 6.9). Most trees are in clumps that vary widely in numbers of stems, size of stems, and tightness of clumping. Large stems are fairly uniformly distributed across the plot, while most small stems are in large clumps or near the windward edge of the ribbon. Nearly all fir stems are associated with discrete clumps that are now within the interior of the ribbon. Conversely, spruce is distributed across the whole ribbon except in areas with dense fir clumps. Spruce clumps typically contain only a few trees, although one large spruce clump is growing along the leeward edge of the ribbon (centered at (-9, 7) in Figure 6.9). Large spruce predominate in the south-leeward area (at X<30, Y>30 in Figure 6.9), while small spruce are abundant near the windward edge. A "peninsula" extending into the windward meadow (at X>40 in Figure 6.9) consists mostly of spruce 5-20 cm in diameter.

Stem density is highest near the windward edge and in the central part of the ribbon, where the fir clumps occur (Figure 6.10). Moderately high densities occur in the "peninsula" and the leeward spruce clump. Basal area shows a much different pattern than stem density (Figure 6.11). High values occur at a variety of locations across the interior of the plot. The large spruce section (at X<30, Y>30 in Figure 6.9), the leeward spruce clump, the "peninsula," and the central area of fir clumps all make distinct contributions to basal area. Thus, despite wide variations in tree diameter and stem density, basal area is roughly uniform across the ribbon.

Establishment by layering produced 79% of the stems and 64% of the basal area in fir, but only 31% of the stems and 24% of the basal area in spruce (Table 6.4). In both species, trees established from seed had a larger mean basal area than trees established by layering (51% larger for spruce, 126% larger for fir). Fir clones were fewer and larger than spruce clones (Figure 6.12); the median size of fir clones was 9.5 trees (N=16), while the median for spruce clones was 2.5 trees (N=33).

Stem density and basal area vary considerably between clonal and nonclonal trees. The highest values of stem density (Figure 6.13) occur within fir clones at the core of the ribbon. Moderately high densities mark several small spruce clones in the "peninsula." The stem density of nonclonal trees is less variable across the ribbon (Figure 6.14), with moderately high values in the region of abundant small stems near the windward edge of the ribbon and at the leeward-edge spruce clump. Basal area shows a different pattern (Figures 6.15 and 6.16). For clonal trees, the highest basal area values occur around the central and southerly fir clumps because these clumps contain relatively large stems compared to other fir clumps. For nonclonal trees, basal area is high in the large spruce area (at X<30, Y>30 in Figure 6.9) and at the leeward spruce clump. These areas contain many large trees (diameter >40 cm). The "peninsula" has a moderately high basal area. Conversely, low basal areas occur in a band across the middle of the ribbon, reflecting the occurrence of several large, clonal fir clumps that have largely excluded nonclonal stems. The fairly uniform basal area across the plot (Figure 6.11) is therefore apportioned between a central peak of clonal fir and several different peaks of nonclonal spruce.

DEMOGRAPHY

Demographic variation here includes all data relating to the dates of tree establishment and, where relevant, mortality. A number of technical points must first be considered, relating to uncertainties in the estimation of these dates and problems with loss of data due to tree decay. The data then permit development of age structures and estimation of changes in the rate of establishment, mortality, and net population change.

Table 6.4. Summary of tree numbers and basal areas for the ribbon plot.

Note: Each line of the table provides summary statistics for a fraction of the ribbon plot tree population: clonal and/or nonclonal, alive and/or dead, spruce and/or fir trees. Basal area is calculated as stem cross-sectional area at breast height; trees shorter than breast height were assigned a DBH of 0.5 cm (area = 0.79 cm^2). "Clonal" indicates the trees are (Y) or are not (N) clonal. Percentages are given relative to the total number of all trees and the total basal area for the plot.

Species	Alive or Dead	Clonal	Number of trees	% of Number	Basal area (m^2ha^{-1})	% of Basal area
spruce	alive+dead	Y	114	17.3%	8.88	19.1%
spruce	alive+dead	N	260	39.4%	28.83	61.9%
fir	alive+dead	Y	228	34.5%	5.63	12.1%
fir	alive+dead	N	58	8.8%	3.23	6.9%
fir+spruce	alive	both	601	91.1%	16.95	91.0%
fir+spruce	dead	both	59	8.9%	1.67	9.0%
spruce	alive+dead	both	374	56.7%	15.08	81.0%
fir	alive+dead	both	286	43.3%	3.54	19.0%
fir+spruce	alive+dead	both	660	100.0%	18.62	100.0%

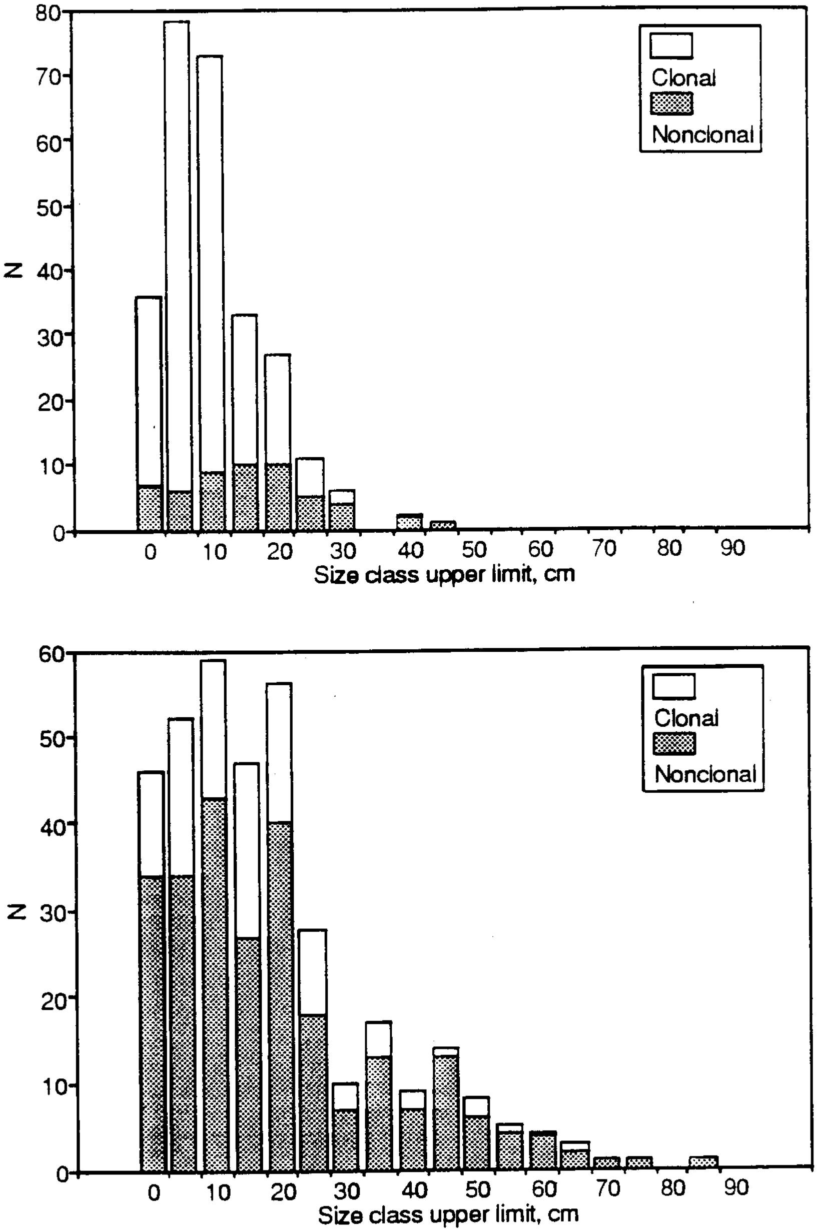


Figure 6.8. Diameter size class histograms for fir (above) and spruce (below) at the ribbon plot.

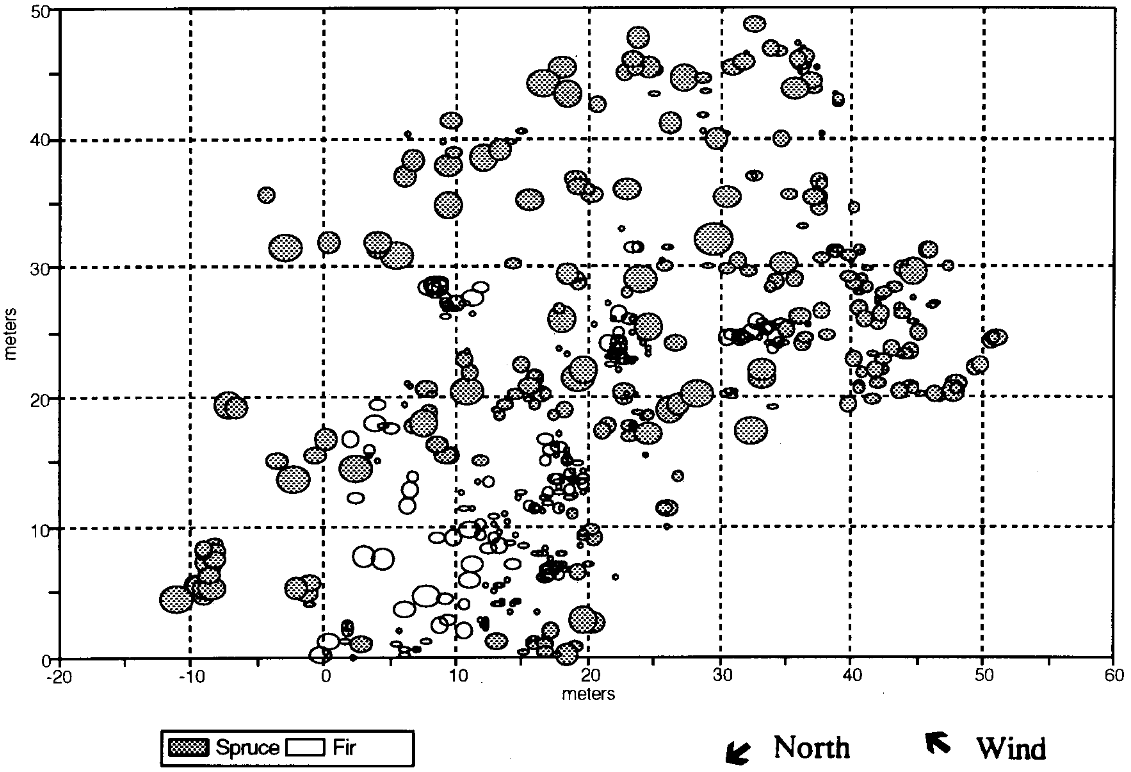
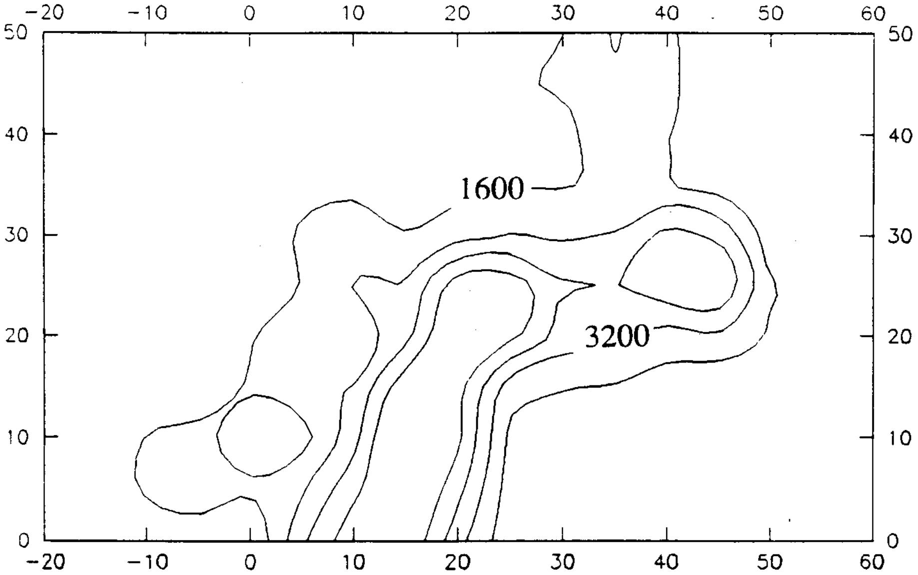


Figure 6.9. Stem map for the ribbon plot. Windward edge of plot is at right. Circle diameter is proportional to DBH but has been exaggerated by 4x.



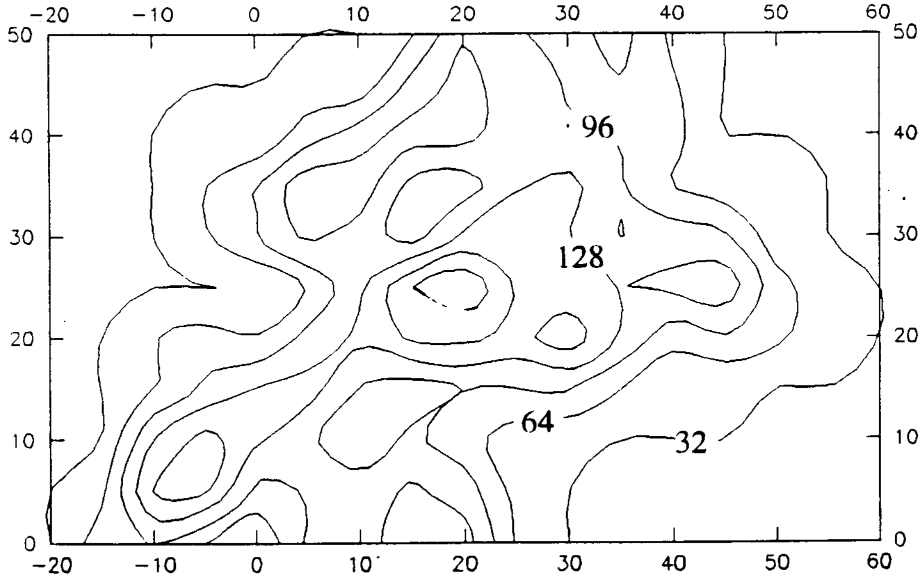


Figure 6.10 (above). Stem density map for all trees at the ribbon site. Contour interval is 1600 trees ha^{-1}, with a value of zero at the windward and leeward plot edges and the maximum contour at 6400 trees ha^{-1}.

Figure 6.11 (below). Basal area density map for all trees at the ribbon site. The contour interval is 32 m^{2}ha^{-1}with the maximum contour at 192 m^{2}ha^{-1}.

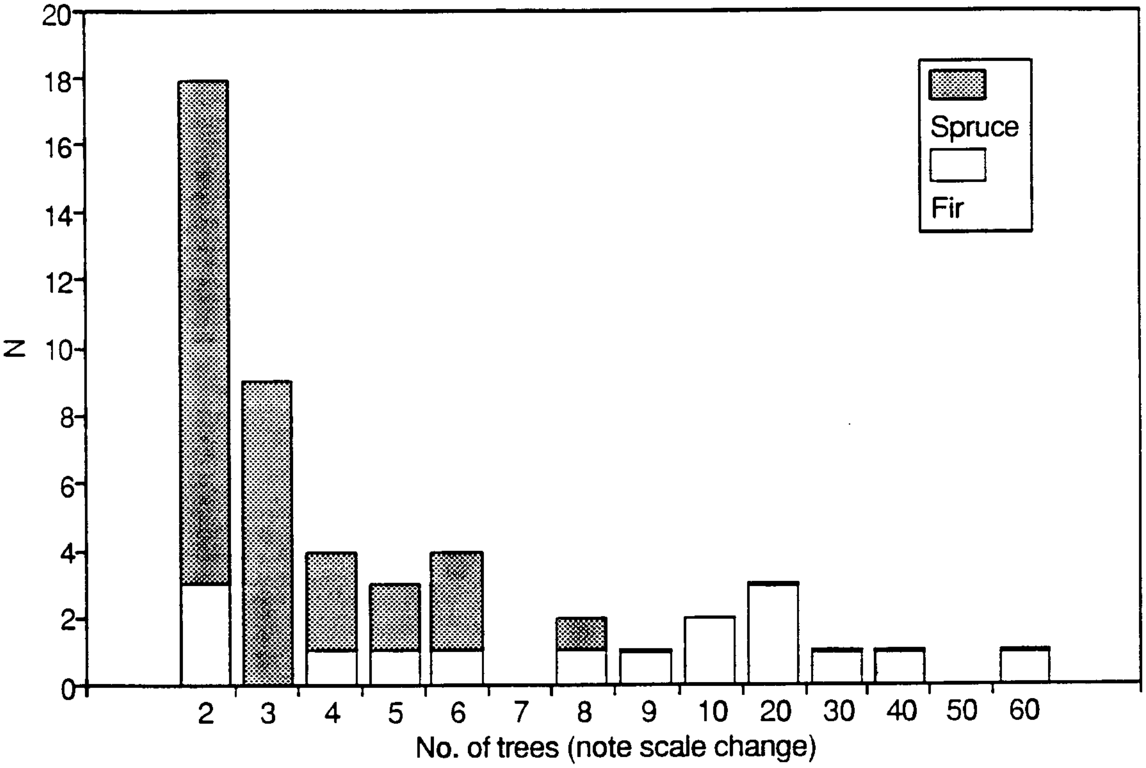
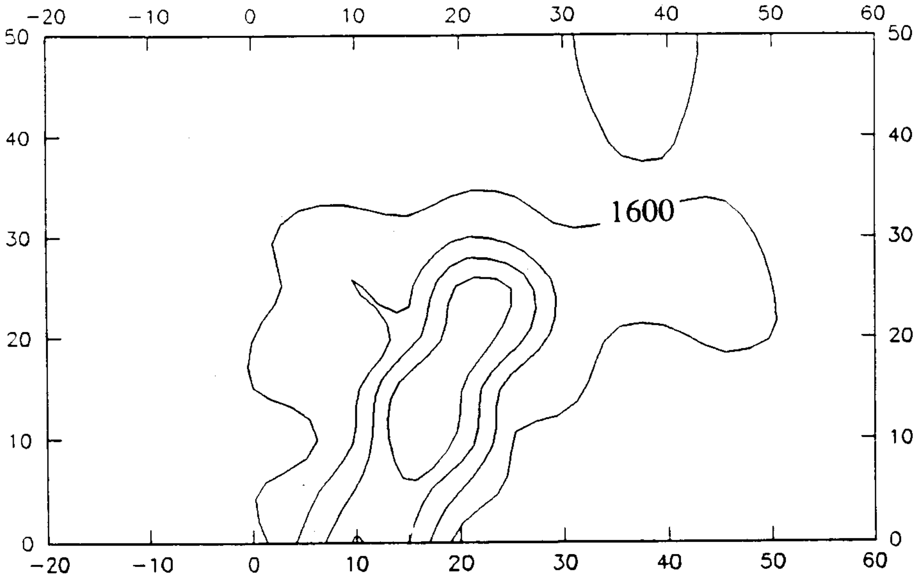


Figure 6.12. Histogram showing size of clones at the ribbon site according to species. 33 spruce and 16 fir clones are represented. Note scale change at 10 trees per clone.



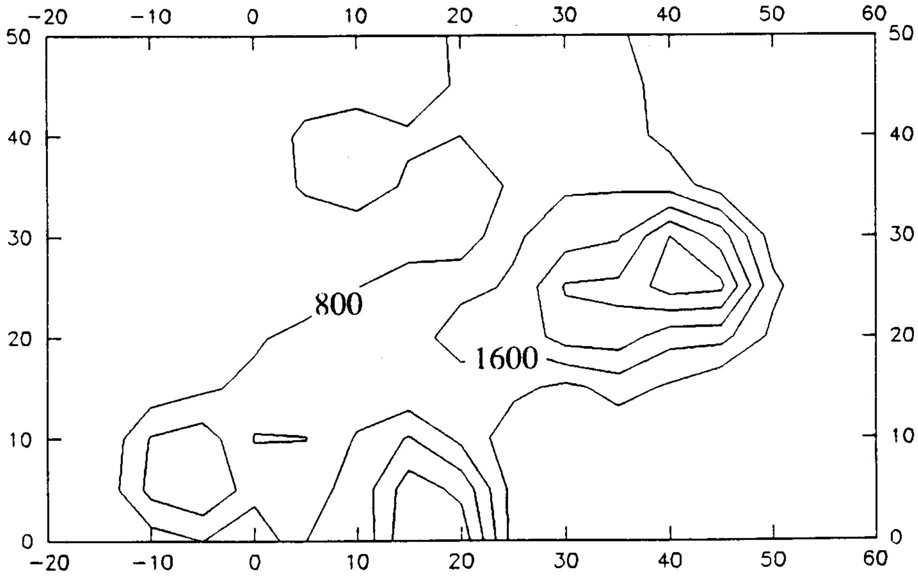
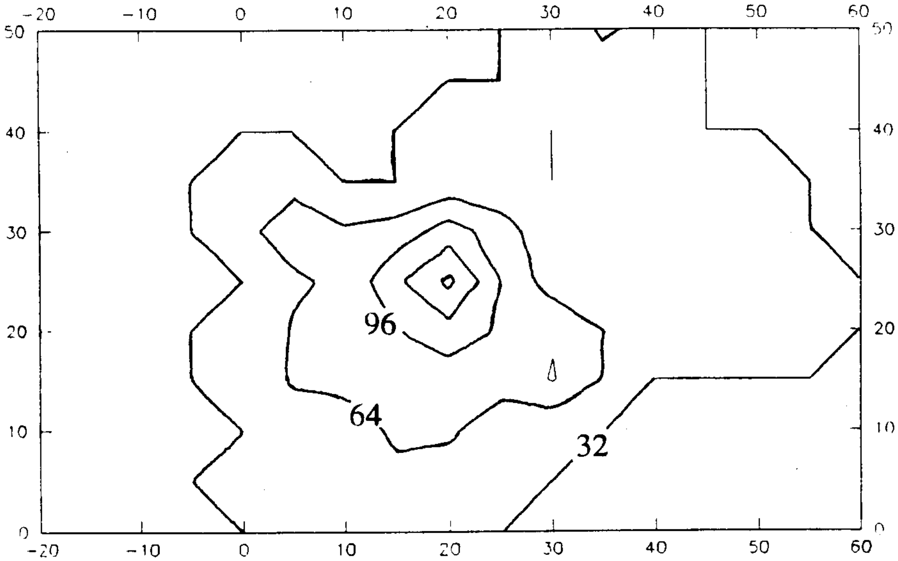


Figure 6.13 (above). Stem number density map for clonal trees at the ribbon site. The contour interval is 1600 trees ha^{-1}, with the maximum contour at 6400 trees ha^{-1}.

Figure 6.14 (below). Stem number density map for seed-established trees at the ribbon site. The contour interval is 800 trees ha^{-1}, with the maximum contour at 4000 trees ha^{-1}.



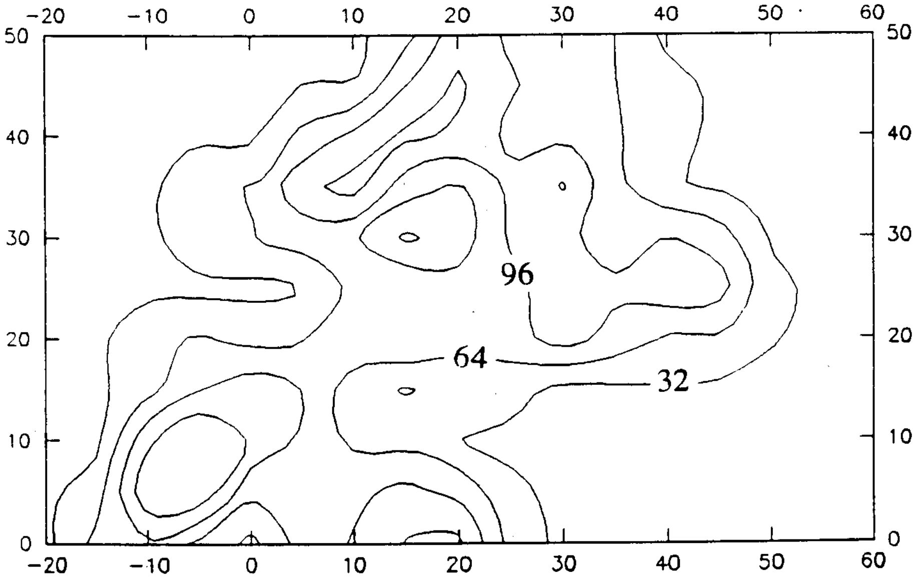


Figure 6.15 (above). Basal area density map for clonal trees at the ribbon site. The contour interval is 32 m^2ha^{-1}, with the maximum contour at 160 m^2ha^{-1}.

Figure 6.16 (below). Basal area density map for seed-established trees at the ribbon site. The contour interval is 32 m^2ha^{-1}, with the maximum contour at 128 m^2ha^{-1}.

Data constraints

Estimation of tree establishment dates required age corrections for distance to pith and for sampling height above the tree's base. The accuracy of these corrections is difficult to estimate. The standard errors for regressions used to estimate the height growth correction were 6.0 yr (75.9% explained variance) for fir and 4.8 yr (85.6% explained variance) for spruce, indicating that the height correction will be accurate to within ±5 yr about 50% of the time for both species.

Estimating rates of establishment and mortality involves three distinct problems:

1. Some trees were present on the site before the establishment of the oldest living trees. This fact is apparent from the existence of a few large (ca. 60 cm diameter) decay class 4 and 5 logs. If we assume that these trees lived to be as old as large spruces now growing on the plot, and that such trees died no later than the early 1800's, then these trees must have established 150-200 yr before the large spruces now present on the plot. Since these trees are not counted as part of the population at any time, they will cause a slight overestimation in estimates of establishment rate. Trees that died more recently are more likely to have remained intact and been sampled, so this bias will decline toward the present as the fraction of unrepresented trees diminishes.

2. Some trees established after the beginning of the record, have since died and fully decayed, and now are absent from the plot. These trees will represent a variable bias on establishment rates and a negative bias on mortality rates. Since a large fraction (53%) of the modern living and dead tree population consists of relatively small (<10 cm DBH) stems and none of these small stems were found to have died before 1800, this bias may be quite important in the early part of the record. However, it is likely to be a relatively minor factor during the period since 1850. For this period, there are many recorded death dates of small trees, suggesting that the record of mortality is largely complete. This period has also seen the establishment of 57% of the stems now present on the plot, and thus accounts for the most detailed period of establishment data. It is therefore treated as the focus period for demographic inferences.

3. Death dates were only determined for 54 out a total of 162 snags, stumps, or logs. As will be shown, decay class is a poor proxy for death date at this site. Therefore this problem is simply corrected by increasing mortality rate estimates for each time interval by a factor of 3 (162 ÷ 54 = 3.0). Although this correction is an oversimplification because it

assumes a constant proportion of undetermined death dates over time, establishment rates are so much greater than mortality rates that errors in mortality rate estimation can only produce a minor bias in net population growth rate estimates.

Clump plot

Establishment

Age corrections for distance to pith and for sampling above the tree's base tend to increase with a tree's estimated age (Table 6.5). Corrections for sampling height were not required for 54% of the trees; the mean correction was 8.5 yr. Corrections for distance to pith were more variable. Although no pith correction was required for 44% of the trees, pith corrections of more than 100 years were required for four of the oldest trees; the mean correction was 8.4 yr (median 1 yr). The 67% of the trees that have established since 1850 required a mean total correction for sampling height and distance to pith of 9 yr or less (median 1 yr).

Tree clump establishment dates fall into two large classes. The largest clumps (clumps 1 to 5 in Figure 6.2) contain decay class 4 and 5 stumps and logs that could not be dated. The presence of these logs indicates that these clumps originated substantially earlier than the oldest trees in the clumps. Since these clumps contained living trees over 300 yr old, the stumps and logs are likely remnants of trees established before 1500. The small spruce clumps, numbered 6 to 14, contain little or no dead wood and probably originated with establishment of the oldest living stem in each clump (*i.e.*, between 1860 and 1927) (Figure 6.17).

Both spruce and fir show a long period of sporadic establishment, then a period of more rapid establishment to a more or less well-defined peak, closing with a decline to low present levels. The timing of these three phases differs between the two species. Fir establishment (Figure 6.18a) spans the interval from 1627 to 1978. Establishment was sporadic until about 1750, increased rapidly until 1820, and remained high from 1821 to 1930, during which time 10 to 15 trees established in most decades. Establishment has declined steeply since the 1930's. Although living spruces established between 1600 and 1977, approximately the same period as fir (Figure 6.18b), spruce establishment was generally less continuous than fir establishment. Only 10 living spruce originated during the period of sporadic establishment (before 1800). Establishment increased from 1810 to

Table 6.5. Age estimation corrections for clump plot trees.

Note: "Height" is the mean correction for sampling height for trees established within an interval, "Pith" is the mean correction for distance to pith, and "Total" is the sum of these corrections. "N" is the number of trees established within the interval. "Percent" is the fraction of the total population of aged trees established within the interval. The last three lines indicate the number and percent of trees established during the entire period of record for which the height, pith, and age corrections, respectively, were zero.

Interval	Height	Pith	Total	N	Percent
<1550	23	>100	>100	4	1.1%
1550-1599	18	>100	>100	1	0.3%
1600-1649	23	56	71	2	0.6%
1650-1699	47	12	58	7	2.3%
1700-1749	42	27	61	7	2.3%
1750-1799	27	20	44	23	7.4%
1800-1849	14	12	26	58	18.6%
1850-1899	8	8	15	87	28.0%
1900-1949	2	4	6	98	31.5%
1950-1989	1	1	2	24	7.7%
1764-1981	0			169	54.3%
1764-1981		0		138	44.4%
1764-1981			0	122	39.2%

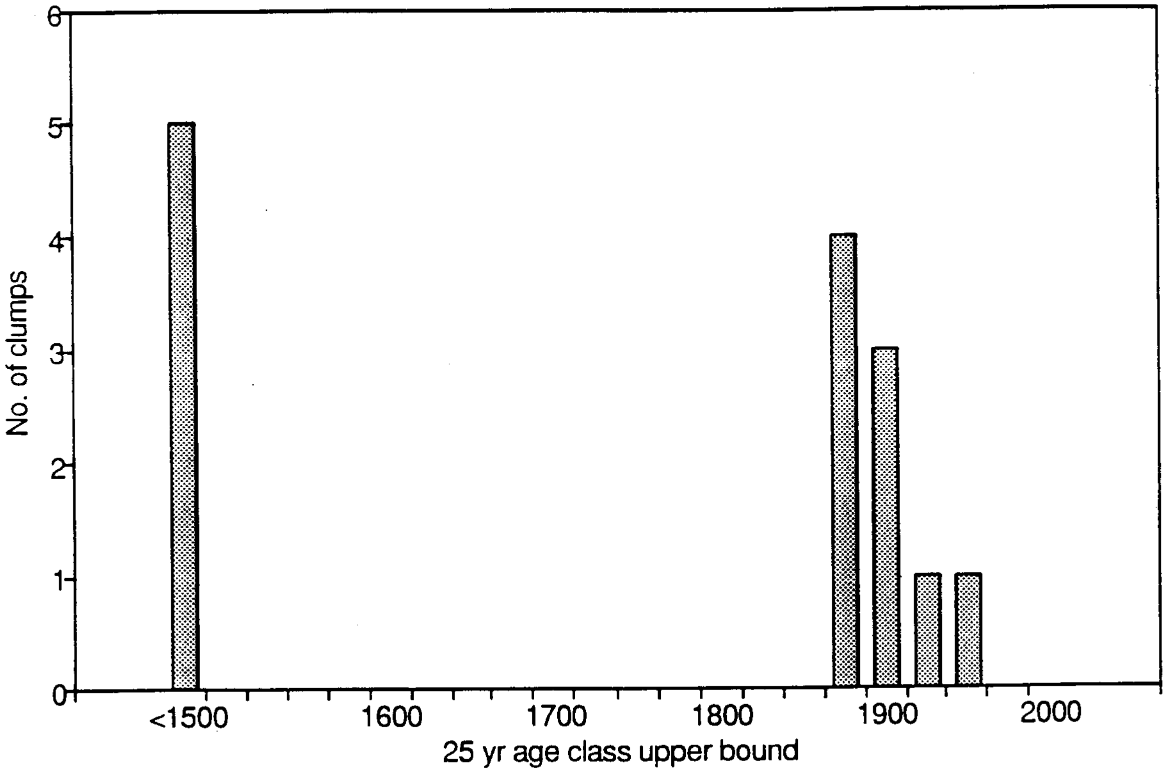


Figure 6.17. Age class histogram for clumps at the clump plot.

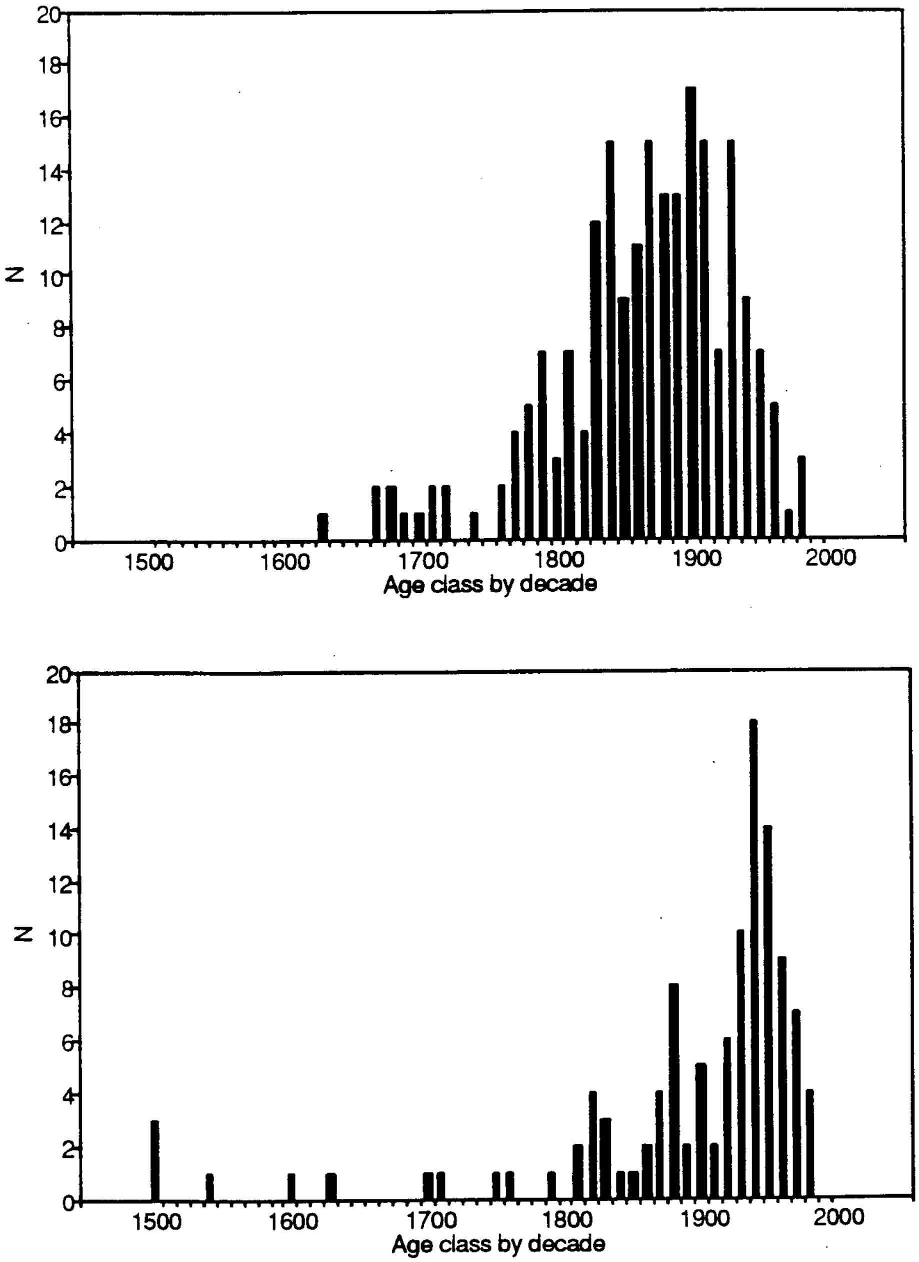


Figure 6.18. Age class histograms for fir (above) and spruce (below) at the clump plot.

1929 and variation in establishment between successive decades is substantially higher than for fir during this period. There was a clear peak of establishment in the 1930's, and then a rapid decline to the present. The period of greatest establishment (*ca.* 1920 to 1960) followed shortly after the establishment of clumps 6 to 14; this constitutes the only period when establishment of spruce has exceeded that of fir.

The spatial pattern of establishment within tree clumps is strongly asymmetric (Figure 6.19). At clump 4, which contains 156 trees, the oldest trees occur near the center of the clump. Most establishment since that time has been on the windward and lateral edges of the clump, with very little establishment in the clump interior or on the leeward edge of the clump. The lateral establishment has caused some elongation of the clump, so that it now measures 8 m from windward to leeward edge but 12 m in the perpendicular direction. Clump 5, the largest spruce clump, contains only 17 trees but also shows predominant establishment on windward and lateral edges and no establishment on the leeward edge. This result supports the hypothesis that a deep leeward snowdrift, which is well-developed in each of these clumps (Figure 6.1), effectively precludes establishment on the lee side of a clump. The slow expansion of clump 4, with trees seldom establishing as much as 0.5 m from their nearest neighbor, is a consequence of the fact that nearly all of the trees in this clump established by layering. Although trees established from seed may grow in close proximity, trees established by layering are compelled to do so. The more open structure of clump 5 similarly suggests that at least some of the trees in this clump may have established from seed; this is particularly true of those trees established since 1931, most of which are located >1 m from their nearest neighbor.

Mortality

Dead stems account for 12.5% of all stems and 16.5% of total basal area in the five oldest clumps. Nearly all of these snags are in decay class 2 or 3, although some decay class 1 leaders occur on living trees. These clumps also contain logs (Figure 6.20) in decay classes 2 to 5, with most (60%) in decay class 4. The amount of down wood in most clumps is approximately proportional to the size of the associated clump, but one old spruce clump (clump 2 in Figure 6.2) contains nearly as many logs as live trees. The logs in this clump represent decay classes 3 to 5 and the cause of this mortality is not apparent. Few logs are associated with the nine small clumps. Since death dates were not determined at the clump plot, mortality rates cannot be estimated.

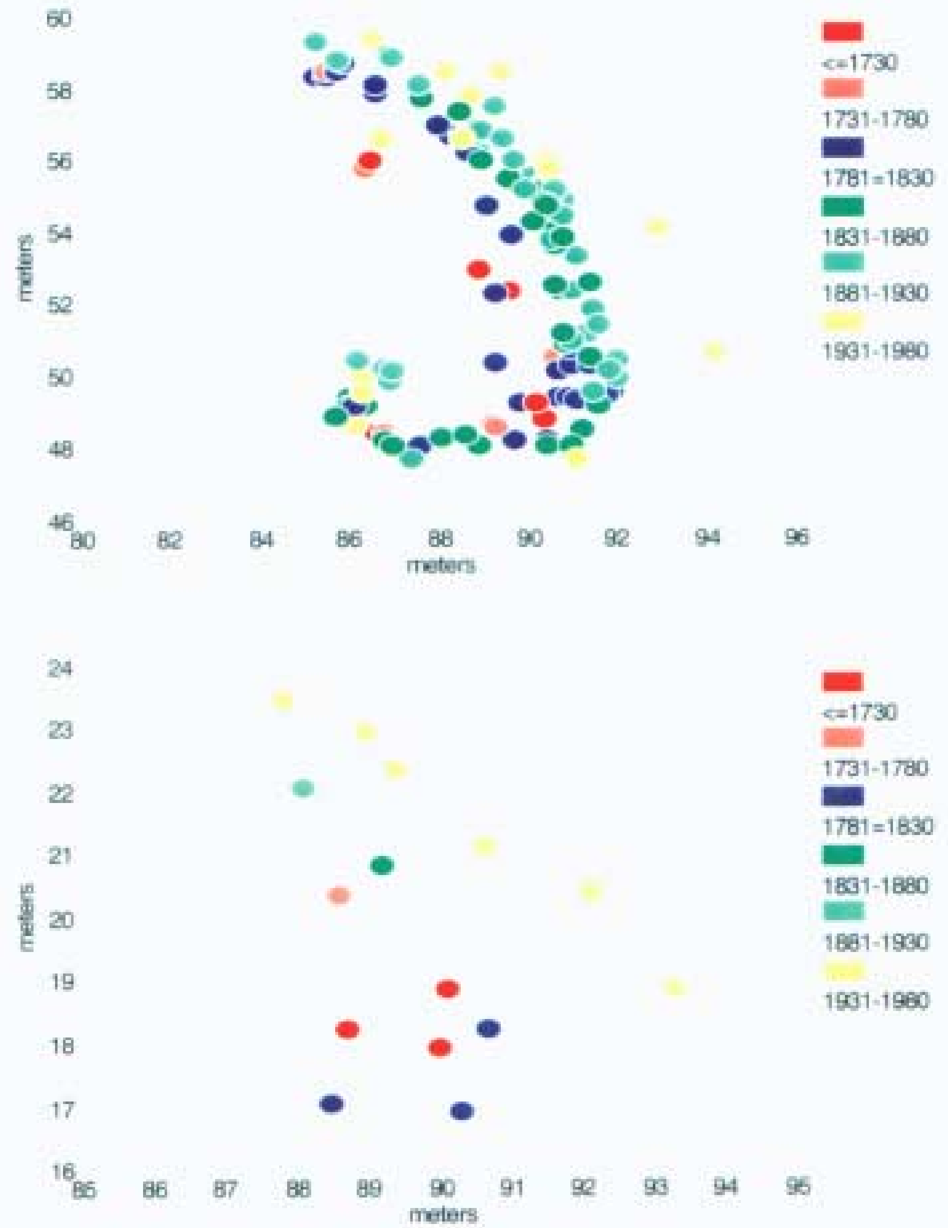


Figure 6.19. Stem map showing dates of establishment for trees in the largest fir and spruce clumps at the clump plot. The fir clump (above) is Clump 4 and the spruce clump (below) is Clump 5.

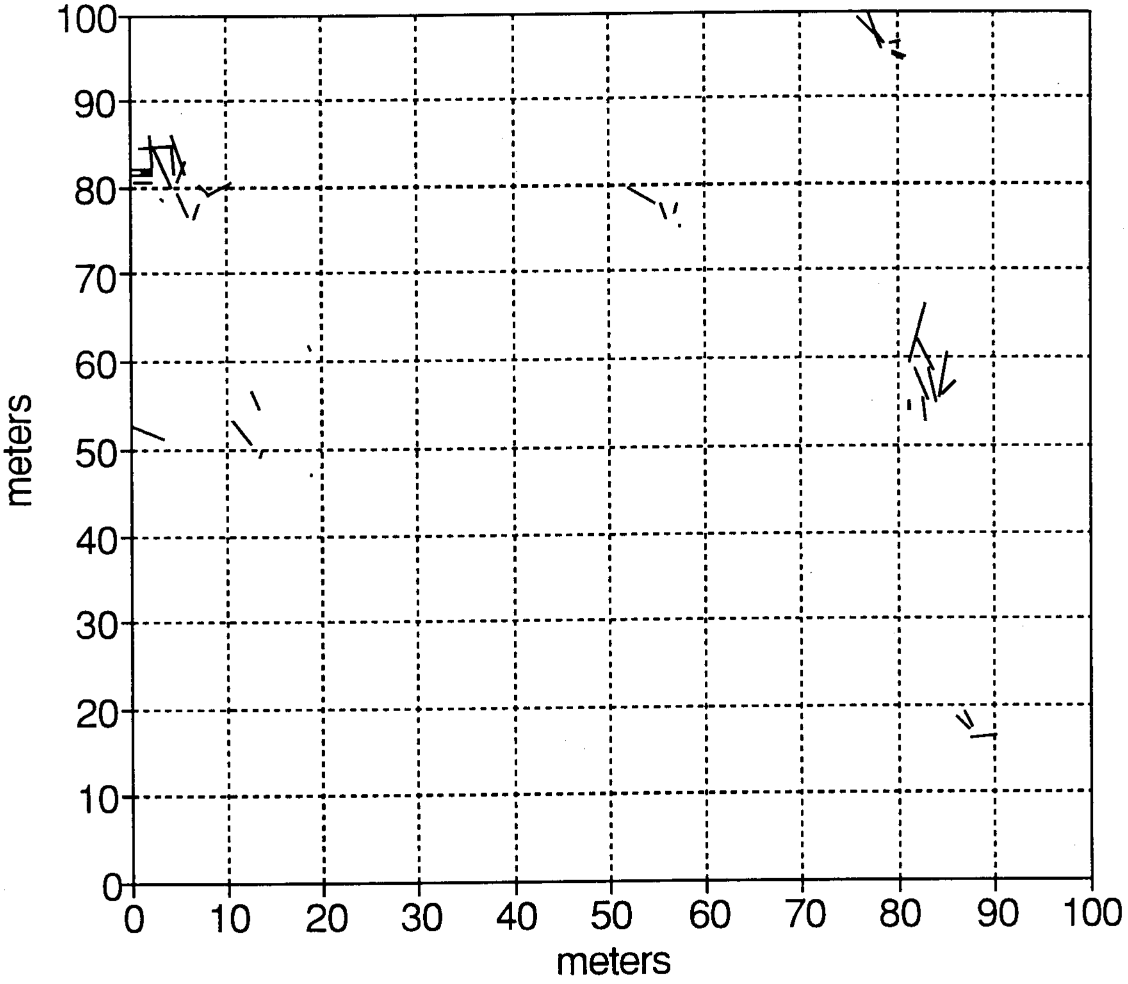


Figure 6.20. Map of log distribution on the clump plot.

Establishment rates

Establishment rates varied between 6% and 18% per decade for most of the last 200 years (Figure 6.21), reaching peak values *ca.* 15.5% per decade between 1780 and 1840. Establishment rates have declined since 1840, even though the absolute number of trees established continued to increase until 1930.

Ribbon plot

Establishment

As at the clump plot, age corrections tend to increase with a tree's estimated age (Table 6.6). Corrections for sampling height were required for 59% of the trees; the mean correction was 11 yr (median 5 yr). Corrections for distance to pith were required for 68% of the trees and ranged up to more than 100 years for most trees established before 1550, totaling 27 trees; the mean correction was 18 yr (median 8 yr). The 54% of the trees established since 1850 required a mean total correction for sampling height and distance to pith of 13 yr (median 9 yr).

Age structures for the ribbon plot (Figure 6.22) show three phases of establishment: a long period of sporadic establishment, a period of continuous establishment during the middle part of the record, and a rapid decline to low modern levels. For spruce, the period of sporadic establishment extended from *ca.* 1400 to the 1620's. The period of increasing establishment was irregular; minor establishment peaks in the 1730's and 1810's preceded the main establishment peak in the 1870's and 1880's. The precipitous recent decline in establishment was also interrupted by a minor peak in the 1910's. Conversely, fir shows a shorter record of establishment with less decade-to-decade variation during each establishment phase. The sporadic period extended from the 1490's to the 1710's, establishment rates increased through the 1830's, and a broad establishment peak appears from 1840 to 1930, reaching a maximum in the 1870's. Since that time, establishment has declined sharply.

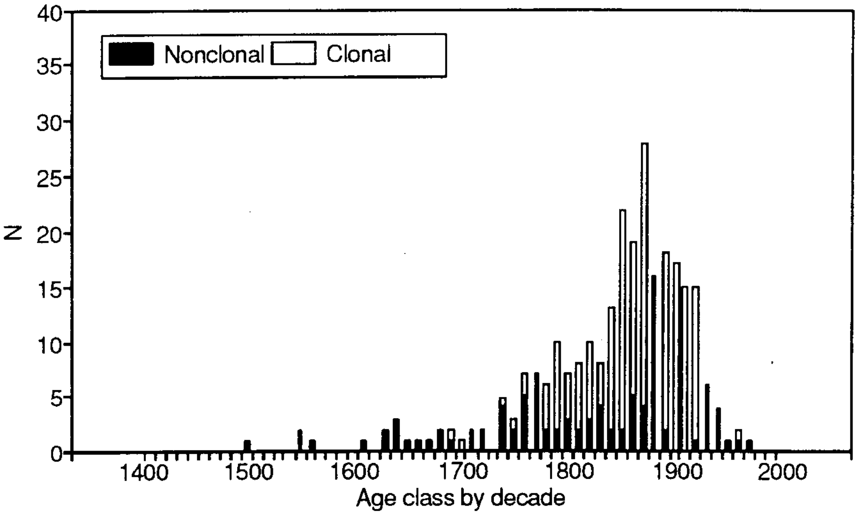
Spruce at both clump and ribbon plots shows considerable decade-to-decade variation in establishment, while fir establishment shows little such variation. Also, the period of peak spruce establishment is shorter than the period of peak fir establishment. The two plots differ in the timing of establishment phases. The sporadic phase begins earlier at the

Figure 6.21. Clump plot establishment rate, 1750 to now.

Table 6.6. Age estimation corrections for ribbon plot trees.

Note: "Height" is the mean correction for sampling height for trees established within an interval, "Pith" is the mean correction for distance to pith, and "Total" is the sum of these corrections. "N" is the number of trees established within the interval. "Percent" is the fraction of the total population of aged trees established within the interval. The last three lines indicate the number and percent of trees established during the entire period of record for which the height, pith, and age corrections, respectively, were zero.

Interval	Height	Pith	Total	N	Percent
1350-1399	74	72	146	2	0.3%
1400-1449	55	140	195	7	1.1%
1450-1499	41	39	79	5	0.8%
1500-1549	30	148	178	8	1.3%
1550-1599	29	118	146	9	1.4%
1600-1649	35	28	63	18	2.8%
1650-1699	19	28	47	24	3.8%
1700-1749	16	20	36	49	7.7%
1750-1799	18	17	35	67	10.5%
1800-1849	12	15	28	105	16.5%
1850-1899	6	10	16	224	35.2%
1900-1949	2	6	7	108	17.0%
1950-1999	0	2	3	11	1.7%
1560-1979	0			261	41.0%
1489-1979		0		205	32.2%
1676-1979			0	120	18.8%



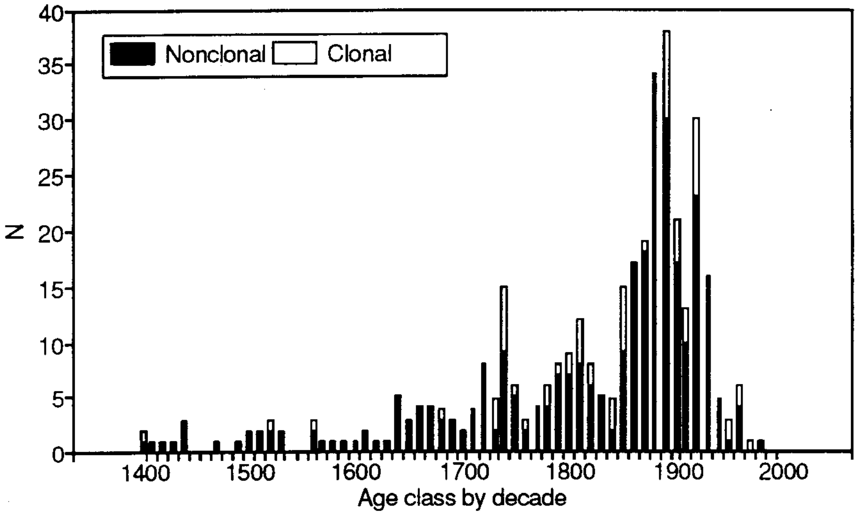


Figure 6.22. Age class histograms for fir (above) and spruce (below) at the ribbon plot.

ribbon plot. The transition from sporadic to increasing establishment is gradual and is approximately concurrent between the two plots. Although peak establishment in fir is concurrent at the two plots, the peak in spruce establishment at the ribbon plot precedes the peak at the clump plot by *ca.* 40 yr.

Clonal establishment in both species is most prevalent in the younger age classes. In spruce, nonclonal establishment is far more prevalent than clonal establishment, although the relative importance of clonal establishment varies from decade to decade. In fir, clonal establishment greatly exceeds nonclonal establishment for most of the period since 1770, while nonclonal establishment has remained approximately constant across the record.

Tree establishment has shown two conspicuous spatial patterns through time (Figure 6.23). First, stem density increases throughout the ribbon; second, establishment is biased toward the windward edge of the ribbon. These patterns appear sequentially, with a gradual transition from the first to the second pattern during the 1800's. The period of stem density increase is shown by a steady decrease in the average distance that a tree establishes from its nearest previously established neighbor (NPN distance). The NPN data show an exponential decline through time (Figure 6.24; $R^2=0.30$, $p<0.01$) beginning in 1390 and continuing until about 1800; after 1810, NPN distances show no long-term trend. Departures from a negative exponential trend for sequential 50 yr establishment intervals from 1381-1430 to 1931-1980 were not significant at $P<0.25$ (t-test of sample means), indicating that there were no periods of significantly aggregated or dispersed establishment relative to the long-term mean. In absolute terms, the mean departures from a lognormal trend did not exceed 10 cm. Thus, until the early 1800's establishment generally followed a space-filling trend in which NPN distances declined as the ribbon became more crowded with trees. This trend is visible in the establishment map (Figure 6.23). Between 1386 and 1780, 23% of the trees now present on the ribbon plot established. These trees are distributed over most of the present extent of the ribbon (red and pink dots in Figure 6.23). Large logs, although not common (Figure 6.25), are similarly widely distributed. These observations suggest that the *ca.* 1780 forest had a much lower stem density, but a similar area, compared to the present ribbon. By 1830, 37% of the trees now present on the plot had established, and the pattern of establishment continued to follow a space-filling trend. This trend did not continue.

The second trend, the biasing of establishment toward the windward edge, cannot be found in the NPN data because it involves expression of spatial pattern at a much larger

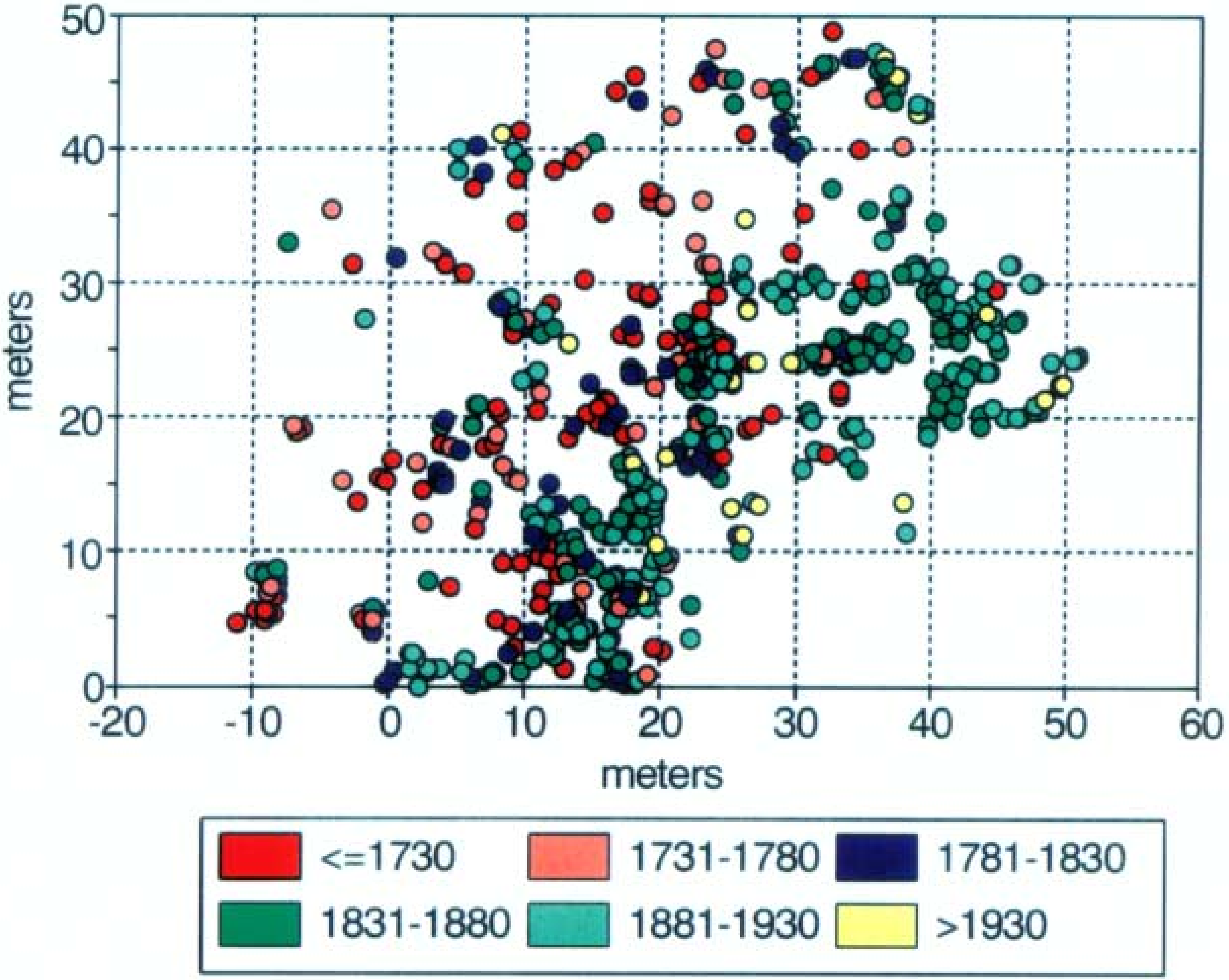


Figure 6.23. Stem map showing dates of establishment for the ribbon plot.

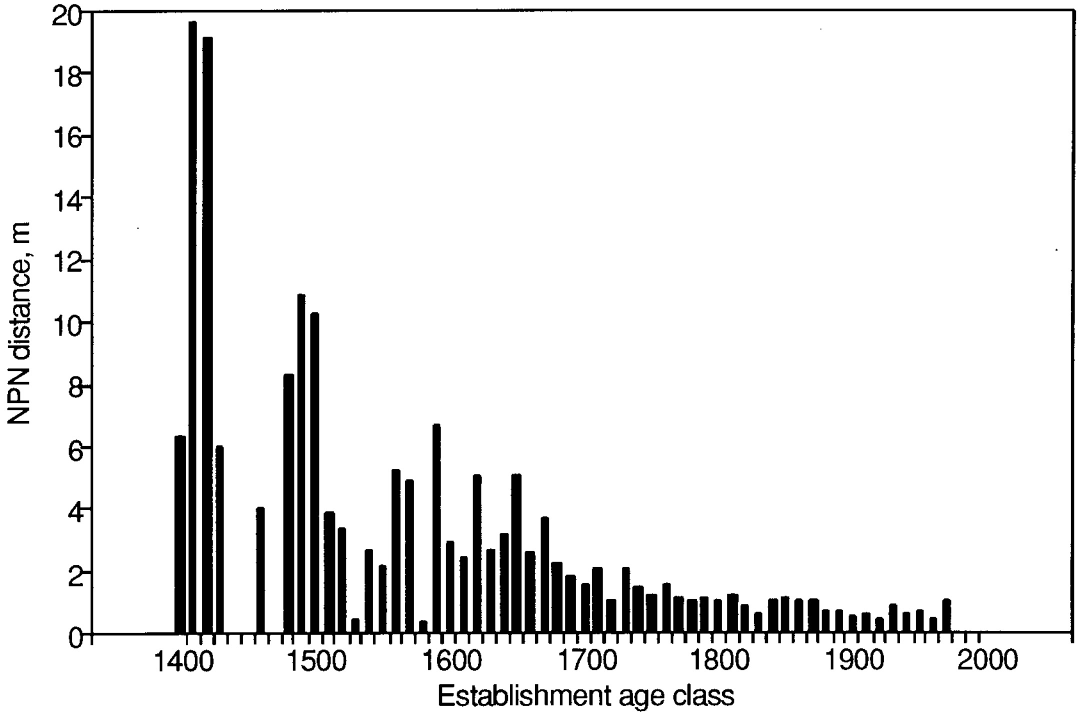


Figure 6.24. Decadal mean NPN (nearest previously-established neighbor) distances for the ribbon plot.

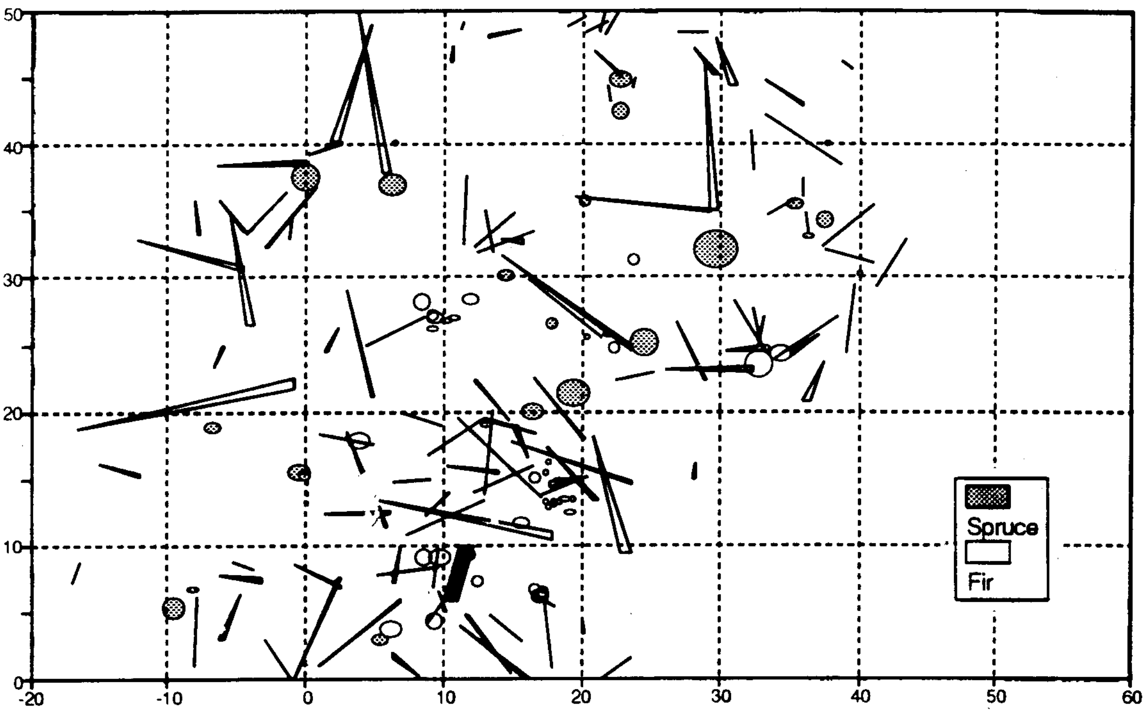


Figure 6.25. Map of stump, snag, and log distribution on the ribbon plot. Stem diameters are exaggerated by 4x.

scale than the distance between a tree and its nearest neighbor, a scale involving the entire ribbon. However, this biasing is apparent from the establishment map (Figure 6.23). The change to a windward-biased establishment pattern occurs between 1830 and 1880; in this interval, a large fraction of total establishment occurred along the windward edge of the ribbon. From 1880 to 1930, most establishment was on the windward edge. Although the 1830-1930 period included 59% of total establishment on the plot, it involved only a slight increase in the forested area of the plot, notably the "peninsula" of about 150 m^2 (centered at about [42,25] in Figure 6.23). Instead, most new trees established between pre-existing trees, at average NPN distances of <1 m. Only 24 trees (4% of the present total) have established since 1931, the most recent establishing in 1979. These trees established primarily near the windward edge of the ribbon, but they do not represent any extension of the forest into the adjacent meadow.

Mortality

The spatial distribution of dead wood within the ribbon plot (Figure 6.25) reflects the present live tree composition (Figure 6.9). For example, fir logs and snags are located within or very near the current fir clumps, spruce logs and snags are distributed throughout the ribbon, and large spruce logs are as widely distributed as large-diameter living spruce. Death dates could be determined for 46 of 59 snags and 8 of 114 logs. Most of the dated logs were large spruce logs. Death dates span the interval from 1730 to the present (Figure 6.26). Relatively few death dates occurred from 1730 to 1830, but some mortality was recorded in nearly every decade from 1840 to the present.

Age at the time of death could be determined for 45 logs and snags (Figure 6.27). The median death age was 180 years. Firs tended to be younger (median 160 yr) and spruces older (median 220 yr) than this. Most of the dead firs were small-diameter stems located in clumps within the ribbon interior; these trees may have been killed by suppression due to competition with canopy dominant trees. A few small fir trees died when large snags fell on them. Most of the dead spruce were large-diameter snags and logs. The cause of death could not be determined. For example, large spruce snags did not display extensive bark beetle galleries. Several large, live spruce had been scarred by lightning strikes, but such scars were not found on any snags or logs. Dead trees seldom had heart rot. Four trees had been cut by axe or saw.

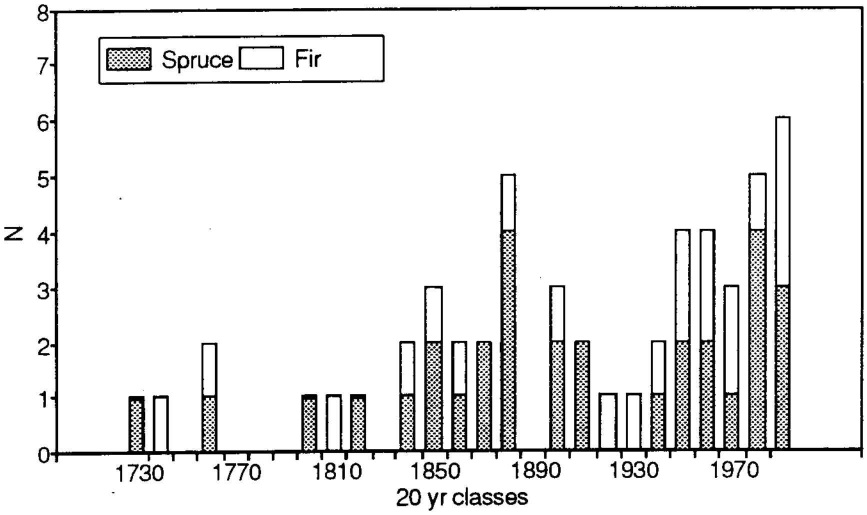


Figure 6.26. Tree death date histogram for the ribbon plot.

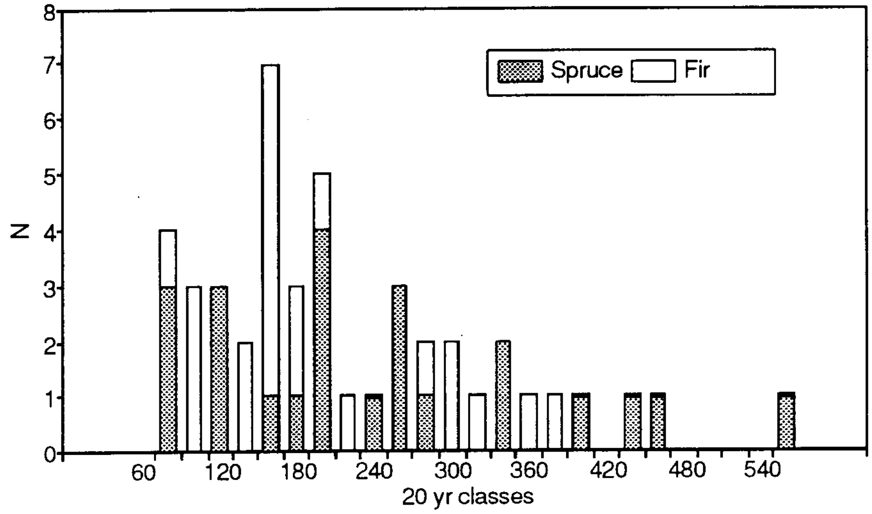


Figure 6.27. Tree death age histogram for the ribbon plot.

Since death dates could not be determined for every dead tree on the ribbon plot, I tried to determine whether tree decay class could be used to estimate the date of tree death. Such an estimate would be desirable because death dates for many trees and logs would otherwise remain undetermined, causing bias in the estimation of mortality rates on the plot. A scatter plot comparing death date to decay class (Figure 6.28) indicates a very weak association between these variables; the 29 decay class 2 trees had a mean death date of 1925 (s.d. = 64 yr), while the 17 decay class 3 trees had a mean death date of 1871 (s.d. = 43 yr). No other decay class contained more than three dated trees. The small difference in time since death for trees of differing decay class, and the absence of clear trend in the scatterplot, suggest that decay class is a very imprecise proxy for estimating time since tree death. However, these data suggest that trees in decay class 4 probably had a mean death date substantially earlier than 1871, perhaps in the early 1800's, and trees in decay class 5 probably died in the 1700's or earlier.

Rates of population change

The mortality rate at the ribbon plot (Figure 6.29) varies greatly from decade to decade. This is probably random variation, reflecting the small number of recorded tree deaths in any one decade; for example, the death of only two trees caused the 4.4% peak in mortality for the 1751-1760 decade. Across the period of record, mortality rates are in the range of 1% to 4%. Since 1850, mortality at the plot has averaged 1.7%. Mortality gradually increased during the 1900's, reaching a maximum of 3% for the 1981-1990 decade. Recorded mortality rates across the period of record are consistent with a rate of 0.1% yr^{-1} to 0.4% yr^{-1} reported for an old-growth spruce-fir forest in Colorado (Rebertus *et al.* 1992).

Establishment rates have varied from 6% to 12% per decade for most of the period of continuous establishment (Figure 6.30). The early period, until about 1830, saw a fairly steady establishment rate of about 8% per decade in a population that grew from 124 trees in 1750 to 241 trees in 1830. This coincides with the period of space-filling establishment. Soon after this, during the period of windward-edge biasing, establishment of both species increased (Figure 6.22) to yield establishment rates of about 12% per decade through most of the latter 1800's. Since 1890 there has been a nearly continuous decline in

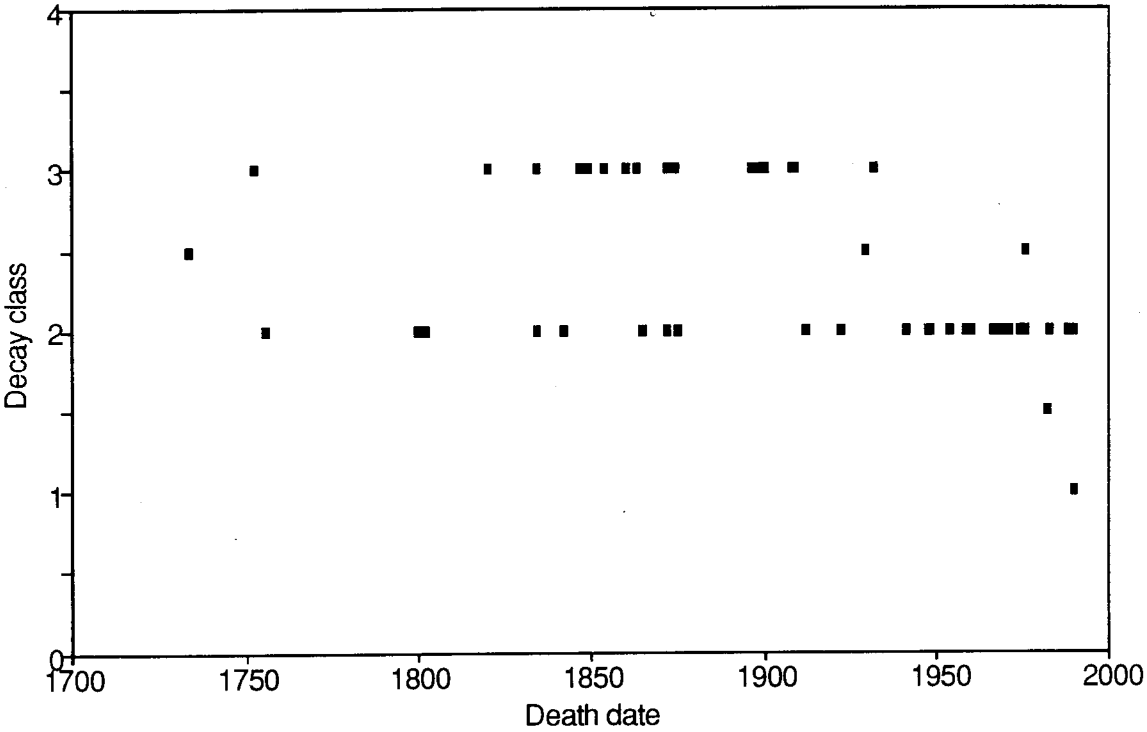


Figure 6.28. Scatterplot comparing death date to decay class.

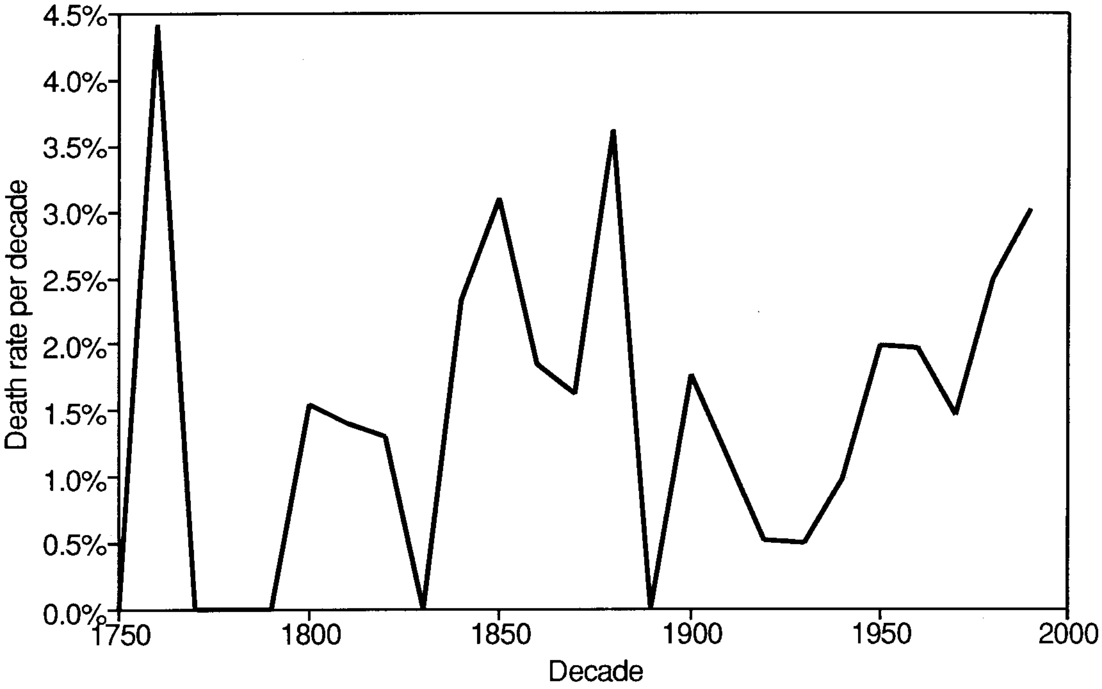


Figure 6.29. Ribbon plot mortality rate, 1750 to now.

Figure 6.30. Ribbon plot establishment rate, 1750 to now.

establishment rates. Very few trees have established recently, and no seedlings less than 5 yr old were observed on the plot in any of the field seasons (1989 to 1991).

The estimates of mortality and establishment rates were summed to yield an estimate of net population growth rate (Figure 6.31). For most of the record the net growth rate has been dominated by establishment, which has often outpaced mortality by a factor of 5×. All of the major features of the establishment rate graph are therefore reflected in the net growth rate graph. During the 1900's the combination of decreasing establishment and increasing mortality have appreciably reduced net growth to approximately 0% since *ca.* 1960.

TREE GROWTH FORM

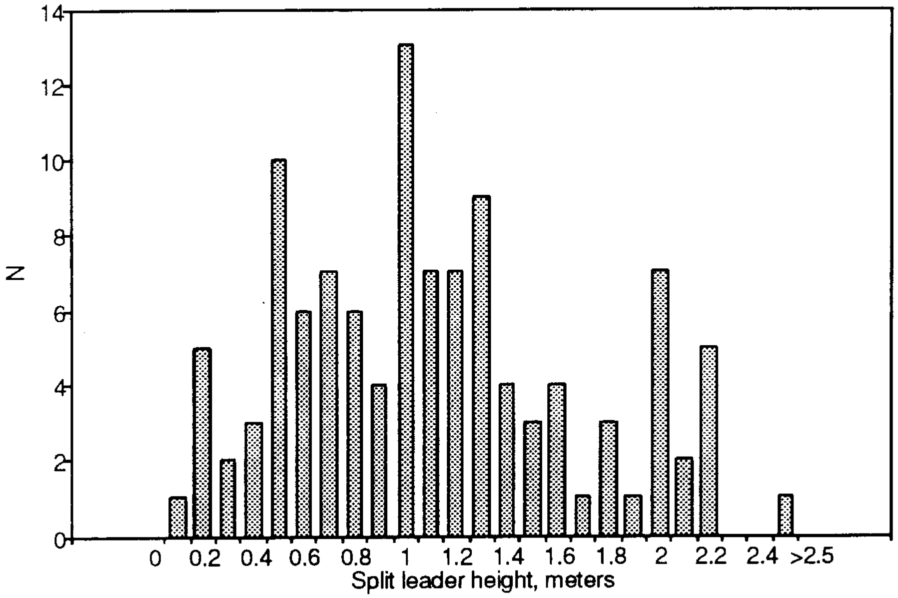
Clump plot

At all tree clumps the depth of snow accumulation corresponds closely to the height of the krummholz mat in the clump (Figures 4.2, 4.3 and 4.4). The erect leaders are branchless on the windward side for up to 1.0 m above the snow surface. Above that height, tree crowns are spire-shaped or wind-flagged. The azimuth of branches on wind-flagged crowns ranges from 73° to 96° (mean 88.4°), indicating that prevailing winter winds at the clump plot are blowing from due west. Many shoots within 25 cm of the snow surface display a mixture of green and brown needles, indicating that winter desiccation has killed some exposed needles. On some branches several years of needle growth had been killed (Figure 4.2).

Most trees (80%) have one leader, 11% have two leaders, and the remaining 9% have from 3 to 10 leaders. Stems split into multiple leaders at heights ranging from 0.1 m to 2.5 m (Figure 6.32a). Nearly all leaders in the largest clump (clump 4 in Figure 6.2) appear to split at a height below the local snowpack level as determined from the height of the krummholz mat and winter photography data. Although multiple leaders occur on trees of widely varying size and age, multiple-leader trees tend to be significantly older, taller, and larger in diameter than single-leader trees (Table 6.7).

Trees with a krummholz base are among the oldest and largest trees on the plot. In clump 3, three old krummholz base spruce each hold several live or recently dead leaders. Although the ages of these three trees could not be accurately determined, release dates of

Figure 6.31. Ribbon plot net population growth rate, 1750 to now.



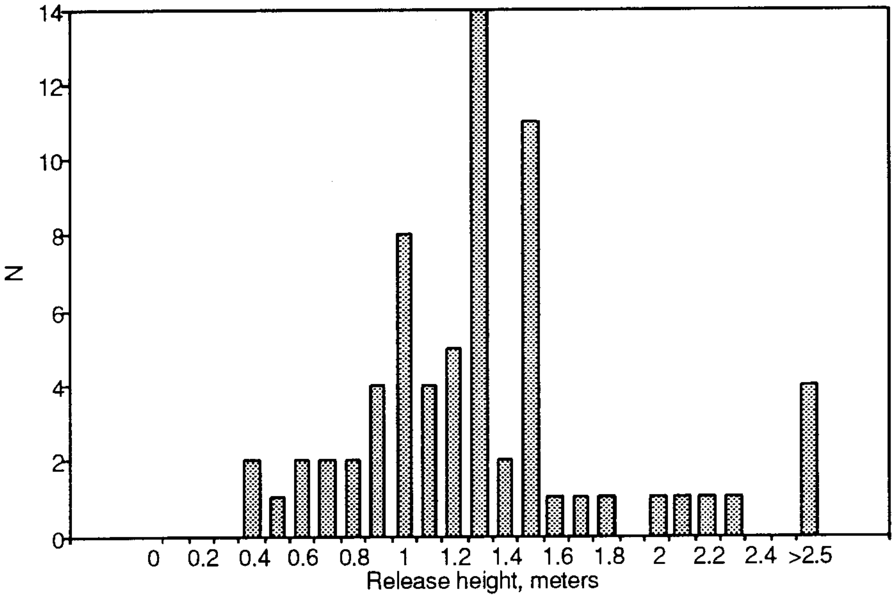


Figure 6.32. Histograms of split leader heights for the clump plot (above) and release heights for the ribbon plot (below).

Table 6.7. Differences between single-leader and split-leader trees in the two largest clumps on the clump plot.

Note: "Probability" is the probability that sample means are identical (t-test for different means, separate variance estimate).

	Tree Age	Height (m)	Diameter (cm)
Split leaders:			
N	64	66	66
Mean	170	4.0	8.9
Std. Dev.	91	2.3	8.0
Single leaders:			
N	248	289	287
Mean	107	2.8	5.1
Std. Dev.	68	1.9	5.7
Probability:	<0.001	<0.001	0.001

the leaders ranged from 1827 to 1935 (Table 6.8). The period of leader release for these trees approximately coincides with the period of new clump establishment (1860 to 1927) and the period of most rapid establishment on the plot (1820 to 1950). This chronology suggests that a period of favorable climate permitted these different forms of increased tree growth.

Krummholz base trees are the oldest trees in the young clumps (clumps 6 to 14 in Figure 6.2). Each of these trees established between 1862 and 1901. Clump 14 was dissected in some detail to determine the history of its development. This clump, currently composed of 9 trees, established in 1892 (Table 6.9). The clump grew below the height of the present krummholz mat for 44 years, long enough for the initial tree to develop a krummholz base. In 1936 a leader began to grow above the krummholz mat; it has now grown into a flagged, erect leader 2.9 m tall. Between 1937 and 1949 the clump acquired eight more trees, most of which were seedlings. These eight trees grew above the height of the present krummholz mat between 1963 and 1976, at tree ages of between 22 and 31 (mean 26.4) yr. That age was between 46% and 67% of their current age, and at that time they were at a height between 47% and 75% of their present height; it therefore seems likely that these trees grew fairly steadily as seedlings, rather than persisting at the height of the krummholz mat for a period before resuming height growth. Since 1976 no new trees have established and no new leaders have been released, and the krummholz mat is now a prominent feature of the clump. These data suggest that conditions at the clump plot were suitable for seedling establishment in 1892, when the clump established. Conditions at clump 14 were again suitable for seedling establishment between 1937 and 1949, but this may have been true either on the plot as a whole (*e.g.*, because of favorable climate) or only at clump 14 (*e.g.*, because of microsite change due to clump growth). Finally, conditions were favorable for tree growth between 1963 and 1976; as the trees growing above the krummholz mat were not protected by the clump, this release may have occurred in response to favorable climate. However, establishment and release data are not sufficient by themselves to determine what constitutes "favorable climate."

Ribbon plot

Most trees at the ribbon plot have a spire growth form; the commonest departure from this is the presence of a release height on a krummholz base tree. This feature was present on 68 trees (10% of the plot total), varying from 0.4-4.0 m, but generally between

Table 6.8. Timing of release for leaders from old krummholz base spruce.

Core I.D.	Height	DBH	Date	Remarks
282	0.5	0	ca.1500	Krummholz base, rotten
283	4.5	10.8	1827	Base of live leader
284	5.0	9.5	1827	Base of live leader, 25 yr pith correction
285	5.5	12.5	1849	Base of live leader, 19 yr pith correction
286	5.0	9.6	1855	Core 0.1m below base of leader; narrow rings before 1855
288	1.1	0	ca.1500	Krummholz base, rotten
292	2.6	9.8	1858	Base of live leader
293	5.5	11.8	1874	Core 0.3m below base of live leader, 11 yr pith correction, core shows no ring width change
290	2.8	4.5	1902	Base of snag leader, died 1985
291	3.4	5.4	1904	Base of live leader, 13 yr pith correction
289	2.9	4.7	1934	Base of live leader, missed pith, upper limit date
294	1.3	0	ca.1500	Krummholz base, rotten
295	3.4	6.2	unkn.	Base of snag leader, unable to crossdate
296	3.7	8.2	1856	Base of snag leader, died 1985
297	5	10.9	1887	Base of live leader
298	5.3	13.1	1890	Base of live leader, 10 yr pith correction

Table 6.9. Establishment and release in a young spruce clump.

Tree	Height	DBH	Est. Date	Release date	Release age
193	2.9	7.1	1892	1936	44
197	1.7	2.3	1937	1965	28
200	1.9	2.5	1940	1963	23
201	1.4	0	1940	1967	27
196	1.4	0	1941	1968	27
198	2.0	2.8	1942	1967	25
199	1.7	1.7	1943	1974	31
195	1.5	0	1948	1976	28
202	1.2	0	1949	1971	22

1.3-1.5 m (Figure 6.32b). Released trees are predominantly (85%) spruce. Most of these trees are presently located within the forest interior (Figure 6.33), but established near the position of the forest edge in ca. 1830 (Figure 6.23). At the time of their establishment, most of these trees were located either at the forest edge or a few meters into the meadow. These spatial patterns suggest that released trees were likely to have been directly affected by snow accumulations in the open meadow during the period following their establishment.

Twenty-four of the released trees were large, old krummholz base trees. The present location of these krummholz-base trees within the interior of the ribbon forest (Figure 4.6) indicates that the stature and density of the ribbon forest has increased over the past several hundred years. Cores from near the base of three of these large, old krummholz base trees show an early period of extremely slow growth, similar to that of large krummholz base spruce currently growing at the clump plot. Despite very different establishment dates, these trees showed contemporaneous abrupt increases in ringwidth between 1750 and 1775 (Figure 6.34), a period of rapid increase in establishment at the ribbon plot (Figure 6.22). Apparently these krummholz-base trees grew more rapidly as a forest interior environment developed around them.

CLIMATE AND ESTABLISHMENT

The association between climate and establishment was assessed in two ways. The first of these used recorded climate data, which are available for the period 1895-1987. The second examined the association between tree-ring widths and climate. The growth of tree rings is often strongly influenced by climate (Fritts 1976), and a long tree-ring record (from about 1500 to the present) is available. However, rather than reflecting variations in establishment, the tree-ring data contained a different message: that the optimum climate for ring growth is different from the optimum climate for establishment.

Climate -- establishment associations

Establishment dates for both species at both study plots were significantly associated with certain monthly climate variables (Figures 6.35 and 6.36). Lagging of the establishment series relative to the climate data resulted in lowered regression coefficients for all lags from -3 to +3 yr. This suggests that in general, the year of germination has been accurately determined.

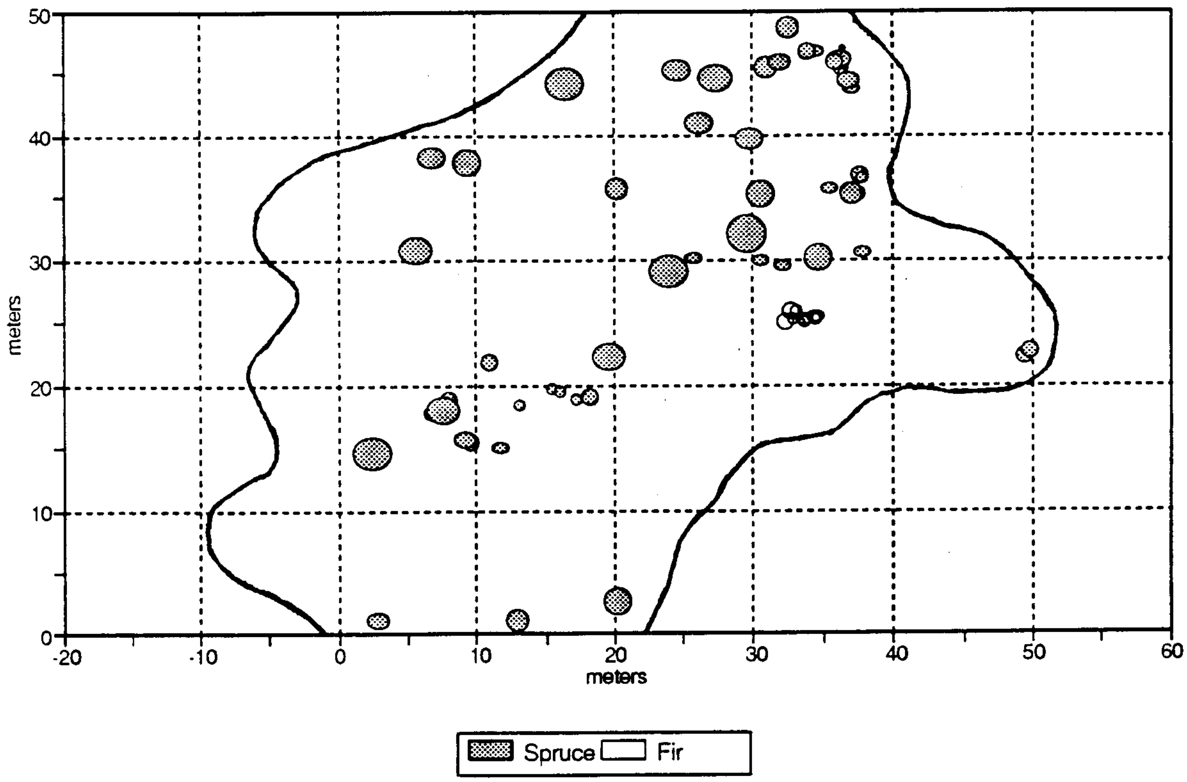


Figure 6.33 Map of released tree locations.

Circle diameter is proportional to DBH but has been exaggerated by 4×. Heavy lines indicate the present extent of the ribbon forest.

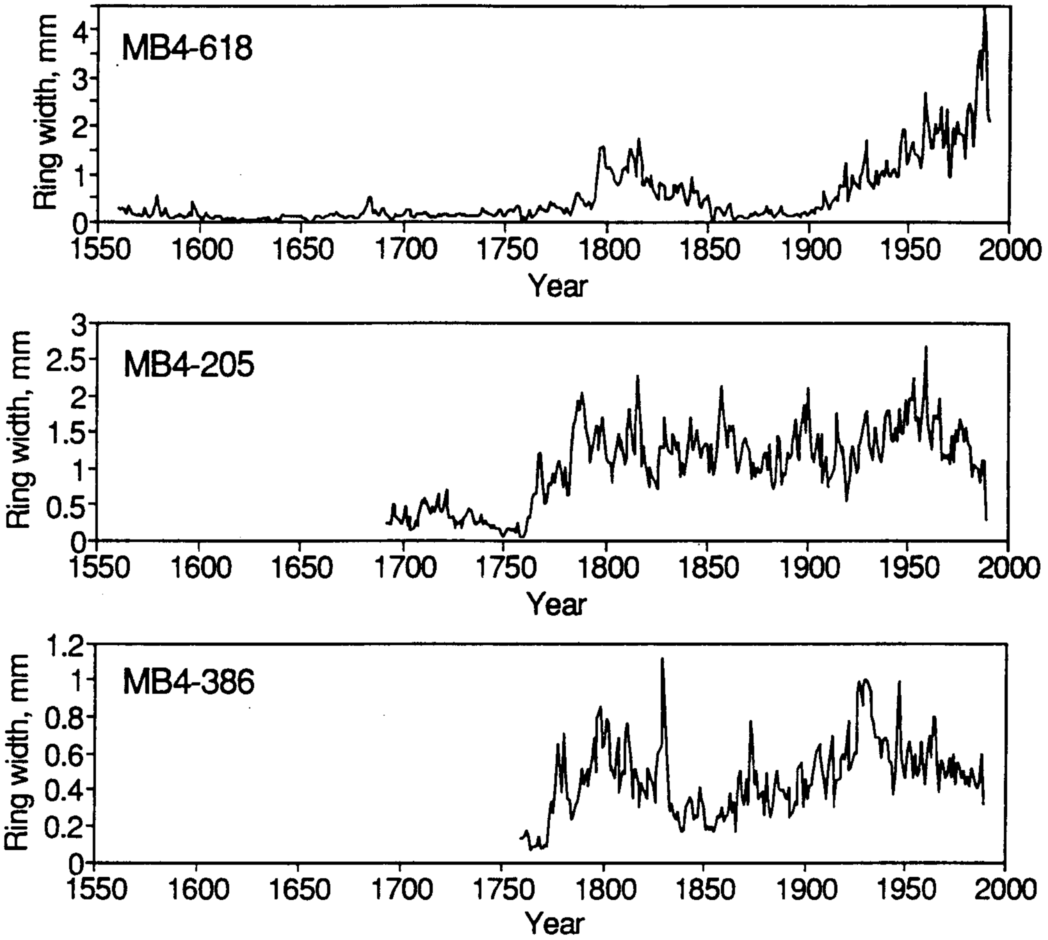


Figure 6.34. Ring width plots for large forest interior spruce trees at the ribbon plot that have a krummholz base.

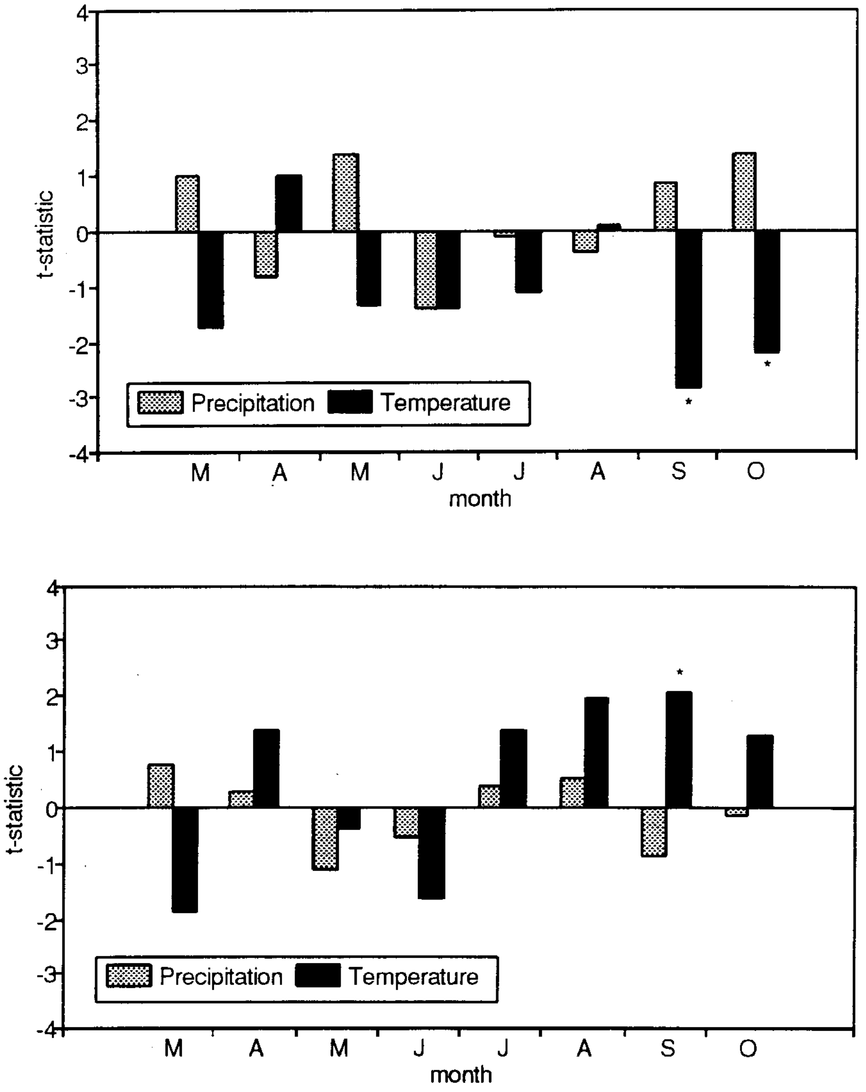


Figure 6.35. Results of climate-establishment regressions for fir (above) and spruce (below) on the clump plot. Values are the "t" statistic for the climate term of the regressions; t > 1.96 indicates significance at p=0.05.

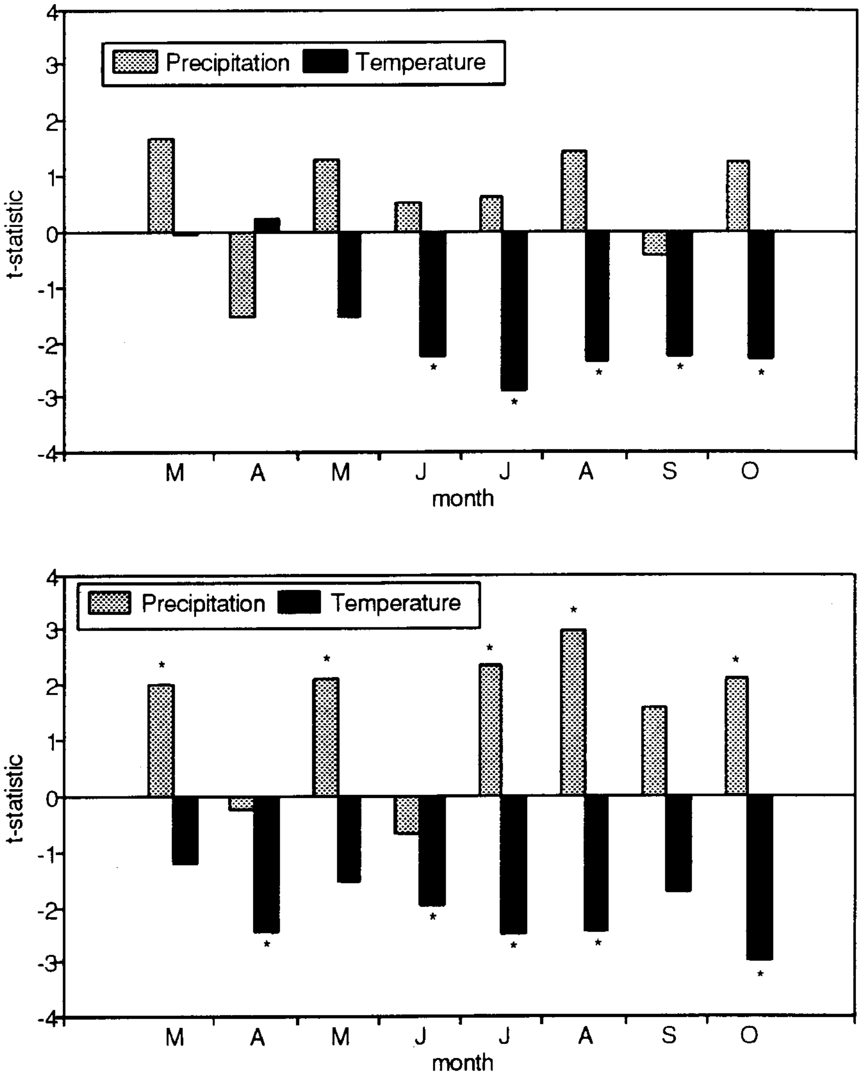


Figure 6.36. Results of climate-establishment regressions for fir (above) and spruce (below) on the ribbon plot.

Although relatively few climate-establishment regression coefficients for the clump plot were significant, the coefficients for both species are generally consistent across several months. Fir establishment was associated with cool September and October temperatures, nad spruce establishment was associated with warm summer temperatures.

At the ribbon plot, climate-establishment regression coefficients were much more significant than at the clump plot. Spruce establishment was associated with relatively cool and moist conditions in nearly every month, with 10 of 16 coefficients significant at p=0.05. Fir establishment shows a similar pattern, but with no significant precipitation coefficients. Fir establishment appears to be most favored in years with a cool June to October.

Ring width - climate associations

The tree-ring chronologies derived from Engelmann spruce and Douglas-fir cover much of the establishment record for the study plots (Table 6.10; Figure 6.37). The Douglas-fir chronology shows a higher standard deviation and mean sensitivity, and a lower first-order autocorrelation, than the Engelmann spruce chronology. Such contrasts are typical between chronologies derived from low and high-elevation sites (Fritts 1974, 1976).

The Douglas-fir chronology generally shows a negative correlation with temperature and positive correlation with precipitation (Figure 6.38a). Correlations are particularly strong and persistent for the growing season (April to October) of the previous and current years, while lower coefficients mark the non-growing season (November to March). The Engelmann spruce chronology shows a more variable and complex association with monthly climate (Figure 6.38b). Growth is positively correlated with temperature for the current July and the previous October, but negatively correlated with temperature for the previous June to September. Growth is positively correlated with precipitation for the current August, but otherwise shows small and variable correlations with precipitation.

Ring width -- establishment associations

Most regression models indicated that tree-ring widths have a weak, inverse association with establishment (Table 6.11). The strongest model, estimating spruce establishment at the ribbon site using both tree-ring chronologies as predictors, explained less than 7% of the variance in the establishment data. The variance explained by all of these models was so low that practically speaking, ring width was not useful as a proxy indicator of

Table 6.10. Summary statistics for the tree-ring chronologies

Note: Mean sensitivity is the mean change between successive ring-width indices, where change is expressed as an absolute value percentage. All statistics are calculated for the interval containing more than 10 cores and were calculated brfore AR modeling of the chronologies.

Site	Lower	Upper
Species	Douglas-fir	Engelmann spruce
Full period	1412-1990	1421-1990
Period with >10 cores	1494-1990	1586-1990
Mean ring-width index	1.011	1.012
Standard Deviation	0.371	0.199
Mean Sensitivity	0.381	0.152
First-order autocorrelation	0.289	0.557

Table 6.11. Regression models using tree-ring chronologies to estimate establishment.

Note: ES is the Engelmann spruce chronology and DF is the Douglas-fir chronology. R^2 is predictand variance explained by the regression model, adjusted for degrees of freedom. Values are calculated for an 1850-1980 data set. These models have all coefficients significant at p=0.05. None of the models estimating establishment at the clump plot contained significant predictors.

Predictand	Predictors	R^2 (%)
Ribbon spruce	ES	4.4
Ribbon spruce	DF	2.1
Ribbon spruce	ES + DF	6.8
Ribbon spruce	DF + (ES * DF)	6.6
Ribbon fir	ES	3.3
Ribbon fir	DF + (ES * DF)	3.1

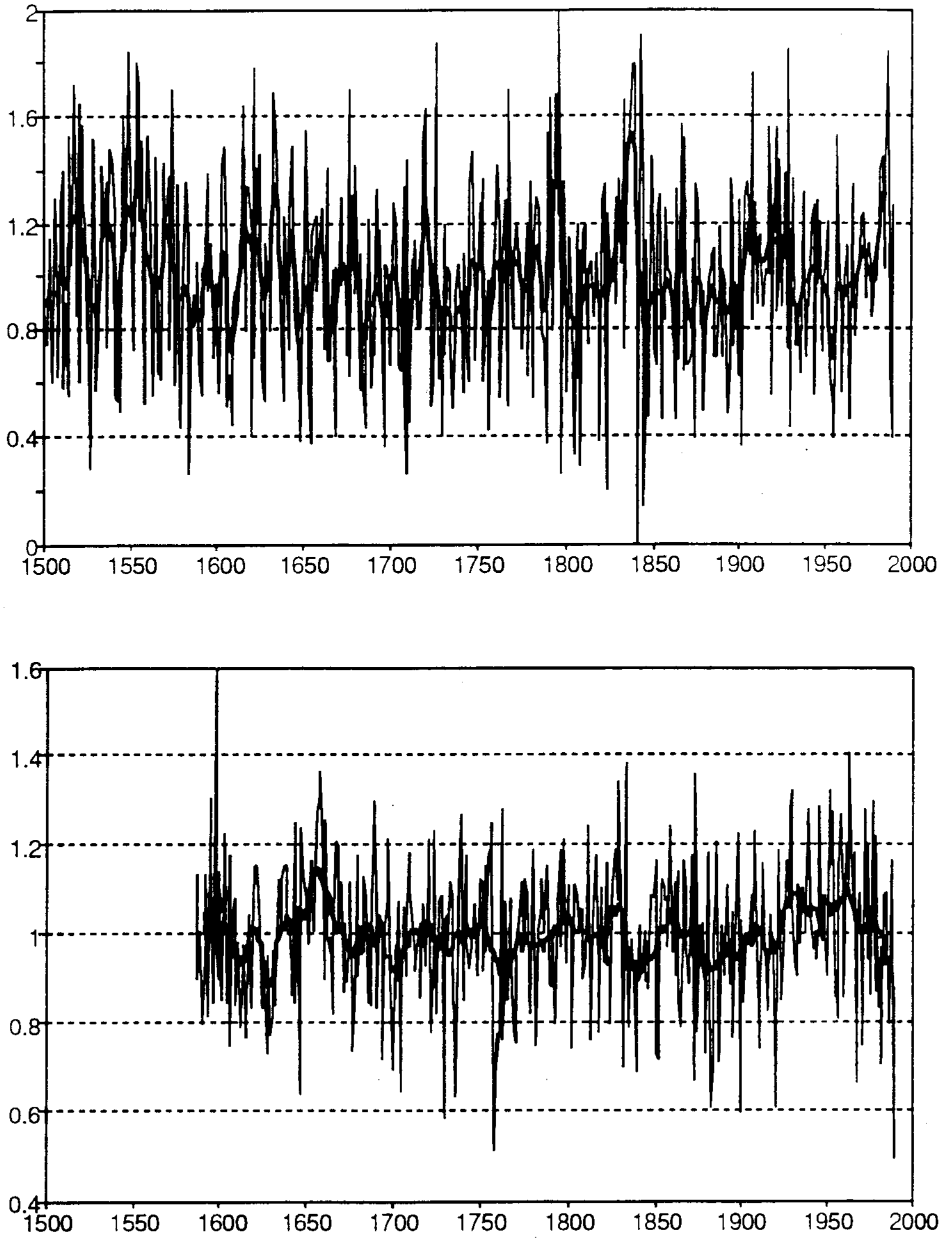


Figure 6.37. Plots of the tree-ring chronologies for the Douglas-fir (above) and Engelmann spruce (below) sites. Both series are plotted for the period represented by > 10 cores and both plots include (heavy dark line) the series as transformed by a 8-year low-pass filter.

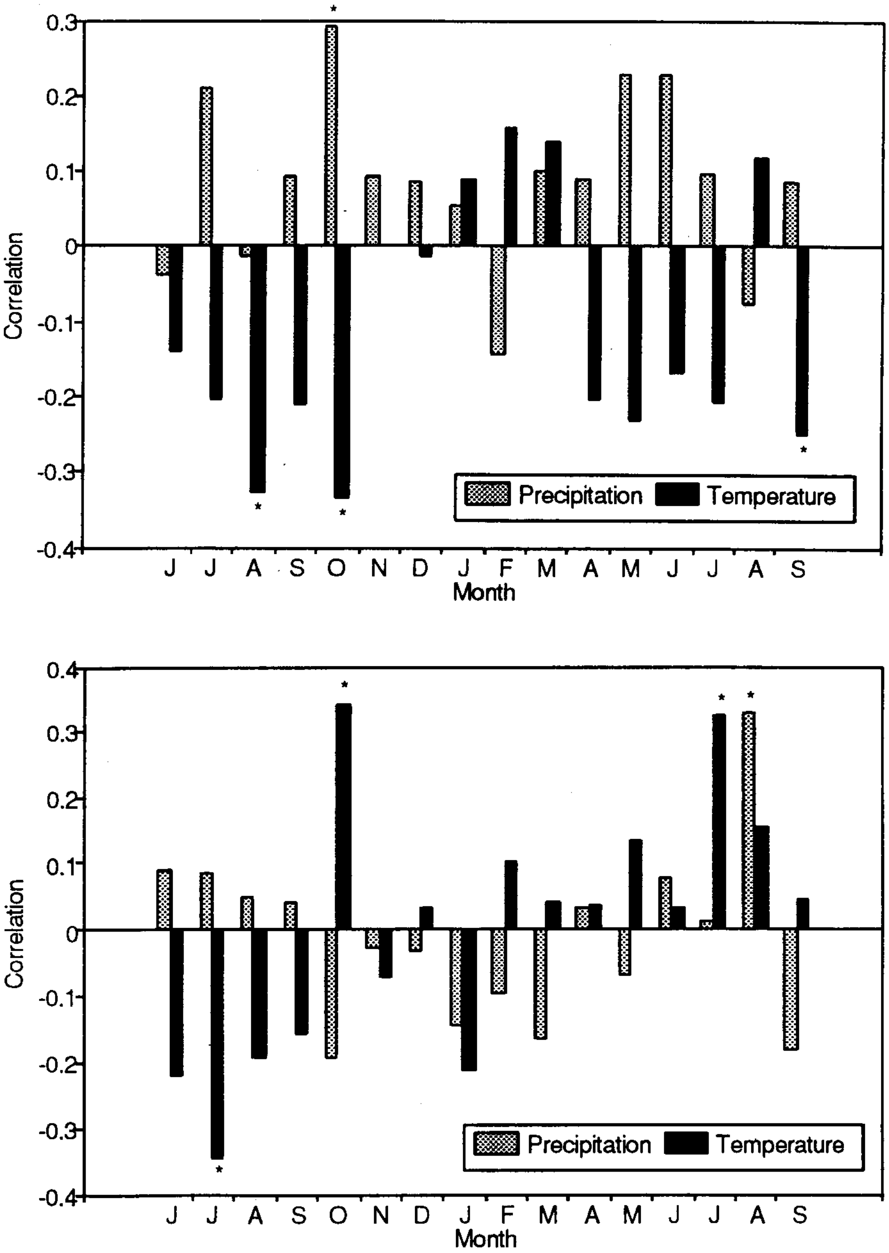


Figure 6.38. Climate-growth correlations for the Douglas-fir (above) and Engelmann spruce (below) tree-ring chronologies. An asterisk (*) indicates values significant at the 95% confidence level.

establishment success. A similar result appeared when regressions were calculated using the entire tree-ring and establishment data set, rather than an 1850-1980 best-dated subset. These regressions, covering the period 1600-1989, achieved predictor significance levels of p=0.01 but explained a maximum of only 1.2% of the variance in the establishment record. More detailed analyses comparing establishment and ring-width data both visually and by cross-spectral analysis also failed to reveal any noteworthy association between the two data types.

Chapter 7. DISCUSSION

The associations observed between climate variables and tree establishment attest to the influence of climate on seedling establishment success. The distribution of meadow vegetation types and the growth form of trees at the clump plot similarly attest to the importance of snow and wind in shaping the development of trees at the study site. These are two salient examples of physical factors that can direct the process of clump and ribbon development. However, autecological factors are equally important in limiting and defining this development. This is why Engelmann spruce and subalpine fir, although subjected to nearly identical physical environments, show differences in size, spatial distribution, and mode of establishment at the study site. Disturbance by grazing animals may have also affected the development of these forests, causing an episode of increased establishment at the clump plot. In this chapter I first consider the relative roles of these physical, autecological and disturbance factors on this site, and then present a conceptual model of how the interaction of these processes can lead to the inception and growth of tree clumps, a transition from tree clumps to ribbon forests, and the growth of those forests to a fixed and relatively constant size. I then discuss the time scales of forest change; these time scales constrain the rate and character of forest response to disturbance, climate change, or structural change. Finally, I note potential lines of further research that would clarify uncertainties encountered in this study and extend our understanding of ribbon forests in general.

PHYSICAL FACTORS

Climatic influences on establishment

The statistical associations between climate and establishment are generally stronger at the ribbon plot than at the clump plot, and are generally stronger for spruce than for fir (Figures 6.35 and 6.36). This probably reflects the prevalence of layering among spruce at the clump plot and among fir at both plots. Since the transition from branch to layered stem is very gradational, occurring over a period of years, it is unlikely that layered stems establish in response to climate in any single year.

Ribbon plot

Establishment at the ribbon plot tends to occur on microsites that experience moderate temperatures and soil moistures. For instance, the meadow near the ribbon edge is shaded by neighboring trees and probably experiences relatively little summer drought due to proximity to a late-melting snowdrift. The statistically significant association between seedling establishment and cool growing season temperatures is implausible; virtually all studies of seedling establishment near the alpine timberline have found that establishment tends to occur during warm periods (*e.g.*, Brink 1959; Franklin *et al.* 1971; Kearney 1982; Kullman 1981, 1989), and soil moisture (rather than temperature) has generally been found to be the most important determinant of seedling survival in spruce (Alexander 1987). Moist soils are important to seedlings of subalpine fir because seedlings have exceptionally low water use efficiency, leading to high mortality rates from water stress caused by both warmth and dryness (Cui and Smith 1991), a problem that may also exist in Engelmann spruce. Engelmann spruce seedlings do suffer high drought mortality due to slow first-year root development (Knapp and Smith 1982). A moist growing season is also likely to be relatively cloudy, reducing mortality due to excessive sun exposure. Such exposure, or "solarization", is a major cause of seedling death in Engelmann spruce seedlings planted at high elevations (Ronco 1970) and presumably would kill natural regeneration as well. Cloudiness would also reduce the risk of high soil surface temperatures, which are an important cause of seedling mortality in Engelmann spruce even at near-timberline elevations (Alexander 1987). If a moist growing season is the principal factor determining establishment success, then the negative association between temperature and seedling establishment may be an artifact reflecting the significant negative correlation between growing season temperature and growing season precipitation for the period of instrumental record ($r = -0.477$, $P<0.0001$). Climate variation appears to be less important to successful establishment of fir than of spruce (Figure 6.35). This is probably because most of the fir originated by layering from a parent tree and did not experience the high levels of water stress encountered by germinants.

Clump plot

Perhaps because of the prevalence of layered establishment, the association between climate and establishment is much weaker at the clump plot than at the ribbon plot.

Precipitation variability does not appear to affect the establishment of either species, although this finding is contradicted by the importance of snow and soil moisture on the plot (see below). Spruce establishment tends to occur in years with a warm growing season (July to October). These spruces are primarily establishing in the open meadow, either in new clumps or at the edges of young, small clumps. In such a situation, a warm growing season may be essential for rapid germination and growth of viable seedlings. However, in view of the weak climate-establishment association at this plot, this conclusion must remain tentative.

Tree rings and climate

The statistical association between tree-ring width and climate provides an indication of the trees' growth response to seasonal climate variations. At the Douglas-fir site, wide rings tend to be formed during cool, moist growing seasons. This pattern is typical of trees growing near the lower timberline, where lack of moisture presents the principal limit to growth and high temperatures increase drought stress (Fritts 1974). The significant positive coefficients for February and March temperature (Figure 6.38b) suggest that the trees may be metabolically active in late winter. Since February average temperatures near this site are above freezing in many years, and March temperatures are above freezing in most years, significant winter photosynthesis may occur.

Wide rings in the spruce chronology (Figure 6.38b) are typically associated with warm July and moist August in the growth year, warm and dry October in the previous year, and cool June to September in the previous year. These findings are similar to those of previous investigators studying Engelmann spruce at Niwot Ridge, 150 km to the south (Hansen-Bristow *et al.* 1988; Yamaguchi 1990). Warmth in July of the growing season should be important because this is the warmest month of the year and time of greatest tree growth (Hansen-Bristow *et al.* 1988). Moisture stress should be low in July because most snowmelt on the site occurs in June and early July, but should increase in August when the late summer drought begins to be important (Knight 1975). Previous October temperature should be important at high elevation sites because frost damage to buds and foliage is minimized by a prolonged period of acclimation to winter temperatures (Hansen-Bristow *et al.* 1988), and survival of these organs will permit greater net photosynthesis during the ensuing growing season. Narrow rings tend to form following a warm previous summer. This may be because a warm summer will lead to abundant radial growth, bud set, and cone formation. In this case growth and growth respiration will place large demands on carbon reserves, leaving relatively little excess carbon for growth the following year.

Tree rings and establishment

Although both establishment and ring width are significantly associated with monthly climate variables, the weak association between ring width and establishment indicates that ring width is not a useful proxy for establishment success. This is because ring width and establishment display different relationships to climate. For example, establishment at the ribbon plot is generally successful when growing seasons are cool. Conversely, ring widths show contrasting responses to summer temperatures in alternate years, so that a wide ring is formed when a cool previous growing season is coupled with a warm current growing season. Ring width can only be a useful proxy for establishment when both variables show a very similar (or opposite) response to seasonal climate variables. In the present case, conditions favoring growth and conditions favoring establishment overlap only slightly. This produces an association between ring width and establishment that is statistically significant, but very weak.

Control of establishment and growth form by snow

One physical factor is paramount at the study site: snow. Snow affects the forests at the study site by limiting seedling establishment and constraining the growth form of the trees. Seedling establishment is limited by deep and persistent snowdrifts that shorten the growing season, while snow affects growth form primarily by protecting foliage from abrasion by windblown snow.

Snow and seedlings

The vegetation survey was undertaken to determine whether spatial variations in vegetation and snow depth were coincident, and whether they indicated corresponding variations in soil moisture. Previous work suggests that snow influences vegetation at the study site primarily by influencing soil moisture. Thilenius (1970) found that variation in the vegetation of alpine meadows in the Medicine Bows is largely a function of available moisture, while Billings and Bliss (1959) demonstrated the close connection between snowmelt and soil moisture at a site 4 km southwest of the study site.

The grass *Deschampsia,* a dominant in dry meadow communities of the Medicine Bows (Thilenius 1970), was most widespread at the clump plot in areas where the snow was less than 1 m deep. These areas included several of the most recently established tree clumps, indicating that dry microsites have been the only sites of successful seedling establishment at the clump plot since the latter 1800's. Establishment in the older and larger clumps has mainly been by layering and has been restricted to the windward and lateral edges of these clumps. These edges are adjoined by *Deschampsia* meadow and thus are relatively dry in comparison with areas dominated by *Sibbaldia*, although snow at these edges is deeper than in the open meadows (up to 1.8 m). Comparable snow depths (1.5-2 m) also prevail over the *Deschampsia* meadow at the ribbon plot. No seedling establishment has occurred in these meadows within the past few decades, suggesting that snow depths >1.5 m are adequate to prevent successful seedling establishment but may permit establishment by layering.

The forb *Sibbaldia* dominates on wet soils near late-melting snowdrifts (Billings and Bliss 1959). At the clump plot, *Sibbaldia* is only dominant in areas leeward of the largest tree clumps, where snow accumulations may exceed 2 m. These sites are completely devoid of establishment by seedlings or by layering. At the ribbon plot, *Sibbaldia* dominates in two areas: a band in front of both the windward and leeward edges of the ribbon, and in patches within the forest interior. These areas coincide with snow depths >2 m and have experienced no seedling or layered establishment within the past several decades. These results suggest that snow depths >2 m are sufficient to preclude all tree establishment.

Snow and growth form

At the clump plot, tree clumps are loci of deep snow accumulation. The growth form of the trees reflects this in that the trees consist of a krummholz mat surmounted by released leaders that show the effects of blowing snow by foliage death and pruning of windward branches. The height of the transition between krummholz and erect leaders conforms precisely to local snow depth. Therefore the presence of growth form features such as a krummholz base or a release height reflect an environment where the trees are sheltered from windblown snow by enclosing snowdrifts. Blowing snow does not significantly affect growth form on the present ribbon plot, which is largely shielded from the full force of the wind by other ribbons located to windward. Nonetheless, many trees located within the ribbon show a release height or a krummholz base. The presence of such relict features on old trees within a modern forest provides compelling evidence of a long-term change in the structure of that forest.

AUTECOLOGICAL FACTORS

Autecological or species-specific factors determine how the trees at a site respond to variation in the physical environment. Two autecological factors are highly significant at this timberline because they tend to affect spruce and fir in markedly different ways. These factors are growth form and establishment mode, and their influence is shown by the contrasting responses of spruce and fir to stress by wind and snow. Fir responds to this stress by adopting a krummholz growth form and by reproducing almost solely by layering, leading to the development of clumps containing large numbers of small stems. Spruce responds to the same stress by developing a krummholz base and by showing a partial shift from seedling toward layered establishment. This produces a less tightly clumped array of larger stems, compared with fir (Figure 6.19).

Growth form changes

Although trees have been present on the clump plot since *ca.* 1500, none of these trees displayed an erect growth form until the mid-1800's, at which time there was also a pulse of new establishment in the open meadows. Disturbance (*e.g.*, grazing) could have contributed to the pulse of new establishment, but could not cause the release of krummholz trees to an erect growth form. Release is typically attributed to a moderation of the harsh timberline environment (Arno and Hammerly 1984). The survival of a released leader probably occurs when the leader grows high enough above the winter snowpack for foliage to escape abrasion by windblown snow. This would require several years of relatively rapid leader growth, which would most likely occur during relatively warm summers.

Although the tree-ring chronologies developed for this study do not show long-term trends suggesting a climatic anomaly corresponding to the period of leader release (Figure 6.37), a long-term climatic reconstruction for the Rocky Mountain region based on a large tree-ring data set from western North America (Blasing 1975, p.489 *in* Fritts 1976) indicates such a possibility. This reconstruction indicates frequent anomalously warm summers in the Northern Rockies from 1824 to 1868 and from 1907 to 1923, with cool summers predominating in the 1700's and 1900's. The transition from low krummholz to erect growth, and the increase in numbers of tree clumps, may have occurred in response to these warm intervals. This warming coincides with the end of the Little Ice Age (*ca.* 1250 to 1850 [Fairbridge 1987]) and thus may represent the first significant warm interval during the period of record at the study site. The same tree-ring reconstruction (Blasing 1975) indicates a virtual absence of warm summer anomalies between 1923 and 1966 (the last year of his study). The relative absence of recent establishment may be a response to this cool period.

Growth form changes at the ribbon plot reflect the gradual development of a continuous forest. Trees showing a release height are primarily located near what was the windward edge of the ribbon at the time of their establishment, suggesting that these trees were exposed to strong winds and partial burial by snow at one time, although many of them are presently located within the forest. The largest of these trees, which have well-developed krummholz bases, are now located well behind the windward edge of the forest ribbon. These krummholz bases are very similar to those presently found on old spruces at the clump plot. Each krummholz base tree shows a transition from very narrow to relatively wide and uniform growth rings between 1750 and 1775 and is presently an erect forest interior tree. The timing of this growth transition coincides with an increase in dispersed, space-filling establishment by spruce at the ribbon plot (Figure 6.23), suggesting that the development of a relatively continuous forest protected the trees from the shallow snow depths and consequent exposure to windblown snow that produces krummholz trees with released leaders at the clump plot. There is a conspicuous lack of evidence that the changes in growth form and increase in establishment during the latter 1700's have a climatic cause. Neither the tree-ring chronology (Figure 6.37) nor the reconstruction by Blasing (1975) suggests a marked climate anomaly for this time, while a more recent analysis by Fritts (1991) finds that temperature and precipitation for this interval were close to the long-term mean. Instead, the growth release and increases in establishment were probably an endogenous response to alteration of the local environment by ongoing tree establishment and growth, a process discussed below.

Establishment mode

Clump plot

Reproduction by layering is far more prevalent at the clump plot than at the ribbon plot. This represents a general trend toward increasing reliance on vegetative reproduction as one approaches timberline (Arno and Hammerly 1984; Black and Bliss 1980; Oosting and Reed 1952; Payette and Gagnon 1979). Although the clump and ribbon plots are at nearly the same elevation and experience similar temperatures, the environment at the clump plot is more harsh because the clump plot accumulates relatively little snow and the trees are more exposed to wind and winter desiccation. Consequently, they must assume a krummholz growth form.

The layering habit strongly constrains clump establishment and growth. Since layered shoots cannot establish farther than the length of a branch (1-2 m at this site) from their parent, tree clumps tend to expand slowly and only on their perimeter. Because the perimeter of a growing clump necessarily increases more slowly than the area, the rate of stem establishment declines through time even though the actual number of new stems establishing may continue to increase. At the clump plot, such a declining establishment rate has prevailed since about 1820 (Figure 6.21).

In an environment where both tree species must reproduce mainly by layering, fir apparently reproduces more readily than spruce. Although only three clumps are dominated by fir, it accounts for almost 70% of the live trees on the plot. Fir has established continuously, with several trees establishing in nearly every decade of the record at the ribbon plot. This suggests that reproduction by layering permits establishment that is not constrained by short-term climate fluctuations. Therefore fir would be expected to have a competitive advantage over spruce if environmental conditions continued to require reproduction by layering. On the other hand, because establishment from seed allows establishment far from the parent plant, the tendency to reproduce from seed confers a competitive advantage on spruce whenever climate (or possibly, disturbance) permits new clump establishment. The ability of spruce to colonize new sites during a short interval of relatively benign climate is seen in the episode of new clump establishment during the 1800's, when all new clumps were established from spruce seedlings.

Ribbon plot

The capacity of spruce to establish from seed while fir establishment is dominated by layering has allowed spruce to dominate the ribbon plot. The presence of a few old fir and spruce clumps indicates that tree clumps and establishment by layering were once structurally important on the plot, but since the mid-1700's expansion of the ribbon forest has been marked by frequent establishment of seedlings in relatively open areas, often several meters from their nearest neighbor. Since the latter 1800's establishment has become biased to the windward edge of the ribbon, but this has not been accompanied by an increase in the frequency of layered establishment. Evidently, the amelioration of the physical environment that permitted widespread spruce seedling establishment to begin in the latter 1700's has not been altered by the subsequent development of a continuous forest on the plot.

DISTURBANCE

Domestic sheep have grazed the subalpine meadows of the Medicine Bows, including the study area, since the 1870's (Thybony *et al.* 1985). Grazing gradually increased in the late 1800's and much of the range was severely overgrazed from about 1900 until grazing was sharply curtailed in 1916 (Bruce 1959; Thybony *et al.* 1985). Grazing may contribute to seedling establishment by removing competitive herbs and grasses and exposing mineral soil (Sims and Mueller-Dombois 1968). Although establishment is low during grazing due to trampling and grazing of seedlings, a high rate of seedling establishment is typical during range recovery after severe overgrazing because seedlings can establish before herbs recolonize exposed mineral seedbeds (Allen 1989). Although several young tree clumps clearly established before grazing started and nearly all established before grazing was curtailed, grazing may have contributed to seedling establishment within the young clumps. At the clump plot, a surge in spruce seedling establishment began in about 1920, reached peak levels in 1937-1938, and ended in about 1956 (Figure 6.18b). This establishment pulse may represent a response to the cessation of intense grazing pressure, particularly in view of the apparent absence of any climatic anomaly (such as relatively warm or wet summers) that might account for increased establishment rates during this period. However, in the absence of more detailed grazing records or any other studies assessing grazing impacts on the local vegetation, this conclusion must remain tentative. The ribbon plot experienced a similar, but smaller establishment pulse that peaked in 1913-

1920 (Figure 6.22b). Although the timing of this establishment pulse correlates well with the 1907-1923 period of warm summers reconstructed by Blasing (1975), it is possible that a reduction in grazing could have contributed to this episode of increased establishment. There is no similar establishment pulse in fir at either study plot; nearly all fir established during the 1900's have been clonal and thus, unlikely to show a marked response to either grazing or benign climate.

CONCEPTUAL MODEL OF CLUMP AND RIBBON DEVELOPMENT

The chronology of forest development on the study site (Figure 7.1) is dominated by two types of processes. Regional processes affect the entire study area and include climate variations and disturbance by grazing. They are external forcing factors that can produce contemporaneous changes in the tree population at both plots. Endogenous processes primarily reflect changes in autecological controls and only affect individual study plots. They represent changes in the tree population such as the establishment of trees or clumps and changes in growth form or establishment mode. Endogenous processes may include both responses to regional processes (*e.g.*, krummholz release due to climate change) and to antecedent endogenous processes that occur because the trees progressively alter the plot environment (*e.g.*, biasing of establishment towards the windward edge of the ribbon). In this section, I first suggest a detailed history for both the clump and ribbon plots, emphasizing these processes. I then extract this information on regional and endogenous processes to present a generalized conceptual model of clump and ribbon development as it occurs in the Medicine Bow Mountains.

History of the clump plot

Regional processes have strongly influenced clump plot development (Figure 7.1). Five clumps probably established by 1500 and persisted as low krummholz with very low tree establishment rates until the early 1800's. At this time relatively warm, dry summers became more common (Blasing 1975), and from about 1821 to 1924, warm summers were more frequent than at any other time between 1700 and the present. This warm interval was accompanied by an increase in the number of trees established, the establishment of nine new clumps, and the release of erect leaders on many krummholz trees. Thus, a single regional process -- warm climate -- dramatically changed the

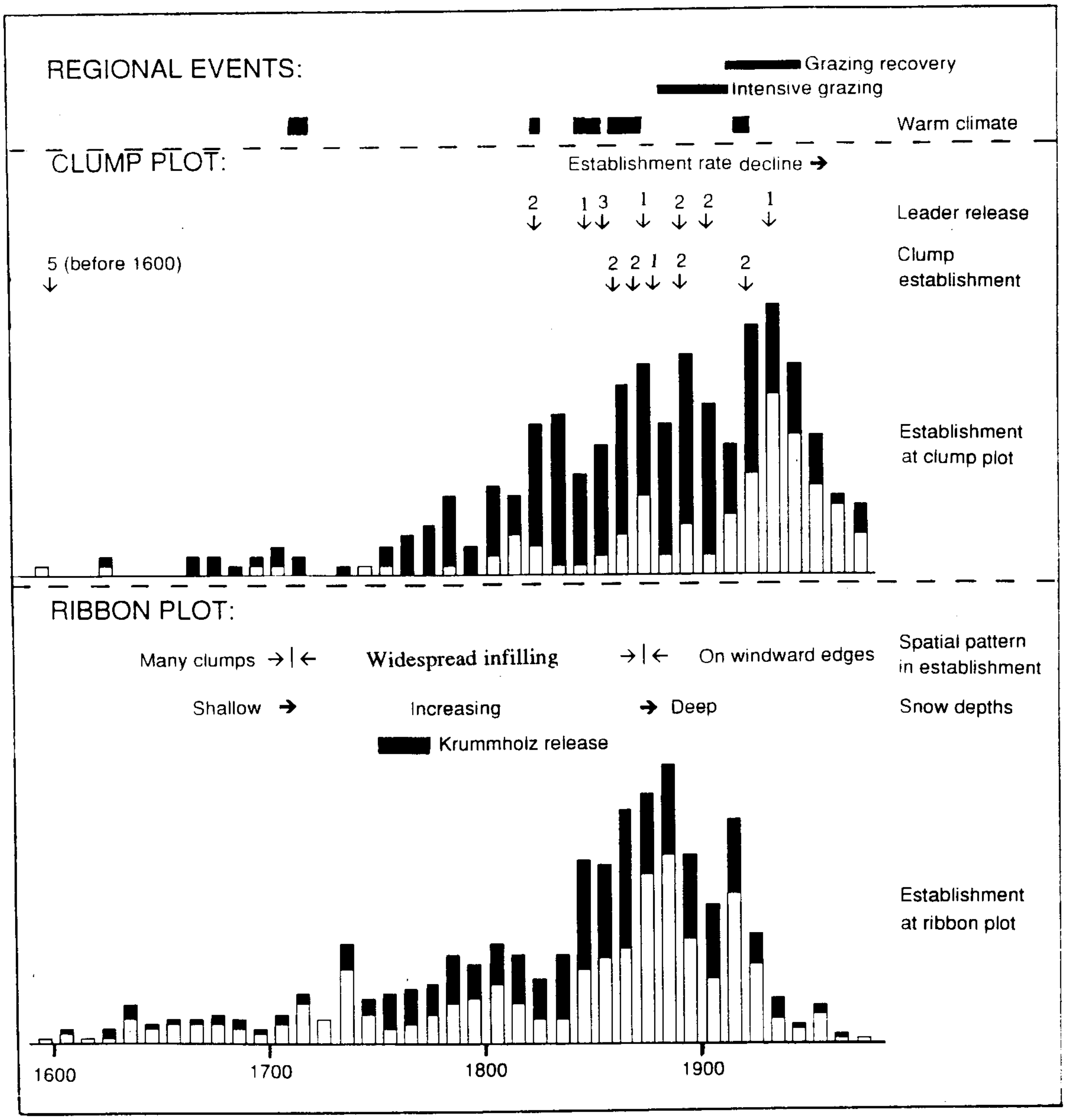


Figure 7.1. Major changes at the study site, 1600 to present. "Regional events" include periods of grazing and recovery and periods of >5 yr with warm summer climate anomalies (as reconstructed by Blasing 1975). "Clump plot" includes the dates of leader release and new clump establishment and a decadal establishment histogram; dark bars represent spruce and white bars, fir. "Ribbon plot" includes phases of plot development, trends in snow depth within the ribbon, the period of krummholz release, and a decadal establishment histogram.

appearance of the plot. Increasingly severe livestock grazing likely affected the plot from the late 1800's to 1916. The cessation of severe grazing pressure may have contributed to a minor peak in spruce establishment from 1920 to 1956. Since that time warm summers have become less frequent, the range has largely recovered from grazing, no new clumps have established, and tree establishment has declined greatly. Thus population changes, clump establishment, and leader release can all be attributed in part to regional factors, chiefly climate change.

There is less evidence of population change due to endogenous factors. The smaller clumps do not have distinct wet meadow vegetation on their leeward edges and apparently experience tree establishment on all edges. It seems likely that only relatively large clumps can trap enough snow to produce deep leeward snowdrifts that preclude tree establishment. If so, the development of deep leeward snowdrifts probably occurred after the release of krummholz allowed the clumps to grow taller. This hypothesis is supported by evidence (Figure 6.19) that establishment has become concentrated on the windward and lateral edges of the largest fir clump only since about 1830, soon after leader release occurred. The current absence of establishment on the leeward edge of large clumps therefore constitutes an endogenous change in the forest. The lack of establishment on leeward edges will cause large clumps to grow into the wind and laterally, perpendicular to the wind. This process has already caused a significant elongation of the largest fir clump (Figure 6.19). Buckner (1977) also observed the progressive elongation of tree clumps perpendicular to the wind and suggested that it represents one pathway for ribbon forest development. However, the data collected in this study suggest that such elongation occurs very slowly, so that it would take many centuries for a ribbon of significant length (*ca*. 100 m) to develop in this manner. In contrast, the transition from tree clumps to forest ribbon at the ribbon plot appears to have occurred in little more than a century.

History of the ribbon plot

Regional processes have also influenced establishment at the ribbon plot, but endogenous processes have played a more important role than at the clump plot. The overall temporal pattern of tree establishment at the ribbon is similar to that seen at the clump plot (Figure 7.1), suggesting that the relatively warm summers of 1821-1924 contributed to establishment at the ribbon plot as well as the clump plot. In particular, the high establishment rates from 1850 to 1929 correlate with the period of new clump establishment at the clump plot, suggesting that this increase was caused in part by climate. There are a number of important structural changes at the ribbon plot that do not coincide with regional events. These include the release of old krummholz trees and the increased growth of fir clumps in 1750-1775, and the windward-edge biasing of establishment in about 1830-1880. These changes may be due to a single endogenous process: the structural evolution of the ribbon. As discussed above, the ribbon may have once been an assemblage of tree clumps. However, probably since the start of the record and certainly since 1600, many trees have established by seed far from their nearest neighbor. The average distance that a tree established from its nearest neighbor declined exponentially from the start of the record until about 1830 (Figure 6.24). Such a decline would be expected if the size of the area in which new trees may establish remained constant while the total number of trees increased. The process of filling in the ribbon with dispersed seedlings operated for much of the establishment record (Figure 6.23); it started as early as the 1600's, when most trees on the plot were in scattered clumps, and persisted until about 1830. At this time, establishment gradually became biased towards the windward edge of the ribbon; this biasing was largely complete by 1880.

The period of krummholz release in about 1750-1775 is conspicuous as a discrete event during the prolonged period of forest infilling by seedling establishment. Trees were scattered across most of the modern ribbon in 1750, but the forest was still fairly open (Figure 6.23). The forest interior trees were therefore increasingly sheltered from strong winds and winter desiccation, permitting krummholz trees to assume an erect growth form. Also, in such an open forest environment the trees could trap a larger amount of snow than is possible in a meadow containing scattered tree clumps. This increase in snow loading would have increased available soil moisture during the growing season, facilitating establishment from seed as well as clonal growth of established clumps. Since it appears that on the modern clump plot snow depths of 0.7 m produce a meadow that is too dry for seedling survival and snow depths of 1.5 m are sufficient to preclude seedling establishment, intermediate snow depths probably will permit successful seedling establishment in a meadow. It is likely that the period of rapid, space-filling population increase at the ribbon plot between about 1750 and 1830 was a response to favorable levels of soil moisture due to the accumulation of intermediate snow depths. Only after about 1830, when a continuous forest was established across most of the potential ribbon habitat, did the space-filling pattern of establishment give way to a pattern of establishment along the ribbon's windward edge.

During this period of ribbon development, establishment was biased towards the windward edge of the ribbon. This was the snowiest phase in ribbon forest development, characterized by snow depths near the modern norm -- that is, suitable for seedling establishment at some sites within the forest but too deep (average 1.8 m) for seedling establishment in the adjacent meadow (Figure 6.3). Establishment probably occurred along the windward edge because early snowmelt along this edge provides a slightly longer growing season than in the rest of the ribbon, and because the edge receives more light than the forest interior. What establishment did occur in the forest interior apparently represented a response to mortality in larger stems; presently, mortality is also increasing in small stems that have been isolated from the warm, sunny windward edge by more recent windward establishment. The result is that the establishment rate has declined since 1900; since 1960, establishment and mortality have been approximately equal.

This interaction between snow, forest structure, and establishment comprises the main difference between the clump and ribbon plots. At the clump plot, snow is largely insufficient to permit seedling establishment, and endogenous alteration of snow accumulation by the trees is minor. Therefore, population changes at the clump plot have largely been driven by a regional factor, climate. Conversely, at the ribbon plot, continuing tree establishment has caused a continuous change in the pattern and depth of snowdrifts. This has caused concurrent changes in the pattern of establishment, so that population changes have been driven by an endogenous feedback between trees and snow. This feedback was positive in the early 1800's, when the increasing density of trees produced snow depths optimally suited for successful seedling establishment. The feedback became negative by the latter 1800's, when snow depths increased to the point that seedling establishment was largely precluded. Today's forest appears to be approximately at equilibrium; rates of establishment and mortality are similar, and seedling establishment occurs only within the extant ribbon.

A conceptual model

The history of clump and ribbon plot development shows that both regional and endogenous processes have been influential throughout the period of record, but that the relative importance of these processes has varied over time. The conceptual model (Figure 7.2) traces this interplay between regional and endogenous process over five relatively distinct phases:

1) In response to either severe disturbance or a regional climate change, seedling establishment occurs in a meadow. If this development follows a catastrophic fire, establishment may tend to occur in areas sheltered by logs or snags. Regardless, the primary control on seedling establishment at this time is a regional process, climate variation. Years suitable for seedling establishment are characterized by relatively warm summers with adequate summer precipitation. Climatic controls on establishment become less important as ensuing phases appear on the site, but the characteristic process in phase 1, establishment of new stems far from living trees, may continue while forested portions of a site experience the other phases of development. This is the longest-lasting phase.

2) As soon as seedlings have begun to establish, the site enters a phase of clump growth that persists for as long as the trees grow in discrete clumps. The clumps trap snow, causing the affected trees to develop a krummholz growth form. Melting of trapped snow and shading of the adjacent meadow increase the probability of seedling establishment on near-clump microsites and allow expansion of the clumps by layering. Establishment around the clump is therefore subject to an endogenous control, microenvironmental variation due to the presence of the clump. However, clumps tend to expand very slowly during this phase, so endogenous controls of establishment do not yield rapid changes in the overall rate of stem establishment or the area covered by tree clumps. Regional climate variation remains influential because relatively warm regional climate may allow clumps to develop released leaders. Released leaders may then cause a further endogenous change: the clumps trap larger snowdrifts and snow accumulations may be large enough to preclude establishment in the lee of the clumps and to cause development of a wet meadow

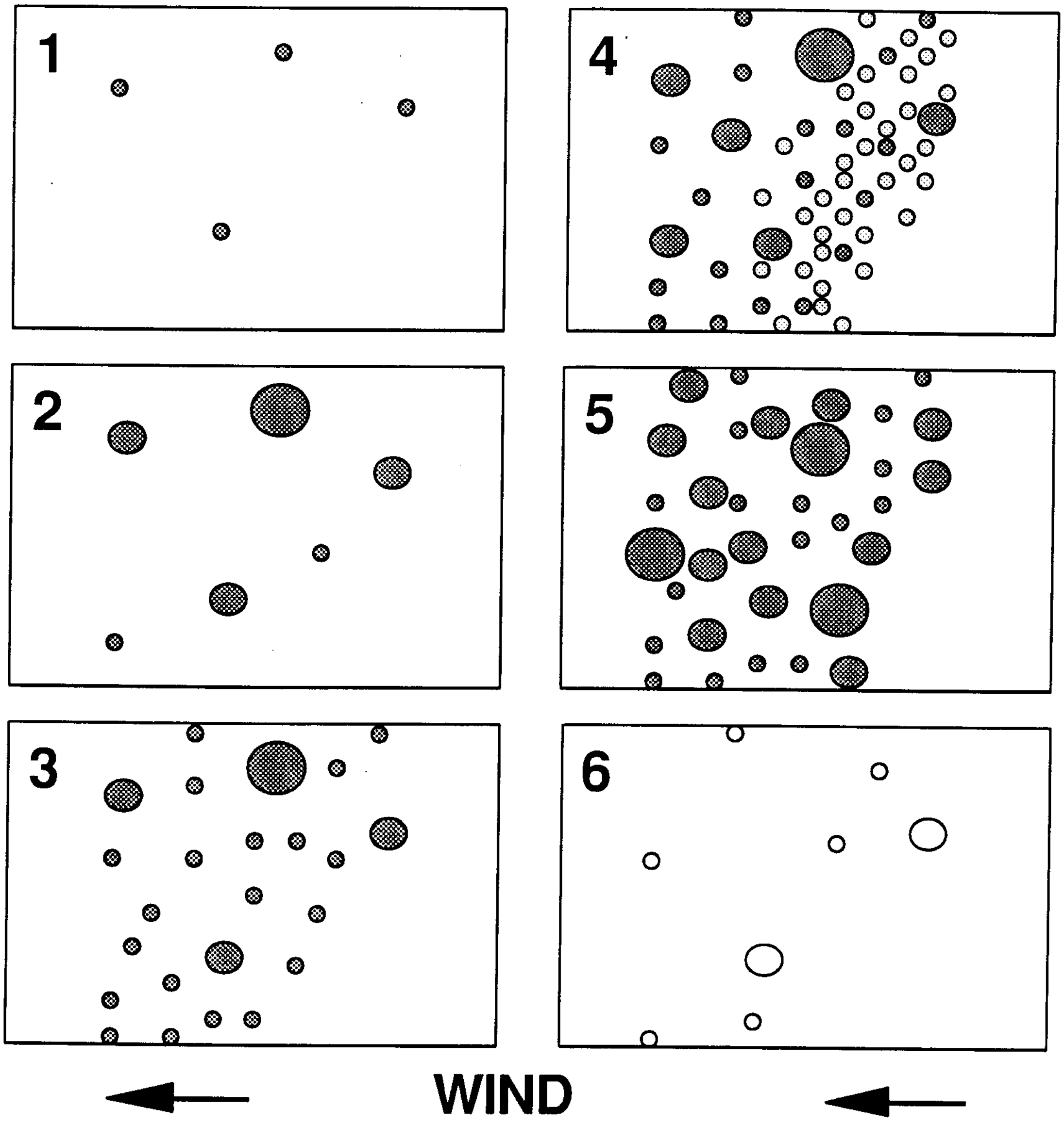


Figure 7.2. Conceptual Model of clump and ribbon development: (1) Seedling establishment in open meadows. (2) Clump growth and continued seedling establishment. (3) Rapid establishment in response to endogenous environmental change causes ribbon forest formation. (4) Establishment is biased to windward edge of ribbon. (5) Ribbon growth ceases and ribbon develops stable age structure. (6) Process reset by catastrophic disturbance, typically fire. See text for detailed explanation.

herb community on these leeward microsites. Because clumps grow so slowly, the site may remain in this phase for many centuries.

3) As new trees continue to establish in open meadow (phase 1) and clump growth proceeds (phase 2), the average snow accumulation across the site increases. An increasingly large proportion of the site is also protected from windblown snow and is shaded by tree crowns. Thus an increasingly large area is comprised of microsites suitable for seedling establishment, resulting in a rapid increase in the rate of seedling establishment. This is an entirely endogenous positive feedback process. The process continues for as long as these changes in snow accumulation, protection from wind, and shading continue to favor seedling establishment. Once these changes cease to favor establishment, primarily because of excessive snow accumulations, the feedback becomes negative and the ribbon enters phase 4. During phase 3 the total forested area on the site experiences a rapid increase and most of the tree clumps coalesce to form a ribbon forest. Most trees in the ribbon are sheltered from windblown snow by other trees, so many krummholz and flagged trees assume a spire-like form. Phase 3 may be the briefest of all phases (*ca.* 100 yr), but it features the largest total growth in forested area. Regional processes are largely unimportant during phase 3, but regional climate change can affect the rate of forest development during this phase.

4) Phase 4 begins as soon as heavy snow accumulations, deep shade, and other endogenous changes in the ribbon forest environment begin to preclude seedling establishment within the ribbon. Because ribbons at the study site (and indeed, all described ribbon forests) are subject to prevailing westerly winds, the windward edge of the forest faces west, receives the afternoon sun, and is warmer than the leeward edge. Therefore snowmelt occurs earlier along the windward edge and seedling establishment becomes biased towards the windward edge of the ribbon. This establishment occurs both within the forest and in the adjacent meadow, causing the edge of the forest to advance into the windward meadow until establishment in the meadow is precluded by the deep snowdrift formed in the lee of the next windward ribbon. Like phase 3, this phase is characterized by changes in establishment due almost entirely to endogenous changes in the physical environment. Any moderate change in regional climate is likely to alter the rate, but not the outcome, of the

process. This phase has a duration similar to phase 3. It features a smaller change in forested area than the preceding phase. The phase closes with a rapid decline in establishment rate to very low levels.

5) The final phase of ribbon forest development is characterized by a fully developed ribbon. The forested area of the ribbon does not change. The presence of forest ribbons on the landscape reduces surface winds to moderate velocities, so winter desiccation of foliage is minor and nearly all trees display a spire-like growth form. Deep and persistent snowdrifts form in meadows between the forests, precluding further seedling establishment in these meadows. Snows are also deep within the forests, but snow depths here are quite variable and some seedling establishment occurs. However, such seedlings may only enter the forest canopy through death of an overstory tree. Phase 5 forests are probably structurally stable and multi-aged, with trees of all ages occurring from the windward to the leeward edge of the forest. The physical environment on the site is strongly influenced by the presence of the trees and thus subject to endogenous control. However, unlike earlier phases, this endogenous control varys little over time. Consequently, variations in regional climate may once more become important; changes in snow accumulation, wind velocity, and temperature could all affect the depth and persistence of snow drifts between the ribbons, thereby changing controls on seedling establishment. The phase is most likely to be terminated by catastrophic fire.

TIME SCALES IN FOREST DEVELOPMENT

Physical, autecological and disturbance factors affect tree population dynamics in markedly different ways. Although these factors are qualitatively very different, all can be characterized according to their expression in the time domain, *i.e.*, the time scales at which these factors are expressed, and at which the forest responds.

Climate, a physical factor, affects tree establishment (as well as clump establishment and krummholz release) at both year-to-year scales, as shown by regressions involving monthly climate variables (Figures 6.35 and 6.36), and at decade scales, as shown by the response of the clump plot to a period of warm summers between 1821 and 1924. Establishment and climate variation may also be associated at century scales; for instance, establishment at both plots apparently increased at the end of the Little Ice Age. These findings are consistent with other studies showing that tree populations may show a response to climate variation at scales of years (Franklin *et al.* 1971; Kullman 1981, 1989, 1991a, 1991c), decades (Agee and Smith 1984; Griggs 1937; Kullman 1979, 1991d; Scott *et al.* 1987), centuries (Lavoie and Payette 1992; Payette et al. 1989a, 1989b; LaMarche and Mooney 1972; Scuderi 1987), and even millennia (Bryson *et al.* 1965; Carrara *et al.* 1991; LaMarche 1973; LaMarche and Mooney 1967; Reider *et al.* 1988). Climate changes that affect establishment tend to be gradual or incremental; for instance, establishment at the clump plot is not strongly associated with individual warm summers, but instead reflects a prolonged period during which warm summers were relatively common.

The primary autecological factors influencing the frequency and spatial pattern of tree establishment are growth form, which alters patterns of snow retention, and mode of establishment, which affects the spatial pattern of establishment. Therefore autecological factors are expressed at the time scales of establishment and growth, which tend to be rather slow. In this study, year-to-year changes in the tree population are generally indetectable, some changes become apparent across decades, and sweeping changes encompassing the entire study area occur across centuries. When autecological factors respond relatively quickly to climatic changes, episodic climate change (*e.g.*, a period of warm summers) can force episodic autecological change (*e.g.*, a period of seedling establishment).

Mode of establishment is an autecological factor that is expressed in two clearly distinct ways. Establishment by seedlings can result in rapid expansion of the tree population because it is possible for a large number of trees to establish in a very short time, and because these trees can establish many meters from their nearest neighbor. For example, seedling establishment allowed the rapid infilling of the ribbon plot between 1750 and 1850. Conversely, establishment by layering necessarily occurs at small nearest-neighbor distances. Because of this, there has been very little net change in the forested area of the clump plot across the period of record (what change has occurred, has been due to new clump establishment by seedlings). Therefore the rate of forest expansion is much greater when trees are establishing by seed than when they are establishing by layering. This finding has been corroborated in the boreal forest-tundra (Payette and Gagnon 1979; Sirois and Payette 1991). A corollary is that an environmental change that permits a transition from layered to seedling establishment (*e.g.*, a change in snow depth from 0.7 m to 1.0 m) will have a much larger effect on the forest than a change that does not induce such a transition (*e.g.*, a change in snow depth from 0.4 m to 0.7 m). Thus, the dichotomous nature of establishment mode enables the forest to show a threshold response to changes in the physical environment.

Although grazing may have affected establishment at the study site, the data do not indicate how long recovery from grazing may require on this site. Wildfire is a more influential disturbance. Wildfire is probably common in the forest-tundra of the Medicine Bows, judging from the frequency of subalpine fire in the range (Romme and Knight 1981) and the broad extent of the one recorded forest-tundra fire (Billings 1957, 1969). It is likely that at some time the study site has experienced catastrophic wildfire, although no record of such an event was found on either plot. The 1809 Libby Flats fire (Billings 1969) provides an excellent example of how such a fire would affect the study site. Recovery from this fire is spatially heterogeneous, including areas with no recovery, areas of former ribbon that are now in clumps, areas of virtually restored ribbon, and areas of seedling establishment in places that were apparently open meadow before the fire. This heterogeneity is due in large part to changes in snow accumulation patterns following destruction of woody structures (clumps and ribbons) by the fire (Billings 1957). Much of the area burned in the Libby Flats fire has shown very little recovery in the ensuing 150 years, suggesting that full recovery from catastrophic fire is likely to require at least several centuries (Billings 1957). Therefore wildfire is an approximately instantaneous event for which the forest's response is limited by the response times of tree establishment and growth.

SUGGESTIONS FOR FURTHER RESEARCH

Since the concept of the ribbon forest was introduced by Billings (1969) there has been little research describing the processes involved in the initiation or development of these forests. Although considerable additional research will be necessary to understand the processes involved in ribbon forest development in complete detail, the present research makes several significant additions to such an understanding. It represents the first attempt to reconstruct the development of a ribbon by determining the dates of establishment for all trees located within the ribbon, and one of the most comprehensive efforts to reconstruct the development of tree clumps by similar means. It is one of the few studies to discuss differences between seedling and layered establishment at a temperate timberline, and consequently adds to our knowledge of the population dynamics of Engelmann spruce and subalpine fir in the Rocky Mountains. Finally, the study presents a model of ribbon forest development from tree clumps that theorizes a systemic interaction between forest structure, snow accumulation patterns and seedling success. This theory is testable by more detailed measurements of the physical environment, by studies of seedling establishment, and by censusing of establishment and mortality, as detailed below. The study has limitations related to site replication, uncertainties in the tree establishment and mortality records, and uncertainties related to microenvironmental determination of seedling establishment success. However, these problems could easily be addressed by further research, and the study has revealed a number of very promising lines for new inquiry.

Controls of Establishment

Physical controls

Although previous studies and the present study suggest that seedling establishment success in the forest-tundra is controlled in large part by the distribution and quantity of snow and by the effects of that snow on soil moisture and length of growing season, these concepts have not been tested by ecophysiological studies or by experimental intervention. In view of the extensive literature inferring the effect of clumps or ribbons on seedling establishment, such a study is overdue. The association between seedling establishment and microsite physical environment should be determined by direct measurement of snowmelt patterns and growing season soil moisture. This would provide detailed empirical data on how climate and snow influence seedling establishment. The mechanism of this influence could be detailed by a physiological study similar to that recently presented by Cui and Smith (1991) for seedling establishment in a subalpine fir forest. Similar uncertainties pertain to ecophysiological controls over establishment by layering in clump and ribbon forest environments. For instance, little is known of the benefits to a layered seedling derived from the contribution of food, water and nutrients from the parent tree.

Grazing controls

Detailed data on grazing intensity, such as annual data on the numbers of animals being grazed and periodic reviews of range condition, are needed to substantiate any claim that seedling establishment has occurred in response to grazing. I know of no such rigorous study for a subalpine meadow region in North America, but in view of the many studies attributing subalpine meadow invasion to grazing (*e.g.* Butler 1986, Dunwiddie 1977, Vankat and Major 1978), such a study would be very useful.

Testing the conceptual model

The conceptual model (Figure 7.2) proposes that the period of rapid establishment during which the ribbon formed from a network of scattered tree clumps occurred in response to an increase in meadow snow depth due to the tendency of seed-established trees in the meadows to trap increasing amounts of snow. This positive feedback caused increasingly rapid seedling establishment in the meadow until trees were so numerous that a ribbon forest had become established, by which time snows became so deep that the feedback became negative. Establishment was then biased towards the windward edge of the ribbon and subsequent establishment slowed, resulting in modern recruitment approximately equal to mortality. If valid, this model suggests five phases of ribbon forest development: (1) seedling establishment in meadows; (2) clump growth; (3) rapid meadow establishment, forming a ribbon; (4) declining ribbon growth dominated by windward-edge establishment; and (5) relative stability. Of course, disturbance could affect or terminate this development. Such a complex model for interaction between trees and their physical environment near timberline has not been previously proposed and warrants intensive study. The research could be accomplished by a real-time study in which populations were periodically recensused to determine the exact dates and locations of seedling establishment and tree death events. Suitable sites for this research are plentiful in the Libby Flats area, where ribbon forests at a wide variety of microsites are regenerating from a serious burn.

Such a study could evaluate the climatic and microenvironmental limitations to seedling establishment that dominate phase 1 by examining seedling establishment in open meadows over a fairly wide area, and could accurately evaluate the role of year-to-year climate variation in determining seedling establishment success. By examining establishment at diverse sites, such a study would be relatively free of any site-specific biases that may exist in the characterization of seedling establishment presented in the current study. Similarly, a variety of sites could be sampled to characterize clump growth (phase 2). A real-time study would also be useful for evaluating the positive feedback that characterizes rapid establishment in phase 3. At the study site, most of this phase happened between 1750 and 1800. At a site where the process is currently underway, very detailed information could be recovered about the changes in snow depth, snow distribution, establishment rate and tree growth form that characterize this phase. It would be similarly useful to examine a ribbon currently in phase 4, when establishment is progressively biased to the windward edge of the ribbon due to excessive within-ribbon snow accumulations. Phase 5, which hypothesizes long-term stability in the forest, requires evaluating forest change over a very long period and so could not be verified by a real-time study. The hypothesis could be tested by developing age-structure transects across a variety of ribbon forests. The presence of old forests that do not show a strong gradient in tree age between windward and leeward edges would tend to support the hypothesis of ribbon stability. Alternatively, very old forests might show senescence or evidence of successional change.

Regional Variability in Ribbon Forests

Every ecosystem displays variations in structure and process across its geographic range, but no study has attempted to document such variation for ribbon forests and few such surveys exist for tree clumps (Buckner [1977] attempted to catalog the distribution of ribbon forests and Arno and Hammerly [1984] provide much information on the extent and variation of tree clumps). The plan for evaluation of the conceptual model presented above would provide regional data about variability in size and age of tree clumps and ribbon forests, and the duration of each phase of the model. If the sample sites were chosen to represent a variety of microsites throughout the study area (*e.g.*, the entire forest-tundra ecotone of the Medicine Bow Mountains), such a study could also reveal ecological gradients within the ribbon forest ecotype, and reveal the variety, frequency and spatial extent of disturbance in ribbon forests.

This study has addressed ribbon forests *sensu* Billings (1969). At least two other types of ribbon forest exist. One is the ridgetop forest, consisting of a single ribbon that acts as a snow fence, described by Daubenmire (1981) and Arno and Hammerly (1984). The second type occurs on alternating ridges and troughs of sedimentary rock and may or may not act as a snow fence; this type has been alluded to by Arno and Hammerly (1984) but never explicitly described. A comparative study of the different types of ribbon forest could answer questions such as: What are the functional similarities and differences between these ribbon forest types? Do they display similar structures? Are they all subject to the endogenous changes encountered in the Medicine Bow ribbons? A similar array of questions may be posed for tree clumps, which also have never been compared on a regional basis.

Experimental interventions

Various predictions of the conceptual model could be tested by experiment. Such a test would be most desirable for phase 3, which predicts a period of rapid seedling establishment due a positive feedback between seedling establishment and changes in snow depth. Such a feedback has not been previously proposed, but can be studied by evaluating the relative impact on seedling establishment of various changes in the physical environment that occur in phase 3. These changes include an increase in average snow depth, increased shading of meadow by tree crowns, and reduced wind velocities due to both of these factors. The increase in snow depth may cause increased soil moisture, lower soil temperatures (but reduced depth of soil freezing in winter) and a shortened growing season. Shading by tree crowns may cause slower snowmelt, lower soil surface temperatures and reduced risk of solarization or high heat and drought stress in seedlings. Reduced wind velocities may cause reduced impacts of windblown snow on exposed foliage in winter and reduced evaporative drought stress in summer. These diverse changes in the physical environment could in turn yield changes in the meadow herb community which might affect seedling establishment by affecting competition between herbs and seedlings. The impact of each of these processes on seedling establishment success and subsequent tree growth can be tested experimentally.

The experiment would begin by locating a relatively large area of homogeneous meadow. It would be desirable to establish this homogeneity by installing a network of soil moisture and temperature measurement points at least a year before beginning experimental intervention, and by conducting a late-winter survey of snow depth and density. It would also be desirable to locate a climate station on the site to measure precipitation, temperature, wind velocity and direction and direct beam solar irradiance, and to accumulate at least a year's baseline data. The precise number of plots established would depend on financial and labor resources, but at a minimum, the effects of altered snow depth, increased soil moisture, increased growing season temperature, and shading by tree crowns should be tested on an array of plots. Snow depth could easily be increased by building snow fences on selected plots; this would affect both soil moisture and growing season temperatures. Soil moisture could be increased by irrigation, preferably using locally-derived snowmelt so that water temperature and chemistry would be the same as if the water came from an overlying snowbank. Growing season temperatures could be increased by erecting temporary plastic shelters during the growing season to increase air temperatures. The shelters should be removed to permit the site to experience a typical physical environment during the nongrowing season. Shading could be tested by erecting artifical "trees" (probably made of plywood) to produce shadows of size and shape comparable to those produced by isolated trees and small clumps in the area. Again, these should be removed during the nongrowing season so as not to affect winter wind and snow accumulation patterns. At least some of the possible interactive effects should be tested; for instance, the combination of increased snow depth and shading by tree crowns would closely approximate the environmental changes predicted under phase 3, and so any failure to observe increased seedling establishment under this treatment would suggest a fundamental flaw in phase 3 of the conceptual model.

The effect of these interventions would be assessed by recording successful establishment of seedlings and growth rates of the established seedlings. Therefore the experiment would have to run long enough to for a significant number of seedlings to establish. ("Significance" is determined by an ability to discriminate between the effect of different treatments relative to the control.) Rates of establishment at the ribbon plot during phase 3 suggest that one or more decades might be required.

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APPENDIX: AGE CORRECTION METHODS

All samples that did not include a tree's pith required age corrections for the time elapsed between pith date and the innermost ring on the sample ("pith corrections").

All samples that were not taken at the base of a tree required age corrections for the time required for the tree to grow to the height of sampling ("height corrections").

Pith corrections

Samples fell into 3 categories: (1) pith date known, (2) core taken close to pith, and (3) core not taken close to pith. Corrections for each of these possibilities are represented in Table A.1.

Type (1) corrections, represented by Tree 1 in Table A.1, were trivial; no pith correction was required for these samples, which included all disks and approximately 25% of all increment cores. For the clump plot, 176 trees (46%) and for the ribbon forest plot, 208 trees (31%) were so dated.

Type (2) corrections, represented by Trees 2 and 3 in Table A.1, were applied to cores of the form shown in Figure A.1. The innermost rings could be envisioned as arcs of concentric circles, permitting calculation of the probable distance to the pith ("Crad" in Figure A.1) by the use of a simple computer program named CHORD. Program CHORD would flag a sample for special consideration if the length of the measured chord (distance "a" in Figure A.1) was greater than 10 times the width of the measured arc (distance "b" in Figure A.1). Next, the average number of rings per centimeter in the innermost portion of the core was estimated by measuring the width of a zone of relatively uniform growth encompassing the innermost 7 to 30 rings (GZ) and counting the number of rings within this zone (CN). The number of missing rings (the pith correction, PCorr) is then:

$$\text{PCorr} = \text{Crad} \times \text{CN} \div \text{GZ}$$

If a sample had been flagged by program CHORD, both type (2) and type (3) corrections would be tried and one estimate selected after examining the sample, consulting the notes for description of the tree, and comparing with data for trees of similar species, height, diameter, vigor, location within the stand, and age. In about 90% of these cases, the CHORD estimate was used. In all, 177 trees (46%) at the clump plot and 405 trees (62%) at the ribbon plot were dated using program CHORD

Table A1. Sample pith correction worksheet.

Note: "Tree" is the ID number of the tree, assigned in the field. "DSH" is the tree's diameter at sampling height, measured in the field. "Start" is the year that the earliest ring on the sample was formed. "Crad" is the radius within (and including) the first ring on the sample. "Rad" is the overall length of the sample. "Rrad" is the hypothetical missing length of an incomplete core. "GZ" is the width of a zone of relatively uniform growth near the pith. "CN" is the number of rings in the zone defined by GZ. "C,R" indicates whether the age estimation was based on extrapolation over the distance measured by Crad or the distance measured by Rrad. "COK" indicates whether a Crad-based extrapolation was excessive. "PCorr" is the magnitude of the pith correction. "PDate" is the estimated pith date, calculated as Start - PCorr.

Tree	DSH (cm)	Start (yr)	Crad (cm)	Rad (cm)	Rrad (cm)	GZ (cm)	CN (yr)	PCorr (yr)	C,R	COK	PDate (yr)
1	1.6	1951	0.00	1.00							1951
2	19.6	1874	0.09			0.152	6	3	C	Y	1871
3	7.5	1944	0.23	1.90		0.110	7	14	C	N	1930
4	35.5	1745		17.45	0.6	0.363	6	9	R		1736

Table A.2. Results of height-age regression for calibration seedlings.

Parameter	Fir	Spruce
Constant	7.17	5.61
S.E. of Y Estimate	6.04	4.82
R^2	75.9%	85.6%
No. of Observations	153	153
Degrees of Freedom	151	151
X Coefficient	4.07	4.46
S.E. of Coefficient	0.186	0.149

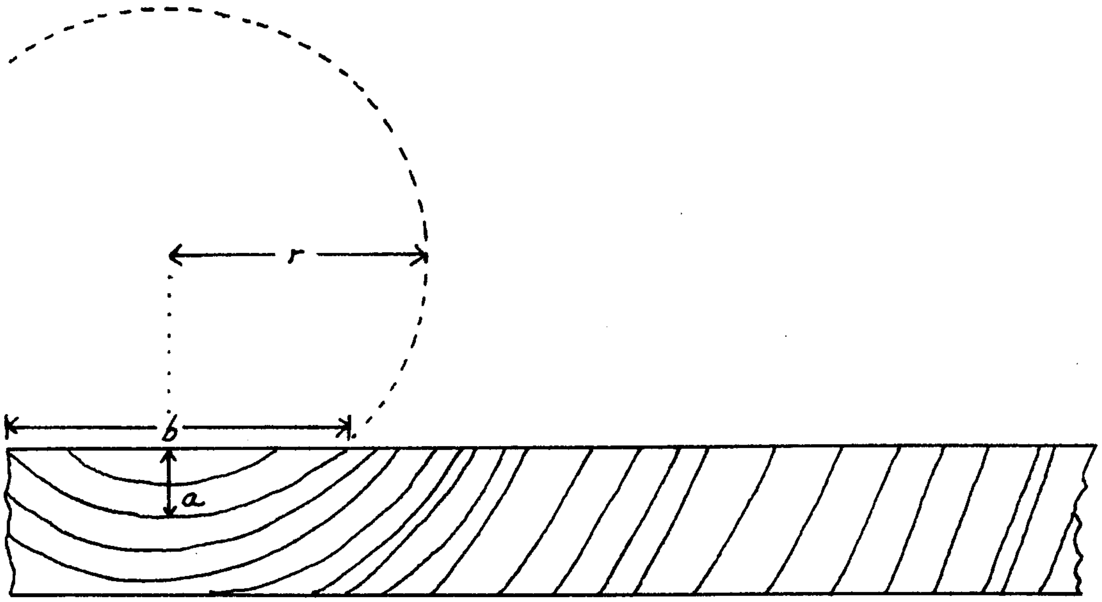

Figure A.1. Estimation of pith dates by chord measurement. Dimensions "a" and "b" are measured using a tree-ring measuring machine. "r" can then be calculated as the radius of the circle that has chord "b", and the distance to pith can be calculated as Crad = r - a.

Type (3) corrections, represented by Tree 4 in Table A.1, were applied to a relatively small number of trees; most of these were so rotten that the recovered core included <75%, and usually <25%, of the probable distance to the pith. For the relatively few trees in which only a small part of the sample appeared to be missing, the probable distance to the pith was calculated from the known diameter of the tree at the height of sampling (DSH) and the measured length of the core (Rad) by assuming that the pith was at the center of the tree; the length of "missing" core, Rrad, is then:

$$\text{Rrad} = (\text{DCH} \div 2) - \text{Rad}$$

and following the procedure outlined above, the appropriate age correction is:

$$\text{PCorr} = \text{Rrad} \times \text{CN} \div \text{GZ}$$

Hovever, only 5 trees at the clump plot (1.3%) and 8 trees at the ribbon plot (1.2%) were dated in this way. The remaining samples (3, or 0.8%, at the clump plot; 35, or 5.3%, at the ribbon plot) were dated by analogy with trees of the same species, known age, comparable (± 10%) diameter at sampling height, and comparable (± 10%) diameter at breast height. A given tree was assigned a pith date corresponding to the mean pith date of the designated similar trees. Finally, 26 dead trees at the clump plot (6.7%) could not be dated either because they were too rotten to sample or because it was not possible to determine establishment and death dates by crossdating with the live tree chronology.

Age corrections

The age correction procedure involved estimating the probable age of spruce and fir seedlings of a given height and then applying this correction to the measured height at which trees on the study plots had been cored. Because a large number of seedlings (50) were cut in order to develop the height-age relationship, they were taken from the windward edge of a ribbon forest located near, but not on, the study plots.

Twenty-five of these seedlings were cut for each species, Engelmann spruce and subalpine fir. For each species, 5 seedlings were cut in each height class from 0-0.2 m to 0.8-1.0 m in order to assure that a wide range of seedling ages was represented and in order to assure that corrections could be applied for sampling heights as great as 1 m without extrapolation. Seedlings were sectioned at 10 cm increments from the base upwards and each of these sections was sanded and counted using the same procedures applied to disk samples from the main study plots. This produced two data arrays (one for each species) containing a large number of height-age values. These data are presented here as scatterplots (Figure A.2); regression statistics are summarized in Table A.2.

Age corrections were calculated for all trees by applying these regression equations to measured sampling heights. The final tree establishment date estimate therefore consisted of a crossdated date for the innermost ring on the sample, minus any necessary pith correction, minus any necessary height correction.

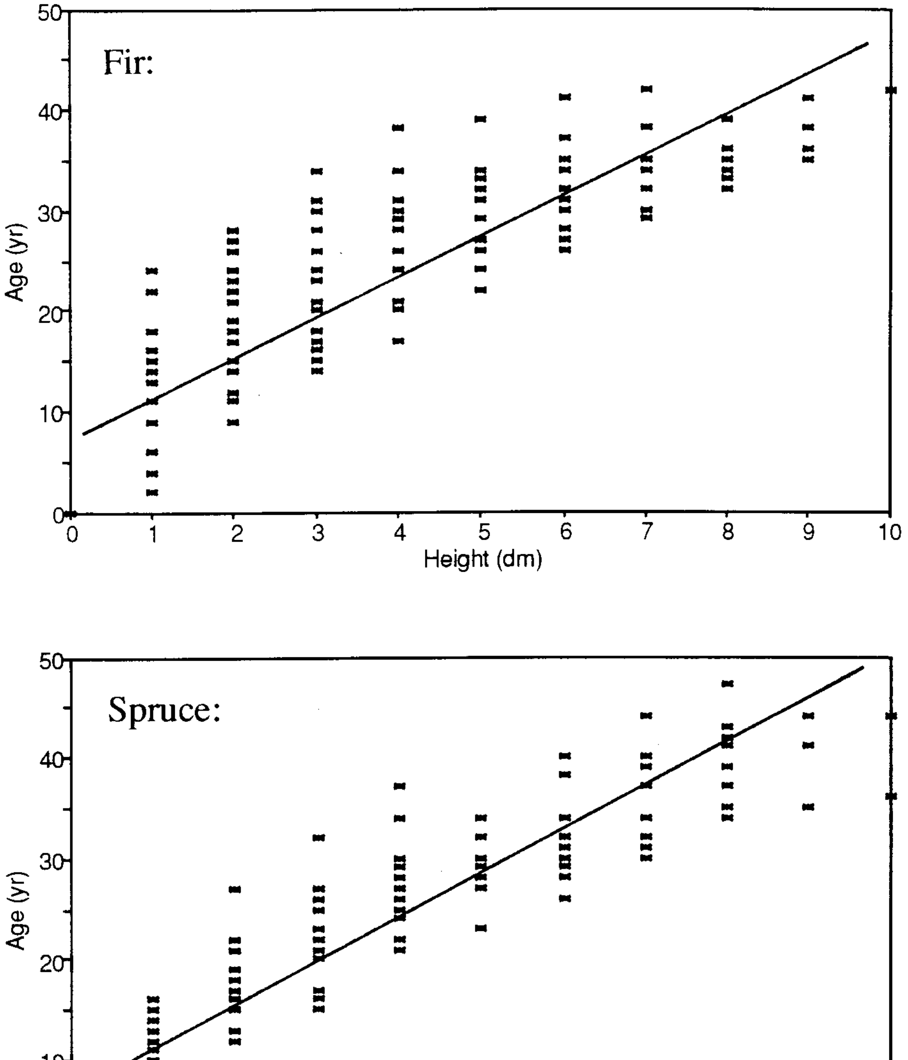

Figure A.2. Scatterplots showing the height and age of disks cut from calibration seedlings of fir (above) and spruce (below), and lines representing the regression equations presented in Table A.2.