THE TREELINE ECOTONE IN INTERIOR ALASKA

- FROM THEORY TO PLANNING AND THE ECOLOGY IN BETWEEN -

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A

THESIS

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Abstract:

Treelines have been the focus of intense research for nearly a hundred years, also because they represent one of the most visible boundaries between two ecological systems. In recent years however, treelines have been studied, because changes in forest ecosystems due to global change, e.g. treeline movement, are expected to manifest first in these areas.

This dissertation focuses on the elevational and latitudinal treelines bordering the boreal forest of interior Alaska. After development of a conceptional model of ecotones as three-dimensional spaces between ecosystems, we offer a historical perspective on treeline research and its broader impact in the Brooks Range, Alaska.

Dendrochronological analysis of >1500 white spruce (Picea glauca (Moench [Voss])) at 13 treeline sites in Alaska revealed both positive and negative growth responses to climate warming, challenging the widespread assumption that northern treeline trees grow better with warming climate. Hot Julys decreased growth of ~40% of white spruce at treeline in Alaska, whereas warm springs enhanced growth of others. Growth increases and decreases appear at temperature thresholds, which have occurred more frequently in the late 20th century.

Based on these relationships between tree-growth and climate as well as using landscape characteristics, we modeled future tree-growth and distribution in two National Parks in Alaska and extrapolated the results into the 21st century using climate scenarios from five General Circulation Models. In Gates of the Arctic National Park, our results indicate enhanced growth at low elevation, whereas other areas will see changes in forest structure (dieback of tree-islands, infilling of existing stands). In Denali National Park, our results indicate possible dieback of white spruce at low elevations and treeline advance and infilling at high elevations. This will affect the road corridor with a forest increase of about 50% along the road, which will decrease the possibility for wildlife viewing. Surprisingly, aspect did not affect tree growth - climate relationships.

Without accounting for opposite growth responses under warming conditions, temperature thresholds, as well as meso-scale changes in forest distribution, climate reconstructions based on ring-width will miscalibrate past climate, and biogeochemical and dynamic vegetation models will overestimate carbon uptake and treeline advance under future warming scenarios.

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General Introduction:

Treelines have long been the focus of intense research (Griggs, 1934; Krebs and Barry, 1970; Wardle, 1971; Troll, 1973; Tranquillini, 1979; Elliot -Fisk, 1983), for a summary see Koerner (1998) or Sveinbjoernsson (2000). Treeline advances and retreats as a result of climate fluctuations have been documented over time scales ranging from thousands of years (MacDonald et al., 1993; Kremenetski et al., 1998) to 20th century warming, in Alaska (Suarez et al., 1999; Lloyd and Fastie, 2003), Canada (Lavoie et al., 1994; Szeicz et al., 1995; Lescop-Sinclair and Payette, 1995) and Scandinavia (Kullman 1993 and 1996). Like climate factors, disturbances can influence position of arctic and alpine treelines, e.g. fire induced shifts in position (Arsenault and Payette, 1992 and 1997; Landhaeusser and Wein, 1993).

Especially in the high latitudes, where warming is expected to be of greatest magnitude (Overpeck et al., 1997; Serreze et al., 2000), large-scale models assume linear correlation between changing climatic conditions (e.g. warming) and subsequently advance of the northern treeline (Elliot-Fisk, 1983; Pielke and Vidale, 1995). However, northern treelines might not react very fast to climate warming (Lavoie and Payette, 1996), or might be relicts of warmer periods and not reflect current climatic conditions (Weisberg and Baker, 1995). Spatially explicit models incorporating topographic influences (Rupp et al., 2001) produce an expansion of boreal forest onto the North slope of Alaska only after thousands of years, because the Brooks Range serves as a barrier.

Position of northern treeline and the extent of the boreal forest are important drivers of the global climate system through albedo (Foley et al., 1994) and the potential to store carbon (Fan et al., 1998; Liski et al., 2003). Summer temperature (July 10°C isotherm, Daubenmire, 1954; Holtmeier, 1974) has historically been reported as the main factor controlling treeline position, while Koerner (1998) recently proposed that soil temperatures of the root zone provide a far better explanation than generalized air temperatures. However, the limiting factor for tree growth may have shifted to moisture supply within the boreal forest (Barber et al., 2000) and parts of the forest-tundra ecotone in Alaska (Jacoby and D'Arrigo, 1995). Briffa et al. (1998) reported a decrease in sensitivity of radial growth and late wood density of high latitude trees to temperature since the mid 20th century.

The current literature at the time I began my Ph.D. could be summarized as follows: Models projected that further warming will enhance tree-growth and will lead to an expansion of forest into tundra, basically assuming that a new steady state between climate and vegetation would be reached. These generalized results were not supported by site studies, however, and the general assumption that temperature was the limiting factor for tree growth began to be questioned (Barber et al., 2000). Within that framework I began planning my dissertation research.

Initial ideas:

At first, my goal was to use a combination of methods to study the tree-environment interactions at treeline in the Brooks and Alaska Range: 1) Microclimatic measurements along elevational gradients including northern and southern aspects to investigate the combination of environmental factors, e.g. climatic or topographic at plot and landscape scale and 2) use dendrochronological methods to investigate past growth of these trees. This combination promised a powerful approach to combine measurements in space (1) and time (2).

I faced the following challenges:

1) Microclimatic instrumentation is cost intensive. During the first year, I was not able to fully instrument all sites. In the following years, however, I established two transects, one in the Alaska Range and one in the Brooks Range. To this day cost-effective data loggers are operating at both transects.

2) However, due to the harsh climate and logistical challenges, not all loggers have been operational at all times. Especially rain gauges were prone to animal disturbance and nearly all sites suffered some data loss. The concept of decentralized logging units (many small loggers instead of one central logger) has proven successful, since we never suffered complete data loss. Especially buried loggers (soil temperature and moisture) performed well. The Brooks Range site (Nutirwik Creek) has been chosen by Bonanza Creek LTER as the northern treeline site. A fully operative weather station has been installed in 2002.

3) Field-work in Alaska is logistically difficult. During the first field season I worked alone, which I do not recommend for a project of this scale. In 2001 and 2002, I had help from two and one field assistant respectively and their help made it possible to

assemble a tree core data set from remote locations in both mountain ranges, while maintaining an intensive sampling protocol of microclimatic site conditions.

4) The extrapolation of plot based measurements (e.g. soil temperature) into space is of crucial importance, and widely used in ecological field studies. The validity of extrapolated results, however, is uncertain and seldom tested. One goal of this study was to use "landscape ecological complex analysis", which basically combines long-term plot measurements (loggers) with short-term spatial measurements of the same variable (Mosimann, 1984; Leser 1997). Given the complexity and logistical challenge, the study is still ongoing and well beyond the scope of this Ph.D. thesis.

5) One of the biggest challenges was to adjust the project to the results, which began to surface after the first two years of research: Temperature was not the only limiting factor for tree-growth at treeline, rather temperature seemed to control parts of the populations at treeline, parts were not responsive to changes in temperature at all, and parts of the populations were controlled by what appeared to be temperature induced drought stress. This finding in itself was puzzling and I refocused my project to test the validity of our results.

By refocusing the research to obtain broad spatial coverage of treeline populations, I was no longer able to work intensely at one site. In addition, initial examination of the environmental gradient data did not show any consistent correlation with the tree growth response and our goal of testing the combination of different microclimatic factors on tree-growth was put on the backburner, since it seemed far more subtle and complex than previously estimated. Therefore the final version of this thesis is the product of an evolving scientific process (as every thesis) and covers research areas which I formerly did not imagine.

Thesis outline:

Treelines are boundaries. To develop a better understanding of the underlying theory and to look at an ecological boundary from a theoretical point of view, Chapter 1 gives an overview of the wide field of ecotone research. Ecotones are the zones of transition, the boundaries, between different ecological systems. In Chapter 1, I develop a conceptual model describing possible ecosystem trajectories of ecotones in a theoretical space-time continuum.

After laying the theoretical foundation, Chapter 2 uses the rediscovery of a treeline research site in the Brooks Range to offer a historical perspective and to argue that research can have far wider consequences than results. In this case, Bob Marshall wrote extensively about his work and travel, which ultimately lead to the establishment of Gates of the Arctic National Park, an eight million-acre wilderness in the central Brooks Range.

Chapter 3 reports the unexpected finding of three distinct population-wide responses of treeline white spruce to warming, positive with warmer temperatures, negative or non significant. We develop temperature threshold values above which the significant effects take place.

In Chapter 4, we use the results of Chapter 3 to build a spatially explicit model, which projects landscape wide changes in forest structure (such as infilling and dieback) and tree distribution under five global circulation models in two National Parks in Alaska.

Chapter 5 applies the general results of this study to the theoretical model developed in Chapter 1 and summarizes the major findings and achievements.

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[1]Chapter 1

Landscape boundaries, ecotones

- There is always something between something -

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There is always something between something:

Boundaries are everywhere. The human eye and mind differentiate and compartmentalize the world around us, the environment, into units: Rooms, chairs, trees, and mountains. If you have a discrete object, there has to be an end and a beginning to it, its boundary. The skin is the boundary for our bodies for example. It seems a two dimensional surface, but when we start changing scale, like use a microscope, the two dimensions dissolve into a space with three dimensions: hairs, pores, parts of skin etc. Two **fundamental concepts** of boundaries emerge:

- every boundary is in reality a boundary space, a three-dimensional body with boundaries of its own, and
- boundaries are scale- and observer-dependent.

For some microbes, our skin is the environment they live in, for us the skin is the transition to our environment. The necessity for formulating boundaries derives itself partly from the "hierarchy principle" (Blumenstein et al. 2000). But those boundaries are analytical in nature and in reality divide a continuous universe. Nevertheless it is practical to delineate subsystems within our universe, simply because our imagination is not able to handle such complexity. The well-known parable of the watchmakers (Simon 1962 in Wu 1999) explains heuristically the need for using systems, subsystems and therefore the boundary concept: Two watchmakers, Hora and Tempus, were making equally fine watches, each consisting of 1,000 parts. Both were frequently interrupted by customers' phone calls, at which time they had to stop working, thus the unfinished watch at hand fell apart. Hora took the hierarchical approach by having his watch built with modules that were further composed by submodules, while Tempus assembled his watch directly from the parts. Eventually, Hora became a rich man, but Tempus went bankrupt. Simple probability calculations reveal that, suppose the probability of an interruption occurring while a part is being added to an assembly is 0.01. Hora makes 111 times as many complete assemblies per watch as Tempus.

If we use this boundary concept in landscape studies, we arrive at the concept of the **ecotone**. Ecotones divide units (homogeneous areas in the scale they are observed), they are often shown as a line on a map, e.g. the coastline on a globe. Clements (in Hansen et al. 1992) first mentioned the term "ecotone" in 1905. He observed that boundary zones between plant communities could combine characteristics of both adjacent communities as well as generate individual features of the transition zone. The roots of the term are Greek, "oikos" meaning household and "tonos" meaning tension. Until the emergence of the "patch dynamics theory", however, the term "ecotone" was unused. It became evident only recently, that ecotones in their function as transition zones actually define patches in the landscape.

A widely accepted **definition of** the term **ecotone** is as follows (Holland 1988): "Zone of transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales and by the strength of the interactions between adjacent ecological systems."

Keeping in mind that an ecotone can vary in size and in ecological functioning it can be expressed in other terms as: "Ecotones can be viewed as zones where spatial or temporal rates of change in ecological structure or function are rapid relative to rates across the landscape as a whole" (Hansen et al. 1992).

Boundaries can be smooth or sharp, curvilinear or straight (Forman 1995). Straight boundaries and edges are mostly related to human activities and are likely to be anthropogenic. Modern agriculture and infrastructure tends to create straight and sharp linear boundaries. Curvilinear boundaries are more organic and often related to natural landscape elements, such as rivers. Most boundaries show spatial arrangements at different scales. They are organized in different fractal dimensions (Figure 2.5-1).

Van Leeuwen (1970) defined the **extremes of boundaries** as "limes convergens" (sharp edge) and "limes divergens" (smooth gradient). Although being addressed initially to plant communities, these terms were adapted to landscape elements of higher levels of organization. Perhaps due to the decline of Latin language in natural sciences, the terms ecocline (for "limes divergens") and ecotone (for "limes convergens") became more successful. Initially, these terms were introduced by Westhoff (1974) to describe limits of plant communities.

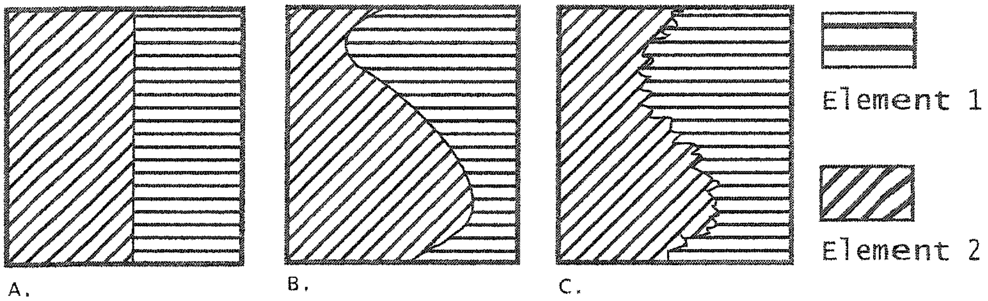

Figure 1.1.: In landscapes different types of boundaries exist showing variability at different fractal dimensions. This is reflected in straight (A), curvilinear (B) or modified at multiple fractal dimensions (C).

Van der Maarel (1976, 1990) suggested that a gradual transition should be called "**ecocline**", while the term "ecotone" should be reserved for a sharp transition, an all-or-nothing scenario. So far, some studies have tested this theoretical concept (e.g. Backeus 1993), but the general definition of ecotone as mentioned above in conjunction with the scale dependency seem to have lead to the usage of ecotone for both scenarios. To clarify the concept of ecotones in relation to other concepts in ecology, Hansen and Di Castri (1992) differentiated the several terms (Table 1.1).

Table 1.1: Terminology for change in space and time

change in space	gradual	ecocline
	abrupt	ecotone
change in time	progressive	ecological succession
	sudden, nonlinear, chaotic	ecotone

Ecotones in theory:

Figure 1.2 shows four ecosystems and their journey through time and space. Each ecosystem can be perceived as a ball rolling along its trajectory towards an unknown attractor. It has its particular place on the earth's surface (or ocean depth for that matter). Each ecosystem is controlled by different factors, their interactions as well as their changes through time. These are called "controlling factors" (Haken and Wunderlin 1991). In Figure 1.2, the array of controlling factors is symbolized by jacks, lifting the space/time continuum, providing possible trajectories and ultimately "channeling" each ecosystem on its way through time and space.

Ecosystem I is running up on a threshold in time, the controlling factors no longer support this particular ecosystem on that particular spot in space. We could imagine a warming climate in northern latitudes leading to an invasion of tundra by trees. The ecosystem I, arctic tundra, is slowly replaced by another type of ecosystem, let's say boreal forest, ecosystem II. The arctic tundra, before a stable ecosystem on our space-time surface and therefore symbolized as a ball, is entering a **temporal ecotone** stage. The controlling factors no longer allow the existence of pure arctic tundra on this spot. In terms of general systems theory, the arctic tundra is moving through the stage of "critical slowing down" towards instability. This instability is symbolized by the ridge, the "threshold in time". From there, chance and the new controlling parameters will determine which new system will establish itself and where it is moving. This newly established system is truly unique and unparalleled. It might to a wide degree be nearly similar to ecosystems we can encounter in other places on the earth. But with a look on the time-space continuum, we can see that this point/ecosystem in time has its special and unique history. To what degree the history of this point will impact the future can only be guessed.

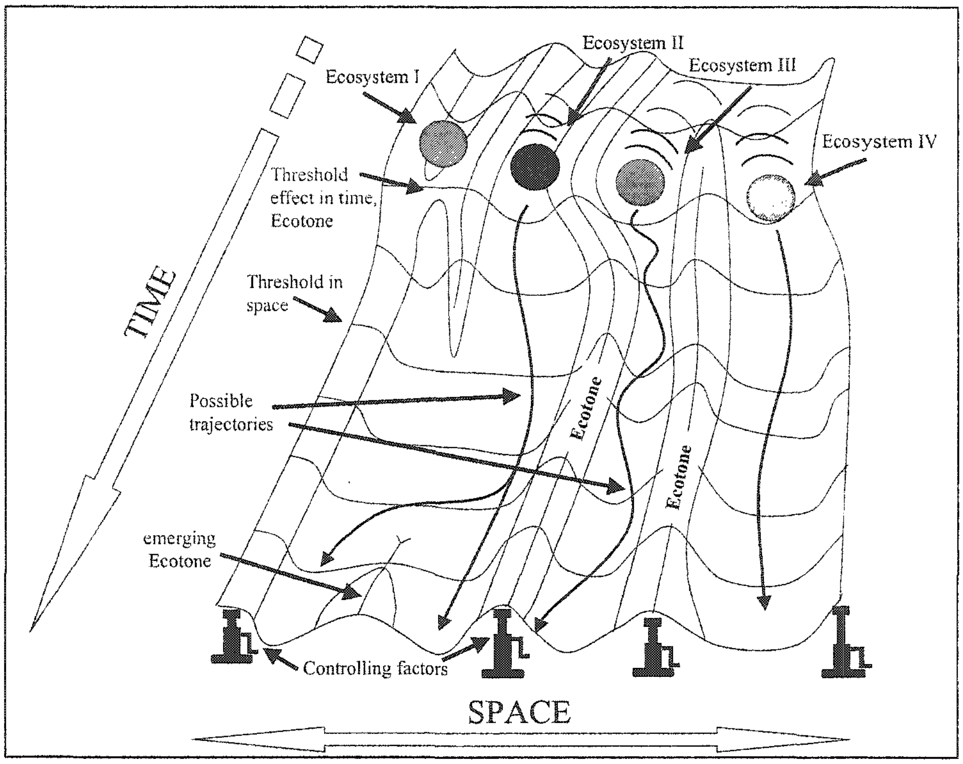

Figure 1.2: Four ecosystems on their journey through time and space. They are following their trajectories, guided by an energetic "landscape". Controlling factors are symbolized by jacks, lifting the time-space continuum, creating the conditions in which ecosystems and their ecotones evolve, exist and perish.

Let us now focus our attention on ecosystem II. It is confined by an array of controlling parameters or environmental factors. They are symbolized by the ridges between ecosystem II and ecosystems I and III. These ridges are transition zones between two adjacent ecosystems, ecotones. They are themselves unstable and need input (energy, matter, information) from both sides/ecosystems to exist. As we can see, time changes the position of the **ecotone in space**. To stick with our image from the beginning, we could imagine shifting biomes due to climate change. The ecotones or transition zones between them shift accordingly. As ecosystem II moves along its trajectory, it encounters a rising ridge, an emerging control parameter. As example we could think of the control parameter "human land use". Ecosystem II can no longer exist where additional energy input through intensive agriculture changes the environmental variables. The new and emerging ecotone might be the transition zone between forest and fields. Ecosystems III and IV are moving along their trajectories, uninterrupted by unexpected, chaotic events or strange attractors. Ecosystem III might be recovering from a disturbance, staggering along. The curvy trajectory symbolizes resilience. The system is pushed and reacts with sideways motion, but does not go "over the edge". It remains stable in its setting.

Ecotones in reality:

The recognition of a transition zone between two ecological systems by Clements (1905, in Hansen et al. 1992) could be called the beginning of ecotone research. Obviously the recognition focussed on the spatial aspect of ecological systems and their boundaries within a given area. Later on, after development of the theoretical foundations (which is still ongoing), the concept was used not only in spatial but also temporal terms (e.g. Delcourt and Delcourt 1992). Keeping in mind that every boundary and its classification is scale dependent, we can identify ecotones where

- a steep environmental gradient exists, that directly affects ecosystem function, structure and composition. Example: Boundary between forest and fields in anthropogenic landscapes, and
- nonlinear response to a gradual change of environmental variables is found, the "threshold effect" or the effect of cumulative impact. For example a pH change below 5.5 in the soil leads to mobility of Al^{3+} -ions with toxic effects on many plants as well as to ground water contamination (Blume 1990).

Ecotones as the boundaries between different ecological systems can emerge on a variety of **scales**. Just as the ecosystem itself can vary in spatial extent as well as occupy different levels in the spatial hierarchy, its boundaries, the ecotones can be found on different hierarchical levels. Gosz (1993) proposed an "ecotone hierarchy" ranging from the biome ecotone (the biome transition area) to the plant ecotone (Table 1.2.). Examples of studies covering the whole range of scales in ecotone research are Bretschko (1995), Kieft et al. (1998), Neilson (1993). The hierarchy is closely linked to probable constraints or controlling factors, which at the biome level are macroclimate and its variation through major topographic structure (Figure 1.3.). The finer the scale and therefore the hierarchical level of the ecotone, the more controlling factors influence the ecotone. In addition to the number of controlling factors, their kind and type change with each hierarchical level. At the lower end of the hierarchy, the **plant**

ecotone level, macroclimate and the major topography are constant, but the differentiation between different ecotones is rather controlled by factors such as microclimate, soil fauna, soil hydrologic regime etc. At increased finer scales the possible combination of controlling factors is much higher than at the coarser levels, simply because it is influenced by all factors above it in the hierarchy! The **biome ecotone** (a large scale phenomenon) may be a result of two or three controlling factors (in our perspective). The **landscape ecotone**, however, is already influenced by the biome it is located in, therefore by its controlling factors, PLUS additional factors on the landscape level. Macroclimate and topography are influencing the landscape ecotone as well as e.g. soil distribution, geomorphic structure and mesoclimate.

The highly differentiated site conditions of ecotones cause special combinations of species and communities, a high richness in species is usual, but ecotones can also display less biodiversity than the neighboring ecosystems (Neilson et al. 1992). But ecotones often act as **barriers** in ecosystems (Blumenstein et al. 2000). They are always areas of discontinuity. This discontinuity explains in part the emergence of structure as part of feedback loops. Once a boundary is manifested, gradients will control the flow of energy, matter and information across it. The different strength of gradients leads to increased differences in the two systems bounding the gradient. In the soil for example, differences in the redox potential of a water saturated sediment layer can lead to different felling of Fe- and Mn-molecules. This is an important prerequisite for the development of rosty patches and concretions in the oxidized layer of a gleyic soil (Scheffer and Schachtschabel 1992).

Table 1.2.: Ecotone hierarchy, based on Gosz (1993)

	ecotone hierarchy focussed on ecology	proposed hierarchy focussed on integral ecological landscape units	controlling factors (each ecotone is influenced by controlling factors of its own level and in addition by every controlling factor above its level)
Macro-scale		land-ocean ecotone (global)	distribution of continents on earth surface
	biome ecotone	ecozonal ecotones	macroclimate, major topography
Meso-scale	landscape ecotone	landscape ecotone	mesoclimate, geomorphic processes, soil characteristics
	patch ecotone	top ecotones	microclimate, microtopography, soil/soil moisture variation, species interactions
Micro-scale	population ecotone, plant pattern		interspecies interactions, intraspecies interactions, physiological controls, population genetics
	plant ecotone		soil fauna, soil flora, soil chemistry

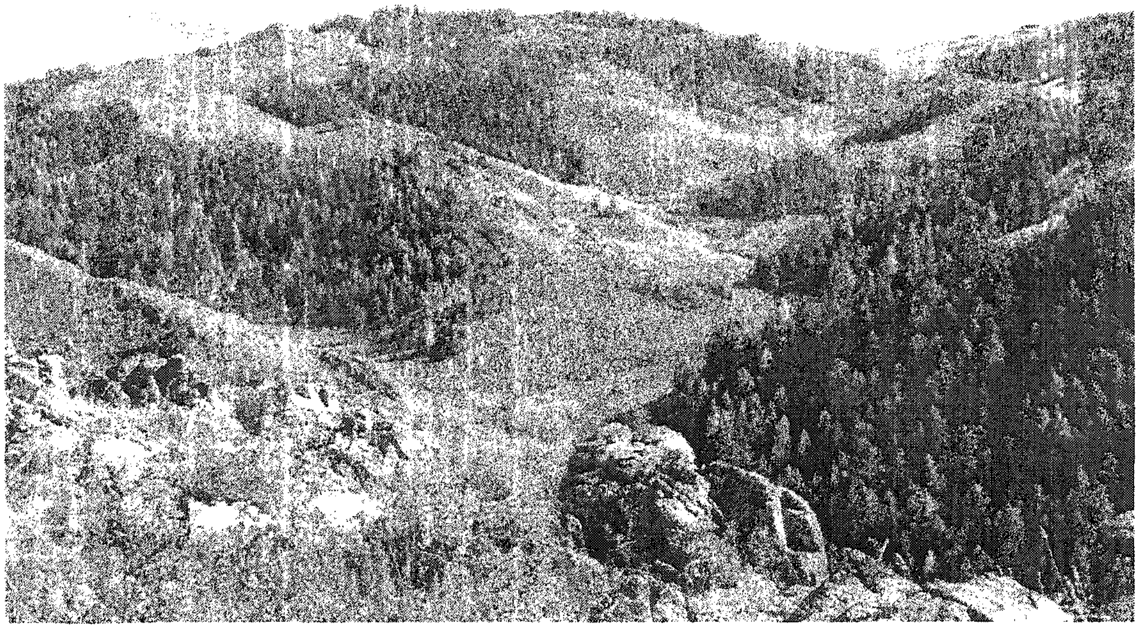

Figure 1.3.: The forest steppe zone in Asia is a broad ecotone between the steppes in the south and the zone of compact forests (taiga) in the north. Due to extreme climatic conditions, and supported by human activities (timber cutting, grazing), in the northern Mongolian mountains mainly northern slopes are covered by forests, while dry southern slopes are dominated by grass and herb steppe ecosystems (Photo: O. Bastian 1994)

The ecotone concept can be applied to both spatial and temporal investigations. If we could directly observe one particular spot on the earth's surface through time, we would always see change under way and never perceive a stable state of this one spot for very long. Through thousands or even millions of years our spot might change from being part of the ocean to a shallow lake to a steppe type ecosystem. We would maybe see a cooling of temperatures, a change in species composition, the advancement of the ice shields, their retreat and the recolonization of our spot starting with gravelly soils, the first lichens arriving, mosses, brushes etc. until we might see a forest. Through some of our observation we could identify an ecosystem in a quasi stable state, meaning that the controlling factors and their "answer by nature", the ecosystem at that time, are in equilibrium. A lot of scientific research has focussed on these "stable states" and only lately has attention been given to the dynamic and change of these systems. These times of increased change, maybe even catastrophic in nature, are ecotones in time.

Delineation of ecotones:

Methods for ecotone detection include spatial analysis (GIS and remote sensing) for the detection of patterns in space (Fortin et al. 2000) and statistical methods applicable to both spatial and temporal datasets. Fortin et al. (2000) also include modeling as detection methods for ecotones by formulating and predicting interactions in multivariate datasets. In general, ecotone detection is the ability to determine spatial or temporal change (Johnson et al. 1992).

For an overview of statistical methods concerning detection of patches in landscapes and therefore ecotones as their boundaries see Fortin et al. (2000), Johnston et al. (1992) and Turner et al. (1991). Some detection mechanisms include: GIS functions (e.g. pattern recognition, optimal corridor location, fractal dimension), "moving (split) window" technique, especially suited for transect data, "wombling" (lattice, triangulation, categorical), essentially a two dimensional form of the moving split-window technique. Once ecotones are detected they can be measured for width, verticality, evenness and curvilinearity (total length divided by straight line length) or sinuosity (length of ecotone per unit area using fractal dimension, Table 1.3.).

Table 1.3.: Overview of statistical methods available for detection, measurement and characterization of ecotones (from Fortin et al. 2000)

ecotone attribute	**data type**		
	grid data (raster format, e.g. in GIS)	**transect data**	**sparse data, unevenly distributed**
detection	edge detection algorithms and kernels	magnitude of first difference	irregular edge detection
location	thresholding of edge operations	maximum of first difference	functional criteria
width	goodness of fit for location statistics	magnitude of first difference	magnitude of first difference
evenness	dispersion of width along boundary		dispersion of width along boundary
sinuosity or Curvilinearity	length of boundary as a function of grid precision; fractal dimension		length of boundary as a function of grid precision; fractal dimension
coherence and significance	boundary statistics overlap statistics (different between boundaries in vegetation, soil, etc.)	coincidence of limits more often than by random chance	boundary statistics overlap statistics (different between boundaries in vegetation, soil, etc.)

Ecotones and change:

Ecotones are often described as "early warning stations" for a change in structure and composition of the adjacent ecosystems (Allen and Breashears 1998). Meaning that if controlling factors are changing (e.g. mean annual temperature increases under global warming scenarios), the change and effects of that change can first be detected in the boundary zone, the ecotone. This is based on the assumption that the limiting factor delineating the spatial extend of that ecosystem at that time continues to be the limiting factor after the change took place. This is not always the case and studies not supporting this view are documented (Neilson 1993).

Let us look at one example, the **treeline-ecotone in interior Alaska:** During the last decades, the Arctic and Subarctic are experiencing warmer temperatures both in summer and winter (Juday et al. 1998) and global change is heavily impacting high latitude ecosystems. One of the most visible natural ecotones is the treeline-ecotone, dividing in our case the boreal forests and the arctic or alpine tundra. Fundamental interest in the question of possible treeline movement under global change is fueled by the question of carbon uptake of the boreal forest ("sink-source question"), albedo changes and other feedback loops between boreal forest and global climate (Foley et al. 1994). This treeline is generally thought to be correlated with the July 10°C isotherm (Daubenmire 1954). The limiting factor for tree growth is therefore believed to be temperature. Under global change scenarios, the vegetation zones will eventually adapt to higher mean annual temperatures and changes summer and winter conditions (Chapin et al. 1995). This logical reasoning is based on the assumption that temperature will still be the limiting factor for tree growth under changed conditions. However, new findings suggest, that the limiting factor for tree growth and establishment may have shifted to moisture supply within the boreal forest and at least parts of the forest-tundra ecotone in Alaska (Jacoby and D'Arrigo 1995). Briffa et al. (1998) reported a decreased sensitivity of radial growth of high latitude trees to temperature since the mid 20th century. This would have a major impact on the forest-tundra distribution in interior Alaska. Two scenarios are most likely:

1. The forest will expand into tundra with increased summer air temperatures, providing a higher CO_2 uptake and a negative feedback to the greenhouse effect (our "limiting factor stays the same scenario")
2. Under increased summer air temperatures the limiting factor of tree growth will shift to moisture supply, possibly leading the ecosystem trajectory towards higher fire frequency, massive die-back of white spruce due to moisture stress and slow change into aspen parkland, resulting in another positive feedback loop with less CO_2 uptake and increased greenhouse effect.

These scenarios make clear that completely different outcomes are possible due to a small change in the ecosystem trajectory. There is no real way of sure prediction. Predictions based on linear causal chains might just be lucky hits, if nothing fundamentally changes within the ecosystems in question. As outlined above, this is not always (actually seldom, Briggs and Peat, 1993) the case. Going back to Figure 1.2. we can now ask, if the boreal forest ecosystem faces the destiny of ecosystem I, running against a threshold in time and subjected to fundamental changes in internal structure, or ecosystem III, shaken, but still on its way through time, adapting by spatial change and shifts in biome location.

As a careful first **conclusion** we might say that:

- Small and slow shifts in controlling factors lead to a gradual spatial shift of the ecosystems involved as long as the limiting factor is not changing. The change can be first detected in the ecotone areas.
- Catastrophic events, nonlinear responses and change in limiting factor can lead to different ecosystem trajectories, change is not first detected in the ecotones.
- If the monitoring interest is focussed on ecotones in time, the core areas of biomes might provide a more suitable homogeneous background for detection of change, e.g. regional drought-stress (Neilson 1993).

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[1]Chapter 2

An Early Treeline Experiment by a Wilderness Advocate - Bob Marshall's Legacy in the Brooks Range, Alaska

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Abstract:

In 1939, the wilderness advocate and conservationist Robert Marshall spent the last summer of his life in the Brooks Range, Alaska. He believed that present environmental conditions did not cause the position of the northern treeline, but that trees simply had not had enough time after the last glaciation to fully occupy their potential distribution. He started a treeline experiment by sowing white spruce seeds in Barrenland Creek, 5 km north of the treeline of his day. Apparently the seeds Marshall sowed had either did not germinate or germinated seedlings did not survive, because there was no sign of them, when in 1968 Sam Wright planted the same plot with 100 four-year old spruce seedlings. To our knowledge nobody had visited the plot until were able to locate it in 2001. We found two seedlings alive of the 100 planted in 1968 and a note from Sam Wright, who had revisited the plot in 1989, and found five seedlings alive at that time. The plot itself is undisturbed and still has three of Bob Marshall's original site markers. Although the experiment lacks detailed information to be of great scientific value, we believe that the site is of historic significance for the National Park Service in Gates of the Arctic National Park, Alaska.

Introduction:

Current debate

Treelines have been the focus of intense research for a long time (Griggs, 1934; Krebs and Barry, 1970; Elliot -Fisk, 1983). Treeline advances and retreats as a result of climate fluctuations have been documented over time scales ranging from thousands of years (MacDonald et al., 1993) to 20th century warming (Suarez et al., 1999, Lloyd et al., 2002).

Especially in the high latitudes, where warming is expected to be of greatest magnitude (Overpeck et al., 1997, Serreze et al., 2000), large-scale models assume linear correlation between changing climatic conditions (e.g. warming) and subsequently advance of the northern treeline (Elliot-Fisk, 1983; Pielke and Vidale, 1995). However, northern treelines might not react very fast to climate warming (Lavoie and Payette, 1996), or might be relicts of warmer periods and not reflect current climatic conditions (Weisberg and Baker, 1995). Spatially explicit models incorporating topographic influences (Rupp et al., 2001) produce an expansion of boreal forest onto the North slope of Alaska only after thousands of years, because the Brooks Range serves as a barrier.

Position of northern treeline and the extent of the boreal forest are important drivers of the global climate system through albedo (Foley et al., 1994) and the potential to store carbon (Fan et al., 1998; Liski et al., 2003). Summer temperature (July 10°C isotherm, Daubenmire, 1954; Holtmeier, 1974) has historically been reported as the main factor controlling treeline position, while Koerner (1998) recently proposed that soil temperatures of the root zone provide a far better explanation than generalized air temperatures. However, the limiting factor for tree growth may have shifted to moisture supply within the boreal forest (Barber et al., 2000) and parts of the forest-tundra ecotone in Alaska (Jacoby and D'Arrigo, 1995). Briffa et al. (1998) reported a decrease in sensitivity of radial growth and late wood density of high latitude trees to temperature since the mid 20th century.

Alaska's northern treeline consists mostly of white spruce (*Picea glauca* (Moench(Voss))). Tests have shown that white spruce seeds can sprout and seedlings can survive on upland tundra sites when transplanted by humans (Hobbie and Chapin, 1998). A more important limitation on the movements of white spruce into tundra is the ability to disperse seeds and Cooper (1986) concluded that white spruce seeds can be dispersed over kilometers, rather than shorter distances as reported earlier (Zasada, 1971; Viereck and Schandelmeier, 1980). Fastie (1995) documented spruce migration rates of 300-400 m/year in Glacier Bay on newly deglaciated terrain and Lloyd et al. (2003) calculated a migration rate of 100 m/year for spruce invading tundra on the northwestern treeline in Alaska. After deglaciation, white spruce arrived in the Brooks Range somewhere between 8500 and 6000 BC. (Edwards et al., 1985) and new dispersal theories using dispersal kernels (Clark et al., 1998) indicate that in fact the slow rate of climate warming may have effectively hindered population spread. Other factors influencing population spread are not only seed dispersal, but also the mechanism of germination and establishment. Survivorship of sowed white spruce seeds in tundra is less than 20% after four years (Hobbie and Chapin, 1998).

Transplanted seedlings, however, showed over 90% of survivorship in shrub and tussock tundra after four years (Hobbie and Chapin, 1998).

Bob Marshall's theory of treeline advance

As early as the 1930s, the forester Bob Marshall was working on this issue in the Upper Koyukuk country of northern Alaska in the Brooks Range. His theory was that trees did not have enough time after the last glaciation to occupy their potential growth range. In his view, the seed dispersal mechanism prevented a fast advance of white spruce into tundra. He calculated the advancement rate of the northern treeline at 1 km/150 years (Marshall, 1956). This was, as we now know, a substantial underestimation. To test his hypothesis, Marshall sowed white spruce seeds north of treeline in three separate watersheds (Grizzly Creek, Barrenland Creek and Kinorrutin Creek). In this paper we present the rediscovery of one of his plots, Barrenland Creek, in 2001.

A short sketch of Bob Marshall's life:

The man later known as a great conservationist and wilderness advocate, Bob Marshall, was born in 1901 as a son of an activist father, the lawyer Louis Marshall. From his father he inherited the urge to stand for what he believed in, be it civil rights or wilderness protection (for a comprehensive tale of Bob Marshall's life, see Glover, 1986). Marshall grew up hiking in the Adirondaks, where he developed a special sense for untamed places and the desire to keep them unspoiled. He chose forestry as a profession. In 1930 he came to Alaska for the first time and spent a winter in Wiseman, a small community on the southern slope of the Brooks Range. His book "Arctic Village" was the result of his stay. Back on the East Coast in 1931, he began to write about wilderness issues, deforestation and conservation. In 1933 he became director of the division of forestry in the Bureau of Indian affairs. In 1935, Marshall was among the principal founders of The Wilderness Society, others included Aldo Leopold and Benton MacKaye, who later helped establish the Appalachian Trail.

A visionary in the truest sense of the word, Marshall set an unprecedented course for wilderness preservation in the United States that few have surpassed. His ideas and dreams continue to be realized long after his death at the young age of 38 in 1939... he was among the first to suggest that large tracts of Alaska be preserved, shaped the U.S. Forest Service's policy on wilderness designation and management, and wrote passionately on all aspects of conservation and preservation (The Wilderness Society, 2003).

After his first trip in 1930 he returned to Alaska three times until his early death in 1939. His legacy in the Brooks Range includes the mapping of more than 30 000 km^2 of wilderness, the book "Arctic Village", which he wrote after living in Wiseman for about a year and "Arctic Wilderness", a book edited by his brother George (Kauffmann, 1992). But perhaps an even more important legacy of his was the naming of two mountains, Frigid Crags and Boreal Mountain: *The mountains became more and more precipitous until finally they culminated in the Gates of the Arctic (Marshall, 1956:14)* He went on to write that: *Alaska is unique among all recreational areas* *belonging to the United States because Alaska is yet largely a wilderness. In the name of a balanced use of American resources, let's keep northern Alaska largely a wilderness.*

The impact of Bob Marshall' writing:

This call for preservation started a long conservation effort in Alaska. It could be argued that the pure name "The Gates of the Arctic" has instilled a sense of adventure, of wilderness and freedom into thousands of readers and conservationists. All the efforts to recognize these values culminated in the establishment and naming of the second biggest National Park in the United States: Gates of the Arctic National Park and Preserve. Kaufmann (1992:69) stated: *Bob Marshall is to the Brooks Range what Henry Thoreau is to the Maine woods and John Muir to the Sierra Nevada.* Gates of the Arctic was awarded National Monument status on December 1, 1978 and became a National Park and Preserve on December 2, 1980. Bob Marshall's dream of keeping northern Alaska largely a wilderness was at least partly realized.

The Barrenland plot - part of Bob Marshall's legacy in the Brooks Range:

In 1939 Bob Marshall spend his last summer in the wilderness of the Brooks Range in northern Alaska. Already in earlier years he had tried to substantiate his theories about the lack of time after glaciation for treeline advance, but his attempts had failed. In 1930 he had sowed spruce seeds on two plots in Grizzly Creek, twelve miles north of treeline of his time (Marshall, 1956). Returning in 1937 he discovered, that the seeds had not sprouted. He wrote: *Well, the seeds had not developed, my experiment was a complete, dismal failure on both plots. (Marshall, 1956:123).*

However, in 1939, while mapping and exploring the upper Koyukuk area, he repeated his early treeline experiment by sowing seeds of white spruce (*Picea glauca*) about 5 km north of current treeline on two 3x3 m plots in Barrenland Creek. He wrote in his journal: *We stopped for lunch on the edge of foaming white water...It was fascinating in its barrenness so we called it Barrenland Creek. After lunch I repeated the experiment I had tried with negative results nine years before - the experiment to test my theory that lack of time, not unfavorable climatic conditions had prevented the progress of the northern timberline... (Marshall, 1956:154).* One plot consisted of mineral soil after removal of the vegetation, on the other Marshall sowed the seeds into undisturbed tundra.

Marshall died four months after this trip (Glover, 1986), and the site was not revisited until Sam Wright and his wife searched for the plot in 1968. On the 5th of August, 1968 Sam wrote: *By seven p.m., rimming up Barrenland Creek's north side, we looked down on the tree planting site where Bob Marshall's stakes still marked his plot after 29 years of arctic freeze and break-up...(Wright, 1988:157).*

No trees had grown, so Wright planted 100 four-year old white spruce seedlings, provided by Les Viereck from a seed stock that was collected and grown in Fairbanks (Viereck, pers. com, April 2001).

Rediscovery in 2001:

Our research group found no evidence that anyone had revisited the plots after 1968. Attempts to contact Sam Wright failed at first. After two unsuccessful attempts to find the plot in 2000 and early 2001, we were able to locate the site in August 2001 and found two seedlings still alive. We also found a note that Wright had returned in 1989 and found five trees alive and one dead. However, we found no trace of any dead trees. In 2001 our research group could find only one of the plots Marshall had established in Barrenland Creek, the other probably washed away. The plot is situated at 67°59.920 N and 150°33.815 W on the north side of Barrenland Creek near the continental divide on top of the Brooks Range (Fig. 2.1), approximately 5 km north of current treeline and 200 m higher in elevation (1050 m a.s.l.). The nearest treeline is situated the valley of the North Fork of the Koyukuk River on north and south facing slopes (Fig. 2.1). White spruce at the North Fork treeline reach 760 m elevation on north facing slopes and 850 m on south facing slopes. Preliminary age data (Wilmking, unpublished data) suggests establishment before 1700, indicating little or no movement during at least the last 300 years. Barrenland Creek runs west - east in a U-shaped valley completely surrounded by mountains with large gravel slides on either flank. The plot occupies 3x3 m on a floodplain north of Barrenland Creek, shortly before the creek enters its canyon. As of the summer of 2001, the four corners were marked with stone piles and three of the four still had Bob Marshall's original willow sticks protruding 50-80 cm above the ground. In one of the stone piles an old peanut can held a note from Sam Wright, reporting that he had found five spruce trees alive in 1989.

The soil is stony and shallow and probably underlain by permafrost. The two spruce trees alive in 2001 are 30 cm in height (Fig. 2.2). They looked healthy and showed recent growth on their tips. An interesting side-note is the fact that Les Viereck planted siblings of the seedlings he gave to Sam Wright in 1968 at the University of Alaska Fairbanks. In 2001 they measured about 9 m in height (Viereck, pers. com., Sept 2001).

Natural white spruce seedlings have been reported naturally several kilometers beyond the last cone bearing trees (Cooper, 1986). However, during our search for the Marshall plot we scanned the entire valley of Barrenland Creek and did not find any evidence of other white spruce trees or seedlings. These two seedlings are growing in an environment that probably has not seen trees for thousands of years. There are several possible explanations for the outcome of Bob Marshall's experiment. We do not know how many seeds he sowed on each plot, but Nienstaedt and Zasada (1990) reported white spruce seed to seedling ratio on mineral soil of 30-50 seeds per seedling and on organic soil 500-1000 seeds per seedling. Marshall may not have sown enough seeds to establish seedlings in this environment. The seeds Bob Marshall used were from Chippewa National Forest near Cass Lake, MN. When tested in 1938 they showed a germination rate of approximately 80%, but they were not genetically ideal for this high latitude site. According to Nienstaedt and Zasada (1990), spruce seeds transplanted either more than 150 m altitudinally, or more than 3° latitudinally will probably show detrimental growth effects.

Seedling survival rates over decades are not well documented for treeline areas, but it could be argued that two out of 100 is quite normal or even above average. On the other hand, environmental conditions may just be unfavorable to growth despite recent warming trends. Soil temperatures might be too low, snowbeds too persistent and therefore the vegetative growth period too short. This plot does not meet the criteria for a "safe spot" (usually south facing, sheltered depressions), the locality most likely to promote survival of seedlings at northern treelines. In addition disturbance by animals or humans might be a factor. After we located the plot in 2001 we had a chance to meet Sam Wright and he told us that in 1989 he had found evidence of human interference on Bob Marshall's plot. But in 2001 the two surviving seedlings seemed healthy and showed recent growth.

And so despite all these scientific explanations and thoughts, the legacy of Bob Marshall in the Brooks Range of Alaska will not only include his life long work for nature conservation, but also two spruce trees growing on his plot about 5 km north of current treeline - a very small but living monument to his research and exploration in what is now called the Gates of the Arctic National Park and Preserve.

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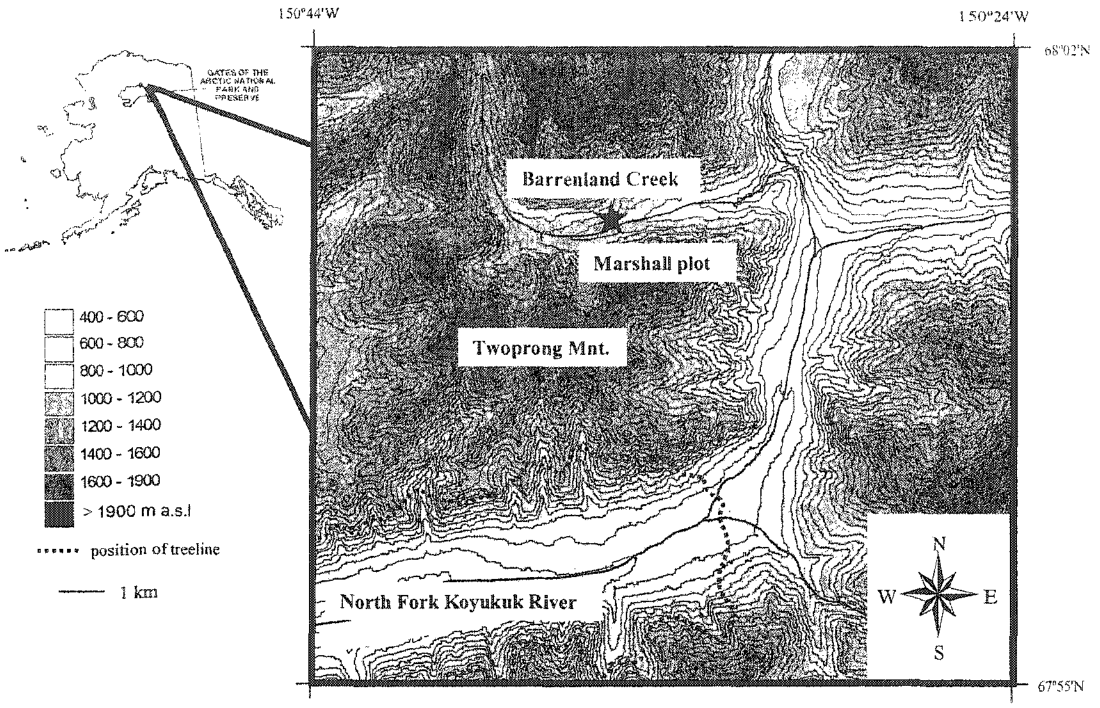

Figure 2.1: Map of the upper North Fork of the Koyukuk River, Brooks Range, Alaska. Bob Marshall's plot is situated approximately 5 km north of current treeline in Barrenland Creek at an altitude of 1050 m a.s.l. Current treeline is situated on north (760 m a.s.l.) and south (850 m a.s.l.) facing slopes in the drainage of the North Fork of the Koyukuk.

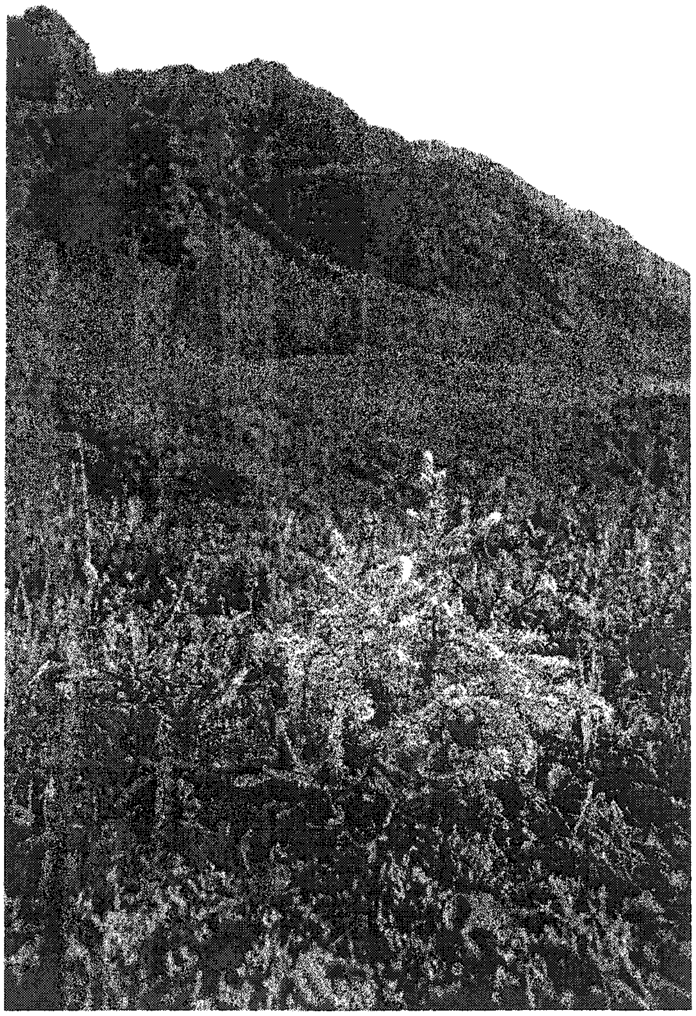

Figure 2.2: One of the two spruce trees still alive on Bob Marshall's plot in Barrenland Creek. Sam Wright planted this tree as a 4 years old seedling in 1968. In 2001, 37 years old, it measured about 30 cm in height, but showed recent growth on the tips. A sibling of this tree, planted at the University of Alaska Fairbanks measures 9 m in height today (Viereck, pers. com., Sept. 2001). Visible in the background is Twoprong Mountain.

[1]Chapter 3

Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds

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[1] Prepared for submission to Ecology Letters: Wilmking, M., Juday, G.P., Ibendorf, J., Barber, V.A. and Zald S.H. Recent climate warming forces opposite growth responses of white spruce at treeline in Alaska through temperature thresholds.

Abstract:

Our findings of both positive and negative growth responses to climate warming at treeline challenge the widespread assumption that arctic treeline trees grow better with warming climate. Hot Julys decrease growth of ~40% of white spruce sampled at treeline in Alaska, whereas warm springs enhance growth of others. Growth increases and decreases appeared at temperature thresholds, which have occurred more frequently in the late 20th century. Without accounting for these opposite responses and temperature thresholds, climate reconstructions based on ring-width will miscalibrate past climate, and biogeochemical and dynamic vegetation models will overestimate carbon uptake and treeline advance under future warming scenarios.

Keywords: Threshold effects, Alaska, climate change, white spruce, treeline, cluster analysis, dendrochronology, carbon uptake

Introduction:

High latitude forests provide important feedbacks to global climate: They contain 49% of the carbon stored in forested ecosystems (Dixon et. al., 1994) and increases in growth and forest area enhance CO_2 uptake (Koerner, 2000). However, replacement of tundra by evergreen conifers (treeline advance), decreases albedo and enhances warming (Bonan et al., 1992; Foley et al., 1994; Foley et. al, 2000). Dendrochronological studies and climate reconstructions of the boreal forest focus on the positive growth response of treeline trees to warmth (Garfinkel and Brubacker, 1980; D'Arrigo and Jacoby, 1993; Briffa et al., 1998), from limited samples on sensitive sites (Pilcher et al., 1990). Using these parameters, vegetation models produce northward expansion of boreal forest under warming climate (Kitttel et al., 2000, Chapin et al., 2000; Rupp et al., 2001). However, positive sensitivity of northern high-latitude trees to temperature has recently declined (Briffa et al, 1998), and temperature-induced drought stress can limit white spruce radial growth (Barber et al., 2000; Lloyd and Fastie, 2002). Population-wide responses of treeline trees to climate remain largely unexamined. Our study identifies diverging population-wide growth responses (enhanced and decreased growth with warming climate) in two mountain ranges in Alaska, quantifies the relative abundance of each growth response and provides a plausible mechanism, through which climate is forcing these divergent growth responses.

Methods:

We collected tree ring samples from 1558 white spruce (*Picea glauca* (Moench (Voss)) in the Brooks Range and Alaska Range of Alaska (Fig. 3.1). Where possible

(11 out of 13 sites), we sampled five site types: floodplain, north- and south-facing forest and north- and south-facing treelimit. We collected nearly exclusively penetrating cores, so that two radial measurements were available for each year. Ring width was measured and both annual ring width measurements were then averaged. This analysis is based on the 1155 trees older than 100 years. The 403 younger trees showed nearly identical results, but were excluded to maintain stable sample size throughout the common period of analysis. Tree growth was compared with the Fairbanks record (1906-2000) of mean monthly temperatures. Fairbanks has the longest record of climate in Interior Alaska, is centrally located between the two mountain ranges and is highly representative of temperature trends in the boreal forest region of Alaska (Garfinkel and Brubaker, 1980; Jacoby and D'Arrigo, 1995; Barber et al., 2000, Lloyd and Fastie, 2002, Lloyd and Fastie, in press).

Tree ring series were crossdated using COFECHA (Cook et al., 1992) and dentrended with ARSTAN (Detrending removes the age effect, Cook et al., 1992). We correlated each tree's record of detrended annual radial growth with the 57 mean monthly temperatures preceding the end of ring formation (results from non-detrended tree ring series exhibited similar results, suggesting that age did not have a significant influence on the tree growth-climate relationship). The Pearson correlation scores for each of the 57 correlations for each tree were used as input into a cluster analysis (STATISTICA). We used "joining" (tree diagram, complete linkage) in the cluster module and visually inspected the results. Based on similar pattern at each site, we then refined the clusters using the "k-means" clustering procedure, where the program calculates a user specified number of clusters. We increased the number of clusters in each step (starting from two) to maximize the difference between clusters. By visually inspecting the means of each clustering run, we were able to stop the procedure as soon as the new run did not produce new clustering pattern (significantly different mean), but merely created a new cluster emulating an existing pattern.

The cluster analysis was used only to mechanise the process of correlating each individual tree with Fairbanks climate parameters. Once we had identified the two dominant climate signals on a population basis (significant correlation of ring width after 1950 with a) July and b) Spring temperature indices, $r > 0.25$, or $r < -0.25$), we calculated the correlation score of each individual tree's detrended radial growth with these two climatic predictors. Other important growth predictors (Summer temperature, average of May-September; Winter temperature, average of November-February) were also tested.

We then manually assembled the clusters based on the common highest correlation scores (July prior, spring temperature index). We grouped first all trees with a significant negative correlation ($p<0.01$, $r < -0.25$) to the mean monthly temperature in Fairbanks after 1950 of the July prior to growth (negative responders). All remaining trees were grouped according to the spring temperature index, significant positive correlation ($p<0.01$, $r > 0.25$) lead to assembly in the group of positive responders, all others were labelled "non-significant". Histograms were inspected to check for normal distribution of correlation scores to predictor indices before and after 1950 as well as for the period of record (1906-2000).

We first assembled the positive and negative responding clusters for each mountain range and then for each site. Five year smoothing was used to assemble Table (3.1).

To examine the consistency of the growth responses throughout the last 200 years, we calculated the decadal mean raw ring width of trees from both mountain ranges belonging to the two clusters that were significantly correlated with temperature. Because the number of trees contributing rings in each decade varied (because of different dates of origin during the 19th century) we calculated the 95% confidence interval in differences of the means of radial growth by decade for the two clusters.

We then developed a regression of the two climatic predictors versus the mean of detrended radial growth of the two significant clusters. Piece-wise linear regression in STATISTICA was used to test, whether a single regression or two regressions showed higher predictive power across the entire range of data. The program calculates two linear regressions for a data array. The breakpoint or "threshold" of these regressions is chosen where the difference in slope of the two models is maximized. We tested the significance of these differences by comparing the slope and p-values of the two resulting equations.

Results:

Based on the relationship between annual radial growth and Fairbanks mean monthly temperature, the initial clustering "tree"-diagram over the entire period (1906-

2000) of climate record revealed a major division between trees with generally positive versus negative correlations with temperature. The "k-means" clustering procedure produced 3 distinctive clusters, revealing three populations of 1) consistently positive, 2) consistently negative and 3) non-significant correlation of growth with temperatures (Fig. 3.2). It is particularly noteworthy that this pattern repeated itself at each of the 13 sites in both mountain ranges (data not shown). More trees belonged to the cluster defined by negative growth responses to warm temperatures (40.1%), than to the cluster with positive growth responses (36.3%). While all 57 monthly correlations define membership in a cluster, statistically significant or near-significant scores are concentrated in only a few specific months (Fig. 3.2). Serial autocorrelation leads to a similar pattern of correlation each year for a period of years prior to ring formation.

Recent findings identify a difference in tree-growth/climate relationships at treeline between the periods pre- and post-1950 (Briffa et al., 1998; Lloyd and Fastie, 2002). Many subregions across the Arctic experienced a period of cooling following 1950 until the late 20th century (Overpeck et al., 1997, Vaganov et al., 2000). However, interior Alaska experienced steadily warming growing season temperatures since 1950 (Barber et al., in press). Clustering runs from our sample restricted to the pre- and post-1950 periods also show distinct differences across this time boundary (Fig. 3.2, C-F). The absolute value of the mean correlation scores of our clusters in both mountain ranges changed from almost uniformly non-significant pre-1950 ($p > 0.01$, Fig. 3.2 C,D) to a pattern after 1950 in which correlation scores of several months were statistically significant (Fig. 3.2 E,F). All further references to statistical significance are based on $p < 0.01$.

At each of the thirteen sites, as well as the combination of data in each mountain range (Fig. 3.2), the three most distinct clusters in the post 1950 data displayed essentially the same pattern of correlation scores: Cluster 1 a highly significant negative response to previous July temperature, Cluster 2 a highly significant positive response to spring temperatures (March one year and April temperatures two years prior in the Alaska Range, and April one and two years prior in the Brooks Range), and Cluster 3 no significant responses. This pattern persisted even at one site where only 15 trees met our age criterion. These July and spring temperatures serve as our climatic predictor-indices for positively and negatively responding trees.

Before 1950 the individual tree correlation scores with the two climatic predictor-indices were distributed normally (Fig. 3.3 A,B) on each axis with the modal class centred near the significance level ($r = \pm 0.25$). However, after 1950 distributions of individual tree correlation scores in both mountain ranges have become either strongly positive or strongly negative (Fig. 3.3 C,D). This divergent response was especially distinct, and underlines the non-overlap of the two significant climate responses. The distinctiveness of the clusters therefore was not the result of a few trees with unique growth patterns, rather trees generally responded either negatively or positively to warming.

To test for site-specific responses, we examined the proportion of negative and positive responders at each site. Negative responders were defined by a correlation score of ≤ -0.25 (threshold of significance) of detrended growth with the July prior temperatures after 1950. Positive responders were all remaining trees with a correlation score ≥ 0.25 of growth versus the spring temperature index (after 1950). In addition, we checked for consistency of predictive power of the climate indices before and after 1950 at each site, by developing site-specific climate predictor indices that maximized the correlation scores of the mean of each positive and each negative population (Table 3.1).

Before 1950 a variety of months best predicted annual growth for positive and negative responders, but after 1950 the months contributing to the best predictor index were highly consistent among sites and identical to the two predictor indices derived from the overall population clustering procedure: Previous July limits radial growth in negative responding trees and warm spring increase growth in positive responding trees. Correlation scores after 1950 are greater in magnitude than before 1950. Unlike previous studies (Garfinkel and Brubaker, 1980; Lloyd and Fastie, 2003), Fairbanks precipitation and cold season temperatures added no independent explanatory power to the climate-tree-growth relationship after 1950.

The smoothed values (five-year running mean) of our climate indices explain up to 81% of the variability in growth of the sampled trees after 1950 (Table 3.1). During the same period, 43% of the Brooks Range trees showed significant negative responses to climate, and 38% positive, while 37% of the Alaska Range trees were negative and 35% positive. The higher correlation of the individual tree-growth-response to climate after 1950, demonstrated by the cluster analysis and the scatter of the two best predictor indices, is also consistent across all sites and site types in both mountain ranges (Table 3.1), suggesting widespread occurrence and unique processes after 1950.

For negative responders, the colder portion of the range of July temperatures (< ~16 °C has no predictive power for radial growth (Fig. 3.5 A,B). July temperatures over ~16 °C however, show a strong significantly negative relationship with growth. This apparent threshold operates at all sites. The relationship of July temperatures in Fairbanks to the actual temperatures at most sites remains unknown. However, at one site (ARRC), climate records exist from Denali National Park Headquarters. July temperatures at Denali Headquarters are on average (1923-1997) ~4.5 °C lower than in Fairbanks. We calculated a similar offset (4 years overlap) for one Brooks Range site (BRNC). Based on these offsets the mean July temperature above which radial growth the following year will be limited would be of about 11-12 °C.

The spring temperature index predictors also appear to be operating above certain thresholds (Fig. 3.5 C,D), but only after 1950. In the Alaska Range after 1950 the years of highest radial growth are associated with the warmest spring index values. There is a similar relationship in the Brooks Range, but the warmest seven springs were all in the 1990s. Therefore we cannot exclude the possibility that the apparent spring temperature threshold of growth acceleration is partly coincidental in the Brooks Range.

Discussion:

The finding of highly significant negative relationships between July temperature and radial growth as the most common climate signal present at treeline and near treeline sites in Alaska is quite surprising, and apparently not consistent with much published literature in North America (Garfinkel and Brubaker, 1980; Jacoby and D'Arrigo, 1989; Jacoby et al., 1996; Overpeck et al., 1997; Lloyd and Fastie, 2003).

Negative response of growth to July temperatures from drought stress is reported for some white spruce in particular habitats (Garfinkel and Brubaker, 1980; D'Arrigo and Jacoby, 1993; Barber et al., 2000; Lloyd and Fastie, 2002). Here we show that trees respond negatively to temperature even at the coldest sites, the northern and altitudinal tree limit and that this response has become stronger with increasing temperatures. In most of the previous studies (exception Lloyd and Fastie, 2002) in this environment the sampled trees were deliberately chosen to obtain a pure climate signal with positive response to temperature (e.g. for climatic reconstructions,). Our sampling, in contrast, was based on landscape parameters and can be taken as representative of the population of trees in this environment.

Dendroclimatological research is often site-specific and includes some subjective elements in the selection of the climatic parameters used in reconstruction. Our clustering approach applied a consistent criterion to all trees across all sites and only then proceeded to site specific analysis. The consistency of white spruce growth response to climate across all sites and both mountain ranges, both negatively and positively, and the strengthening of this response in the post 1950 time period, suggests that a true climatic control is involved.

This strengthening of the climate-growth relationship after 1950 in our sample contrasts with the hemisphere-wide decrease in positive sensitivity of northern tree growth to summer warmth (Briffa et al., 1998). Possible explanations for this discrepancy include a) we did not assume a coherent climatic signal at each site, but tested each tree explicitly for its growth response to climate and thus did not average opposite responses b) warm season temperature trends in the western North American

Arctic have been the opposite of hemisphere-wide trends (Barber et al., 2003; Juday et al., in press) c) we exclusively examined white spruce and not a variety of species that may have included opposite trends.

Most negative-responding trees in our sample (but not all!) grow on south-facing slopes just below, or in tree islands at, treeline. South-facing sites below treeline are the most productive locally, with higher stem density than in the treeline ecotone. At these sites physiological limitation on water transport due to low soil temperatures (Goldstein et al., 1985) and increases in shrublayer (Sturm et al., 2001) result in higher competition for below-ground resources such as water, and may ultimately lead to drought stress. Growth of boreal conifers is affected mostly by previous year temperatures (Jacoby and D'Arrigo, 1995; Jarvis and Lindner, 2000). Thus the pattern in negative responders of maximized correlation scores with previous July temperature is consistent with a drought stress mechanism.

Positively responding trees may be benefiting from lengthening of the growing season observed in high-latitude environments (Keeling et al., 1996; Myneni et al., 1997), leading to earlier onset of ring formation and increased CO_2 assimilation early in spring (Keeling et al., 1996). Lengthening of the growing season may be due largely to the timing of snowmelt, which in turn may be strongly influenced by late winter/early spring temperatures (our predictor index). In the case of the spring temperature index in the Alaska Range, the mean of March and April temperatures at Denali National Park Headquarters is only about 2K lower than in Fairbanks, so that the upper half (above threshold) of spring temperature index values may actually reflect the onset of snowmelt at the sites. Timing differene of these events between the Alaska and Brooks

Range caused by latitudinal difference also support the hypothesis, that threshold values for positive responders reflect onset of snowmelt. In the Alaska Range the positive correlation of growth with temperature is maximized earlier than in the Brooks Range (Fig. 3.1 E,F, Table 3.1), which is further north and experiences later snowmelt.

Boreal coniferous trees need soil water to reinitiate photosynthetic activity in spring (Jarvis and Lindner, 2000). Liquid water can be available at the soil surface as soon as overlying snow starts to melt, even though mean air temperatures are below freezing (Jarvis and Lindner, 2000). We infer that warmer spring temperatures produce earlier onset of snowmelt leading to the positive growth response of a sub-population of white spruce. Although this explanation is consistent with our data, further work needs to be done to confirm this mechanism. On the other hand, the consistency of this positive response from individual trees to sites to entire mountain ranges suggests that a true threshold mechanism is involved.

Carbon sequestration in deciduous boreal ecosystems is positively related to early thaw (Jarvis and Lindner, 2000; Black et al., 2000; Barr et al., 2002). We show that also in coniferous forests ring width and therefore above-ground carbon uptake can increase due to warm springs, but only in our positive responding population. Some boreal systems switch from carbon-sink to -source over periods of years and net ecosystem productivity (NEP) in them is actually controlled by respiration (Valentini et al., 2000). Carbon flux measurements, needed to calculate respiration and ultimately NEP, are not available for our sites.

The similarity of the percentages of positive and negative responders in both mountain ranges after 1950 could lead to the conclusion that in the short term there has been no net change in carbon uptake on a regional scale by trees in these environments. However, it appears that positive responders are more frequent in environments with lower stem density than negative responders, so that calculated per unit area, the carbon uptake potential of positive responders may be far less than that of negative responders. Even more significantly, the majority of trees now responding positively, historically grew less than negative responders until the late 20th century (Fig. 3.4) and as a result are smaller (avg. dbh 16.0 cm, height 8.4 m) than negative responders (avg. dbh 23.0 cm, height 10.4 m). Negative responders have achieved significantly less growth than positive responders since the 1970s (Fig. 3.4), a period of especially strong climate warming. Therefore in these environments future climate warming might not be associated with a significant increase in carbon uptake and sequestration, but carbon uptake overall may actually decline. Surprisingly, in our results, age as an independent factor did not affect the correlation of trees to temperature as reported elsewhere (Lloyd and Fastie, 2002; Szeicz and MacDonald, 1994).

Conclusions:

Recent climate warming has intensified the negative growth response of a large proportion of trees at locally productive sites near treeline in Alaska. Trees on less favourable sites may be benefiting from earlier thaw and are now outperforming productive sites, reversing the historical growth relationship (Fig. 3.4). Any assumption that white spruce growth at treeline will change uniformly in relation to climate appears unjustified, and this changing sensitivity to climate is an obvious contributor to the error-term in ring-width based reconstruction of past climate. Our results indicate that climate-tree growth relationships of treeline white spruce in Alaska can be modelled successfully as two distinct responses across entire mountain ranges. For modeling applications at larger scales the main question becomes the relative proportion of positive spring responders and negative summer-drought responders in the area of interest. The consistency of the proportion of trees displaying these two responses in the Brooks Range and Alaska Range suggests that these ratios are applicable to similar areas of the boreal forest. The unprecedented levels of high temperatures in the last decades (Barber et al., 2003) have led to non-linear patterns of white spruce growth responses to warming at Alaska's treelines and temperature thresholds appear to be operating. Drought stress is now even affecting treelines at the cold margin of the boreal forest. In the longer term, intensification of warming could lead to the elimination of these negative responding trees through stress related mortality. Dynamic vegetation and biogeochemical models need to incorporate these divergent responses and apparent temperature thresholds to avoid overestimation of treeline advance, high latitude carbon uptake and future aboveground carbon storage.

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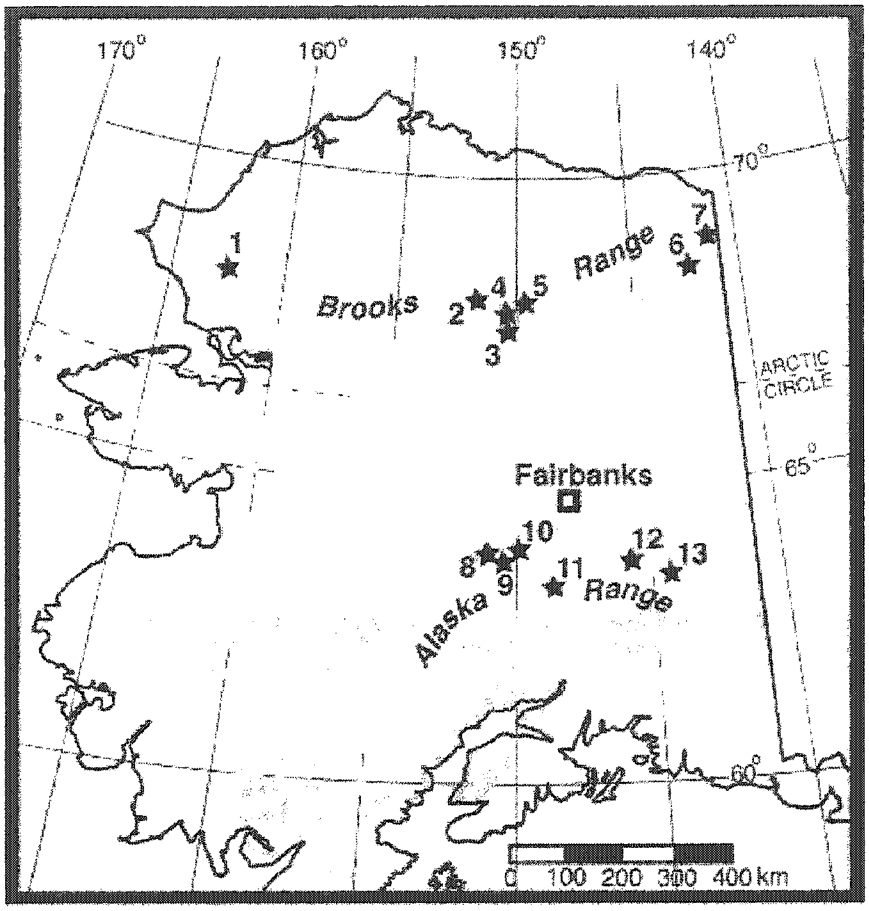

Figure 3.1: Location of study sites in Brooks Range and Alaska Range in Alaska. Shaded area is extent of boreal forest. All sites are at or near treeline. Brooks Range sites: **1**, BRKG (68.0 °N, 161.5 °W), **2**, BRHF (67.8 °N, 152.4 °W), **3**, BRCL (67.7 °N, 150.5 °W), **4**, BRNF (67.9°N, 150.5°W), **5**, BRNC (67.9°N, 149.8°W), **6**, BRSJ (68.5 °N, 143.8 °W), **7**, BRFR (68.6°N, 141.6°W). Alaska Range sites: **8**, ARCC (63.6°N, 150.0 °W), **9**, ARTL (63.4°N, 149.2 °W), **10**, ARRC (63.7 °N, 149.0 °W), **11**, ARSC (63.5°N, 148.8 °W), **12**, ARBC (63.4 °N, 146.4 °W), **13**, ARTK (63.3 °N, 143.3 °W).

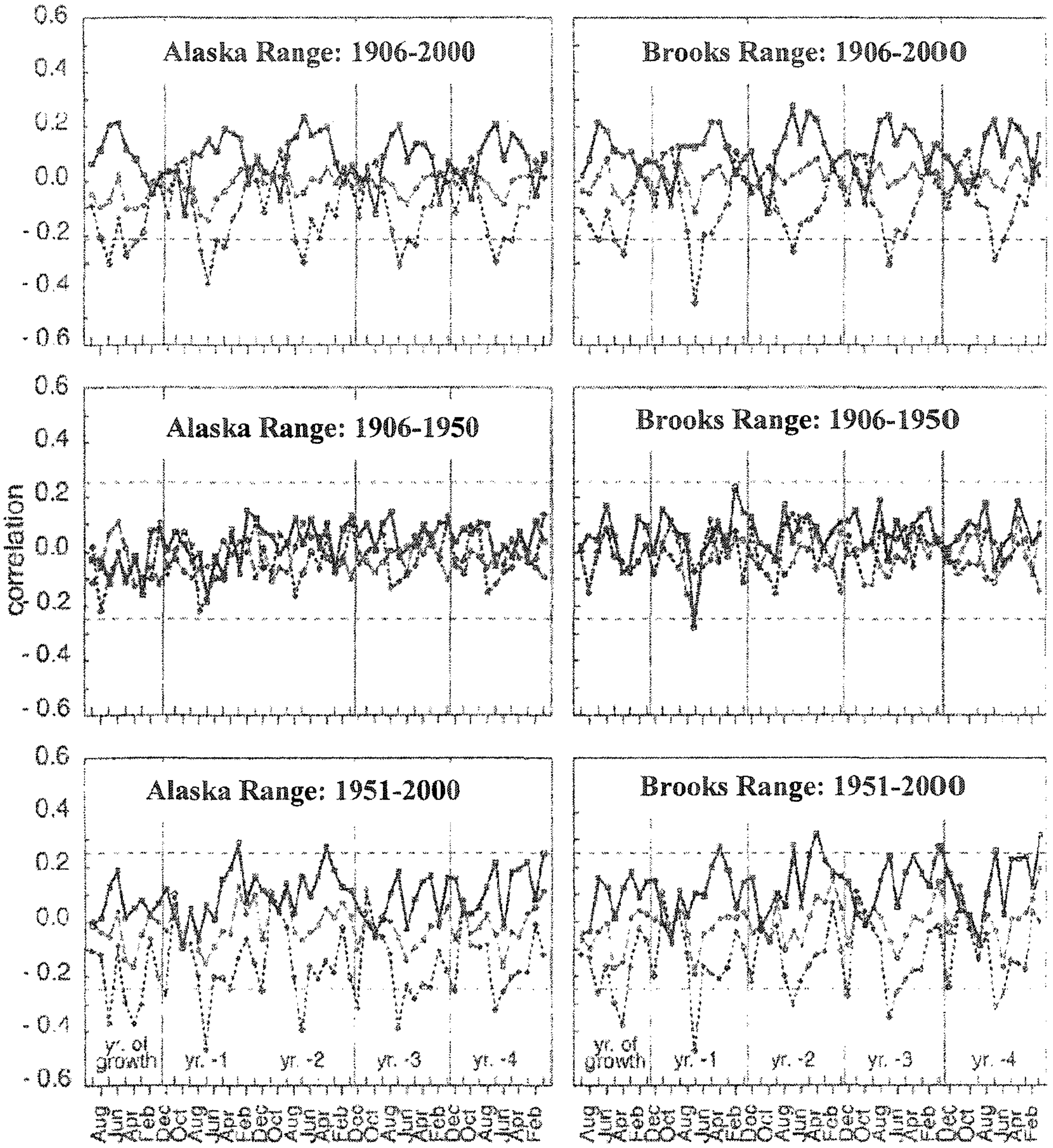

Figure 3.2: Cluster analysis of climate - tree correlation scores. Correlation scores of annual radial growth with Fairbanks mean monthly temperature over a 57 month period prior to the end of each yearly ring formation. The three lines depict the mean of the three most destinctive clusters developed using "k-means" clustering. Solid lines represent the mean correlation scores of all trees included in the cluster with positive

radial growth responses to monthly temperatures, dotted lines represent the cluster defined by negative responses, and dashed line represents clusters defined by trees with no consistent growth response. Level of statistical significance ($p \sim 0.01$) indicated by horizontal dashed lines. Note intensification of growth response after 1950 period and the maximization of correlation scores in the July prior to ring formation for negative responders in both mountain ranges and in the spring (March and/or April) for the positive responding population. Because of a high degree of serial autocorrelation most explanatory power is concentrated in the maximum correlation scores of the two years prior to ring formation.

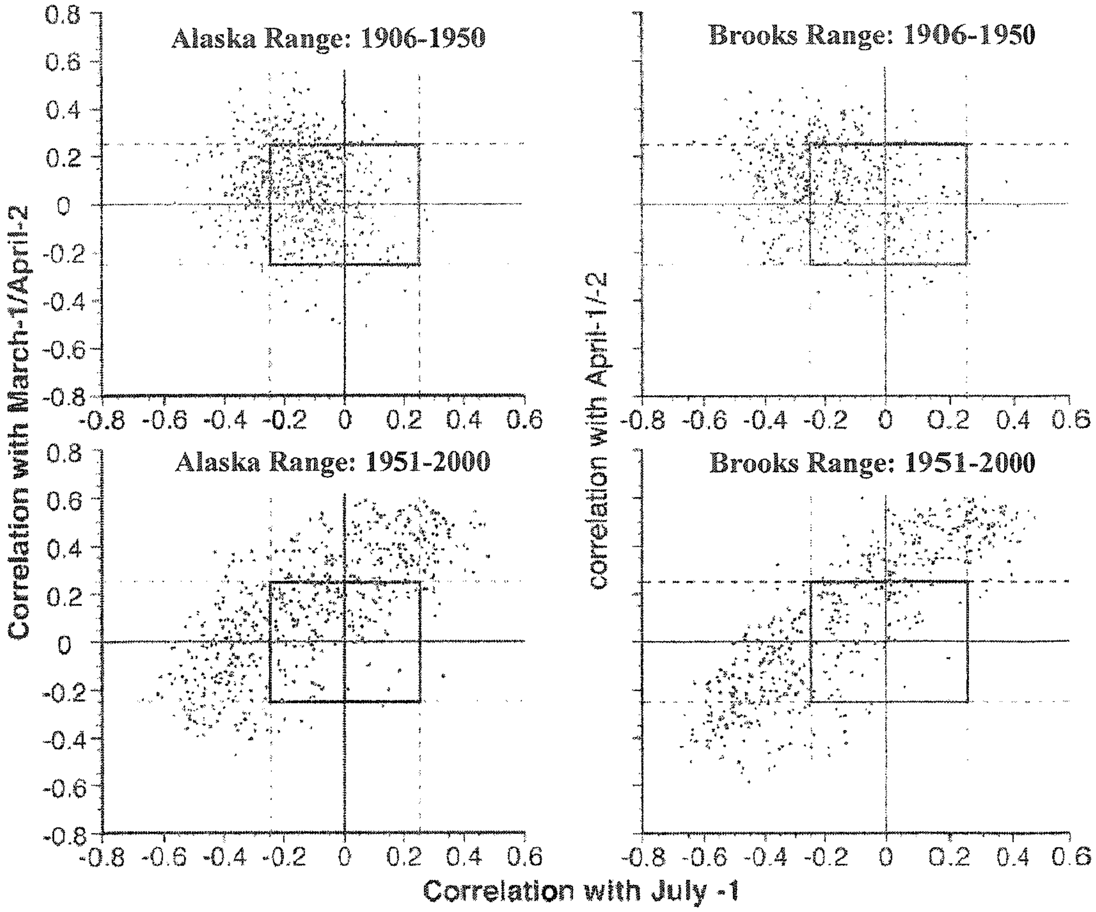

Figure 3.3: Growth predictor indices before and after 1950. Scatterdiagram of correlation scores of individual tree radial growth with previous July temperature (x-axis) and spring temperature index (y-axis) for Alaska Range (n=600) and Brooks Range (n=555) before and after 1950. Level of statistical significance indicated by dashed lines. The values inside the box are non-significant. Note the scatter before 1950 (top row) indicating normal distribution along both axis. After 1950 the distribution shifts in the direction of strong positive and strong negative correlations. Note that the majority of trees display either negative or positive correlation with predictor indices, rather then both responses simultaneously.

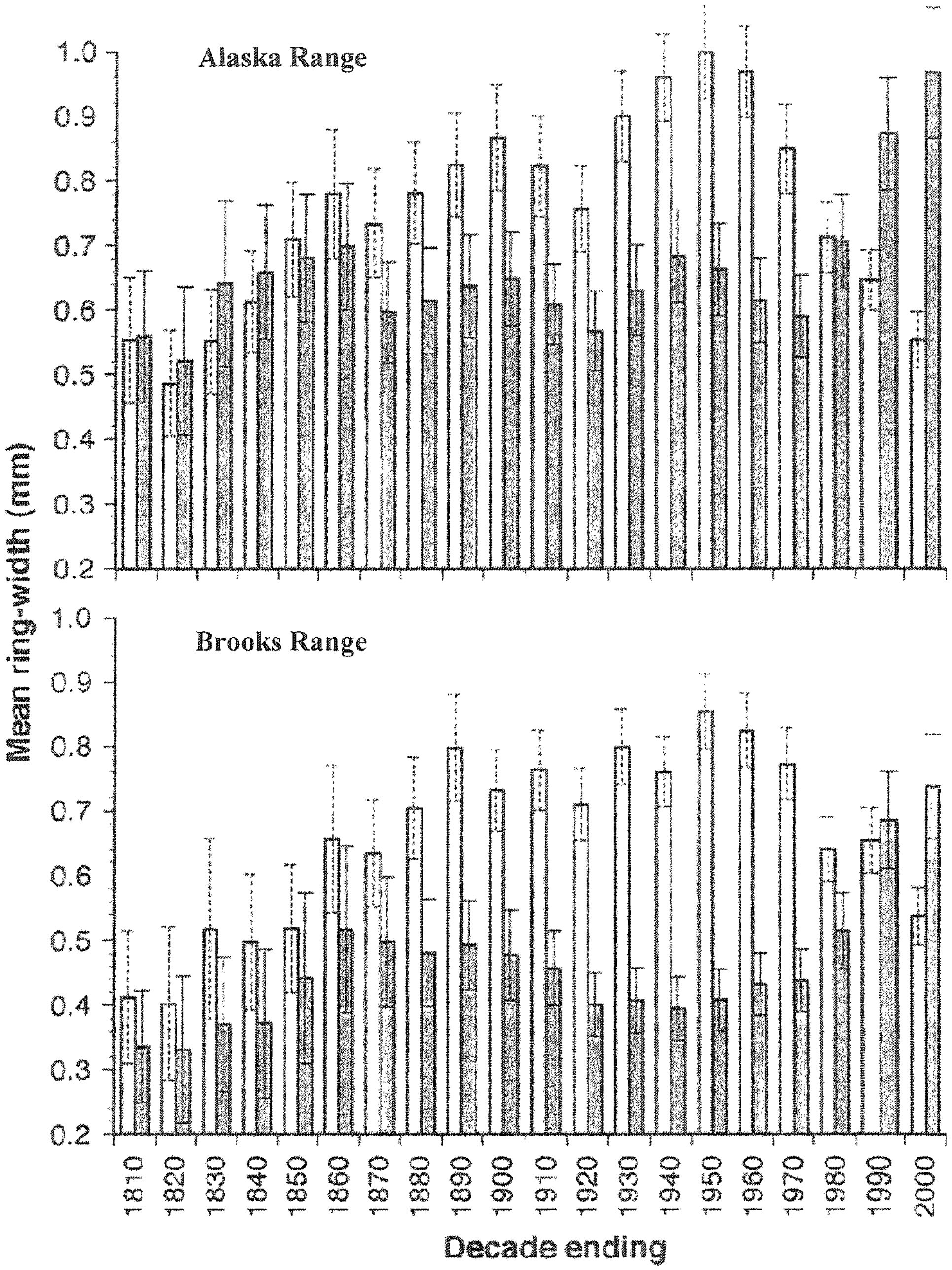

Figure 3.4: Mean raw radial growth by decade of negative and positive responders. Negatively (white colums) and positively (grey columns) responding populations in the Alaska Range and Brooks Range. Note the reversal of historic relationship of growth in the last part of the 20^{th} century, consistent with recent climate warming.

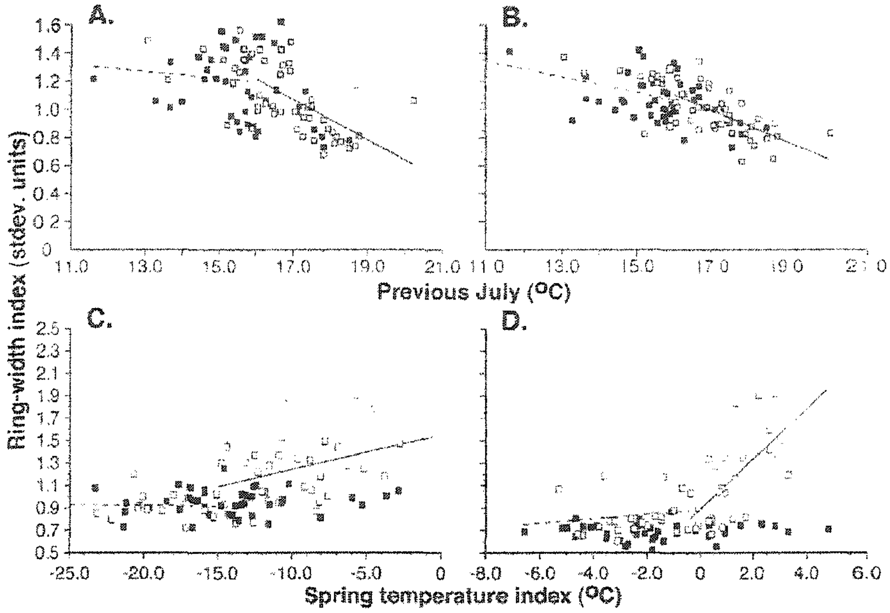

Figure 3.5: Ring width controlled by temperature thresholds. Piecewise linear regression of annual correlation scores of detrended radial growth (standardized values) versus temperature indices in the Alaska Range (**A**,**C**) and Brooks Range (**B**,**D**) before 1950 (solid squares) and after 1950 (hollow squares). Two regression lines are produced for each data set, maximizing the difference in slope to estimate "breakpoint" or threshold. Dashed lines indicate regression line before threshold, solid lines after threshold. July temperature (in °C) displays little predictive power for growth in both the Alaska Range (**A**) and Brooks Range (**B**) until an apparent ~16 °C threshold. (**C**,**D**) Detrended radial growth of positive responding trees to temperature predictor index (mean March-1/April-2 in the Alaska Range, and mean of April-1/-2 in the Brooks Range). Growth shows little response to temperature before 1950. After 1950, growth responds positively to an increase in temperature index in the upper portion of the range of values (warm springs). The absolute values of the apparent spring temperature thresholds differ between the mountain ranges, because of the different months used in calculating each temperature index.

Table 3.1:

Pre and post 1950 correlation scores of growth with temperature by site

Site	n > 100 yrs. at site	% sig.	Post 1950	r	5 yr. smooth	Pre 1950	r
ARBC	167	19.8	Jul -1	-0.63	-0.85	Aug	-0.41
ARCC	28	78.6	Jul -1	-0.50	-0.82	Jul-1/-3	-0.33
ARRC	121	38.0	Jul -1	-0.59	-0.86	Aug/Aug-1/Apr-3	-0.47
ARSC	15	33.3	Jul -1	-0.52	-0.80	Aug	-0.35
ARTL	123	52.8	Jul -1	-0.77	-0.81	July-1/Aug-1	-0.38
ARTK	146	35.6	Jul -1	-0.54	-0.85	Aug/Aug-1	-0.37
BRCL	68	38.2	Jul -1	-0.68	-0.86	Apr/Jul-1/Jul -3	+0.55
BRFR	59	67.8	Jul -1	-0.64	-0.90	Jul/Feb-1	+0.35
BRHF	73	42.5	Jul -1	-0.66	-0.83	Jun/May-2	+0.42
BRKG	67	8.9	Jul -1	-0.58	-0.75	Jan-1/Jul-1	+0.48
BRNC	109	46.8	Jul -1	-0.65	-0.87	Jul-1/Apr-4	-0.53
BRNF	79	51.9	Jul -1	-0.64	-0.88	Jul-1	-0.52
BRSJ	100	46.0	Jul -1	-0.66	-0.87	Jul-1/Apr-4	-0.41
ARBC	167	33.1	Mar-1/Apr-2	+0.53	+0.78	Mar/Jul-1	-0.41
ARCC	28	7.1	Mar-1/Apr-2	+0.56	+0.65	Aug/Aug-2	-0.36
ARRC	121	49.5	Mar-1/Apr-2	+0.60	+0.85	Mar/Jul-1	-0.44
ARSC	15	53.3	Apr-1/Apr-2	+0.61	+0.75	Aug	-0.40
ARTL	123	36.5	Mar-1/Apr-2	+0.63	+0.84	Jul-1/Aug-1	-0.38
ARTK	146	27.4	Mar-1/Apr-2	+0.60	+0.81	Aug-1/-2	-0.42
BRCL	68	51.5	Apr -1/-2/-3	+0.67	+0.77	Jun/Jan-2/-3	+0.50
BRFR	59	16.9	Jul/Apr -2	+0.70	+0.76	Aug/Feb-1/Aug-2	+0.50
BRHF	73	30.1	Apr-2/Feb-2/Jan-3	+0.54	+0.82	Jul/Aug -2	+0.43
BRKG	67	76.1	Apr-2/Jul-2/Dec-2	+0.55	+0.87	Aug -1/-2	+0.51
BRNC	109	43.1	Apr-1/-2	+0.62	+0.74	Jul-1/Apr -4	-0.47
BRNF	79	32.9	Apr -1/-2	+0.60	+0.70	Jan -3/-4	-0.30
BRSJ	100	20.0	Apr-1/-2	+0.58	+0.73	May-1/Dec-1	+0.37

Correlation scores of growth with temperature pre and post 1950 by site for negative responders (upper portion) and positive responders (lower portion). Correlation was performed using the mean of all negative or positive responders including all site types. Each of the 57 months preceding the end of each ring formation was tested as a possible growth predictor. Combination of months with highest predictive power is shown. After 1950, the unifying explanatory variable for negative responders is prior July (indicating drought stress) at each site. The smoothed (5-year running mean) values explain up to 81% of variation in growth at these sites. March and April temperatures one and two years prior to ring formation are the months with peak correlation for the positive responding populations at each site after 1950, consistent with the earlier onset of spring in this period. For site locations see Fig. 3.1.

[1]Chapter 4

Modeling spatial variability of treeline white spruce growth responses to Climate Change - Outlook for two National Parks in Alaska

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Abstract:

National Parks in Alaska are among the largest protected areas in the northern high latitudes. They are mostly intact ecosystems where human modifications have been and will be very low. The biggest threats to their biodiversity are large-scale and rapid changes in climate. In this paper we present a study of tree-growth - environment relationships of the treeline species white spruce (Picea glauca (Moench[Voss])) in two National Parks in Alaska: Gates of the Arctic National Park (GAAR) and Denali National Park (DNP). For each park, we modeled tree-growth based on landscape characteristics and extrapolated the results into the 21st century using data from five General Circulation Models (GCMs). In GAAR, one of the most remote and pristine parks of North America, our results based on the application of these scenarios, indicate enhanced growth at low elevation, whereas other areas will see changes in forest structure (dieback of tree-islands, infilling of existing stands). In DNP our results indicate possible dieback of white spruce at low elevations and treeline advance and infilling at high elevations. This will affect the road corridor with a forest increase of about 50% along the road, which will decrease the possibility for wildlife viewing. Surprisingly, aspect did not affect tree growth - climate relationships. Our results provide maps of possible forest dieback and expansion, which can be tools for future park planning.

Keywords: National Park, Alaska, Treeline advance, Decision tree model, White Spruce

Introduction:

Treelines are the limit of upright woody trees, beyond which only prostrate vegetation can survive. High-latitude and alpine treeline areas are zones of transition between two major biomes, boreal forest and alpine or arctic tundra. While sometimes conceived of as a broader transition zone, treelines in our study areas, representing two northern mountainous regions, are relatively sharply defined borders between forested sites and tundra. In this paper we apply the term treeline to an imaginary line connecting the highest patches of forests on a given slope (Körner, 1998).

Historically, the survival and growth of trees at treeline were seen as limited by only one environmental factor. The lack of available warmth has generally been interpreted as the limiting factor for tree growth in cold regions. This apparent simplicity of only one controlling factor has made treeline environments the focus of sustained research interest (Griggs, 1934; Krebs and Barry, 1970; Elliot-Fisk, 1983; Grudd et al. 2002).

Treeline ecotones have been investigated as potential "early warning stations" for Climate Change (Lescop-Sinclair and Payette, 1995; Hogg and Schwarz, 1997). Warming has been greatest in the high latitudes (Overpeck et al., 1997, Serreze et al., 2000), for example during the last century, Alaska experienced one of the strongest warming trends on a global basis (Chapman and Walsh, 1993).

Given the historical relationship between temperature and treeline position, the warming trend of the last decades could be expected to cause treeline advances in Alaska, which have been documented in some places (Suarez et al., 1999; Lloyd and

Fastie, 2002). However, arctic treelines might be more stable than expected (Szeicz and MacDonald, 1994), may not react quickly to climate warming (Lavoie and Payette, 1996), or might be relicts of warmer periods and not reflect current climatic conditions (Weisberg and Baker, 1995).

Large-scale climate-vegetation models assume linear correlation between changing climatic conditions and subsequent position of the boreal treeline (Pielke and Vidale, 1995; Elliot-Fisk, 1983). Site-specific studies, on the other hand, do not document significant changes in treeline position associated with recent climate warming of the last few decades (Holtmeier, 1995; Baker and Weisberg, 1997). Topography represents a barrier to treeline advances in response to climate warming. Models incorporating the topographic influences of mountain masses (Rupp et al., 2001) produce expansion of boreal forest onto the North Slope of Alaska after thousands of years.

Historically summer temperature (especially the July 10°C isotherm (Daubenmire, 1954; Holtmeier, 1974)) is reported as the main factor controlling treeline position. Körner (1998) and Chapin and Shaver (1985) proposed that soil temperatures of the root zone provide a far better explanation than generalized air temperatures, and Goldstein et al. (1985) suggested that colder soil temperatures can limit tree growth through increased resistance of water flow in white spruce at treeline. However, within the boreal forest, well south of the treeline areas, the limiting factor for white spruce growth is moisture supply (Barber et al., 2000). In parts of the forest-tundra ecotone in Alaska, growth limitations may have shifted from lack of warmth to lack of moisture (Jacoby and D'Arrigo, 1995, Chapter 3). Across the northern hemisphere, the sensitivity of radial growth and late wood density of high latitude trees to temperature has decreased since the mid 20th century (Briffa et al., 1998).

Alaska's northern treeline consists mostly of white spruce (Picea glauca (Moench (Voss))). In Alaska, white spruce populations at or near treeline in the Brooks Range and Alaska Range are mixed with positive, negative and no significant growth response to temperature (Chapter 3). Roughly equal proportions (~30 - 40%) of these trees display negative and positive sensitivity to temperature. Warm mean July temperature prior to the year of growth results in the reduction of growth in negative responding trees, and, warm spring temperatures one and two year prior to growth control growth increases in positive responding trees. During the second half of the 20th century, when most northern hemisphere trees at treeline sites experienced reduced sensitivity to temperature (Briffa et al, 1998), the Alaska trees increased in sensitivity (Chapter 3).

About 1975 Alaska's climate regime shifted to the warmest and driest in the last century (Barber et al., in press), so that these temperature thresholds are occurring more frequently in the later part of the 20th century. Future climate warming will likely have even greater effects on growth of Alaska treeline trees than has been seen in the past, because thresholds will be exceeded even more frequently.

In this paper we explore the spatial distribution of white spruce affected by these temperature thresholds in two National Parks in Alaska and attempt to build a simplified, medium scale, spatially explicit model of tree-growth climate relationships.

National Parks have multiple roles of protecting natural ecosystem processes and natural habitat, and providing for the enjoyment, education and recreation of visitors. Park boundaries are stable, but ecosystems are constantly responding to changing environmental conditions. Treeline advance is one example of the response to a change in environmental conditions that can be relatively rapid, with extreme rates of up to one km/decade on level terrain (Lloyd and Fastie, 2002).

GAAR is one of the most pristine areas of North America. Visitor frequency in GAAR is very low, and implications of treeline advance or retreat will be of importance primarily to the relative area occupied by tundra and boreal forest, the associated changes in habitat structure and the feedbacks to wildlife and the global climate system. DNP is the most visited National Park in Alaska with more than 280,000 visitors per year (http://www.nps.gov/dena/pphtml/facts.html). Bus tours provide the main visitor experience with viewing of wildlife and scenery along the park road, which leads from boreal forest through treeline into broad expanses of tundra. The general vision statement of the DNP goals states: "The National Park Service will preserve outstanding opportunities to view wildlife and mountain scenery, ..." (Denali National Park and Preserve, 2003). Small-scale changes in treeline position in our study areas, i.e. treeline advance and infilling, would reduce the ability of visitors to see wildlife from the road.

Description of study areas:

GAAR in the Brooks Range and DNP in the Alaska Range both encompass boreal forest and arctic or alpine tundra (Table 4. 1). GAAR became a National Park and Preserve in 1980. It encompasses over 34 000 km^2 in the central portion of the Brooks Range, Alaska. Boreal forest reaches from the southern foothills nearly to the continental divide, stretching along large river valleys, occupying 18% of the park area. Treeline occurs at elevations of about 800 to 900 m on south-facing slopes and 700 to 800 m on north-facing slopes and is a mixture between alpine (elevational) and latitudinal treeline. North of the continental divide, no naturally occurring white spruce is found. Our four study sites in GAAR (one site (BRNC) is actually 2 km outside the eastern border of GAAR) were located at or close to the northern limit of white spruce in Alaska (Fig. 4.1).

Denali National Park and Preserve was originally established as Mt. McKinley National Park in 1917. Today it consists of over 24 000 km^2, 38% of which is boreal forest. Our study sites (Fig. 4.1) were located at treeline in three watersheds within the park. Road tours into the park began in the 1920s and a comparison of historic photographs from that time period with the views of today suggests infilling of trees in scattered stands (Viereck, pers. com).

Methods:

Tree cores:

We collected tree ring samples from 793 white spruce (Picea glauca (Moench [Voss]) in GAAR and DNP. Site conditions (aspect, slope angle, elevation) were estimated at each tree location using GPS, altimeter and clinometer. We selected trees with no visible mechanical damage and cored mostly dominant and co-dominant individuals along transects from south-facing treeline through south-facing forest, through floodplain into north-facing forest and up to north-facing treeline.

For each tree, we recorded diameter at breast height (dbh), tree height (dbh and tree height were used to calculate green weight (Manning et al., 1984)) and position with a handheld GPS. Penetrating tree-cores were collected from each tree with a Hagloef increment borer. Cores were mounted, sanded (to 600 grit), rings counted, marked and measured using a Velmex measuring stage. Annual ring-width values were then averaged from both sides of the core. Averaged values were crossdated using standard techniques (Fritts, 1976). We verified the crossdating using COFECHA. Our goal was to include two 25-year periods before and after a major climate shift in 1975 (Barber et al., in press). Therefore we included only the 753 trees, which were 50 years or older and contributed rings continuously over that 50 year period in the analysis.

To establish membership in a responder class, we used the annual raw ring-width values. We compared averaged raw ring width of the time periods 1950-1974 and 1975-2000 and calculated the amount of decreased or increased rates of growth for those two time periods. Trees suffering a decline in growth we called "losers", trees with increased growth we called "winners" (there was only minimal change in membership if we used detrended values).

We then detrended and standardized the raw ring width values using ARSTAN (Cook and Kairiukstis, 1990) to remove the age effect. Tree growth was then correlated (Pearson correlation) with the Fairbanks record (1906-2000) of mean monthly temperatures. Fairbanks has the longest record of climate in Interior Alaska and is highly representative of temperature trends in the boreal forest region of Alaska (Garfinkel and Brubaker, 1980; Jacoby and D'Arrigo, 1995; Barber et al., 2000, Lloyd and Fastie, 2002 and 2003).

Based on empirical relationships of tree-growth and climate (Chapter 3), we used data from five GCMs (Kattsov et al., in press) for the 21st century to examine future rates of growth that might be expected under elevated temperatures. For the loser population of trees, we assumed a linear reduction in rate of growth under scenario temperatures based on the observed values (Fig. 4.2). Our standard for projecting the elimination of trees was when the projected empirical relationship reached zero growth. We used a responder function (Chapter 3), which models zero growth at a Fairbanks July temperature higher than about 22°C (Fig. 4.2).

Decision-tree model:

We developed two models of the relationships between tree growth and environment for white spruce, one for GAAR and one for DNP. Our goal was to predict where, within our catchment areas, trees suffered a decline in growth versus areas where growth accelerated after the major climate regime shift in 1975 (Barber et al., in press). Input parameters (predictors) included characteristics of each tree (age, dbh, tree-height, green weight) and environmental variables of the site where the tree grew. Environmental variables were both categorical: aspect, competition factor, stand characteristic (closed canopy, open canopy, outlier etc.), and continuous: elevation, height above valley floor.

We used the "classification tree" module in STATISTICA for model development. "Classification trees" are used to predict membership in classes of categorical dependent variables (in our case "winner" or "loser") on the basis of measured predictor variables.

In essence the program asks a series of hierarchical questions. Each answer leads to a univariate split in the data, in our case separating mostly winners from mostly losers, i.e. all tree weighing more than 310kg are assembled in one group of mostly losers, all lighter trees in the other (Fig. 4.3). After each split a new set of questions is tested against the remainder of the data-points to optimize the classification, e.g. if a tree is lighter than 310kg AND grows higher than 38.5m above the creek level. The C&RT-univariate split selection method employs an exhaustive grid search of all possible combinations of univariate splits to compute the classification tree (STATISTICA, help file). Predictive power is optimized by using half of the sample (randomly selected) for model development and the other half for model testing.

The main advantage of using "classification trees" was that they produce an easy to use "flowchart" with "if - then" questions and that the ecological validity can be tested with expert knowledge. In addition "classification trees" are organized hierarchically (as the environment), use univariate splits, which ecologically can be translated as "thresholds", they are nonparametric and numeral and categorical variables can be used as input. In each National Park we developed the model first for all trees within that area and then tested that model against each study site within the area.

Spatial translation of decision-tree model:

After model development, we used a GIS to "translate" our simplified schematic model into space. We obtained landcover classification from the National Park Service (2003; 60 m resolution). In order to apply the classification results spatially, we used elevational buffers to calculate area around streams (our model uses elevation above stream as a base for classification) and the treeline polygon (border of forested area to shrub and/or tundra). The treeline polygon obtained by this procedure was about 50 m lower in elevation in DNP than the highest trees we cored. Therefore, we used the treeline polygon and buffered it 50 m upward to estimate area occupied by these highest communities (winners).

For GAAR we applied our model to the entire park area. In DNP, large areas classified as boreal forest are occupied by black spruce. Since our model was developed on the basis of white spruce, we used only a subsection in the northeast of the park (~25% of park area) to extrapolate our decision-tree model results into space. Boreal forest in the area chosen is dominated by white spruce forests and treeline. In addition we used a 7.2 km wide corridor in DNP with the park road in the center to examine the extent and magnitude of the projected change in the area most heavily visited.

Results:

Winners and Losers:

Out of 753 trees tested for winner and loser status (both parks), 388 were winners and 365 were losers. In GAAR (n = 381) 57% of tested trees were winners, 43% losers. Winners in GAAR increased in radial growth 26.6% on average between the two test periods, losers decreased 17.3%. In DNP (n = 372) 46% of tested trees were winners, 54% losers. Winners in DNP increased radial growth on average by 28%, losers decreased 27%.

Decision tree model and model test:

The decision-tree model correctly classified between two-thirds and three-fourths winners and losers in both parks (Tables 4.2 and 4.3). Rates of correct classifications were generally higher at DNP (Table 4.3) than at GAAR (Table 4.2). The highest rate of misclassification of winners predicted as losers (31.4%) occurred at one site in GAAR (BRNF). The highest misclassification of losers as winners (21.7%) occured at the BRNC site in GAAR. For site nomenclature see Fig. 4.1.

The model for GAAR was developed on the basis of four study sites and 378 trees (three trees lacked complete site information). The model predicted 68% of class membership correctly and mis-classified 13% winners and 19% losers (Table 4.2).

The model for DNP was developed on the basis of three study sites and 306 trees (66 trees lacked complete site characteristics) and was tested against the 372 trees older than 50 years. The model predicted 74% of class membership correctly and miss-classified 14% winners and 13% losers (Table 4.3).

In GAAR the decision-tree model proceeds in four steps to reach the final level of classification (Fig. 4.3A), including, in order, tree biomass, relative elevation, competition status and tree height. First, all trees above 310 kg (15% of sample) of green weight are predicted as losers (Node 3, for miss-classification see Table 4.4). From the remaining trees, all trees growing up to an elevation of about 40 m above the floodplain are classified as winners (Node 4). If trees above the 40 m threshold grow in tree-islands, they are classified as losers (Node 6) and the remainder of trees in our sample (mostly the trees on middle to upper slopes) are classified as winners if they are smaller than 8.45 m in height (Node 8). All residual trees following the last step are classified as losers (Node 9). However, node 9 contains nearly an equal number of winners and losers and is the main contributor to the overall misclassification. In easy terms, these model parameters can be summarized as follows:

Statement 1: Big trees do not benefit from warmer and drier conditions regardless of landscape position.

Statement 2: Trees growing on lower slopes close to the creeks benefit from warming.

Statement 3: Tree-island competition is not beneficial for trees under warming conditions.

Statement 4: Small trees on middle and upper slopes benefit from warmer conditions.

The DNP decision tree uses five decision levels (Fig. 4.3B), which are low relative elevation, high relative elevation, tree age, mid-elevation position and dbh and height. In this model, all trees growing in the lower belt around the floodplains (lower than 65 m above creek-bed) are classified as losers (Fig. 4.3B, Node 2; for misclassification see Table 4.5). Trees growing higher than 305 m above the creek-bed, however, are classified as winners (Node 5), and form the highest current treeline communities. The trees growing on the remaining middle slopes are classified as winners if they are younger than 64 years (Node 6). The model also classifies trees as winners if they occur lower than 135 m above the valley floor and have a dbh over 39 cm (Node 11), or are relatively tall trees (> 8.45 m) and occur higher than 135 m above the valley floor (Node 13). This seemingly more complex model can also be summarized in more intuitive terms as follows:

Statement 1: Trees growing on lower slopes do not benefit from a warmer, drier climate.

Statement 2: The highest treeline communities are able to take advantage of warmer conditions.

Statement 3: Young trees on mid-slopes show accelerated growth after the regime shift.

Statement 4: Established, larger trees in existing stands do benefit from warming.

Ecological translation - projection into space:

Since our decision-tree-models incorporate both environmental parameters and tree information, such as age or green weight, which is not necessarily related to landscape position, extrapolating these models into space requires substitution of tree-specific parameters by the landscape parameters that are the best proxies for them. We tested each tree-specific predictor for it's relationship to landscape position, but did not find any reliable predictive relationship. As a result, the adaptation of the model we applied in order to identify areas predicted to support winners, losers and mixed populations consisted only of landscape parameters. The output of the spatial models can be seen in Fig. 4.4 for GAAR and Fig. 4.5 for the subsection of DNP.

In GAAR all areas up to 40 m above the main creek or river in a catchment are classified as landscapes currently occupied by winners. These areas total 2100 - 2500 km^2 or 35 - 40% of the existing boreal forest within the park. We infer that these areas would experience increasing tree growth and vigor under a warming climate. The decision tree model of GAAR also classifies 1) younger and smaller trees located higher than 40 m above a creeks or river as winners, and 2) tree-islands and older and bigger trees in the above 40 m elevation zone as losers. Since these parameters express tree to tree variability, they cannot be modeled using landscape information. Therefore, we consider the zone above the 40 m limit as "mixed", consisting of winners and losers. This mixed zone totals 60 - 65% or 3500 - 4000 km^2 of the existing boreal forest within the park. We infer that these areas would experience continuous forest cover in a warming climate, but composed of an increasing proportion of winners.

Boreal forest in DNP is a mixture between black and white spruce. Since our land-cover classification did not differentiate between the two forest types, we ran the spatial model only for areas most likely occupied by white spruce, e.g. areas close to treeline, mountainous terrain (see box in Fig.4.1). All areas up to about 65 m above the main creek or river in a catchment are classified as landscapes currently occupied by losers, which is the opposite response type compared with the similar landscape position in GAAR. These areas total about 383 km^2 or 49% of the existing boreal forest within the area of extrapolation in DNP. We infer that these areas would experience substantial growth decreases under a warming climate, possibly including elimination of white spruce with sufficient warming. The next node in the decision tree model of DNP classifies all trees higher than 305 m above the creek or river as winners. We infer that these areas, which include the highest current treeline communities, would support increased tree growth, tree establishment and infilling, and possibly treeline advance into alpine tundra under future warming conditions. Infilling and treeline advance during the last few decades of unusual warmth have been reported from other high elevation treeline areas in Alaska (Lloyd and Fastie, 2003). In the decision tree model of DNP, areas between 65 m and 305 m above creeks or rivers (400 km^2) are classified as supporting mixed populations of winners and losers. In these areas very young trees (< 65 years, 10% of sample) are classified as winners similar to GAAR. Well established bigger trees are also classified as winners in the decision tree model of DNP. However, in the middle elevation zone in DNP shorter trees and smaller diameter trees are classified as losers, suggesting that competition may be a factor in their negative response to warming. As a result we infer that in this mixed population zone warming would be associated with decreasing tree stem density.

Changing environment - projection in time:

A high percentage of the trees in our sample and other similar sites in the Alaska Range and Brooks Range show a statistically significant correlation between mean monthly temperatures in Fairbanks and annual radial growth, including both positive and negative correlations (Chapter 3). Negative correlations were maximized using the mean monthly temperature of July in the year prior to ring formation. This negative response is consistent with temperature-induced drought stress as a controlling factor for growth of white spruce in central Alaska (Barber et al., 2000) and at treeline (Jacoby and D'Arrigo, 1995). Negative effects of July temperature on treeline white spruce occur only above the threshold of 16°C at the Fairbanks station, which probably translates to a temperature of 11-12°C at treeline sites (Chapter 3). This temperature function predicts tree growth reduced to zero at about 22°C at Fairbanks (Fig. 4.2). Sustained periods of time at or even near July temperatures that produce zero growth are likely to result in the death of white spruce negatively correlated with July temperature in our study area, through stress related factors such as insects (Hard, 1985 and 1987).

During the 20th century, mean monthly July temperatures in Fairbanks reached or exceeded the 16°C growth reduction threshold in 52 of 93 years (record 1906-1999). The five GCMs project temperatures at Fairbanks above the threshold ranging from 85 out of 99 years (CSM-model) to 98 out of 99 (CCC-model) in the 21st century (Kattsov et al., in press).

Mean monthly July temperature of the Fairbanks grid-cell modeled by ECHAM, HAD and GFDL reach and/or exceed the 22°C zero growth threshold in the second half of the 21st century. The CCC and CSM models project highest July temperatures of around 20°C during the scenario period (Kattsov et al., in press).

Discussion:

Winners and Losers:

Most published literature on treeline studies in the northern-hemisphere focuses on the positive growth response of trees with warming climate (Garfinkel and Brubaker, 1980; D'Arrigo and Jacoby, 1993; Briffa et al., 1998). In our sample, however, negative growth responses of treeline trees with warming are widespread (48% of trees greater than 50 years old). Temperature-induced drought stress as the major factor controlling tree growth has been reported within the boreal forest (Barber et al., 2000) and at treeline (Jacoby and D'Arrigo, 1995). Recent warming and a shift around 1975 to the warmest and driest climate regime of the last century (Barber et al., in press) have intensified the negative growth responses of trees to warming. We report here that large areas of white spruce at or near treeline in two National Parks in Alaska are also showing reduced growth consistent with the drought stress hypothesis.

More trees responded positively to warming in the northern study areas of GAAR (57%) than in DNP (46%). While the average growth increase after 1975 is about similar in both parks, the average rate of growth decrease is higher in DNP. Both of these trends suggest that the northern treeline (the colder environment) benefits from warming more than elevational treelines within the boreal forest. In addition, summer and winter precipitation in DNP is higher than in GAAR (Hammond and Yarie, 1996) and probably offsets some of the drought stress there.

Error structure of the decision tree model:

In GAAR, most trees misclassified as winners, which are in fact losers, grew either on south-facing forests in one study site (BRNC), or as small scattered trees on north-facing slopes. Half of the trees misclassified as losers (which are winners) grew on south-facing forest sites. A further 25% of winners misclassified as losers represent scattered trees on north-facing slopes, and the remaining 25% are large trees growing in floodplains. Since winners and losers are mostly misclassified in the same environments (south facing forests and scattered trees on north-facing slopes) misclassification is partly offset and the outcome of the overall classification is more accurate than would otherwise be the case. Site variations (as in BRNC) can play a role in changing the general relationship between tree growth and environment. It is therefore important to employ an extensive sampling design, rather than concentrating on a few sampling locations in order to control for this spatial variability.

The vast majority of trees in DNP which our model classified as losers but in fact are winners, belong to one of the following groups: 1) south-facing forests or 2) forest in floodplains. Interestingly enough, the trees classified as winners (which are in fact losers) also belong mostly to one of these categories, leading to two conclusions: First, here again the classification errors partly compensate for each other and decrease the overall misclassification as in GAAR. Second, trees in these environments can be winners or losers, but those traits are apparently not controlled by any of our predictor variables, and thus might be controlled by variables we did not measure, or variables on a smaller scale than our investigation, e.g. local moisture supply. However, plot scale correlation of soil temperature and soil moisture with growth response (Wilmking, unpublished data) does not support this hypothesis. Alternate explanations of opposite responses of trees in apparently similar environments, such as genetic differences between winners and losers, await further study.

Projection into space:

The application of our decision-tree models spatially in both National Parks projects strongly reduced growth of trees at low elevations in DNP and larger trees in GAAR, possibly eliminating these trees through stress-related mortality as climate warms within the next 100 years. By contrast, at higher elevations in DNP all trees show a growth increase under warmer conditions. Positive growth responses and future recruitment in these highest elevation environments is a prerequisite for future treeline advance. Actual treeline advance in the last decades in Alaska (Lloyd and Fastie, 2002 and 2003) occurred during a period of climate warming, empirically validating this projection. In GAAR trees at higher elevations only show increased growth with warming if these trees are not hindered by tree-to-tree competition. Nearly all trees in tree islands show reduced growth after the regime shift to a warmer climate in 1975. Single trees at high elevations in GAAR are mostly winners. Tree-to-tree competition also seems to be a factor in the mixed mid-elevation zones in both parks where positive and negative responders can grow in close proximity to each other (sometimes < 3m!). In DNP bigger, established trees have a competitive advantage over smaller trees in the mid-elevation zones. We hypothesize that small-scale differences in soil, nutrients, and light can be overcome by trees able to integrate across these differences with larger rooting volumes and crowns. On the other hand, most trees between 50 and 60 years old in this elevation zone did increase their growth with warmer and drier conditions, suggesting that these trees are utilizing growth resources not used by established trees. In GAAR, small trees in the mid-elevation zone are mostly winners (Fig 3A, Node 8). These inconsistent results lead us to two conclusions: Growth response in these areas is mostly controlled by 1) factors we did not measure (e.g. genetic variability, nutrient availability), and/or 2) by factors acting on a smaller scale than our investigation. As a result, in both national parks our models show the highest misclassification rates in these zones.

Trees growing close to creeks or rivers (low-elevation slopes and floodplains) show opposite growth responses to temperature in the two National Parks. In GAAR, low-elevation slopes and floodplains are the areas of increased growth with warming climate, whereas in DNP under the same warming conditions trees on such sites show decreasing growth. Floodplains and low-elevation sites in DNP are locally the most productive sites, supporting closed canopy forest with high stem densities. The soils are silty. In GAAR, floodplain sites in our sample areas are one of two types, either young gravelly floodplains supporting widely spaced individual trees, or older floodplains underlain by permafrost, also supporting widely spaced trees. Low elevation sites in GAAR are locally also the most productive, but stem densities are lower than in DNP. In low-elevation and floodplain areas, as in the high elevation areas, tree to tree competition seems to be an important factor determining growth response under warming climate. Trees not hindered by other trees (as in GAAR floodplains) are able to take advantage of warmer air and soil temperatures with increased growth. If the depth of the active layer in permafrost sites increases with warming climate, larger rooting volume and new nutrient sources probably benefit the trees. In DNP by contrast, these sites are already fully occupied by established trees and warming probably intensifies existing competition.

Surprisingly, neither tree age (Szeicz and MacDonald, 1994) nor aspect showed any significant relationship with growth response. Age was only used once as a deciding factor in our decision-tree models. Instead, tree weight and dimensions of the tree (dbh, height) seem to play an important role in the climate-tree growth relationship.

Projection in time:

Opposite growth responses of treeline white spruce in Alaska have intensified in the latter part of the 20th century due to climate warming (Chapter 3). If this warming continues (as modeled by five GCMs), we expect a further intensification of diverging growth responses of white spruce at treeline in Alaska. Winners will take advantage of warmer conditions and enhance growth, thereby increasing their carbon uptake. Losers will experience further decline in growth and drought stress-related mortality of these trees is likely due to several reasons. 1) Growth rates of zero are associated with the range of temperatures projected by the scenarios for the 21st century; 2) Growth rates are averaged over a population; single trees will reach zero growth far earlier; 3) Stressed trees are more likely to attract and sustain damage from factors such as insects (Hard 1985 and 1987); 4) Prolonged growth rates of only 30 - 40% of historical levels may severely diminish their ability to compete with other plants for resources. In addition, such rates of reduction might lead to population responses far larger than we project for individual trees.

It is therefore likely that under further warming conditions landscape-scale changes in white spruce distribution will take place. Areas of declining growth (lower hillsides in the DNP or tree islands in GAAR) would have high rates of tree mortality, and areas experiencing enhanced growth (treeline areas in DNP and lower hillsides in GAAR) would experience infilling and higher productivity.

Example: The Park Road

We chose the road corridor in DNP as an example to illustrate the magnitude, extent and impact of possible advance of treelines and dieback of white spruce. In 2002, DNP was visited by 280,911 recreational visitors (a drop from the 350,000 visitors/year at the end of 90s). The overwhelming majority of those visitors drove into the park with a shuttle bus. Wildlife viewing (e.g. Moose, Caribou, Dall Sheep, Grizzly Bear, Wolf, Fox etc.) and the view of Mt. McKinley are the major attractions of the park. Increased traffic in the last 30 years has apparently had no negative effect on the number of wildlife sightings from the road (Burson et al., 2000) and, while moose behavior indicated possible traffic avoidance, this does not hold true for the distribution of grizzly and caribou (Yost and Wright, 2001).

We define the road corridor as an area extending 3.6 km out on either side of the road. In 2000, 21.1% of the road corridor (187.0 km^2) was classified as boreal forest (Fig. 4.6A, Table 4.6), where the distance in which wildlife can be seen (< 100m from the road) is far smaller than in terrain not forested. The application of our spatial model of tree-growth landscape relationships for the road corridor identifies areas of possible forest expansion and dieback (Fig. 4.6B). If climate warming occurs according to the pattern simulated by the climate scenarios during the 21st century, boreal forest area would increase to 289 km^2 and occupy 33% of the road corridor (Table 4.6), an increase of about 50% over the current forested area. Dieback of trees would occur at low-elevation areas at the park entrance and along major river valleys (about 10% of road corridor), which are now occupied by boreal forest. More important for visitors though, the tundra areas south of the western portion of the park road (see arrows) would experience increases in tree density (infilling) and treeline advance (Fig. 4.6B). These are the prime areas of wildlife viewing and allow stunning views of Mount McKinley on clear days. Repeating the general vision statement of the DNP goal: "The National Park Service will preserve outstanding opportunities to view wildlife and mountain scenery, ..." (Denali National Park and Preserve, 2003), it will be a challenge to address the dichotomy of preserving natural ecosystems and all associated changes and the impact of these changes on its visitors.

Conclusions:

White spruce populations at and near treeline in the Brooks Range and Alaska Range of Alaska include roughly equal numbers of trees that have increased (winners) or decreased (losers) in growth after a major shift in 1975 to a warmer climate. The occurrence of winners and losers was effectively modeled in GAAR and DNP using tree and site characteristics, primarily size of trees, relative elevation and age. The models were different for both National Parks, expressing regional variability. In GAAR, trees that respond to climate warming with increased vigor and growth (winners) are generally found at low-elevation slopes and on floodplains. Similar environments in DNP are occupied by losers. Trees currently at the highest elevations in DNP are all winners. All other zones showed mixed growth responses. One possible explanatory factor that ties together the responses and spatial distribution of winners and losers at different scales appears to be tree to tree competition. Areas of low competition, e.g. highest treeline sites or low density floodplains, show generally positive growth responses with warming. Areas of high competition, e.g. high tree density floodplains and forests, are primarily occupied by losers. The partly opposite model outputs in both National Parks lead to the conclusion that a generalization of our results is only possible within the context of our sample area and the results cannot be applied broadly.

Growth of loser white spruce is predicted by temperatures of the previous July, if it exceeds 16.5°C at the reference station in Fairbanks. Temperatures greater than 22°C at Fairbanks are projected to result in zero growth of losers. Five GCM scenarios for the 21st century produced temperatures above the growth reduction threshold more than 85% of all years, and three of the five scenarios produced temperatures which reached or exceeded 22°C in the second half of the 21st century. This result suggests that areas now occupied by losers would no longer be able to sustain the species under scenario conditions.

The combination of the decision-tree model of DNP with the five GCM scenarios for the 21st century projected treeline advance of about 50 m in elevation. As a result, our spatial model for the road corridor in DNP projects a significant increase in forest cover from now 22% to 32%, even though dieback of white spruce in low elevation areas would occur. This increase in forest cover would significantly decrease the ability of visitors to see wildlife and scenery from the road, and should be carefully considered when planning the future park infrastructure.

In summary, if recent warming trends continue, changes in distribution of white spruce forests are within the range of possibility on a regional scale (treeline advance, dieback) and structural changes within existing forest are possible on a medium (landscape) scale (changes in tree density through infilling and dieback). Our results show that changes in growth performance of individual trees due to climate warming are already underway, that further warming would intensify these changes and that they would have landscape-wide consequences.

In a global context, our results indicate that large-scale models of climate-vegetation interaction will have to be coupled with medium-scale topographically based models. As an example, structural changes (dieback, infilling and treeline advance) can happen in an area smaller than 4 km^2 which might be within the extent of one grid-cell in global vegetation models. Albedo as well as carbon uptake or release-potential are directly linked to these structural changes and therefore cannot be captured using large-scale models. Spatially explicit medium-scale models, however, can capture this variability so that a combination of large-scale and medium-scale models will greatly increase the predictive power of such approaches.

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Tables:

Table 4.1: Landcover types in study areas (km^2), (National Park Service, 2003)

	GAAR	**DNP**
Boreal forest	6241.3	9531.6
Shrubs	17746.4	4126.2
Tundra	5358.9	3434.6
Water bodies	335.7	438.0
Bare/burned area	2962.8	2605.6
Snow/ice	145.0	2717.0
Indeterminate/clouds	1523.5	1750.9
Total area	34313.6	24603.9

Table 4.2: Model classification of winner and loser trees in GAAR, based on comparison between "decision tree" modeling versus actual growth performance:

		TEST	correct	Loser misclassified as winners	Winner misclassified as loser
GAAR	n	381	260	50	71
	%	100.0	**68.3**	**13.1**	**18.6**
BRNC	n	129	88	28	13
	%	100.0	**68.2**	**21.7**	**10.1**
BRNF	n	86	52	7	27
	%	100.0	**60.5**	**8.1**	**31.4**
BRCL	n	77	59	9	9
	%	100.0	**76.6**	**11.7**	**11.7**
BRHF	n	89	61	6	22
	%	100.0	**68.5**	**6.7**	**24.7**

Table 4.3: Model classification of winner and loser trees in DNP, based on comparison between "decision tree" modeling versus actual growth performance:

		TEST	correct	Loser misclassified as winners	Winner misclassified as loser
DNP	n	372	269	53	50
	%	100.0	**72.4**	**14.2**	**13.4**
ARRC	n	142	97	25	20
	%	100.0	**68.3**	**17.6**	**14.1**
ARCC	n	33	29	3	1
	%	100.0	**87.9**	**9.1**	**3.0**
ARTL	n	165	125	19	21
	%	100.0	**75.8**	**11.5**	**12.7**

Table 4.4: Misclassification of trees as winners or losers at decision nodes in the GAAR "decision tree" model

Node	n	winners n	losers n	misclassification rate [%]
3	28	5	23	18
4	42	35	7	17
6	12	2	10	17
8	52	40	12	23
9	55	25	30	45

Table 4.5: Misclassification of trees as winners or losers at decision nodes in the DNP "decision tree" model

Node	n	winners n	losers n	misclassification rate [%]
2	47	5	42	11
5	13	13	0	0
6	16	13	3	19
10	30	6	24	20
11	7	5	2	29
12	4	0	4	0
13	35	23	12	34

Table 4.6: Aggregate area of spatially predicted actual tree performance under climate warming in the DNP road corridor

Road-corridor (RC)	km^2	% of existing forest in RC	% of RC
Total area of RC	883.4		100.0
Existing forest in RC	187.4	100.0	21.2
Potential forest loss	85.3	45.5	9.7
Potential forest gain	186.5	99.5	21.1
Net forest after change	288.6	154.0	32.7

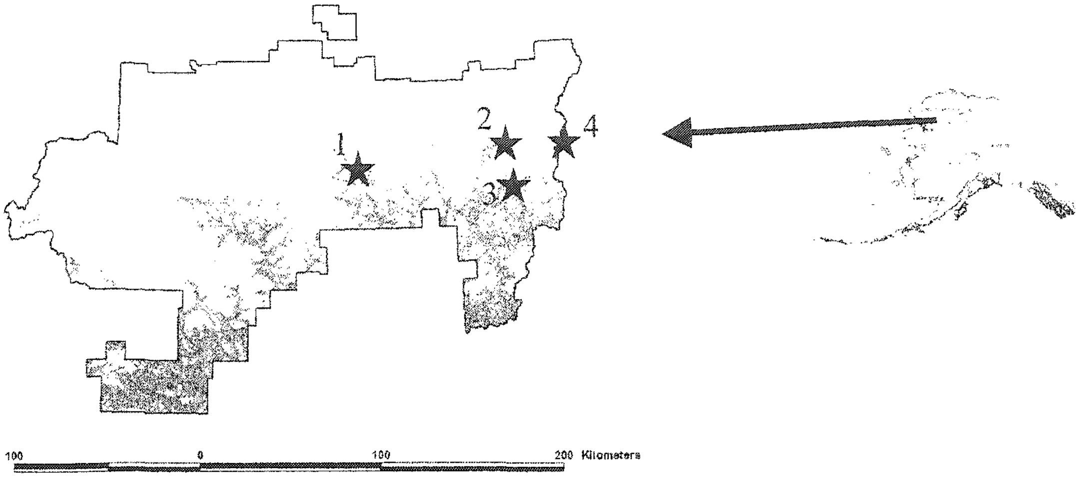
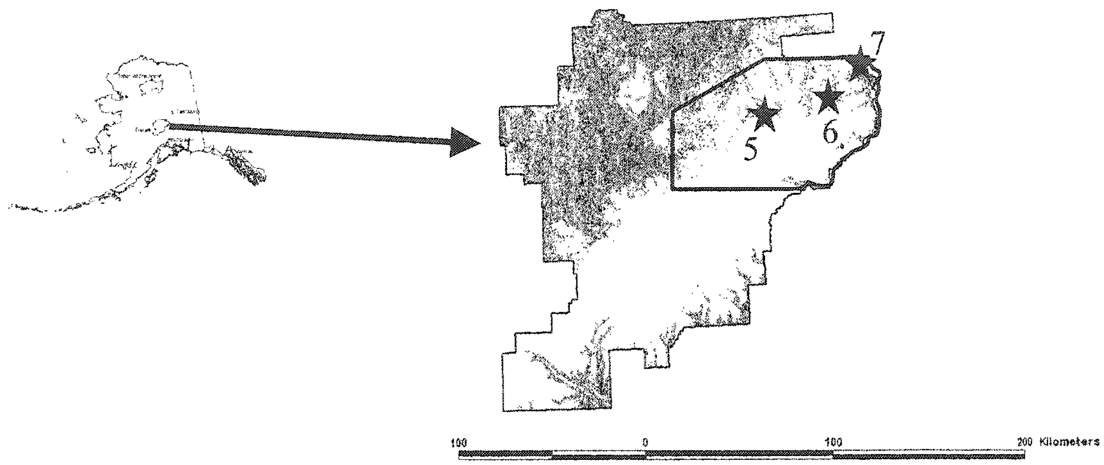


Figure 4.1: Location of study sites:

(A) Gates of the Arctic National Park, Brooks Range (BR), Alaska. All study sites are at or close to treeline. At each study site cores were sampled from north and south-facing slopes at and below treeline and where possible in the floodplain. Location of study sites: 1) Hunt Fork, BRHF (67.8 °N, 152.4 °W), 2) North Fork Koyukuk, BRNF (67.9°N, 150.5°W), 3) Chimney Lake, BRCL (67.7 °N, 150.5 °W), 4) Nutirwik Creek, BRNC (67.9°N, 149.8°W).



(B) Denali National Park, Alaska Range (AR), Alaska. All study sites are at or close to treeline. At each study site cores were sampled from north and south-facing slopes at and below treeline and where possible in the floodplain. Location of study sites: 5) Cabin Creek, ARCC (63.6°N, 150.0 °W), 6) Savage River, ARTL (63.4°N, 149.2 °W), 7) Rock Creek, ARRC (63.7 °N, 149.0 °W).

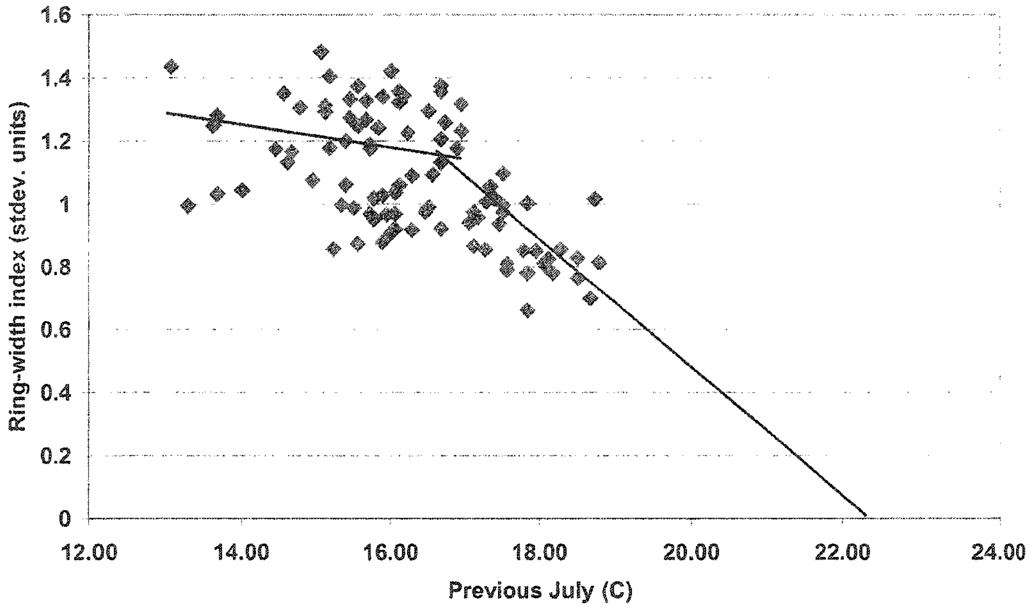
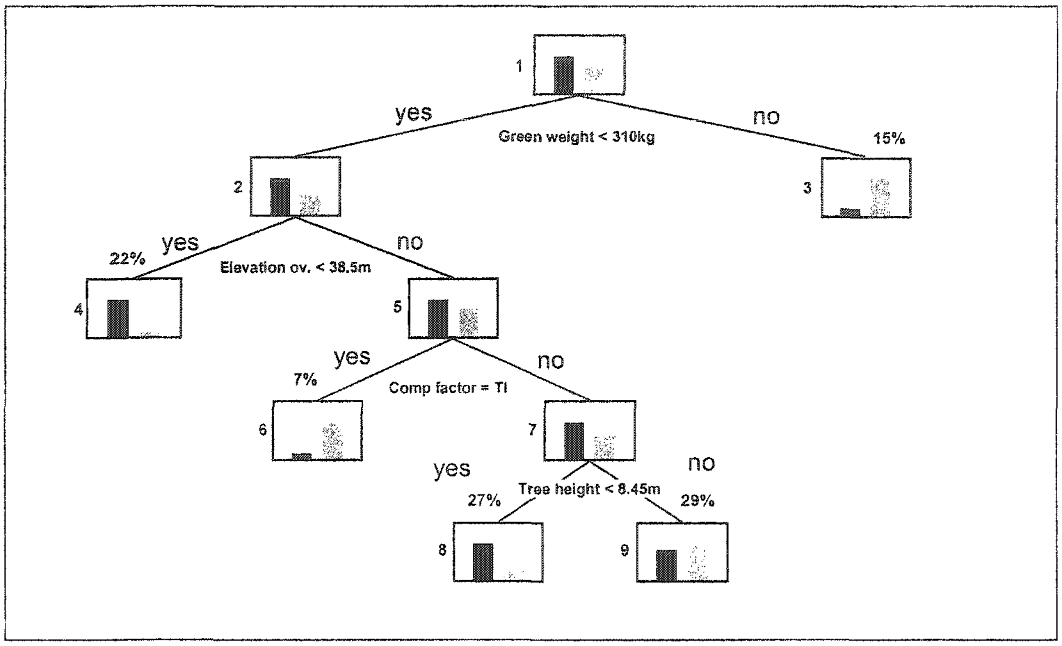


Figure 4.2: Temperature threshold controlling negative growth response (modified from Chapter 3). Mean ring width index (MRWI) as a measure of growth (y-axis) of all sampled trees older than 50 years with a negative growth response versus Fairbanks mean monthly July temperatures of the year prior to ring formation. A MRWI of 1 is the mean average growth over the life-span of each tree of the sampled population until we cored it. Piecewise linear regression was used to calculate the threshold, by maximizing the difference in slope between the two regression lines. Mean monthly temperatures below 16.5°C do not affect MRWI of the following year (r^2=0.05, n=55). Above 16.5°C however, tree growth is strongly negatively correlated with warmer July temperatures (r^2=0.51, n=38).

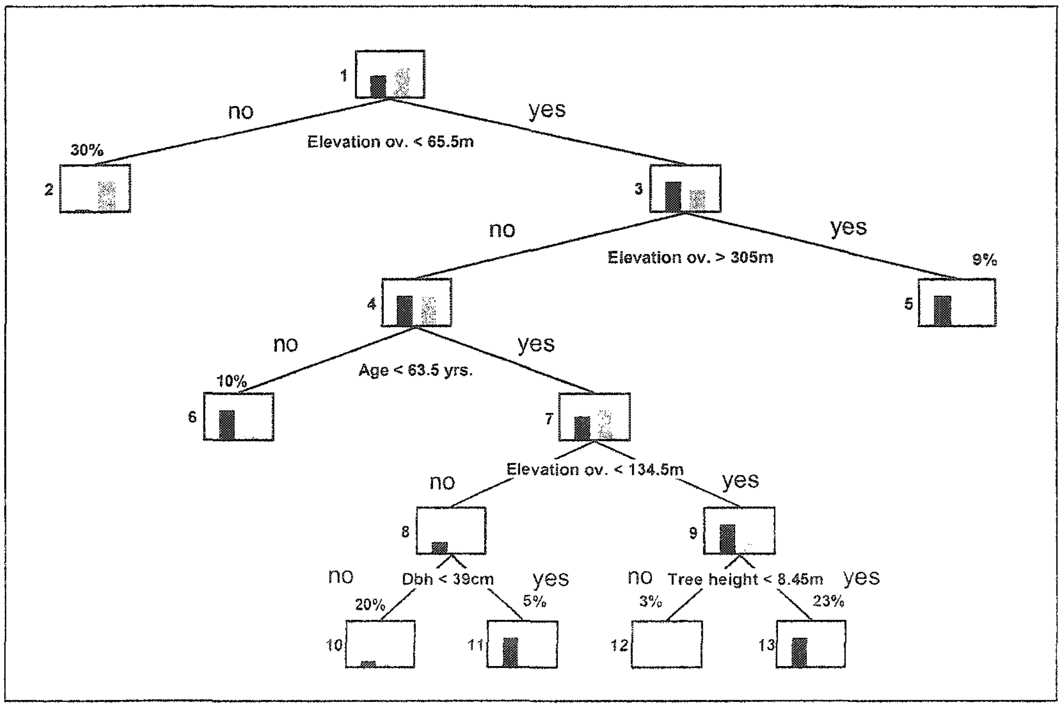
Figure 4.3: Decision tree model for GAAR (A) and DNP (B)

Tree and landscape characteristics are used to compute the decision-trees in each National Park. The model asks a series of hierarchical if-then questions (most important questions at the top) to classify the trees into "winners" and "losers". Winners are symbolized by black and losers by gray columns in every box (Node). All trees belonging to the group characterized by a positive answer to the question (below the box) move to the left, all others to the right (e.g. if a tree's green weight is less than 310 kg it will be moved to box 2 in (A), if a tree is heavier, it will be moved to box 3 in (A) and classified as "loser"). Numbers to the left of each box indicate "node" number. Misclassifications for each node can be found in Tables 4 and 5. The number on top of each box represents percentage of trees in that box of total sample within each park. Column height corresponds to percentage of winners and losers in each box (as in a histogram). "Elevation ov." equals the relative altitude of a tree over the creek below, e.g. a low "elevation ov." corresponds to a site on the lower slopes. TI: Tree-Island, Dbh: Diameter at breast height.

A)


1
yes
no
Green weight < 310kg
15%
2
3
22%
yes
no
Elevation ov. < 38.5m
4
5
yes
no
7%
Comp factor = TI
6
7
yes
no
Tree height < 8.45m
27%
29%
8
9

(B)


1
no
yes
30%
Elevation ov. < 65.5m
2
3
no
yes
Elevation ov. > 305m
9%
4
5
no
yes
10%
Age < 63.5 yrs.
6
7
no
Elevation ov. < 134.5m
yes
8
9
no
Dbh < 39cm
yes
20%
5%
no
Tree height < 8.45m
yes
3%
23%
10
11
12
13

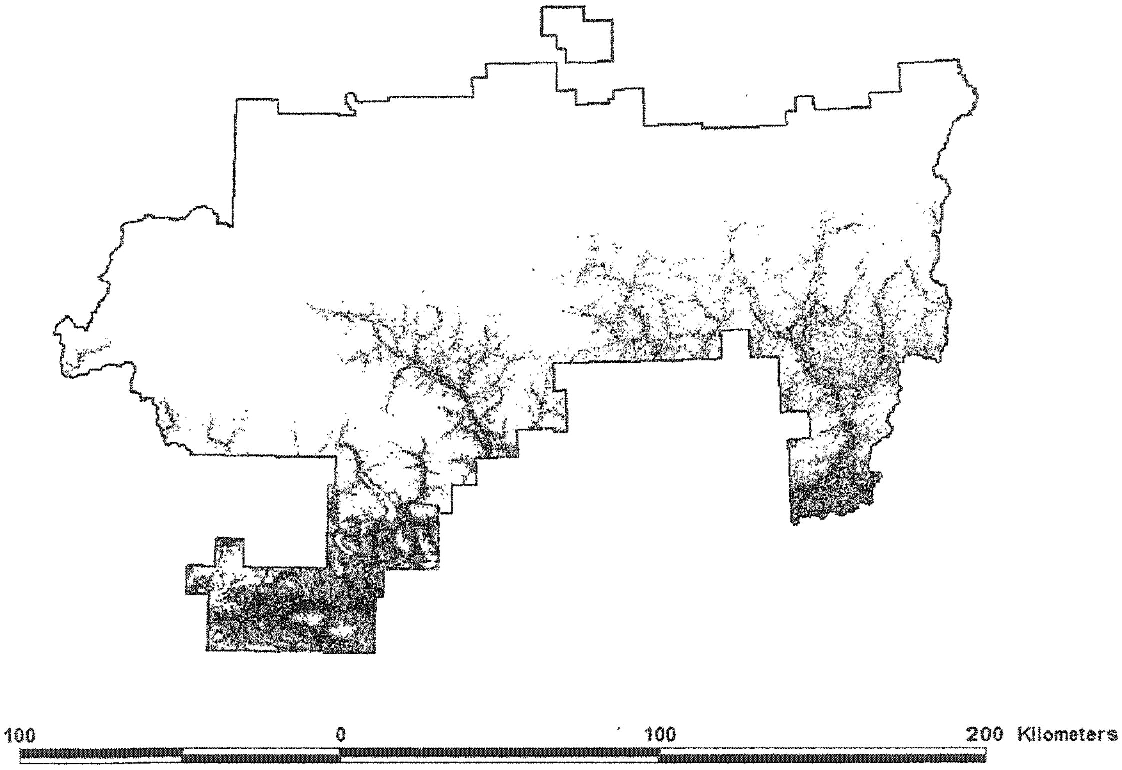


Figure 4.4: Effect of further warming on GAAR. The spatial application of our decision-tree model for GAAR projects no major treeline advances. However, within the existing boreal forest (6241.3 km^2) our model identifies areas currently occupied by winners (black shading). These areas, amounting to 35 - 40% of existing forests along the creeks and rivers are projected to increase in tree growth under a warming climate. Gray shaded areas represent mixed populations of winners and losers, which cannot be modeled using only landscape information.

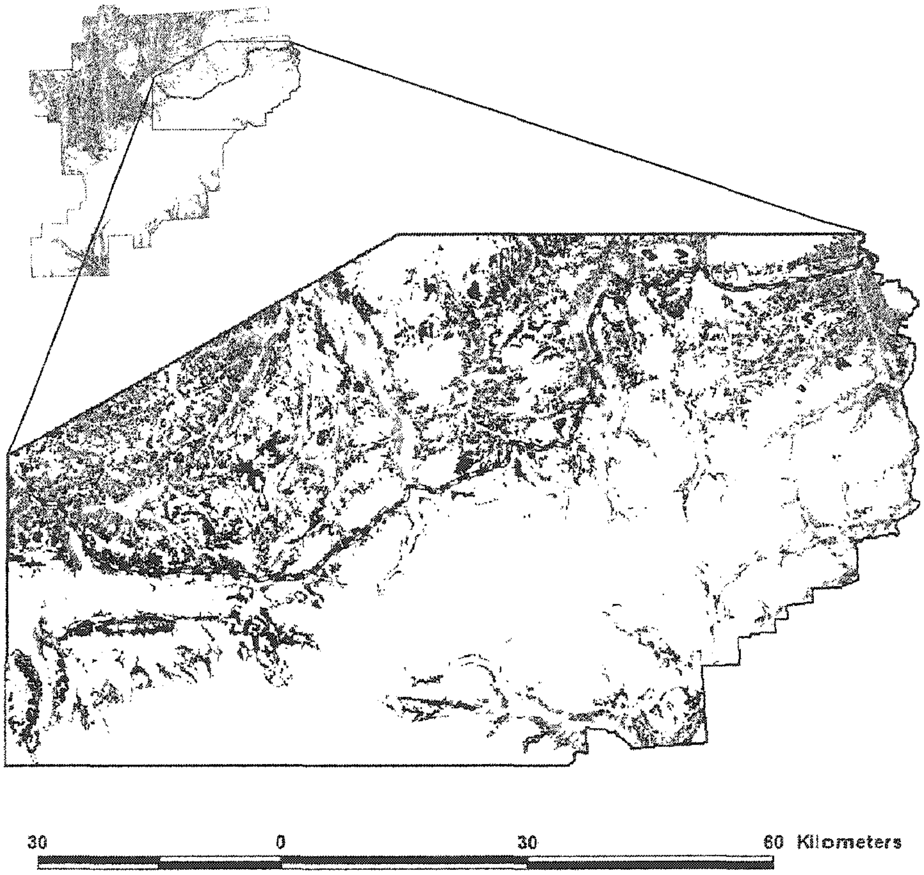


Figure 4.5: Effect of further warming on DNP. We restricted the spatial application of our decision-tree model for DNP to the area where white spruce is the dominant tree species. Total area occupied by boreal forest in 2000 in the box was 784 km^2. Spatial application of our decision-tree model projects treeline advances at higher elevations (black shading), in an area of 801 km^2 (=102% of existing forest) and dieback in areas currently occupied by losers (light gray), amounting to 384 km^2 (49% of existing forest). Taking together these two processes, the forest would expand by about 50% and occupy 1201 km^2. Dark gray shaded areas represent mixed populations of winners and losers, which cannot be modeled using only landscape information.

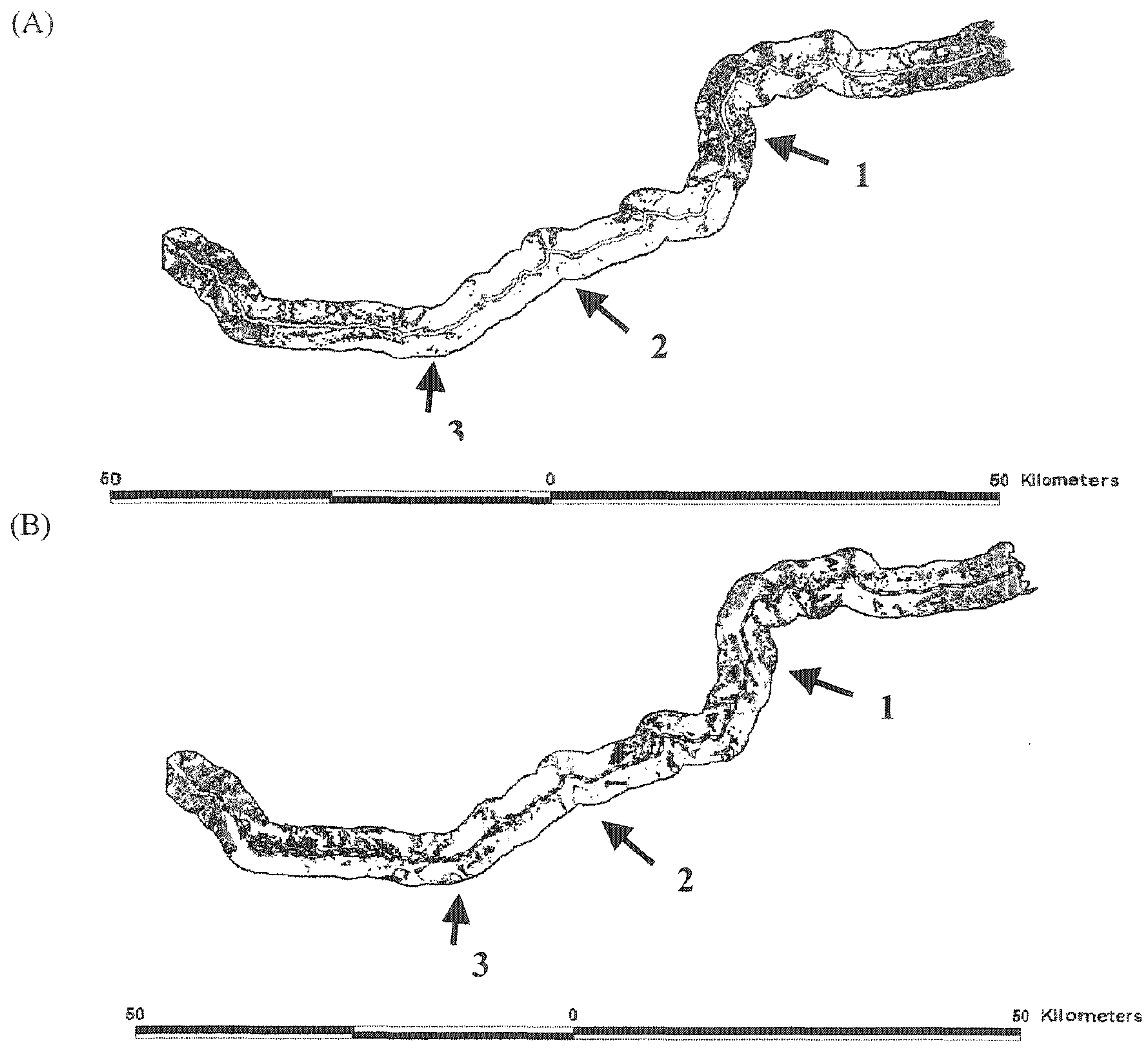


Figure 4.6: Boreal forest distribution in DNP road corridor today and after 21st century climate warming scenarios. In 2000, 21% of the road corridor (187.0 km^2) was classified as boreal forest (National Park Service, 2003; Fig. 4.6A). Using the existing relationship of winners and losers to landscape position, the spatial model for the road corridor (Fig. 4.6B) produces areas of possible forest expansion (black) and dieback (light gray). Areas in light gray represent existing boreal forest, classified as losers and projected to lose all forest cover as a result of climate warming produced by the

scenarios. Areas in medium gray are currently occupied by existing boreal forest classified as mixed winners and losers that would remain in forest cover throughout the scenario period. Areas in black depict all pixels 50 m higher than and adjacent to highest elevation existing forest pixels, representing areas of forest expansion into tundra under further warming similar to climate scenarios. Boreal forest area would increase to 288.6 km^2 and occupy 32.7% of the road corridor. Note that some forest areas, especially along low lying river corridors will experience forest decline (arrow 1). Some tundra areas (arrows 2 and 3) south of the park road (Fig. 4.6B), now prime areas of wildlife viewing, would experience increases in tree density (infilling) and treeline advance leading to reductions in scenic views along the road.

Chapter 5

Closing the circle:

Application of the theoretical model from Chapter 1

and a general summary

Closing the circle - Application of theoretical model:

Let us remember look at Fig. 5.1 (Fig. 1.2.) for a minute. Four ecosystems are on their journey through space and time, their paths controlled by unknown attractors and resulting trajectories. This general concept can be applied to the content of this thesis and vice versa, the results of this thesis can enhance the readability of our figure. Let us replace "Ecosystem 1" with "Mammoth Steppe", an ecosystem prevalent during the last glacial maximum (Walker et al. 2001); since then environmental conditions have changed, and controlling factors (jacks in the figure) have lead to an extinction of this ecosystem type at this place (Fig. 5.2). A threshold effect in time has "stopped" it's trajectory. If we make the space axis more applicable to the northern high latitudes, we see the latitudinal relationship of major biomes: "Boreal Forest", further north "Arctic Tundra" and then "Polar desert", which does not exist in Alaska, in northern Canada. While the "Mammoth Steppe" does not exist any more, our three current ecosystems roll parallel in time, adjusting their position slightly to the spatial change in controlling factors, the resilience of these systems symbolized by their "curvy" trajectory. The

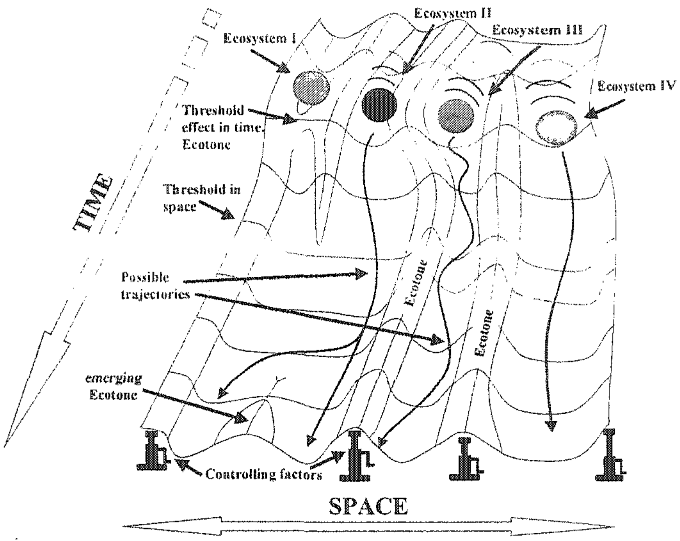


Figure 5.1: Four ecosystems on their journey through time and space, see chapter 1.

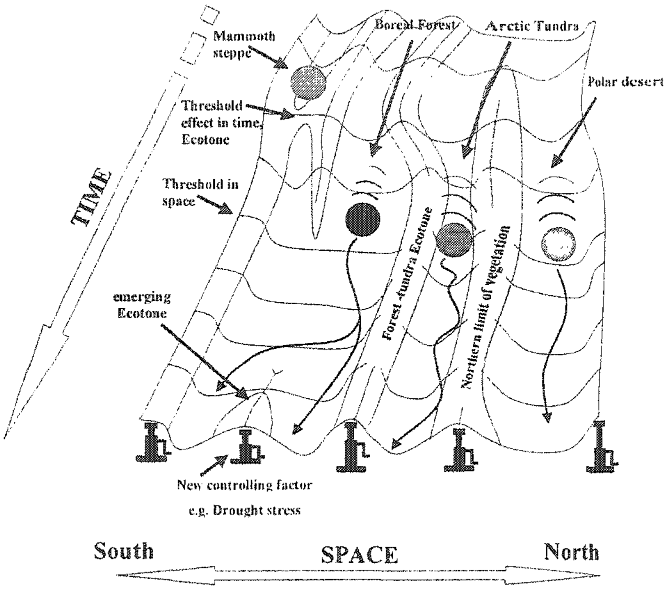


Figure 5.2: Present trajectories of northern high latitude ecosystems.

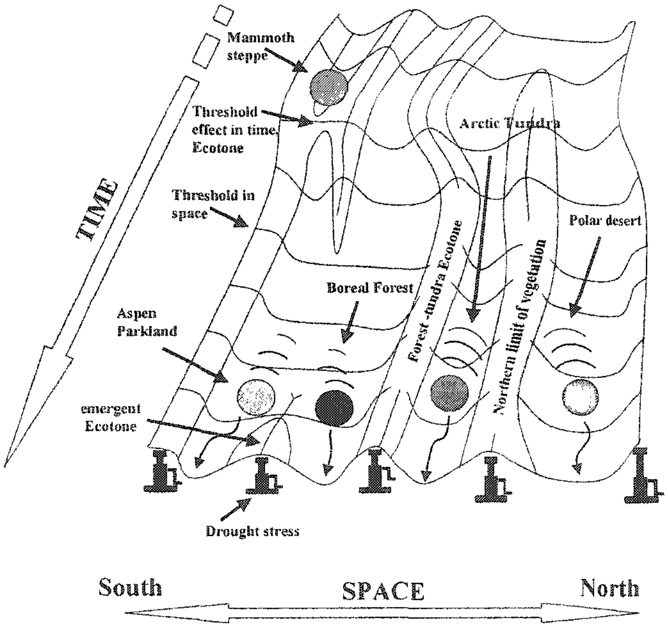


Figure 5.3: New controlling factors lead to an emergent ecotone, which gives rise to a new ecosystem type, Aspen Parkland.

boundaries dividing these ecosystems are the "Forest-tundra ecotone" and the "Northern limit of vegetation".

But a new controlling factor is appearing, "Drought stress" (Jacoby and D'Arrigo, 1995; Barber et al., 2000; Chapter 3 and 4). This controlling factor influences in our case the ecosystem "Boreal Forest". There might be new controlling factors in "Arctic Tundra" as well, e.g. thermokarst and drainage of large areas, but we will restrict our exercise to boreal forest.

The ecosystem "Boreal Forest" will reach a bifurcation, where some areas now occupied by boreal forest will experience the control of drought stress mechanism and switch to a new ecosystem, e.g. "Aspen Parkland" (Fig. 5.3.), now prevalent in the southern extend of the Canadian boreal forest (Hogg and Hurdle, 1995; Barber et al., 2000). In addition, the controlling factor now symbolized by drought stress might also include other factors, which become more prevalent in the future, e.g. a shortening of the fire-return interval.

Therefore, in the future, we might see four ecosystems on this slice of the earth's surface, symbolized by this space-time continuum: "Aspen Parkland" might replace the "Boreal Forest" in the south, which reduces the area of this ecosystem. Only small-scale invasion of "Arctic Tundra" seems likely at the northern edge of the boreal forest in the near future (Rupp et al., 2001, Chapter 4). How "Arctic Tundra" and "Polar desert" will change in the future is also an open question.

This short excursion into general system theory provides a tool to tie results of different studies together to provide an overview. We can use it to highlight a particular characteristic of these environments (e.g. emergent controlling factor). In addition it offers the option to, at least mentally, assess the impacts of change and it offers the possibility to communicate different scenarios and ideas.

General summary and conclusions of this thesis:

The overall significance and contributions of this thesis summarized as follows:

1) The generalized systems model of space-time continua, controlling factors, attractors and trajectories can be applied as a theoretical foundation to ecotone research (Chapter 1 and 5).
2) Rediscovery of a treeline research plot from 1939 in the Brooks Range is of general interest to the arctic scientific community (Chapter 2).
3) Contrary to previous results, white spruce treeline communities in the Alaska Range and Brooks Range display positive **and** negative relationships with climatic indicators (temperature, Chapter 3).
4) Contrary to previous results, these relationships with climatic indicators are not decreasing but increasing in significance in the last decades (Chapter 3).
5) The negative response to increasing temperature is most likely produced by a drought stress mechanism. This mechanism operates at every site in two mountain ranges, it is a widespread phenomenon and, especially under future warming conditions, would be increasingly important (Chapter 3 and 4).
6) Positive and negative responses of tree growth to climate are controlled by temperature thresholds (Chapter 3). Using temperature - growth relationships and projection of future temperature regimes in interior Alaska (five General Circulation Models), elimination of white spruce from some sites is within range of probability during the present century (Chapter 4).

7) Landscape position alone can only partly explain why certain individual trees display positive or negative relationships of growth with climate. Genetic variability and other environmental factors should be considered (Chapter 4).

Based on these results, it seems likely that under future warming conditions changes in white spruce distribution and structure of current forest stands will take place: Treelines will probably advance at some altitudinal tree limits in the Alaska Range and infilling will occur at northern treeline in the Brooks Range. It seems unlikely however that a widespread invasion of trees into arctic tundra will take place in the near future, but some areas (especially around streams and creeks) at northern treeline will increase in stand density and above-ground carbon uptake. Other areas (low-lying areas in the Alaska Range, tree-islands in the Brooks Range) will experience decreases in tree growth. **Any assumption that white spruce growth at treeline will change uniformly in relation to climate is unjustified**, and this changing sensitivity to climate also is an obvious contributor to the error-term in ring-width based reconstruction of past climate. Tree growth at treeline is not only controlled by one environmental factor, but by a combination of many factors acting on varying scales. For example, precipitation varies regionally, effective soil moisture, however, locally. Future research should include hypothesis of which environmental factor operates on what scale and test explicitly of how far extrapolations can be made based on each factor.

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