CLIMATE AND THE AUTUMNAL MOTH (*Epirrita autumnata*) AT MOUNTAIN BIRCH (*Betula pubecens* ssp. *czerepanovii*) TREELINES IN NORTHERN SWEDEN

A Thesis

by

AMANDA BEATRICE YOUNG

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2008

Major Subject: Geography

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Approved by:

Chair of Committee,	David M. Cairns
Committee Members,	Charles Lafon
	Fred Smeins
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ABSTRACT

Climate and the Autumnal Moth (*Epirrita autumnata*) at Mountain Birch (*Betula pubecens* ssp. *czerepanovii*) Treelines in Northern Sweden. (August 2008)

Amanda Beatrice Young, B.A., Gustavus Adolphus College

Chair of Advisory Committee: Dr. David M. Cairns

The main objectives of this investigation were to determine the impact of climate on mountain birch (*Betula pubecens* ssp. *czerepanovii* (Orlova)) growth and to develop a regional chronology of autumnal moth outbreaks. To accomplish the objective, cores of mountain birch were taken from 21 sites in Norrbotten, Sweden. Tree-ring chronologies were developed for each site. Climatic influences were determined by correlating ring widths to climatic variables (average monthly temperature, average monthly precipitation and NAO). Outbreaks were recovered from the ring width indices using the non-host method with Scots pine (*Pinus sylvestris* (L.)) as the non-host. This method removes the climatic influence on growth to enhance other factors. Patterns of synchrony and regional outbreaks were detected using regression and cluster analysis techniques.

The primary climatic influences on the tree ring growth of mountain birch are June and July temperatures; precipitation during October is of secondary importance. Climate explained 46% of yearly tree ring width variation. Outbreaks of the autumnal moth occur at varying time intervals depending on the scale of study. Intervals between outbreaks on the tree level are twice as long as at the plot level. On the regional scale plots within the same valley had more similar outbreak intervals and magnitudes of outbreaks. Elevation is a driver in determining the length of outbreaks and length between outbreaks. The percent monocormicity of a plot is also a determining factor of the length between outbreaks.

This study is the first regional scale study on climate and outbreaks of the autumnal moth on mountain birch. The results complement research being conducted on autumnal moth larval densities and will help in modeling and assessing the effects of outbreaks with increasing climatic change.

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CHAPTER I

INTRODUCTION

Treeline ecosystems are dynamic and subject to changes due to climatic variation as well as non-climatic factors. The treeline of Northern Sweden is primarily composed of mountain birch (*Betula pubecens* ssp. *czerepanovii* (Orlova)), Scots Pine (*Pinus sylvestris* (L.)) and Norway Spruce (*Picea abies* (L.)). Though all of these species can occur at treeline, mountain birch dominates the upper limits. The mountain birch treeline ecosystem are sensitive to variations in climatic variables, primarily temperature, though precipitation and the North Atlantic Oscillation (NAO) also play a role (Dalen & Hofgaard, 2005; Hofgaard, 1997; Kullman, 2002b; Löffler *et al.*, 2004; Moen *et al.*, 2004; Stevens & Fox, 1991; Sveinbjörnsson, 2000; Truong *et al.*, 2007). The classic climatically-induced treeline is one where trees growing at their physiological limit at high altitudes and high latitudes become stunted and form krummholz (Arno & Hammerly, 1984; Ellenberg, 1988; Körner, 1998; Körner & Paulsen, 2004; Sveinbjörnsson, 2000). However this is not the case in Northern Sweden where mountain birch krummholz are rare (Cairns & Moen, 2004).

Mountain birch are susceptible to non-climatic variables such as reindeer (*Rangifer tarandus* (L.)) herbivory and defoliation by cyclical moth outbreaks (*Epirrita autumnata* (Borkhausen)) (Bylund, 1997; Cairns & Moen, 2004; Moen & Danell, 2003; Tenow, 1972; Tenow *et al.*, 2007). The 9-10 year cyclical outbreaks of moths results in

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the establishment of new cohorts of trees and growth releases in the previously established trees (Bylund, 1997; Ruohomäki *et al.*, 2000; Sveinbjörnsson *et al.*, 1996; Tenow, 1972; Tenow & Bylund, 2000; Tenow *et al.*, 2004). Understanding the controls on treeline formation is important in understanding how proposed changes in the climate will affect future treeline dynamics (Tenow, 1972).

In this study, I present a regional-scale dendroecological investigation of climate and non-climatic influences on mountain birch at treeline in Northern Sweden. I use tree cores, climatic records, and records of moth outbreaks to determine the impacts of climate and disturbance on tree growth. Few studies have used dendrochronology to view the influences of climate and moth outbreaks in mountain birch (Eckstein *et al.*, 1991; Karlsson & Weih, 2003; Kirchhefer, 1996; Levanič & Eggertsson, 2008; Sonesson & Hoogesteger, 1983). Many of the studies that have been conducted on mountain birch have been carried out in a small area (Eckstein *et al.*, 1991; Karlsson & Weih, 2003; Kirchhefer, 1996; Levanič & Eggertsson, 2008; Sonesson & Hoogesteger, 1983). This study provides a regional analysis of the influences of climate and moth outbreaks on mountain birch at treeline in Northern Sweden.

SPECIFIC AIMS OF RESEARCH

- Establish a tree-ring chronology for mountain birch and Scots pine
- Detect the climatic signal found in mountain birch and Scots pine on a local and regional level
- Detect and establish an outbreak record of the autumnal moth on a local and regional level

CHAPTER II

LITERATURE REVIEW

TREELINE

Definition

Variations in climate are expected to be expressed more dramatically at high elevation and areas at high latitude. An ecotone that is frequently studied to detect these changes is ‘treeline’. One of the things that makes studying treelines difficult is that it is hard to classify and though the name implies a line of trees, treeline is not a distinct line (Grace 1989; Grace *et al.* 2002; Holtmeier 2003; Sveinbjörnsson 2000; Sveinbjörnsson *et al.* 1996). Usage of the term treeline varies from ‘northern range margins’ as the physiological species limit (Pederson *et al.* 2004), a boundary between upright trees and dwarf (krumholtz) trees (Takahashi *et al.* 2005; Tømmervik *et al.* 2004), and sometimes treeline is associated with a height limit (2m) (Kullman 2005b; Kullman & Kjällgren 2000). Typically treeline is defined as being an ecotone of scattered trees that are between the upright forest and the tundra (Holtmeier 2003; Holtmeier & Broll 2005; Körner 1998; Körner & Paulsen 2004; Macdonald *et al.* 1993; Smith *et al.* 2003; Sveinbjörnsson 2000; Sveinbjörnsson *et al.* 1996). This definition of treeline allows for a gradient of trees from upright to dwarf or even krumholtz up to the point that the vegetation is not dominated by trees (Dalen & Hofgaard 2005; Hofgaard 1997; Tømmervik *et al.* 2004).

The upper limit of treeline is believed to be the result of minimum summer temperature (8-11^{o}C) (Brubaker 1986; Esper & Schweingruber 2004; Körner 1998; Körner & Paulsen 2004; Sveinbjörnsson 2000; Sveinbjörnsson *et al.* 1996). Temperature is a good proxy for treeline distribution in landscape and regional treeline studies, however, finer scale studies should look at additional variables (Holtmeier & Broll 2005). The treeline ecotone is highly heterogeneous and increases in variability at finer the scales (Holtmeier & Broll 2005).

The mountain birch belt of Fennoscandia has a combination of both arctic and alpine characteristics (Sveinbjörnsson *et al.* 1996; Wielgolaski 2001). However, the winters create a characteristically arctic system (Sveinbjörnsson *et al.* 1996; Wielgolaski 2001). The mountain birch treeline is abrupt without a gradual transition between forest and tundra (Cairns & Moen 2004; Moen & Danell 2003).

Types of Treeline

Orographic, anthropogenic, and climatic are the three types of treeline (Holtmeier & Broll 2005). Orographic treelines are controlled by physical factors other than climate: i.e. topography (Butler *et al.* 2007), rock slides (Butler & Walsh 1994), soil conditions (Cairns 2002; Resler 2006), and avalanches (Walsh *et al.* 1994).

Anthropogenic treelines are common worldwide. Anthropogenic treelines are artificially depressed below their climatic limits and are not being restrained by orographic factors. Common causes of anthropogenic treelines are logging and grazing (Hofgaard 1999; Holtmeier & Broll 2005; Löffler 2000; Löffler *et al.* 2004). When anthropogenic treelines are released they increase dramatically upslope towards their climatic potential (Gehrig-Fasel *et al.* 2007; Rapp 1996).

Climatic treelines are primarily a result of low temperature (Körner 1998; Körner & Hoch 2006; Körner & Paulsen 2004; Weih & Karlsson 2001). Treeline is not directly limited by temperature but by its in ability to gain enough carbon in low temperature environments (Smith *et al.* 2003). Temperature is controlled by elevation, wind, moisture and aspect (Holtmeier & Broll 2005). Wind and aspect are controlled by local topography (Holtmeier & Broll 2005). Temperatures fluctuate depending on the slope, aspect and albedo of ground cover (Holtmeier & Broll 2005). There are more factors controlling treeline than just physiological tolerance, local site conditions are important (Holtmeier & Broll 2005; Stevens & Fox 1991).

Advancement of treeline has been documented from the tropics to the arctic due to increased temperatures over the past (Körner 1998; Kullman 2001a, b, 2004, 2005b, 2007; Kullman & Kjällgren 2006; Löffler *et al.* 2004; Luckman & Kavanagh 2000; Rhemtulla *et al.* 2002; Truong *et al.* 2007). However, not all treelines are migrating up slope (Kullman 1989, 1993). Trees are highly adapted to be able to withstand temporary climatic changes in their environment (Arno & Hammerly 1984; Brubaker 1986; Dalen & Hofgaard 2005; Holtmeier 2003; Kullman 1993)

Climate Change in Fennoscandia

Annual increases in mean temperatures due to atmospheric warming are higher in Fennoscandia than the rest of Europe and the Northern Hemisphere (Christensen *et al.* 2007; Moberg *et al.* 2005; Serreze *et al.* 2000). Spring temperatures have increased significantly in Fennoscandia by an average of 0.94^{o}C since the 1900's (Moberg *et al.* 2005). Winter temperatures have increased 0.7^{o}C, however, not significantly (Christensen *et al.* 2007; Moberg *et al.* 2005; Serreze *et al.* 2000). Summer temperatures have increased as well but not by more than half a degree or significantly (Moberg *et al.* 2005). Sweden and Norway have had a 5-20 % increase in precipitation, variability is due to exposure to the westerly winds off the Atlantic Ocean (Moberg *et al.* 2005). Areas exposed to these westerly winds have increased winter and spring precipitation (Moberg *et al.* 2005; Serreze *et al.* 2000). Variability in precipitation is much higher than for temperature (Moberg *et al.* 2005). Future increases in precipitation are expected to come in the form of winter storms at an increased frequency (Christensen *et al.* 2007).

The North Atlantic Oscillation (NAO) is an oscillation in the atmosphere over the Atlantic Ocean, with its poles in Iceland and the Azores (Hurrell *et al.* 2003; Hurrell 1995; Meincke 2002; Rogers 1985; Serreze *et al.* 2000). NAO is a measure of the influence of the Gulf Stream (Westerlies) across the Atlantic (Rogers 1985). When NAO indices are in a positive phase the pressure difference between the Azores and Iceland are high, creating strong Westerlies directed towards northern Europe (Hurrell *et al.* 2003; Hurrell 1995; Hurrell & Dickson 2003; Meincke 2002; Serreze *et al.* 2000). During positive phases winters are warm and wet in northern Europe while southern Europe is hot and dry (Christensen *et al.* 2007; Hurrell *et al.* 2003; Hurrell 1995; Rogers 1985). Negative phases of NAO result in weaker pressure differences between Iceland and the Azores islands resulting in weaker Westerlies which are directed towards southern Europe (Christensen *et al.* 2007; Hurrell *et al.* 2003; Hurrell 1995; Rogers

1985). Negative phases are cooler and wetter than normal in southern Europe and there for dry, cold winters in northern Europe (Hurrell *et al.* 2003; Meincke 2002).

Phases of NAO last for several years in either positive or negative phases. The most recent negative phase lasted from the 1940's to the 1970's, since the 1970's a positive phases with indices higher than previously recorded (Hurrell 1995; Hurrell & Dickson 2003). Departures in NAO values parallel departures in temperature (Hurrell 1995; Hurrell & Dickson 2003; Rogers 1985). The correlation between NAO indices and temperature are well documented by Rogers (1985), Hurrell (1995, 2003), Chen and Hellström (1999). Correlations between NAO and temperatures in northern Sweden are highest from May-August (Chen & Hellström 1999). NAO indices explain 21% of temperature variation in Sweden (Chen and Hellström 1999), while it accounts for 31% of wintertime temperature variance (Hurrell *et al.* 2003). The mildest winters during the last 250 years have occurred during the winters of 1988-89 and the 1930's, corresponding to periods of positive NAO phases (Moberg *et al.* 2005). The influence of NAO decreases with increased latitude and in an easterly direction due to reduced influence by the westerly winds (Chen & Hellström 1999).

Climate and Treeline

Recent climate change scenarios show that the most drastic climate changes will likely occur in the arctic and in mountainous environments. Moen et al. (2004) modeled three scenarios of the effects of increased temperature on the treeline position in northern Sweden. With a temperature increases of 1.4-4 ^{o}C the three models used in this study showed a rise of treeline of 233-667 m at a rate of 100m for every increase of 0.6 ^{o}C (Moen *et al.* 2004).

Treeline ecotones occur at the boundaries of adjacent vegetation types are considered to be potentially good monitoring locations for the effects of climate change on vegetation (Holtmeier 2003; Holtmeier & Broll 2005; Körner 1998; Kullman 1998). With increasing temperatures treelines that are not orographically or anthropogenically controlled will migrate upslope. Trees in a stunted or krumholtz state produce leader stems and the viability of seeds will increase after numerous seasons of warm temperatures (Holtmeier & Broll 2005). The regeneration and infilling by seedlings at treeline is potentially a better indicator of climate change than radial growth for seedlings are more susceptible to change that trees (Daniels & Veblen 2004; Smith *et al.* 2003).

MOUNTAIN BIRCH

Distribution

Mountain birch is found in Fennoscandinavia, Iceland, and the Kola Peninsula, Russia (Väre 2001). In northern Sweden mountain birch composes the treeline from 600-950 m.a.s.l. (Kullman 1979, 2005a). The treeline decreases in elevation with increased latitude as well as from continental to maritime environments (Kullman 2005a; Väre 2001).

Growth Forms

There are two growth forms of mountain birch: monocormic (single stemmed) and polycormic (multiple stems). The level of polycormicity a tree has is attributed to its hybridization between *B. pubescens* and *B. nana* (Väre 2001). Polycormic trees are known to grow on poorer nutrient sites dominated by heaths (Tenow 1972). Mountain birch forests are composed of scattered islands of trees and this pattern is consistent up to the treeline where the density of islands decreases (Sveinbjörnsson 2001). Monocormic trees are found in meadow habitats that have higher pH levels and precipitation than heaths (Tenow 1972; Wielgolaski & Nilsen 2001). Polycormic trees are found in more continental environments than more costal and maritime environments where monocormic trees are found (Oksanen *et al.* 1995)

A study of forest structure at Abisko has shown that the forests in that region are composed of 79% polycormic trees (Bylund & Nordell 2001). This study also demonstrated that polycormic trees had larger stems and were taller than monocormic trees (Bylund & Nordell 2001). Similar studies in the area showed there was no statistical difference between monocormic and polycormic stems in relation to size (Oksanen *et al.* 1995; Sonesson & Hoogesteger 1983).

Potential Effects of Climate Change on Mountain Birch

The growing season in temperate and cold climates corresponds to photoperiods and thermoperiods (Larcher 2003). Transition into a dormant state is more influenced by photoperiod than by temperature (Skre *et al.* 2008). During this transitional state leaf buds for the next years growth develop (Larcher 2003). Temperature influences the development of the buds and timing of spring budburst (Skre *et al.* 2008). Once in a dormant state the cambium becomes hardened and resistant to frost and dehydration (Larcher 2003). Dormancy is a state in which the plants can survive below 5^{o}C and not respond to temporary warming (Karlsson *et al.* 2007; Larcher 2003). Woody plants must endure a certain length of chilling before they can exit dormancy (Myking & Heide 1995). Chilling is a period of time with temperatures below which any growth can occur (Myking & Heide 1995). This period of chilling can exist beyond the required period before the plant is triggered to activate by increased temperatures (Heide 2003; Larcher 2003; Myking & Heide 1995).

Winter temperatures play a significant role in the ability of mountain birch to achieve their chilling requirements. If winter temperatures rise and trees are not able to chill for long enough periods and bud break maybe delayed thus reducing the growing season (Myking & Heide 1995). This may also occur if pre-dormant temperatures are high delaying the onset of dormancy and budburst (Heide 2003; Skre *et al.* 2008). Alternatively, and more likely in the case in Scandinavia, warmer winters will still be below the chilling requirement but they will be closer to reactivation temperatures in the spring allowing bud break to occur earlier thereby extending the growing season (Myking & Heide 1995). Chilling requirements decrease with increased latitude, increased elevation and with increased continentality (Myking & Heide 1995; Skre *et al.* 2008; Taulavuori *et al.* 2004).

Bud break is entirely related to spring temperatures once dormancy has been broken (Myking & Heide 1995). May temperatures are particularly important (Karlsson *et al.* 2003). Earlier budburst will lengthen the growing season, but will also increase the potential for frost injury (Myking & Heide 1995; Skre *et al.* 2008; Taulavuori *et al.* 2004). Snow storms in early and late spring have a high mortality rate on leaves and can reduce carbon intake by 90% (Sveinbjörnsson *et al.* 1996). Additional reduction in growth may come from a decreased carbon balance due to the high levels of respiration at warm temperatures, while low levels of photosynthesis occurs during the shortened photoperiods of spring (Skre *et al.* 2008). Serreze et al. (2000) argue that early bud break will increase the annual photosynthetic activity in northern latitudes by 10-12%.

Saplings of mountain birch treated with warmer winter minimum temperatures came out of dormancy earlier and went straight into budburst compared to saplings treated with cold temperatures that came out of dormancy but did not proceed to outbreaks immediately (Skre *et al.* 2005). This is potentially an adaptation to prevent bursting too early and being effected by frost (Skre *et al.* 2005).

Currently bud break occurs around the middle of June when solar irradiance is highest (Holmgren *et al.* 1996). In the Abisko region the growing season lasts from 75-80 days of full foliage in the continuous forest and decreases by up to 10 days at treeline (Sveinbjörnsson *et al.* 1996). Budburst has been modeled to increase by 3-8 days per degree change in the average temperature (Karlsson *et al.* 2003). An increase of 1^{o}C has the potential to raise the treeline by 200m in the Abisko region (Holmgren & Tjus 1996). However it has only been observed to have increased by 20-50 m (Holmgren & Tjus 1996). The optimal late summer temperature for mountain birch in Abisko is 11^{o}C (Sveinbjörnsson *et al.* 1996). With increased temperatures it has been hypothesized that the treeline will infill becoming denser and the expansion of mountain birches will be on leeward sides of mountains sheltered from the wind (Kullman 2005a).

Nitrogen is a limiting nutrient at treeline and increases with lower latitudes and elevations (Sveinbjörnsson *et al.* 1992). Soil temperatures are a limiting factor in the mineralization of nitrogen into a state the mountain birch can absorb (Sveinbjörnsson *et al.* 1992). With increasing temperatures and the lengthening of growing season, soil temperatures will rise and nitrogen mineralization will increase resulting in increased growth (Sveinbjörnsson *et al.* 1992). Growth of mountain birch under elevated temperature regimes has shown a tripling in growth compared to current temperatures (Kellomäki & Kolström 1994).

Mountain birch is responsive to short-term climatic changes. Reports of a retrogressive treeline occurred from 1980 to 1990 after the effects of the cooling period of the 1940-1970's were noticed in tree populations (Kullman 1989; Kullman & Hogberg 1989). With increasing temperatures since the 1980's noticeable tree growth and range expansion have been noted (Kullman 1993, 2001a, 2002, 2003). The birch treeline occurs higher on south and southwestern slopes than on north-facing slopes (Kjällgren & Kullman 1998; Kullman 1979, 1989, 1993; Kullman & Hogberg 1989; Sonesson & Hoogesteger 1983; Sveinbjörnsson 2001; Sveinbjörnsson *et al.* 1996). Temperatures fluctuate, however, so the potential treeline changes over time (Kullman 1976, Aas 2001).

Disturbance

Non-climatic factors play a role on treeline dynamics by killing and stimulating portions of the forest naturally (e.g. insect outbreaks) and through anthropogenically-mediated processes (e.g. stock grazing and logging). The two primary non-climatic forces in the northern Sweden are the natural cyclical outbreaks of the autumnal moth and browsing of semi-domestic reindeer. The cyclical outbreaks of autumnal moths can change the distributions of the forest by killing large portions of the forest (Bylund 1997; Klemola *et al.* 2003; Klemola *et al.* 2006; Tenow 1972, 1975, 1996; Tenow & Bylund 2000; Tenow *et al.* 2004; Tenow *et al.* 2007). Additionally, herbivory by reindeer potentially keeps the treeline from developing to its climatic potential (Cairns & Moen 2004; Herder *et al.* 2004; Holtmeier *et al.* 2003; Kullman 2005c; Lehtonen & Heikkinen 1995; Moen & Danell 2003; Olofsson & Oksanen 2005; Olofsson *et al.* 2004; Tenow 1996).

Other insect defoliators of the mountain birch are the winter moth, leaf miners and saw flies (Tenow 1972, 1996). The winter moth (*Operophtera brumata* (L.)) is sympatric with the autumnal moth and behaves similarly though occurs in more maritime climates (Tenow 1975). Its main host is the mountain birch (Tenow 1975).

AUTUMNAL MOTH

Distribution

The autumnal moth (*Epirrita autumnata* (Borkhausen)) is a hemi-polar (Northern/Western Hemisphere) species found commonly in Scandinavia and occasionally in Canada. Autumnal moths are commonly found throughout the Scandes, though they only reach outbreak levels in the northern mountains (Bylund 1997; Ruohomäki *et al.* 2000; Ruohomäki *et al.* 1997; Tenow 1972, 1975; Tenow *et al.* 2004). Outbreaks in Northern Sweden occur every 9-10 years and last for two to four years (Hoogesteger & Karlsson 1992; Klemola *et al.* 2006; Ruohomäki *et al.* 2000; Tenow

1972, 1975; Tenow & Bylund 2000; Tenow *et al.* 2004). Whether these cyclical outbreaks occur locally or regionally is still not well understood (Bylund 1997; Ruohomäki *et al.* 2000; Ruohomäki *et al.* 1997; Tenow & Bylund 2000; Tenow *et al.* 2007).

Life History

The life of the autumnal moth starts in the fall when the adult moths fly and mate. The female lays up to 240 eggs in cracks and lichens on the stems of mountain birch (Bylund 1997; Ruohomäki *et al.* 1997; Tenow 1972). The eggs hatch in the spring at bud break (Tenow 1972). Larvae feast on the leaves of the mountain birch for about a month before pupating at the base of trees in the duff and litter (Tenow 1972). They reemerge in the fall to start the cycle over again. Each individual only persists for one year (Tenow 1972). The eggs of autumnal moth are sensitive to winter temperatures below -36°C (Nilssen & Tenow 1990). Outbreaks have been reported to occur more intensely in older stands (Bylund 1997; Ruohomäki *et al.* 1997).

Outbreaks

Defoliation reduces the amount of photosynthetic area a tree has to fulfill its carbohydrate needs and thus reduces radial growth (Brubaker 1978; Fritts 1976; Kulman 1971; Swetnam & Lynch 1989). In addition to reducing the radial growth, extensive outbreaks can also kill off large portions of the forest. Forests at treeline can be depressed from their climatic potential by moth outbreaks (Nuorteva 1963). Outbreaks do not occur at low elevations nor at low latitudes due to higher numbers of parasitic ants and wasps which cannot survive in the cooler temperatures of higher elevations (Nuorteva 1963).

Outbreaks of the autumnal moth have been reported to occur in both monocormic and polycormic stands of mountain birch throughout the Scandes and into Northern Finland and the Kola Peninsula (Bylund 1997; Nuorteva 1963; Sonesson & Hoogesteger 1983; Tenow 1972, 1996; Tenow *et al.* 2004). Outbreaks do not occur across the entire landscape. They are patchy attacking one stand at a time with an interval of 9-12 years between landscape outbreaks (Bylund 1997; Klemola *et al.* 2006; Ruohomäki *et al.* 2000; Tenow 1972, 1996; Tenow *et al.* 2007).

Occurance of Outbreaks

Three types of outbreaks patterns have been proposed for the autumnal moth: synchrony (simultaneous outbreaks), moving outbreaks (one region to the next in a wave), and diffuse outbreaks (random outbreaks with no pattern) (Tenow 1972). Fifteen outbreaks have been recorded by Tenow (1972) and Nilssen et al (2007) through an analysis of historic documents, outbreaks have probably been occurring for much longer. Eight of the historic outbreaks have been synchronous, four have had a distinct wave pattern from north to south, one has been diffuse and the earliest two outbreaks are from limited records and the outbreak type is inconclusive (Nilssen *et al.* 2007; Tenow 1972). Synchronous outbreaks have occurred more commonly throughout the historical record however wave and diffuse outbreaks do also occur.

During the last forty years, outbreaks across Fennoscandia have appeared regionally synchronous in local waves occurring within 3-4 years across the region at intervals of 9-13 years (Klemola *et al.* 2006). Outbreaks appeared to occur in waves from the northeast/ east to southwest/west (Klemola *et al.* 2006) although some outbreaks have proceeded in the opposite direction (Nilssen *et al.* 2007; Tenow 1972). Synchrony of outbreaks is strongest along the east side of the Scandes from 65-67^{o}N (Klemola *et al.* 2006). It has been reported that increases of larvae densities occur synchronously up to distances of 60 km (Tenow *et al.* 2007), however; another study showed that synchrony of larvae densities occurred up to 700 km (Klemola *et al.* 2006). Synchrony among outbreaks decreases with distance (Klemola *et al.* 2006; Tenow *et al.* 2007; Williams & Liebhold 2000).

Distribution of Outbreaks

Outbreaks have primarily been found in older stands of mountain birch (Bylund 1997; Ruohomäki *et al.* 1997; Tenow 1972). Females prefer to lay their eggs on lichens and in cracks that are present on older stems (Bylund 1997). Apical buds may be more easily disturbed by the autumnal moth on older trees inducing new leaves to develop that are more nutritious (Ruohomäki *et al.* 2000; Ruohomäki *et al.* 1997). Trees that were able to establish lichen communities in the Abisko region were 15 to 32 years old (Sonesson 2001). However, it has also been reported that females are poor fliers and unselective about where they lay their eggs (Ruohomäki *et al.* 1997; Tammaru *et al.* 2001). Eggs have been noticed on non-host species that are unsuitable to the larva when it hatches in the spring (Ruohomäki *et al.* 1997). Ruohomaki (1997) proposes that although eggs are laid indiscriminately, they do have a higher likelihood to survive when they are in protected locations such as in lichens and cracks in the bark. It is also suggested that eggs that over winter beneath the snow pack are protected from severe winter temperatures and have a better likelihood of survival (Ruohomäki *et al.* 1997).

Older birch stands grow at a slower rate than young trees and produce fewer apical spouts (Ruohomäki *et al.* 1997). The reduced growth rates found in older trees allows for more nutrients in the leaves that are produced (Bylund 1997; Ruohomäki *et al.* 1997). Larvae of the autumnal moth prefer eating the young leaves and buds of the mountain birch (Klemola *et al.* 2008; Klemola *et al.* 2004; Ruuhola *et al.* 2008; Ruusila *et al.* 2005; Tenow 1972). If the larvae eat the buds of these mature trees, further canopy growth is stopped for one to two years because buds develop a year before they emerge (Larcher 2003; Skre *et al.* 2005; Skre *et al.* 2008). When this happen, the tree then puts more energy towards photosynthesizing which adds nutrients to the remaining leaves (Ruohomäki *et al.* 1997).

Another proposed reason that outbreaks occur in mature stands of mountain birch is due to reproduction. Mature trees invest more resources into reproducing during masts which, reduces leaf quality during these periods (Selås *et al.* 2001). Selås (2001) found that older trees' outbreaks occurred between large masting events. The moths reached outbreak levels after a mast, when leaves were the most nutritious, and before another masting event began (Selås *et al.* 2001).

Local climate affected by topography and edaphic conditions plays a role in the location of outbreaks. An intensive study on the topographic dependence of outbreaks was conducted in the Abisko valley by Tenow (1975). The study found that a strong local control of outbreaks were local topography and zones of temperature inversion.

Within inversion layers (along streams and lakes) temperatures were low enough to kill over wintering eggs. Additionally, the forest limit not defoliated in most areas along the Abisko valley even where the stands were mature (Tenow 1975).

The density of eggs laid per females during outbreaks is half the density seen during low levels of moths (Klemola *et al.* 2008). Additionally, body size decreases with increased densities (Kaitaniemi *et al.* 1999; Klemola *et al.* 2008).

Indirect Controls of Outbreaks

Ruohomaki et al. (2000) suggest that outbreaks are linked with the last 3-4 years of the sunspot cycle. The first outbreak that was predicted to occur after this publication was for 2003, though the location could not be predicted (Ruohomäki *et al.* 2000). There have been reports of outbreaks occurring throughout Fennoscandia in 2003 including northern Sweden (personal observation David Cairns – Texas A&M University and Jon Moen – Umeå University) and northern Norway (Klemola *et al.* 2008). Populations in northern Norway over the past 40 years seemed to be in line with the solar cycles (Selås *et al.* 2004). If the solar cycles were controlling outbreaks, they should occur synchronously and not in waves (Nilssen *et al.* 2007). Nilssen et al (2007) noticed in their data set that outbreaks shifted from being in to out of phase with the sunspot cycles over a 110 year period.

Limitations

The autumnal moth does not reach outbreak levels in southern Scandinavia or in the maritime climates of Norway, but it does in the Scandes. Why outbreaks reach outbreak status in the Scandes is still a mystery, but some potential agents of outbreak control have been ruled out. Biotic factors that control outbreaks are predicted to increase in response to the number of moths, if these biotic controls do not increase with moth populations they cannot control the cyclical behavior of outbreaks (Ruohomäki *et al.* 2000; Tammaru *et al.* 2001). There are reports of low level parasitism and predation from birds, mammals, and insects. There are seven types of larvae and three types of pupae, all hymenptera that parasite on autumnal moths (Ruohomäki *et al.* 2000). During the 2002-2003 outbreak in northern Norway, parasitism was found in all stages of moth development (Klemola *et al.* 2008; Tenow 1972). Though parasites are known, it is unclear how they effect the growth and development of moths (Klemola *et al.* 2008). Passerine birds prey on adult female autumnal moths and may consume between 20-30% of the population (Tammaru *et al.* 2001). There is some evidence that voles and lemmings will eat the pupae, however this is not well documented (Neuvonen 1988). Wood ants are one of the more active predators of the autumnal moth (Punttila *et al.* 2004; Ruohomäki *et al.* 2000; Tammaru *et al.* 2001). Ants protect trees from larvae and adult autumnal moths (Punttila *et al.* 2004; Tammaru *et al.* 2001). However, because there are stable populations of wood ants from year to year they probably do not control outbreaks (Punttila *et al.* 2004; Tammaru *et al.* 2001). The ants are, however, potentially one of the evolutionary drivers explaining why the autumnal moth flies in the autumn (Tammaru *et al.* 2001). They fly after the ants behavior starts to slow down for the winter, prolonging the livelihood of adult moths and the eggs that are laid (Tammaru *et al.* 2001). Pupae predation is lower in the north than in the south due to there being fewer ant colonies (Ruohomäki *et al.* 2000)

Influence of Current and Future Climate

The relationship between climate and moth populations is starting to be understood. Autumnal moths are highly plastic with regard to their thermal environment though not linear (Yang *et al.* 2007). Hatching occurs around midsummer when bud break of mountain birch occurs (Ruohomäki *et al.* 2000). Hatching too much earlier could be detrimental due to a lack of spring leaves to eat (Ruohomäki *et al.* 2000). The survival rate of early hatched larvae is higher during cool temperatures than during warmer periods (Yang *et al.* 2007). If they hatch too late, the foliage has matured beyond the requirements for young caterpillars (Ruohomäki *et al.* 2000). Delayed hatching also increases the rate of predation and parasitism (Ruohomäki *et al.* 2000).

Warmer winters do not affect the survival of mountain birches, although it does affect the survival of autumnal moth eggs. Eggs cannot survive temperatures below -36 ^{o}C during midwinter or below -29 ^{o}C, while the eggs are coming out of dormancy (Nilssen & Tenow 1990; Ruohomäki *et al.* 1997). In years after temperatures below -36 ^{o}C no outbreaks can occur due to the high egg mortality (Ruohomäki *et al.* 2000). Freezing temperatures that produce a high mortality rate, potentially occur synchronously across a region thereby resulting in a synchrony of populations across the region (Ruohomäki *et al.* 2000; Tenow & Bylund 1989).

Cold temperatures are frequently controlled by local topographic variation (Tenow 1975, 1996; Tenow & Bylund 1989). Valleys with lakes and streams cause temperature inversions creating lakes of cold air that are below the lethal limit for autumnal moths (Kallio & Lehtonen 1973; Ruohomäki *et al.* 2000; Tenow 1975).

Warm spring temperatures may allow eggs to hatch earlier (Karlsson *et al.* 2003). Hatching before budburst induces ballooning in search for food (Bylund 1997). Development of larvae is twice as fast at 45 ^{o}C than at 12 ^{o}C (Yang *et al.* 2007). The survival rate of larvae is highest between 10-20 ^{o}C and lowest at 5 ^{o}C or above 25 ^{o}C (Yang *et al.* 2007). Warm summer temperatures will allow the moths predators to survive and increase their populations thereby reducing moth populations (Jepsen *et al.* 2008; Klemola *et al.* 2002; Neuvonen & Wielgolaski 2005; Ruohomäki *et al.* 2000; Tammaru *et al.* 2001).

Outbreaks of the autumnal moth tend to occur after warm winters and cool spring/summers (Niemela *et al.* 2001; Nilssen & Tenow 1990; Yang *et al.* 2007). Yang et al. (2007) found that survival rates of both larvae and adults decreased with increased temperatures. Eckstien (1991) however found that birch grows best during warm winters and during warm summers.

Over an elevational gradient autumnal moths are able to match the phenology of the mountain birch and hatch during bud break (Mjaaseth *et al.* 2005). This does not mean that if bud break were to occur earlier than normal due to climatic change they would also be able to match bud break. Hatching of the eggs is highly dependent on temperature accumulation, which may or may not occur simultaneously with bud break (Karlsson et al 2003). Early snowfall in the fall can cause high mortality in moth populations by freezing pupae and adults (Mjaaseth *et al.* 2005).

Egg mortality is normally due to winter temperatures (Klemola *et al.* 2006). Survival is partially dependent upon low spring and summer temperatures (Klemola *et* *al.* 2006). During the most recent outbreak (1999-2006) occurrences of the winter moth were seen the year after the autumnal moth population peaked in 2003 (Klemola *et al.* 2008). This was the first recorded outbreak of the winter moth in the region (Klemola *et al.* 2008). The winter moth is a more maritime species that survives best in warmer climates than the autumnal moth (Tenow 1972; Tenow *et al.* 2007). The appearance of the winter moth is potentially due to increased temperatures (Klemola *et al.* 2008). During the outbreak temperatures in northern Norway the temperature never dropped below -36°C (Jepsen *et al.* 2008).

Increased temperatures may allow outbreaks of the winter moth to reach outbreak levels throughout Fennoscandia (Tenow *et al.* 2001). Additionally, increased minimum winter temperatures could raise the risk of defoliation (Neuvonen & Wielgolaski 2005).

Interactions with Mountain Birch

Monocormic and polycormic birches are not equally susceptible to outbreaks of the autumnal moth. In northern Finland during the 1964 outbreak it was recorded that 77% of the monocormic trees (n =3044 trees) were defoliated compared to the 45% of polycormic trees (n =11,756 trees) (Kallio & Lehtonen 1973). Outbreaks in monocormic stands are typically detrimental (Kallio & Lehtonen 1973; Tenow 1996; Tenow *et al.* 2001). Only 10% of the monocormic trees were reported to have made a recovery compared to 50% in the polycormic trees (Kallio & Lehtonen 1973). Polycormic stands respond to outbreaks by sending up basal sprouts (Kallio & Lehtonen 1973; Tenow & Bylund 1989; Tenow *et al.* 2001). The main stem may die but the individual tree will still be present. It has been proposed that the autumnal moth is selecting towards a more polycormic growth form of mountain birch (Kallio & Lehtonen 1973).

Similar to the 1964 outbreak in Ustiski, in 1955 an intense outbreak occurred at Abisko in Northern Sweden. This outbreak has been the most intensely studied outbreak of autumnal moths to date. The outbreak occurred across the entire valley, though there are a few areas that escaped (Tenow 1975). During 1955 alone 80-90% of the leaf carrying shoots died (Tenow 1975). Starvation triggered the larvae to descend from the mountain birch and defoliated the ground vegetation changing the entire composition of the ecosystem (Tenow 1975).

The impacts of an outbreak can be seen for many years after an attack due to dead standing stems on the landscape; however the impacts can last much longer. In northern Finland the 1964 outbreak in the Utsjoki region depressed the forest up to a kilometer due to the mass die off of trees during the outbreak (Kallio & Lehtonen 1973; Lehtonen 1987). In polycormic stands after severe outbreaks, the dead crowns will be found standing in a cluster of young sprouts (Tenow 1972, 1975; Tenow & Bylund 1989). Tenow (1972, 1975, 1989) reports that outbreaks have been documented to occur across the entire slope, in a belt, leaving the treeline and valley bottoms unscathed. After severe outbreaks the extent of decimated stands can be mapped years latter due to the time it takes to recover. Mountain birch forest needs at least 70 years to reestablish (Bylund 1997; Tenow & Bylund 2000).

The humid environment in Fennoscandia and the wood morphology on mountain birch makes it susceptible to rot. Both monocormic and polycormic trees are susceptible to this rot. After an outbreak the dead main stem can be a vector for rot that will eventually kill the tree. The rot initially will reduce the recovery often an outbreak by limiting the number of shoots a tree can produce and it will likely kill the tree in the end (Karlsson *et al.* 2005; Lehtonen 1987).

Since seed production at high elevations is poor, disturbances by moth outbreaks that triggers basal sprouts keeps the forest alive (Kullman 1995; Kullman 2003; Sveinbjörnsson *et al.* 1996; Tenow & Bylund 2000).

Like most host plants, mountain birch produces a set of delayed inducible resistance (DIR) in response to herbivory. These responses can range from producing toxins that inhibit consumption to just altering composition so that it is unappealing to insects (Ruohomäki *et al.* 1996). Defoliation must reach a certain level before DIRs become active (Bylund 1997). A DIR can occur within 12 hours of an outbreak (Yang *et al.* 2007). DIR increases innately at high temperatures, while defoliation at cool temperatures reduces quantities of DIR produced (Yang *et al.* 2007). DIR of previously damage trees do not stop larvae during their last instar (Yang *et al.* 2007).

Mountain birch leaves have a set of varying chemical compositions that they produces throughout their lives (Ruusila *et al.* 2005). This variation keeps the moth from just adapting to one type of DIR, and it must keep adapting throughout its life (Ruusila *et al.* 2005). The role that DIR plays in controlling outbreaks is unclear, though it is unlikely that they are controllers of regional outbreaks (Ruohomäki *et al.* 2000). Outbreaks during cool temperatures could benefit the moth by keeping levels of DIR down and increasing the quality of the food (Yang *et al.* 2007).

Due to the reduction of carbon and nutrients trees have stored after defoliation, there maybe a delay in budburst the following year (Neuvonen *et al.* 2001). Though delayed, the trees will produce leaves the year after an outbreak although this comes as a cost to radial growth (Kaitaniemi *et al.* 1999). This crop of leaves is high in DIR making them poor food for the autumnal moth even though they have higher concentrations of nitrogen than non-defoliated trees (Haukioja 1979).

There are relatively few studies that mention the effects of moth outbreaks on treelines. During the 1955 outbreak of the Abisko valley, Tenow (1975) mentioned that the treeline was spared from outbreaks along with the valley bottoms. Outbreaks occurring at treeline often have poor re-growth due to the extreme climatic conditions in which they live (Tenow 1972). In contrast, Haukioja (1979) suggests that trees growing at treeline can respond to outbreaks quicker since they have a higher belowground/aboveground biomass ratio. The 1965 outbreak near Kevo, Finland was highest at mid elevations. Growth limitations in mountain birch at high elevations can not be attributed to low levels of nitrogen; higher concentrations of nitrogen occur at treeline than within the forest (Sveinbjörnsson *et al.* 1996; Sveinbjörnsson *et al.* 1992).

With increasing temperatures there is a potential for increased intensities of outbreaks and an increased recovery time (Neuvonen *et al.* 2001; Neuvonen & Wielgolaski 2005). New insects (e.g. winter moth) may expand their distributions with increased temperatures (Neuvonen *et al.* 2001; Tenow 1996; Tenow *et al.* 2007).

DENDROCHRONOLOGY

Dendrochronology is the study of time through trees. The process of conducting dendrochronological research is based on observing, measuring and comparing tree rings from one sample to another. Dendrochronology has been used to study archeological ruins, hydrology, climate, and disturbance patterns. Physical disturbances to trees can be seen through scars and reduced ring widths. The primary types of physical disturbance are: fire (Margolis *et al.* 2007; Pohl *et al.* 2006; Swetnam *et al.* 1999), ice storms (Lafon & Speer 2002), wind (Frelich & Lorimer 1991), and herbivory (e.g. mammalian (Boudreau *et al.* 2003; McLaren & Peterson 1994; Payette 1986); insects (Brubaker 1978; Swetnam & Lynch 1989). Variations in the local environment can also be detected by comparing the measured ring widths to time series of climatic variables (temperature, precipitation, or drought) (Linderholm 2001; Lindholm *et al.* 2000; Macias *et al.* 2004).

Studies on Treeline

Trees at their physiological limit have a stronger radial response fluctuation in growth due to changes in climate (especially temperature) than do trees at lower elevations and latitudes (Briffa *et al.* 1990; Brubaker 1986; Eckstein *et al.* 1991; Fritts 1976; Gunnarson & Linderholm 2002; Helama *et al.* 2004; Kirchhefer 2001; Linderholm 2002; Pederson *et al.* 2004). Another factor that amplifies the climatic signal is a lack of competition for resources with other trees at the treeline since they are more widely spread out (Lindholm & Eronen 2000).

Detection of Outbreaks

Insect outbreaks can be detected by using dendrochronological techniques. Some of the major studies in defoliating insects have been conducted on the Douglas fir tussock moth (*Orgyia vetusta* (Boisduval)) (Brubaker 1978), false hemlock looper (*Nepytia freemanii* (Munroe)) (Alfaro & Macdonald 1988), larch budmoth (*Zeiraphera diniana* (Guenée)) (Esper *et al.* 2007), spruce budworm (*Choristoneura fumiferana* (Clemens)) (Filion *et al.* 1998; Fraver *et al.* 2007), western spruce budworm (*Choristoneura occidentalis* (Freeman)) (Campbell *et al.* 2006; Ryerson *et al.* 2003; Swetnam & Lynch 1989), two-year cycle spruce budworm (*Choristoneura biennis* (Freeman)) (Zhang & Alfaro 2002), forest tent caterpillars (*Malacosoma disstria* (Hübner)) (Cooke & Roland 2007) and the Pandora moth (*Coloradia Pandora* (Blake)) (Pohl *et al.* 2006; Speer *et al.* 2001).

In order to detect the outbreaks, knowledge of the insect's life history is important to help identify the signal left in the wood by defoliation (Brubaker 1978; Zhang & Alfaro 2002). To find this signal it is useful to compare ring widths from known outbreak periods (Speer *et al.* 2001). This signal is not always apparent in the raw ring width index (Ryerson *et al.* 2003). In order to enhance the outbreak signal one can use a non-host species to eliminate the climatic variation frequency, which helps distinguishes the outbreak frequency in the ring width indices (Brubaker 1978; Campbell *et al.* 2006; Swetnam & Lynch 1989; Swetnam *et al.* 1995). Low severity outbreaks can be overlooked in analysis due to the low level of defoliation they caused to the tree.

Outbreaks under 50% defoliation are not distinguishable from noise in the tree ring width indices (Brubaker 1978; Hoogesteger & Karlsson 1992).

Studies in Fennoscandia

Climate studies on trees at high elevations and high latitude have been extensive in Fennoscandia, however, few of these studies have been on mountain birch. A majority of studies on climate change in Fennoscandia have been done on Scots pine. These studies have included temperature (Briffa *et al.* 1990; Briffa *et al.* 1992; Lindholm & Eronen 2000), precipitation (Linderholm & Chen 2005), and NAO (Lindholm *et al.* 2001) reconstructions. Additionally, studies on the spatial variation of climate trends have been conducted (Helama *et al.* 2005; Linderholm 2002; Linderholm & Chen 2005; Linderholm *et al.* 2003; Macias *et al.* 2004). Other studies have focused on the growth of Scots pine (Hustich 1945, 1956, 1978; Linderholm *et al.* 2003; Tuovinen 2005).

Common trends across these studies are that in most cases the most significant factors that influence growth are July temperatures followed by May precipitation. The studies that looked at NAO found that winter NAO was significant in both maritime and continental climates, while summer NAO was significant on the western slope of the Scandes and at the physiological limits of Scots pine in the continental regions (Helama *et al.* 2005; Linderholm *et al.* 2003; Lindholm *et al.* 2001; Macias *et al.* 2004).

On the other hand the lack of dendrochronological studies preformed on mountain birch may be because it is of little economic value (Sonesson & Hoogesteger 1983). On the other hand, according to Kirchhefer (1996), studies could be limited because, “This is presumably the upshot of difficulties in studying birch rings due to wood morphology, irregular growth, extreme and irregular growth reductions due to insect outbreaks, many missing rings, a short life span, and rapid decay of dead wood”. Kirchhefer is not the only one that expresses difficulties in working with mountain birch. Missing rings due to insect outbreaks and early/late frost are numerous (Hoogesteger & Karlsson 1992; Kullman 1979; Levanič & Eggertsson 2008). Levanič and Eggertsson (2008) could cross-date just over half of their collected samples due to ring morphology and suppressed rings.

There are three categories of papers written on mountain birch: treeline progression, climate analysis and response to insect outbreaks. Studies on treeline have primarily been limited to ring counts which give a relative age of trees growing at these extreme levels (Kullman 1979; Kullman 1991; Kullman & Kjällgren 2000; Löffler *et al.* 2004; Sonesson & Hoogesteger 1983). These studies have shown that at some treelines, trees were established 75-150 years ago. Though it is believed that these are recovering anthropogenic treelines that have not yet reached their climatic potential (Löffler *et al.* 2004).

Four papers address climatic influences on mountain birch (Eckstein *et al.* 1991; Karlsson *et al.* 2004; Kirchhefer 1996; Levanič & Eggertsson 2008). These studies cover a large area of the mountain birch’s distribution (e.g. northern Norway: (Kirchhefer 1996); northern Sweden: (Eckstein *et al.* 1991; Karlsson *et al.* 2004); and Iceland: (Levanič & Eggertsson 2008)). Each of these studies found that mountain birch responds most strongly to June and July temperatures of the current growing season. In Iceland there was a positive growth response, though not significantly, to January precipitation (Levanič & Eggertsson 2008). In Norway and Sweden two of the studies showed no response to precipitation (Karlsson *et al.* 2004; Kirchhefer 1996), while the third showed a response to the previous year's precipitation (Eckstein *et al.* 1991).

Seven papers have addressed the topic of outbreaks of autumnal moth and mountain birch through the use of dendrochronology (Eckstein *et al.* 1991; Hoogesteger & Karlsson 1992; Karlsson *et al.* 2003; Karlsson *et al.* 2004; Kirchhefer 1996; Nuorteva 1963; Tenow *et al.* 2004). Four of these studies were conducted looking at the direct response of trees to a specific outbreak by either growth reduction (Karlsson *et al.* 2003; Karlsson *et al.* 2004; Nuorteva 1963) or the age of sprouts that have established since the outbreaks (Nuorteva 1963; Tenow *et al.* 2004). One paper is based on growth reductions of an experimental defoliation (Hoogesteger & Karlsson 1992). Two reports used modern techniques for detecting defoliation events over a long time series (Eckstein *et al.* 1991; Kirchhefer 1996).

Karlsson et al. (2004) examined tree ring widths before and after known outbreaks of the autumnal moth. Levels of defoliation were known for the study areas, so they were able to compare ring width variations to percent defoliation. They found that low levels of defoliation were not detected in the rings. Defoliation at 80% and higher showed reduction of ring widths for 1-4 years and foliage reductions of 100% for at least one year produced initially suppressed rings but then had larger than average growth. All of these conclusions are however, based on a samples size of only one for each level of defoliation.

Karlsson and Weih (2003) evaluated ring width reductions over an eight year period in relation to apical dominance as a response to defoliation during the 1995 outbreak at Torneträsk Railway Station. They showed that ring widths during the year of defoliation decreased.

Nuorteva (1963) showed that the response to the 1927 outbreak in northern Finland where large portions of the forest were defoliated and killed, the raw ring width series displayed a decrease in growth during 1927. Not all samples were from before 1927 thus they are probably basal sprouts responding to the outbreak. This study was limited to 11 trees from around the Utsjoki area.

Tenow et al (2004) used tree ring analysis to determine the rejuvenation of mountain birch after a 50 year old outbreak compared to the number of caterpillars found during the outbreak.

Hoogesteger and Karlsson (1992) took a different approach to detecting outbreaks. They experimentally created an outbreak situation of different intensities by clipping leaves from birch trees. During and after their experimental outbreak they recorded photosynthetic rates and ring widths. Trees that were 100% defoliated had a new canopy by mid July however the resources put into establishing a new canopy reduced ring widths on average 15-22% and the effect lasted up to 3 years (Hoogesteger & Karlsson 1992). Simulated outbreaks of 50% defoliation did not produce new leaves during the growing season yet they did not show a reduced ring width. This was due to increased photosynthetic rates up to 35% caused by increased nitrogen content. The nitrogen content went up due to an equal amount of nitrogen but a decreased leaf area.

An increase in nitrogen directly increased the photosynthetic rate of the remaining leaves thus causing no ring width reduction (Hoogesteger & Karlsson 1992).

Kirchhefer (1996) and Eckstein (1991) use modern techniques to detect outbreaks. Their method used a non-host tree as a comparison to the host tree to eliminate factors other than the outbreak that may be affecting the trees growth. Kirchhefer's (1996) analysis was an exploratory paper to determine if detection of outbreaks was possible in mountain birch using tree rings and attempted to detect environmental variables leading up to an outbreak. The use of Scots pine in this analysis was just a visual comparison. His research was conducted on 10 sites in northern Norway.

Eckstein (1991) examined outbreaks of the autumnal moth by subtracting a mountain birch chronology from a Scots pine chronology to remove climatic variability. Comparing this corrected chronology to Tenow's (1972) historical documentation of past outbreaks he found that by this method 6 of the 10 outbreaks that were known to have occurred in the area. The missing outbreaks were explained by the heterogeneity both spatially and in the intensity of outbreaks. Additionally he speculated that there might be some kind of variability between the pines and birches that 'removed' the other outbreaks.

Additional, studies on mountain birch in relationship to climate and autumnal moth outbreaks are needed. The interactions between climate and moth are two of the drivers that create the treeline ecotone between the forest and tundra. Increased temperatures will theoretically raise the treeline while occasional large scale outbreaks have the potential to lower the treeline. The location of the mountain birch treeline is important economically as forage for the reindeer, aesthetically for tourist and species richness region between the tundra and forest.

CHAPTER III

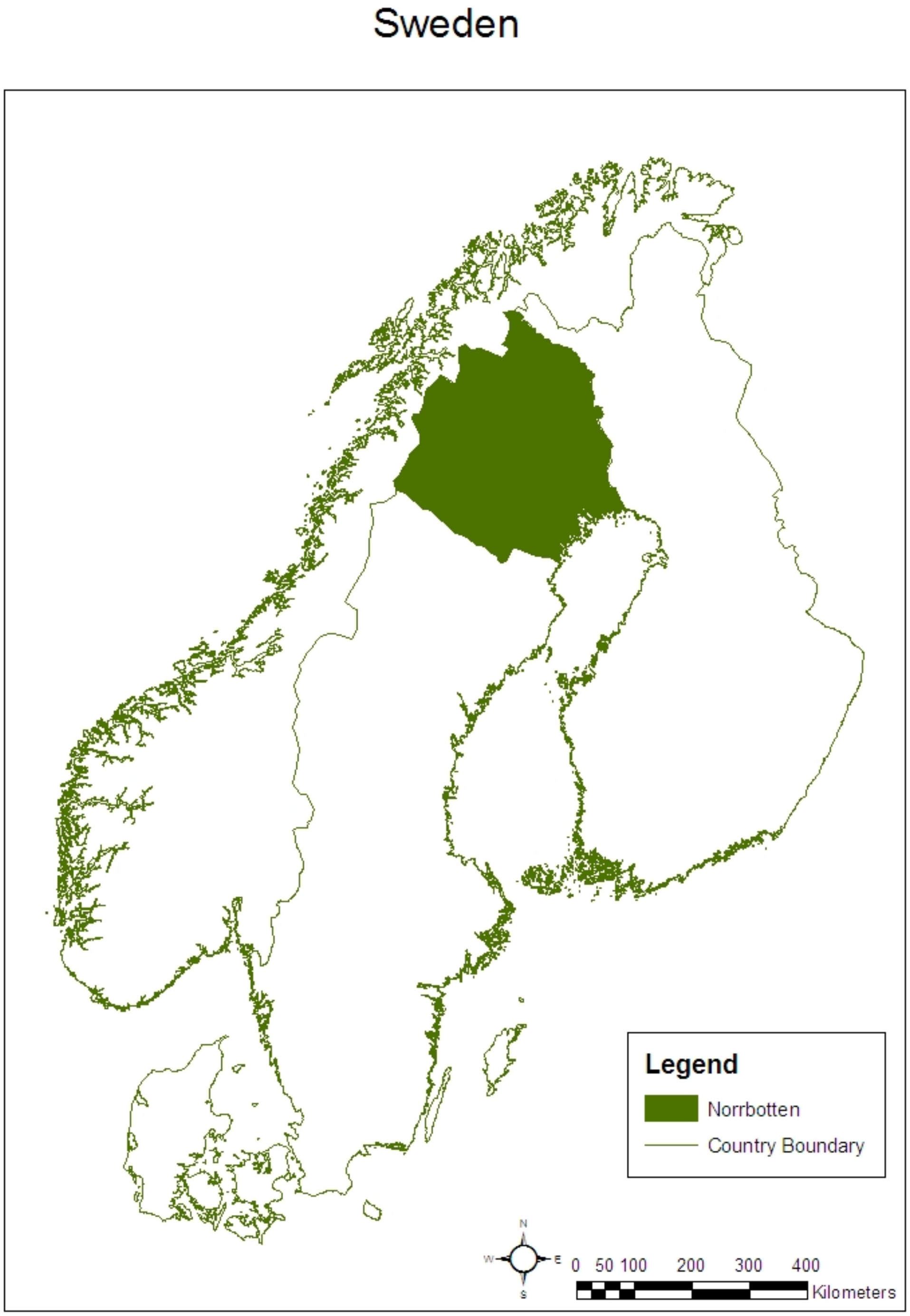
METHODS

STUDY SITE

The region of my study is the Scandes Mountains in Norrbotten province, Sweden which is above the Arctic Circle (66.5^{o}N) (Figure 1). Norrbotten province is the northernmost province of Sweden and shares borders with Norway and Finland. The Scandes are a mountain chain composed primarily of Pre-Cambium granites and gneisses that divide the Scandinavian Peninsula between Norway and Sweden (Lidmar-Bergström & Näslund 2005). Climatically the Norwegian side of the mountains is considered maritime and the Swedish side is a mix between maritime and continental (Tikkanen 2005). The Scandes are dissected by numerous large, glacially-carved valleys. The valleys on the Swedish side are gentle compared to the Norwegian side and run down to the Baltic Sea (Corner 2005). The primary forest type found in the Scandes is a mix of mountain birch and Scots pine or Norway spruce. The regional average annual precipitation is 435 mm, with average July precipitation of 709 mm (Figure 2) (Tuomenvirta *et al.* 2001). The regional average annual temperature is -.2 ^{o}C, with average July temperatures of 13.5 ^{o}C (Figure 2) (Tuomenvirta *et al.* 2001).

SAMPLE DESIGN

I established 21 sample sites throughout Norrbotten (Figure 3). Sample sites are located within seven regions: Vuoggatjålme (3), Kvikkjokk (1), Ritsem (7), Nikkaluokta



Amanda B. Young
May 12, 2008

Figure 1. Map of Fennoscandia (without Iceland). Study region is located in Norrbotten province in northern Sweden.

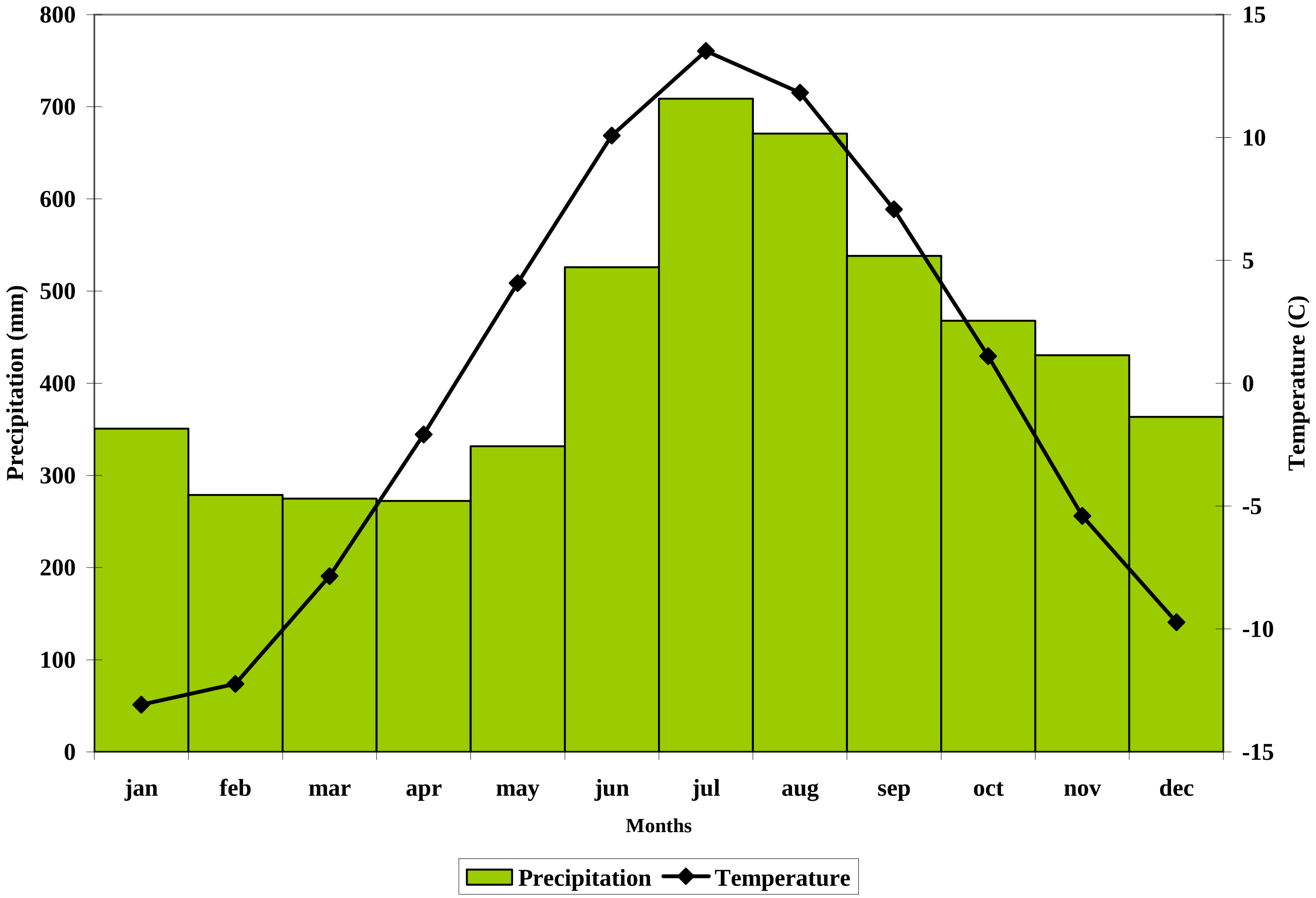


Figure 2. Climograph of the regional monthly average precipitation and temperature for Norbotten, Sweden.

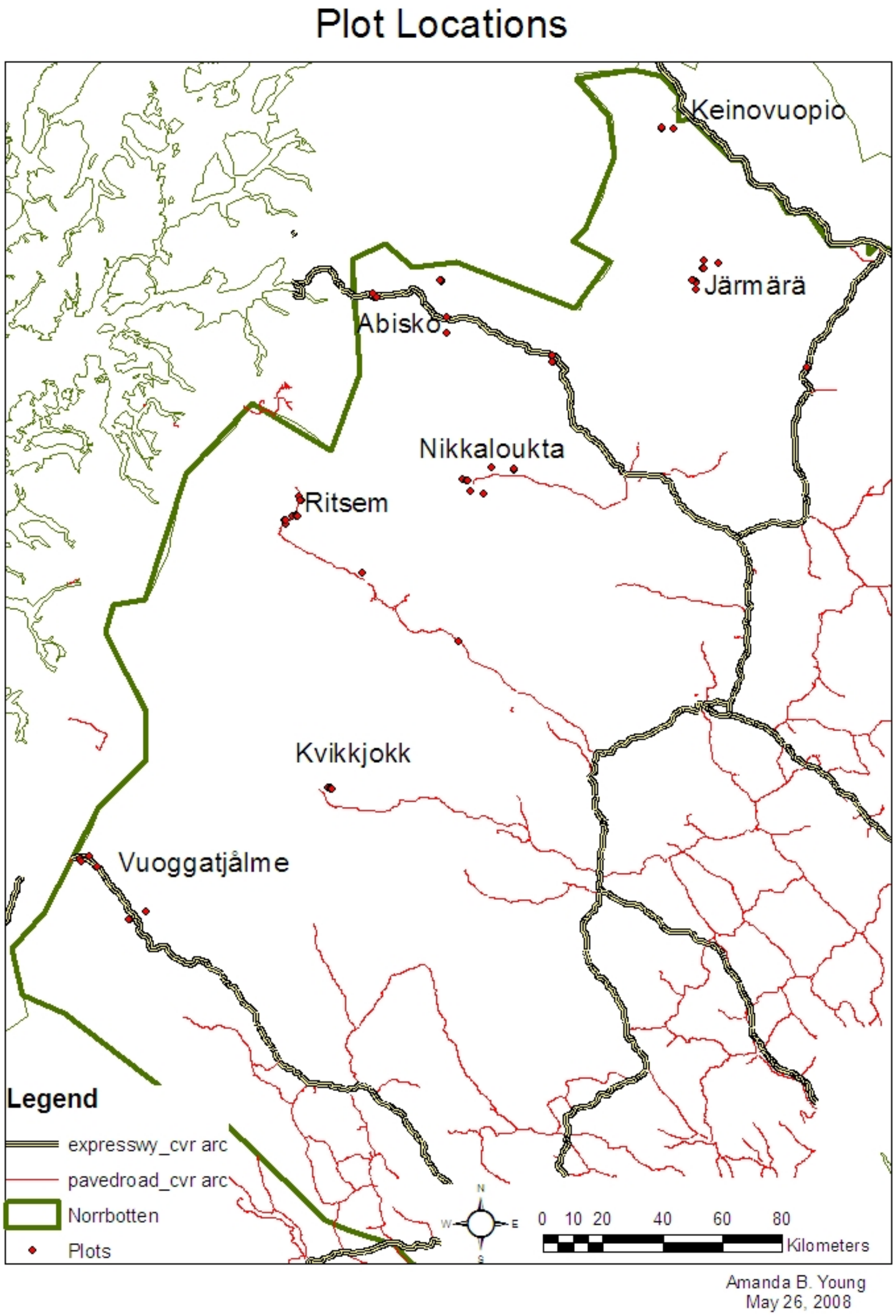


Figure 3. Location of study plots in Norrbotten, Sweden. All study regions were accessible by road. All plots are mapped though not all were used in the study.

(2), Torneträsk (3), Järmärä (2), and Keinivuopio (3). Each of these regions was accessible by road.

Sample sites are characteristic of the area and each contains at least 20 trees. At each sample site 15-20 mountain birch trees greater than 5 cm at base were cored (n = 464) (Figure 4). Coring was conducted cross slope at the base of the tree in attempts to reduce slope-related growth variation. One core all the way through the tree or two cores (one from each side of the tree) were taken using a Haglöf increment borer (Haglöf Sweden AB., Långsele, Sweden). For each tree growth form (monocormic or polycormic), height of lichen up the main stem, diameter at base, and past signs of outbreaks were recorded. Evidence of past outbreaks included dead main stems and intense basal sprouting. Height of the lichen *Parmelia olivacea* was recorded as an estimate for average snow depth (Sonesson *et al.* 1994).

Six sites of Scots pine were also sampled at the highest possible elevations (Figure 3 and 5). These trees encounter their physiological limit while still in a continuous forest of mountain birch. At these sites 8-20 Scots pines were cored across the slope and at breast height. These samples were used in climatic comparisons and as the non-host in detecting herbivory. Cores of both species were stored in paper straws and stored in a dry environment.

SAMPLE PREPARATION

Tree cores were glued to core mounts. Cores were then processed by sanding with progressively less abrasive sanding belts (80 to 400 grit) in order to draw out the cellular structure of each year’s ring (Fritts 1976). Birch cores were then dyed using

Figure 4. Example of a mountain birch plot. Cores taken at the base of trees over 5 cm in diameter.

Figure 5. Example of a typical Scots pine plot. Cores were taken at breast height.

Phloroglucinol. Phloroglucionl is used to detect ring boundaries in diffuse porous species that have hard to see ring boundaries (Patterson 1957). Phloroglucinol is mixed with ethyl alcohol (95%) and applied to the cores. It is then washed with a solution of 10% hydrochloric acid (HCl) which reacts with the phloroglucionol and stains the lignin. The dye is fixed to the wood when the HCl is washed off in a bath of water. Dyed cores were re-sanded due to moisture from the dying process opening up the cells thereby creating an obscured surface.

Ring counts and visual cross-dating was conducted on each core (Stokes & Smiley 1968). Due to small ring widths and unusual growth some samples could not be cross-dated. Even after dying the wood the rings of mountain birch are very small and hard to see. Following the visual cross-dating, rings were measured using a stereomicroscope and Velmex measuring system (Velmex Inc., Bloomfield, New York, USA) and the software Measure J2X (VoorTech Consulting, Holderness, NH, USA).

DATA ANALYSIS

Cross-dating and Correlation

Measured ring widths were run through COFECHA a statistical program that helps verify cross-dating (Holmes 1986, 1994). Cross-dating is an important part of dendrochronology. It takes all of the samples in a plot into consideration and helps identify missing and/or false rings (Fritts 1976). This can be done manually with skeleton plots or digitally with computer programs such as COFECHA. COFECHA assesses cross-dating by using correlations of segmented time lengths of the series and compares them to a master series (Grissino-Mayer 2001). The program also identifies segments that have outliers in the data from missing or false rings (Grissino-Mayer 2001). The default 32 year spline with a 50% frequency response was used in this analysis because it has been proven to be the optimal spline size to detect errors in ring width series (Grissino-Mayer 2001). Segment lengths of 30years with a 15 year overlap and 20 years with 10 year overlap were used to detect missing and false rings in the series. Cores that could not be cross-dated were removed from the data set.

Standardization

Ring width standardization is also important process in dendrochronology. It was originally developed to remove yearly variation and allow long-term climatic trends to be detected (Fritts 1976). The standardization process creates a ring width index that allows numerous samples to be compared by setting their means to one, allowing young and old wood to be compared to each other (Cook & Holmes 1986; Fritts 1976). Depending on the purpose of the study and standardization techniques applied it can remove growth related trends, yearly variations, long-term variations or disturbances found in the rings. This study is looking at short-term variations caused by interannual climatic influences and cyclical moth outbreaks thus the removal of long-term trends is necessary. Due to the aims of this study double detrending (two standardization methods) will be used: negative exponential and 20 year cubic spline.

The first standardization method used is a negative exponential curve (Figure 6). Typical growth related trends for trees in the open or in the canopy are negatively exponential, having larger rings as young trees and slowly decreasing size over time (Fritts 1976). Removing this trend is important because not all the cores start the same

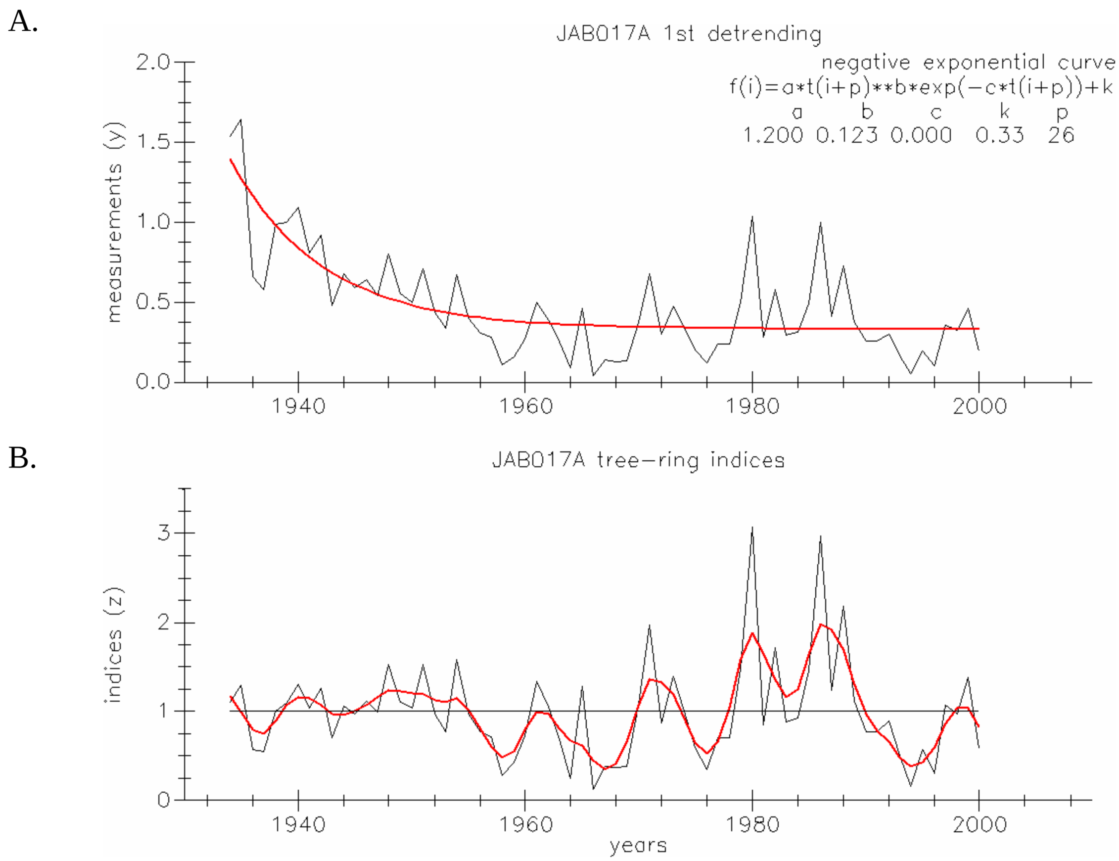


Figure 6. First method of standardization A). Application of a negative exponential curve to the raw ring widths. Measurements are in mm (y), B). Standardized ring width indices with a mean at one (z).

year; otherwise comparisons of young growth on one core to older wood on another might skew the data (Figure 7). Not all of the cores have this growth trend and a horizontal mean was used as the first detrending method in these cases (Fritts 1976).

The second detrending technique used was a cubic spline (Figure 8). Cubic spline is a low-pass filter method that has a flexible curve that follows the rings. A flexible cubic spline (e.g. 20 year) removes long-term cycles to better express interannual variation; a stiffer cubic spline (e.g. 60 year) better expresses the long-term cycles. An additional factor to consider when using a cubic spline is the life history of the tree. The stiffness of the spline should compose a large percent of the series length for removing annual variation and smaller percentage to focus in on the annual variation (Cook & Holmes 1986; Fritts 1976). Mountain birch typically has a life span from 50-120 years though some specimens are known to be over 200 years old (Eckstein *et al.* 1991; Kullman 1979; Sonesson & Hoogesteger 1983). Due to the life history of mountain birch and the aims at detecting annual and inter-annual variation a 20 year cubic spline was used to remove long-term trends in the data.

Standardization was conducted using the program ARSTAN40c (Holmes 1994; Holmes *et al.* 1986) Cook and Krusic 2006). This program was specifically designed to standardize tree rings. ARSTAN40c computes both standardization on the individual chronologies but also produces a mean chronology. ARSTAN40c produces both individual core and series averages of the raw, standardized, residual, and autoregressive values (Figure 9). The residual values will be used in the dendroclimatology section below. Residual chronology has the autocorrelation between years removed. The

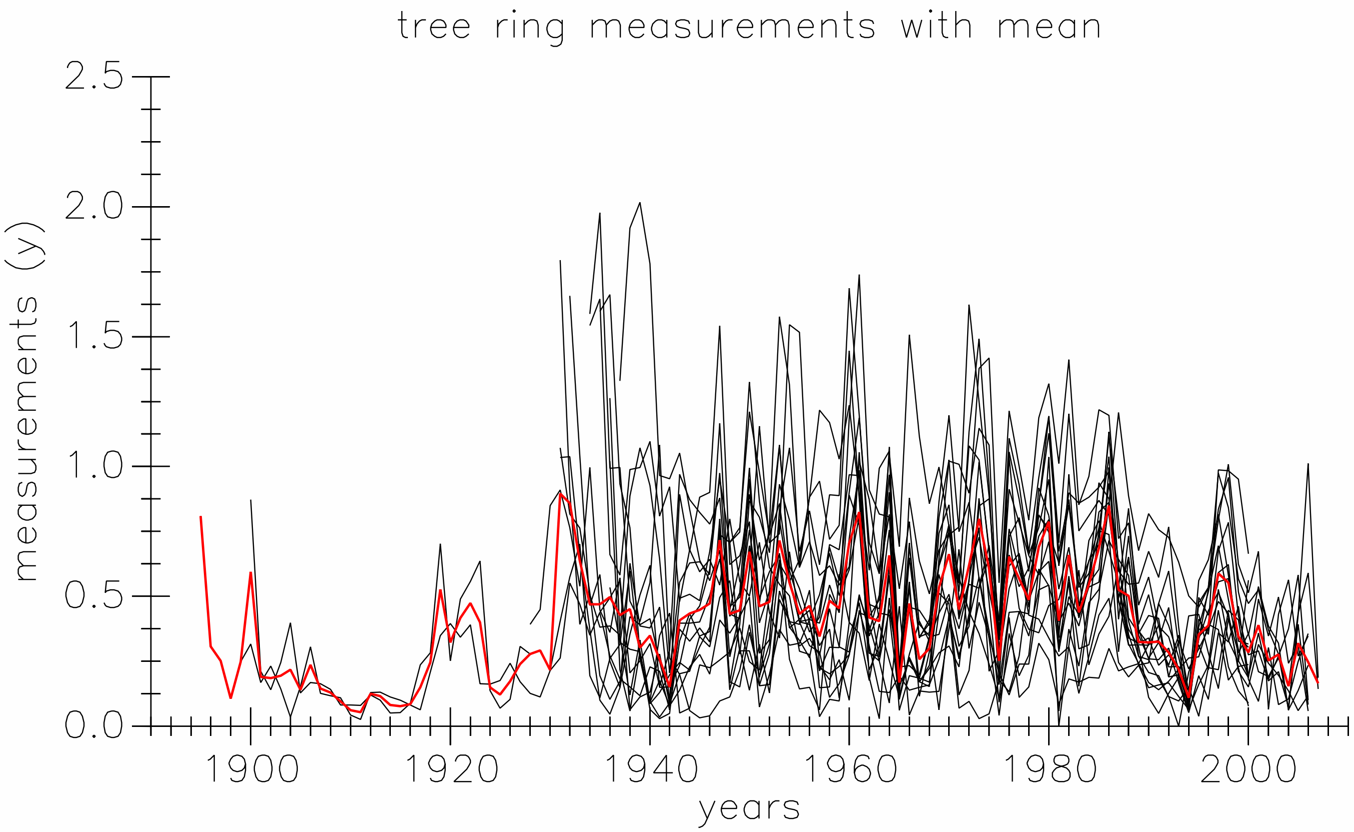


Figure 7. Raw tree ring width indices of all cores (black) and the mean (red) at Järmärä site (JAB). Measurements by mm (y).

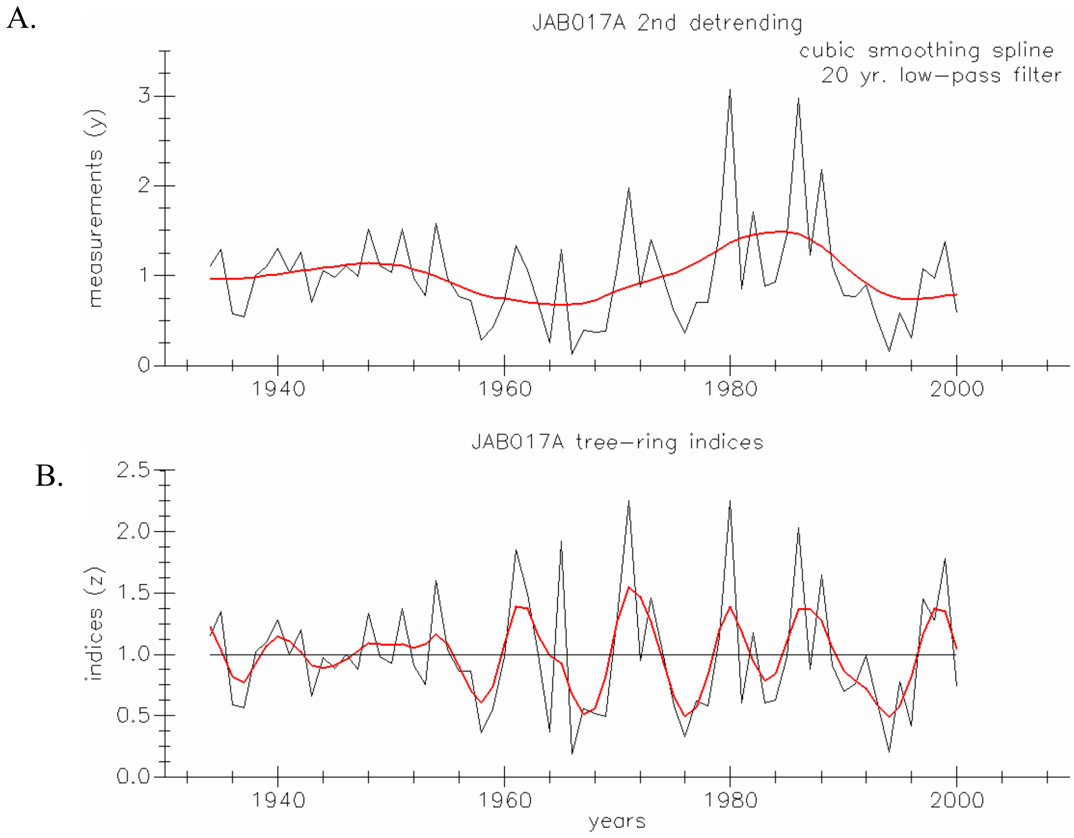


Figure 8. Second method of standardization. a). Application of a 20 year cubic spline to the ring width indice after the application of a negative exponential curve.   b). Double detrended ring width indice with a mean of one.

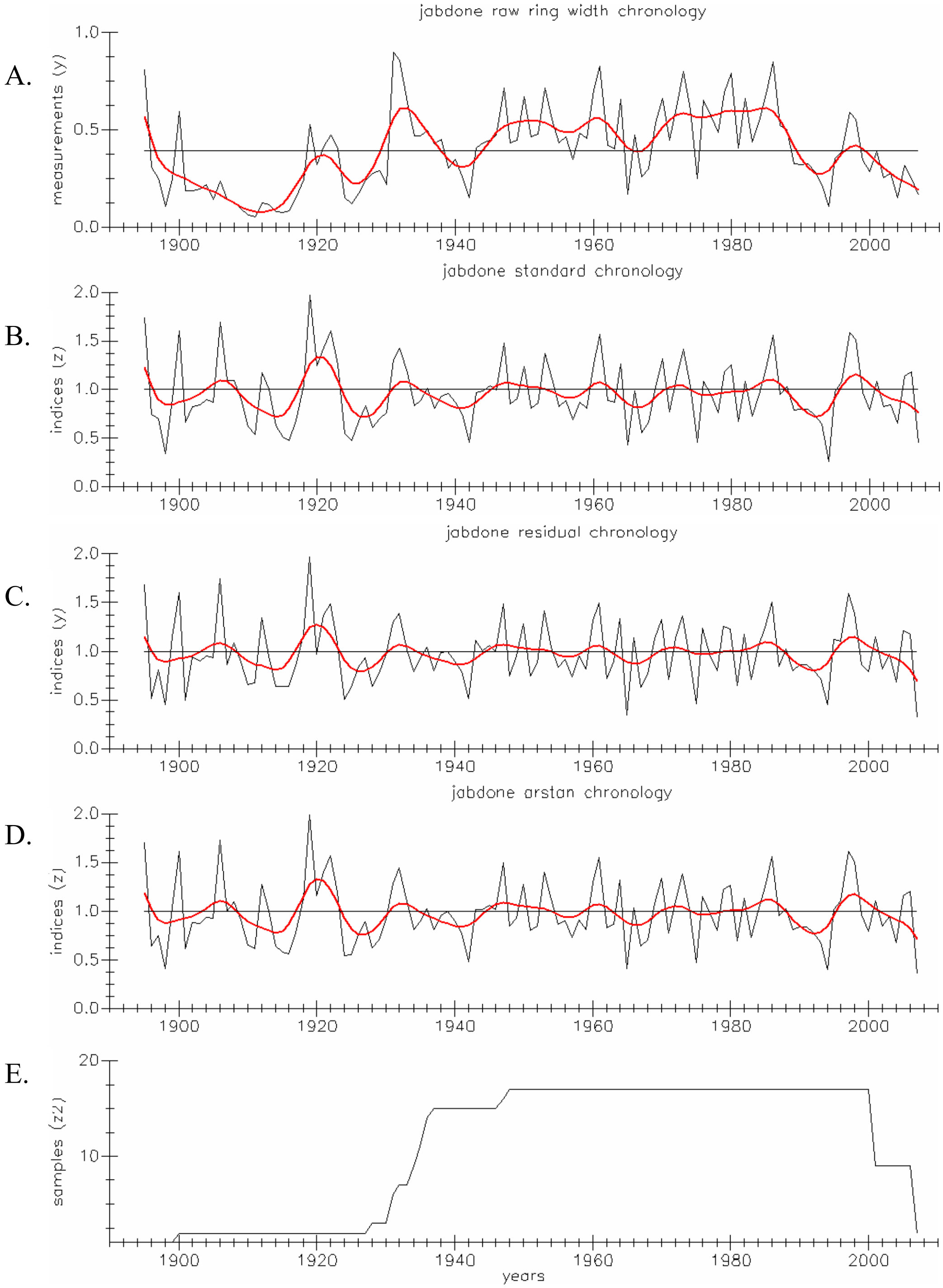


Figure 9. Averaged chronologies produced by ARSTAN. a). raw ring width index, b). Standardized ring index, c). Residual index, d). Arstan index, e). Size of sample pool.

double detrended individual series will be used in the in the OUTBREAK analysis below.

Dendroclimatology

This portion of the analysis is composed of two parts. Creating a regional climatic data set and detecting the response of climate in the tree rings.

Climate Data

Climate data came from the Nordklim 2.0 dataset (Tuomenvirta *et al.* 2001). Nordklim is a cooperative project run by the metrological institutes of Denmark, Iceland, Finland, Norway, and Sweden with 114 weather stations running from the 1870's to 2001. This effort was established to create a uniform climatic data set between the five countries. The variables included are mean monthly temperature, mean monthly maximum temperature, highest maximum temperature, mean monthly minimum temperature, lowest monthly minimum temperature, mean monthly pressure, monthly precipitation sum, maximum 1-day precipitation, number of days with snow cover, and mean monthly cloud cover. The data that I used in this study are mean temperature, highest maximum temperature, lowest minimum temperature, precipitation sum and mean cloud cover (Table 1). Weather stations from both east and west sides of the Scandes in Sweden, Norway and Finland are used in this analysis. These weather stations cover the time period 1890 to 2001. All stations have data from 1913 to 2001 (Table 1).

I plotted all the weather stations located in or adjacent to Norrbotten from the Nordklim data set in ArcGIS. A Voronoi diagram was created using the Geostatistic

Table 1. Intervals of Nordklim data fields for each weather station.

	Abisko	Kvikkjokk	Jokkmokk	Karesuando	Stensele	Tænaby	Tjåmotis	Piteå	Haparanda	Sodankylan	Kiruna	Glömfjord	Kråkmo	Tromsö
mean monthly temp	1913-2001	1890-2001	1890-2001	1890-2001	1890-2001	1901-2001		1890-2001	1890-2001	1908-2002		1890-2001		1890-2001
max monthly temp			1885-2001	1885-2001	1885-2001				1873-2001	1908-2002		1957-2001		1931-2001
min monthly temp			1885-2002	1885-2002	1885-2002				1873-2001	1908-2002		1957-2001		1876-2001
monthly precip	1913-2001	1890-2001	1890-2002	1890-2003	1890-2004	1890-2005	1909-2001	1890-2001	1890-2001	1908-2002	1898-2001	1895-2001	1895-2001	1890-2001
monthly cloud cover			1890-1999		1890-2000				1890-2001	1908-2002		1990-2001		1890-2001

Toolbar. Voronoi diagrams are commonly used to calculate area weighted values (Mu 2004). The Voronoi diagram was then clipped with the Norrbotten polygon to display areas of influence of weather stations within Norrbotten. The Voronoi diagram determined that 14 weather stations record the weather for the Norrbotten area. This analysis did not take elevation into account. Ten stations are located in Sweden (Karesuando (68.26°N, 22.31°E), Abisko (68.21°N, 18.49°E), Jokkmokk (66.37°N, 19.38°E), Tjåmotis (66.55°N, 18.32°E), Kvikkjokk (66.57°N, 17.44°E), Stensele (65.04°N, 17.09°E), Tærnaby (65.49°N, 15.05°E), Piteå (65.32°N, 21.29°E), Haparanda (65.49°N, 24.08°E), and Kiruna (67.49°N, 20.20°E)). Three stations are located in Norway (Glömfjord (66.49°N, 13.59°E), Kråkmo (67.48°N, 15.59°E), and Tromsö (69.39°N, 18.56°E)) and one station is in Finland (Sodankylan (67.22°N, 26.39°E)).

The 14 weather stations were used to calculate a regional climate record. This was done by calculating an area weighted average for each meteorological field based on the percent of area each weather station covered in Norrbotten from the Voronoi diagram. Each weather station's data were multiplied by the proportion of Norrbotten that they represented and then summed to produce a regional climate record for Norrbotten for both precipitation (Figures 10 & 11) and temperature (Figures 12 & 13). The larger percent of area a weather station covers the more its data will weigh in the regional climate data (Table 2).

Variations in the data are largely due to the location of the weather stations. Three of the weather stations in Sweden are found in valleys in the mountains (Abisko (388 m.a.s.l.), Kvikkjokk (337 m.a.s.l.), and Tærnaby (475 m.a.s.l.)). The other seven

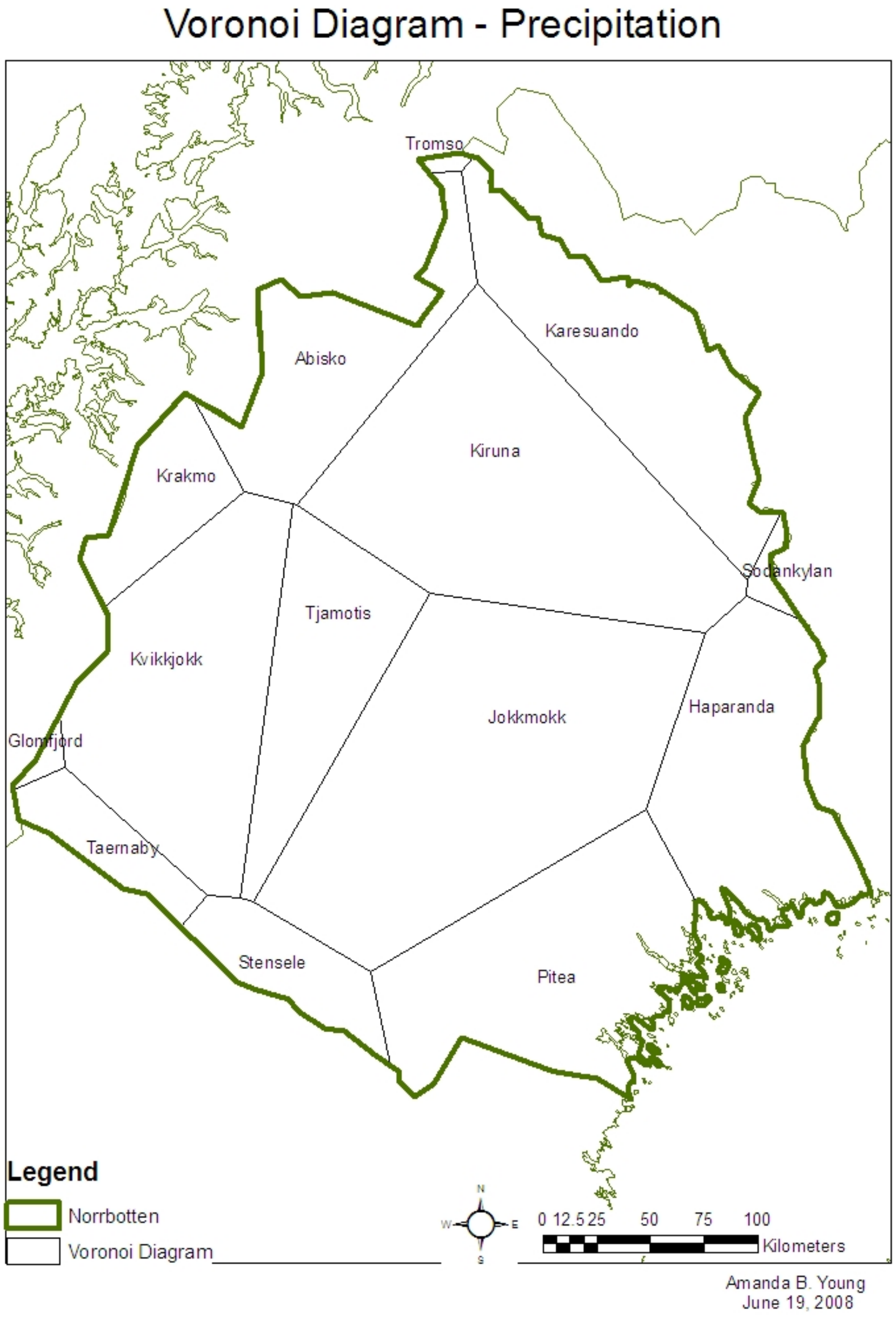


Figure 10. Voronoi diagram of precipitation for weather stations percent area coverage in Norrbotten, Sweden.

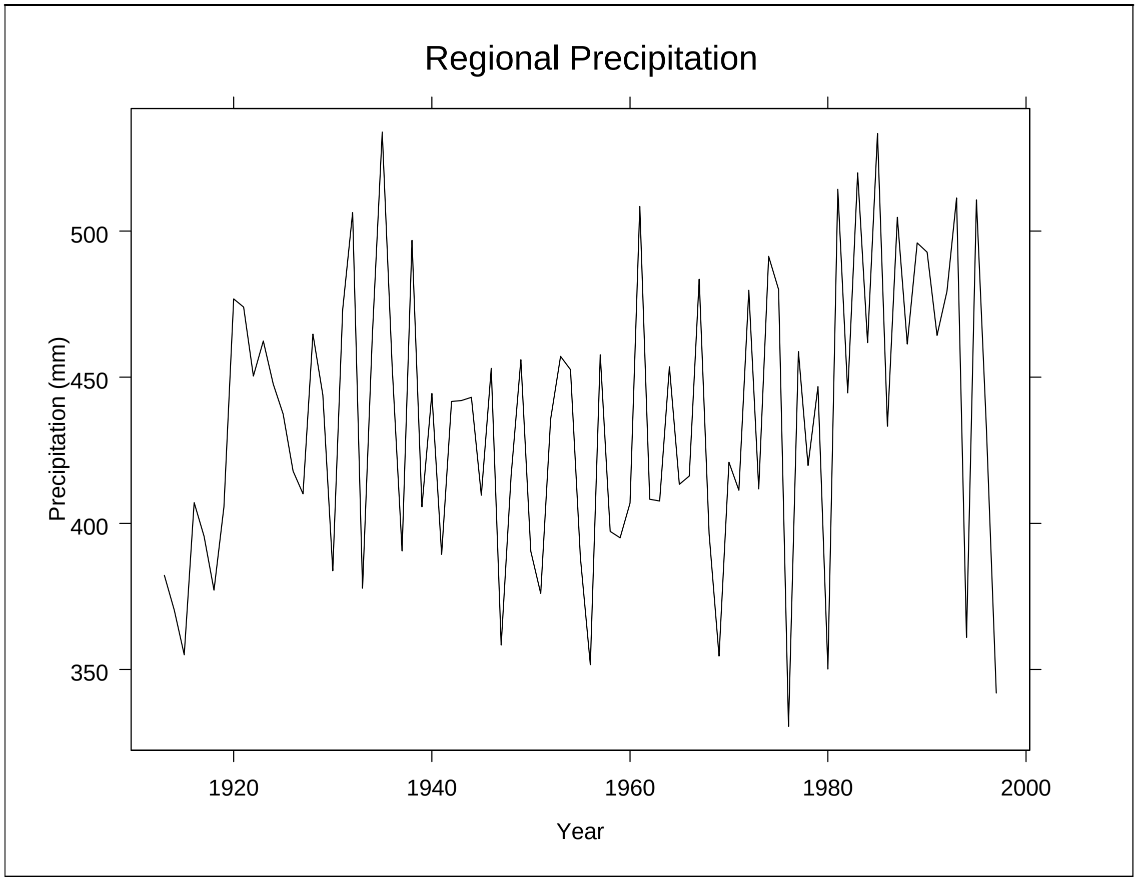


Figure 11. Regional precipitation series from 1913-1997.

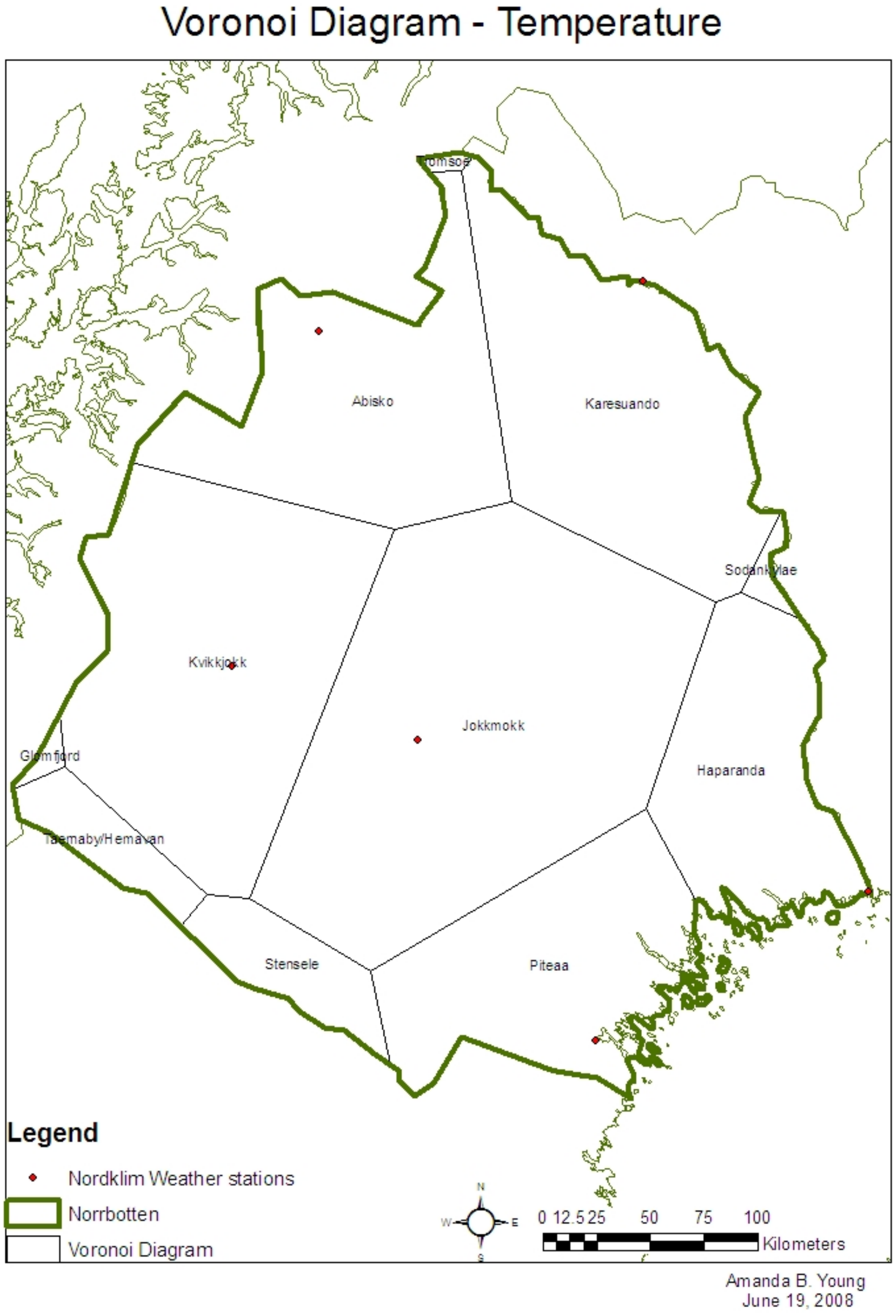


Figure 12. Voronoi diagram of temperature for weather stations percent area coverage in Norrbotten, Sweden.

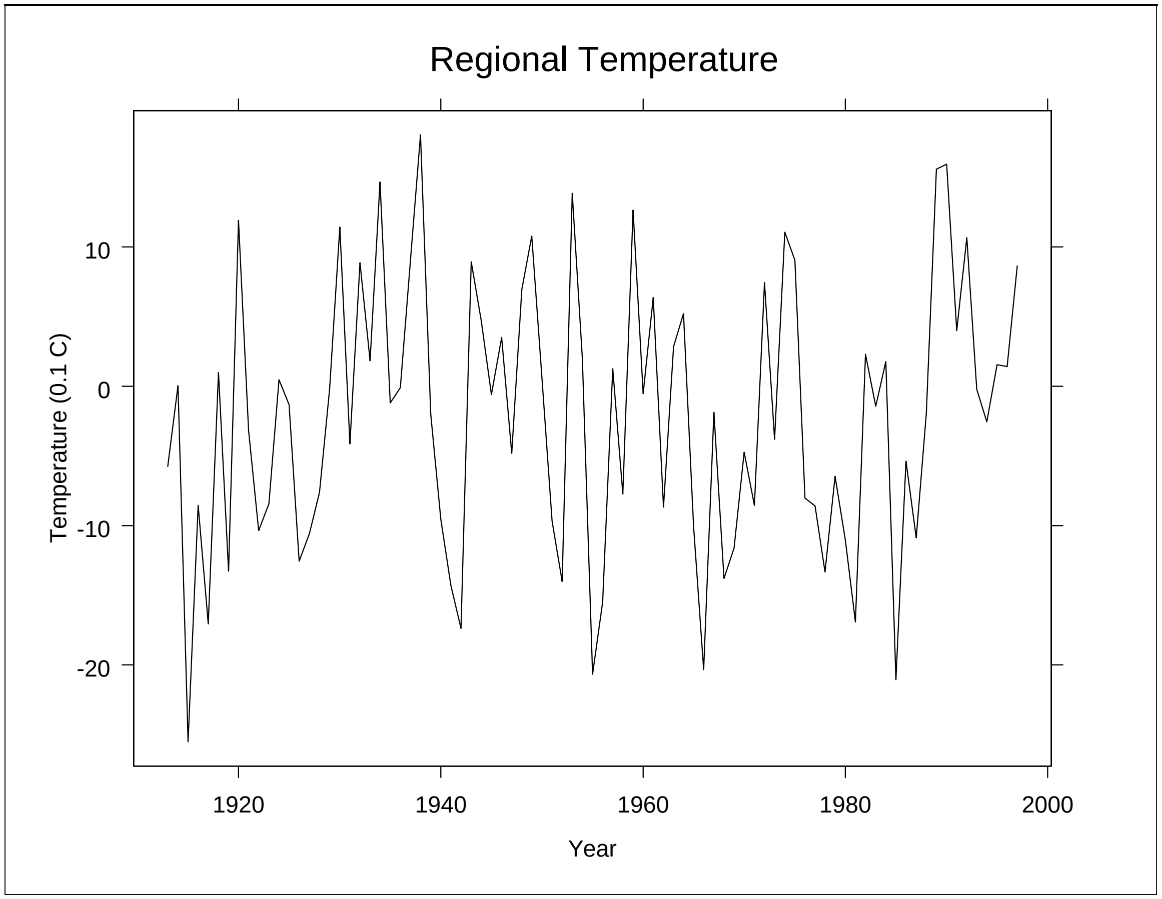


Figure 13. Regional temperature series 1913-1997.

Table 2. Area of coverage for Voronoi polygons for mean monthly precipitation and mean monthly temperature. Elevation of Weather Station in meters above sea level (m.a.s.l).

	Voronoi Area (km2)		
Station	Temp	Precip	m.a.s.l
Jokkmokk	28464.66	21060.97	260
Kiruna	NA	17346.48	442
Kvikkjokk	19485.47	12391.02	337
Piteå	12022.75	12022.75	6
Karesuando	16131.33	9967.39	327
Haparanda	9834.59	9729.32	5
Tjåmotis	NA	6899.91	300
Abisko	13745.06	6897.23	388
Kråkmo	NA	3380.56	76
Stensele	3136.40	3134.00	325
Tænaby	2339.05	2339.05	475
Sodankylan	441.34	431.98	179
Glömfjord	299.08	299.08	39
Tromsö	156.09	156.09	100

Swedish stations are found at slightly lower elevations east of the mountains (5-327 m.a.s.l) (Table 3). The three Norwegian plots are located close to the coast and at low elevations (39-100 m.a.s.l.). The shortest distance between two weather stations is Tjåmotis and Kvikkjokk (35km) (Table 3). The distance between Sodankylan and Tænaby (540km) is the greatest distance between two weather stations. The only weather stations located in close proximity to my study sites are Abisko and Kvikkjokk.

I calculated correlations between meteorological stations for each field. There is a small difference between the monthly temperature correlations across Norrbotten (Table 4b). The lowest temperature correlation exists between Glömfjord and Piteå (0.17) and the highest is between Jokkmokk and Kvikkjokk (0.96) (Table 4b). Temperature correlations that involve Piteå are much lower than all other correlations. This maybe due to Piteå's easterly location, low elevation (6 m.a.s.l.) and proximity to the Baltic Sea.

Precipitation correlations between weather stations are much lower. The lowest precipitation correlation is between Abisko and Stensele (0.14) and the highest is between Tjåmotis and Kvikkjokk (0.82) (Table 4a). The precipitation correlations relate to the distance between weather stations on the east side of the Scandes. Abisko and Stensele are two of the farthest separated stations in Sweden (373 km), while Tjåmotis and Kvikkjokk are the closest weather stations (35km).

The highest precipitation correlations are between stations on the east side of the mountains. The only weather stations located on the east side of the Scandes that correlates well with the Norwegian weather stations for precipitation are Abisko and

Table 3. Distances between weather stations (km).

km	Abisko	Kvikkjokk	Jokkmokk	Karesuando	Stensele	Tænaby	Tjåmotis	Piteå	Haparanda	Sodankylan	Kiruna	Glömfjord	Kråkmo	Tromsö
Abisko														
Kvikkjokk	161.38													
Jokkmokk	195.41	92.15												
Karesuando	152.62	261.01	236.19											
Stensele	373.21	212.87	207.89	242.15										
Tænaby	324.71	173.43	223.87	120.87	127.67									
Tjåmotis	160.11	35.9	58.34	200.19	215.76	196.97								
Piteå	355.19	242.83	163.63	353.24	193.5	289.81	216.6							
Haparanda	365.89	313.72	221.63	302.04	333.99	413.31	278.98	144.35						
Sodankylan	345.85	388.25	316.31	208.78	498.6	540.03	354.44	334.77	208.95					
Kiruna	85.87	146.85	136.67	114.19	338.24	320.12	126.62	283.26	280.65	272.96				
Glömfjord	267.28	164.9	250.49	404.74	242.15	120.87	200.19	368.54	468.1	552.25	294.75			
Kråkmo	132.29	120.37	206.89	280.51	310.37	225.06	148.52	363.44	421.9	455.16	182.75	140.52		
Tromsö	146.6	305.26	339.98	198.01	518.1	457.67	306.64	495.3	483.1	404.13	212.71	377.59	238.4	

Table 4. Correlations of temperature and precipitation between weather stations. a). Precipitation. b). Temperature.

A.

	Abisko	Kvikkjokk	Jokkmokk	Karesuando	Stensele	Tænaby	Tjåmotis	Piteå	Haparanda	Sodankylan	Kiruna	Glömfjord	Kråkmo	Tromsö
Abisko														
Kvikkjokk	0.35													
Jokkmokk	0.24	0.73												
Karesuando	0.42	0.53	0.62											
Stensele	0.14	0.66	0.7	0.44										
Tænaby	0.49	0.56	0.33	0.35	0.37									
Tjåmotis	0.28	0.82	0.77	0.52	0.65	0.47								
Piteå	0.07	0.53	0.69	0.45	0.64	0.19	0.57							
Haparanda	0.18	0.53	0.61	0.51	0.5	0.29	0.52	0.62						
Sodankylan	0.27	0.44	0.52	0.6	0.38	0.28	0.43	0.46	0.7					
Kiruna	0.39	0.61	0.71	0.67	0.50	0.31	0.65	0.53	0.55	0.54				
Glömfjord	0.44	0.05	-0.11	0.12	-0.14	0.43	-0.02	-0.19	0.02	0.09	-0.02			
Kråkmo	0.49	0.06	-0.07	0.09	-0.15	0.42	-0.03	-0.21	0.01	0.08	-0.02	0.94		
Tromsö	0.42	-0.09	-0.21	0.06	-0.22	0.29	-0.09	-0.28	-0.11	0	-0.08	0.72	0.71	

B.

	Abisko	Kvikkjokk	Jokkmokk	Karesuando	Stensele	Tænaby	Piteå	Haparanda	Sodankylan	Glömfjord	Tromsö
Abisko											
Kvikkjokk	0.92										
Jokkmokk	0.89	0.96									
Karesuando	0.92	0.9	0.92								
Stensele	0.84	0.93	0.95	0.86							
Tænaby	0.86	0.93	0.92	0.92	0.95						
Piteå	0.23	0.23	0.25	0.23	0.24	0.21					
Haparanda	0.85	0.86	0.91	0.9	0.89	0.86	0.24				
Sodankylan	0.85	0.84	0.25	0.91	0.84	0.81	0.24	0.94			
Glömfjord	0.86	0.86	0.85	0.83	0.86	0.9	0.17	0.81	0.79		
Tromsö	0.89	0.81	0.8	0.85	0.76	0.79	0.18	0.8	0.82	0.89	

Tænaby (Table 4a). This is interesting because both of these locations are in the mountains in large east-west oriented valleys that are potentially influenced to a higher degree by the maritime climate found on the west side of the Scandes. Additionally, precipitation correlations on the east side of the Scandes that involve Abisko are all much lower than those correlations without Abisko (Table 4a). This is most likely due to the east-west orientation, maritime climate and rain shadow in the Torneträsk Valley in which Abisko is located.

The correlations between the regional climate record and the weather stations are not straightforward. The correlations between temperatures of different weather stations (Table 4b) had higher correlations than those of precipitation (Table 4b). There is a higher correlation between the regional climate record and precipitation than with temperature (Table 5). There are only three weather stations that have higher temperature correlations than precipitation, the two Norwegian stations that have temperature data (Tromsö and Glömfjord) and one Swedish station (Piteå). Piteå was the only station that did not correlate well with the other weather stations, but it is also the only station east of the Scandes that correlates well with the regional temperature signal. All three of the Norwegian stations have low correlations with the regional precipitation. This is due to only having a small influence on the regional climate data. If we ignore the Piteå correlation there seems to be a correlation between area of influence and correlation in the for the temperature data. Interestingly, the three stations that correlate the highest to the regional climate data for precipitation are those in its center (Jokkmokk, Kvikkjokk, and Tjåmotis) (Figure 10).

Table 5. Correlations between weather station data and regional climate variables.

	Station to Region Correlation	
	Temp	Precip
Jokkmokk	0.359	0.810
Kiruna	NA	0.707
Kvikkjokk	0.346	0.812
Piteå	0.980	0.679
Karesuando	0.345	0.661
Haparanda	0.324	0.684
Tjåmotis	NA	0.834
Abisko	0.344	0.448
Kråkmo	NA	0.168
Stensele	0.331	0.668
Tænaby	0.311	0.568
Sodankylan	0.331	0.586
Glömfjord	0.276	0.173
Tromsö	0.287	0.020

Not included in the Nordklim data set are North Atlantic Oscillation (NAO) indices. Monthly NAO indices were acquired from Dr. Hurrell's (National Center of Atmospheric Research) online database of NAO indices (Hurrell 2008)(Figure 14). Correlations were run between NAO monthly indices and temperature and precipitation to justify the use of NAO as a growth response variable (Figure 15).

Correlations and Response Functions

Detecting the influence of interannual climatic variations on tree-rings was undertaken in DENDROCLILM2002 (Biondi & Waikul 2004). Using DENDROCLIM2002 Pearson's correlations and response functions were calculated between monthly climatic variables (mean monthly temperature, mean monthly precipitation, and mean monthly NAO) and the residual chronology produced from double detrending in ARSTAN. These functions were calculated for an 18 month interval from April of the previous year to October of the current year. This was done because tree ring growth is influenced by indirect factors such as the temperature and precipitation in the previous year and stored as carbohydrates in the roots (Fritts 1976). In the case of trees, the previous year affects the current year by limiting the amount of energy that can be stored.

A PCA was run with the response functions of the three climatic variables for each 19 month period for all 21 mountain birch and six Scots pine plots in order to detect the amount of variation in the ring widths that can be attributed to climate. Analyses was run in PC-ORD (McCune & Grace 2002) with sample sites as the independent variables and climatic variables as the independent variables (Briffa & Cook 1990; Fritts 1974).

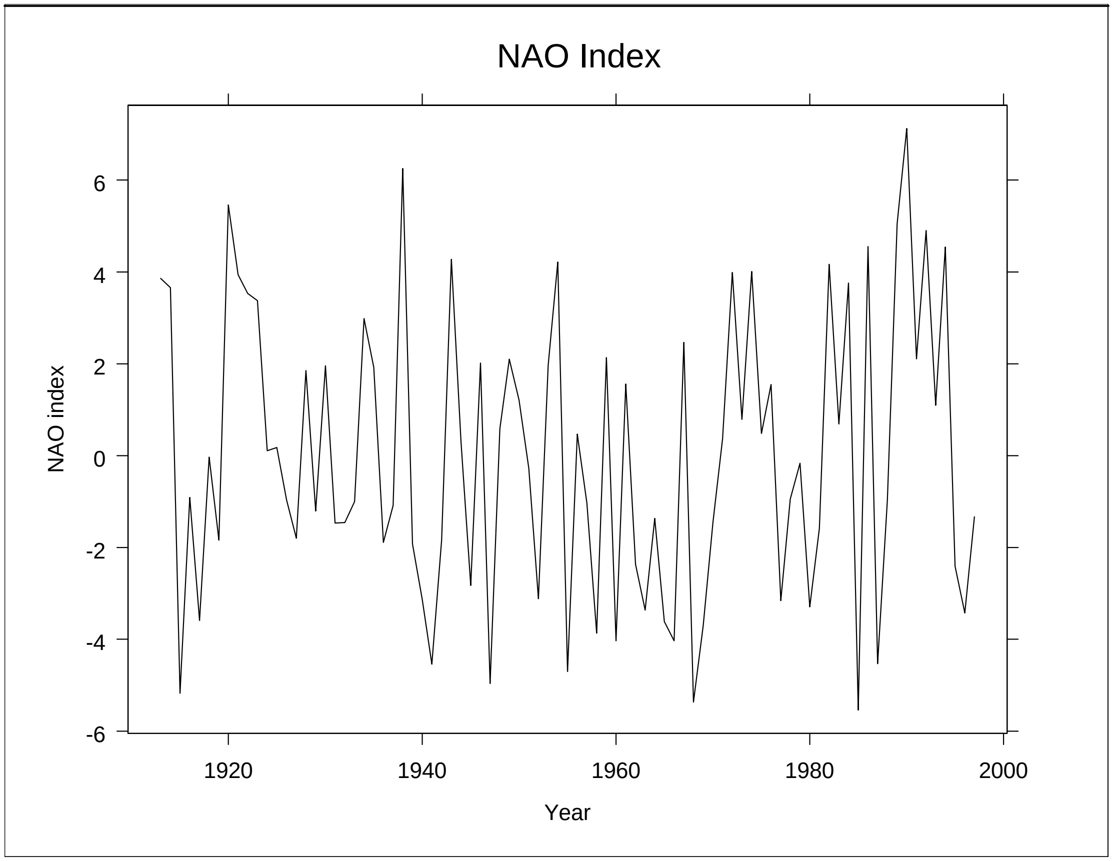


Figure 14. North Atlantic Oscillation (NAO) series 1913 -1997.

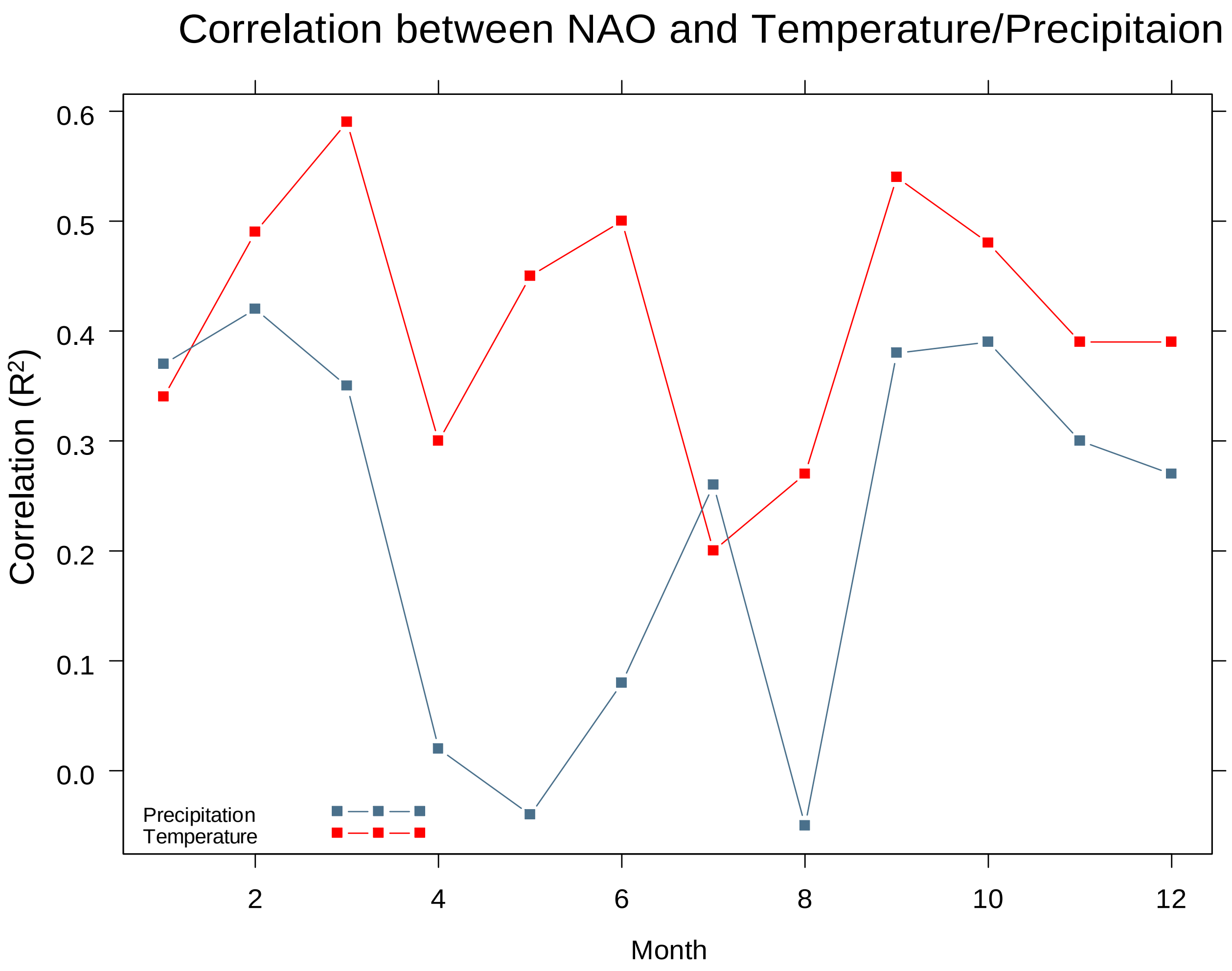


Figure 15. Correlations between regional precipitation and temperature data with NAO.

Axes are determined significant if they contain more information than is expected by chance (McCune & Grace 2002). If eigenvalues for an axis are higher than its broken eigenvalue it is considered to have more information than chance alone (McCune & Grace 2002).

DETECTING OUTBREAKS

Program OUTBREAK

Outbreaks of the autumnal moth are detected using the program OUTBREAK. OUTBREAK was developed to analyze outbreaks of spruce budworm, tussock moth and Pandora moth. In order to detect the outbreaks this program takes a species that is not afflicted by an insect species (non-host) (e.g. Scots pine) and creates an average chronology. The average chronology is created by averaging all each standardized core in the plot together to create an average chronology. Species that are afflicted by insect outbreaks (host) (e.g. mountain birch) have their chronologies subtracted from the non-host average chronology. This removes climatic variability from each tree core and is considered to be a corrected chronology. Potential outbreaks are considered to occur when the ring width indices of the host chronologies are less than those of the non-host chronology. All potential outbreaks are first checked to see if they reach the maximum growth reduction and secondly to see if they fit the length of an outbreak. If it does not accomplish these two factors it is eliminated as an outbreak. For each outbreak a maximum growth reduction is calculated to determine the year of the peak outbreak.

OUTBREAK in the Literature

The methods used by the OUTBREAK program were developed in the Rocky Mountains of the western United States for western spruce budworm (Swetnam and Lynch 1989, Swetnam et al. 1995, Ryerson et al 2003). OUTBREAK has been applied to western spruce budworm in the northern Rockies (Campbell et al 2005; 2006), tussock moth in the southern Rockies (Swetnam et al 1995), Pandora moth in Oregon, USA (Speer et al 2001; Pohl et al. 2006), and on tent caterpillars in Ontario, Canada (Cooke and Roland, 2007).

Parameters Used in OUTBREAK

OUTBREAK requires that two parameters be set by the user, standard deviation of maximum growth reduction and the number of years an outbreak lasts. The default standard deviation is 1.28 which for tussock moth and Pandora moths represents the smallest 10% of the corrected ring index (Speer 2001, Swetnam 1995). The standard deviation that encapsulates the smallest 10% of the values in my chronologies is calculated by finding the mean (-3.61182E-06) and standard deviation (1.000) of all corrected value for rings in the study. The standard deviation is then multiplied by the value that occurs at the smallest 10% from the data set (-1.235). The resulting value (-1.235) is then subtracted from the mean giving a standard deviation (-1.235) that comprised the smallest 10% of the corrected values. The number of years of an outbreak was taken from Tenow (1972) who reported that outbreaks lasted 2-4 years in any one location.

A count of the number of outbreaks that occurs in any given year is interesting but not a very useful measure. The count data was standardized by dividing the number of cores expressing an outbreak but the total number of cores in the plot. The occurrence of outbreaks is more accurately expressed with this measure. In order to better define the outbreaks a filter (10, 20, 30, 40, and 50%) is applied to the proportion of outbreaks data with filters. That is for each filter outbreaks that occurred in at least 10% (20, 30, 40, 50%) of the plot are considered to be outbreaks. A filter of 20% was chosen after comparing it to the historical visual documents that confirmed when outbreaks had occurred (Table 6).

Historical documentation of outbreaks was determined from Tenow (1972), Nilsson et al. (2007) and Klemola et al (2008). Outbreaks of the autumnal moth have been reported since the 1860's by travelers and forest service personnel throughout Fennoscandia. Tenow (1972) made a collection of all the known outbreaks from the 1860's to 1965. The record has been updated by Nilssen et al (2007) for 1965 to 2001. Tenow (1972) and Nilsson et al (2007) established 15 periods of outbreaks across the Scandes (Table 6). Each of these outbreaks has been classified as being a synchronous, a wave with directionality, or a diffuse outbreak. From the historical records Tenow (1972) determined that the average length of an outbreak throughout the Scandes is 5-15 years. The length of an outbreak at a single location is between 2-4 years (Tenow 1972). Periodic outbreaks occur every 9-10 years and moth population densities are highest around the middle of each decade (Tenow 1972).

Table 6. Historically documented outbreak periods (Tenow, 1972; Nilssen et al., 2007).

Period	Outbreak	Period
I	1862 -64?	?
II	? - 1875- ?	?
III	1882-84 ?	Synchronous
IV	1888-92	Synchronous
V	1897-1905	Wave N to S
VI	1905-09	Synchronous
VII	1915-22	Wave N to S
VIII	1922-28	Synchronous
IX	1933-39	Diffuse
X	1942-50	Synchronous
XI	1954-56	Synchronous
XII	1960, 1962-68	Synchronous
XIII	1974-1977	Wave N to S
XIV	1984-87	Synchronous
XV	1992-2001	Wave N to S

There have been numerous papers written on the 1927 outbreak in northern Finland (Kallio & Lehtonen 1973; Lehtonen 1987; Nuorteva 1963; Tenow 1972); the 1955 outbreak in northern Sweden and Norway(Bylund 1997; Eckstein *et al.* 1991; Karlsson *et al.* 2004; Karlsson & Weih 2003; Karlsson *et al.* 2005; Kirchhefer 1996; Sonesson & Hoogesteger 1983; Sveinbjörnsson 2001; Sveinbjörnsson *et al.* 1996; Tenow 1972, 1975, 1996; Tenow & Bylund 2000; Tenow *et al.* 2004)), 1965 (northern Finland (Holtmeier *et al.* 2003; Lehtonen & Heikkinen 1995); the mid-1990's outbreak in northern Norway and Sweden (Tenow *et al.* 2007; Tømmervik *et al.* 2001) and the 2003-2004 outbreak in northern Finland, Sweden and Norway (Klemola *et al.* 2008). These articles helped in determining outbreaks that should appear in my data set.

The majority of the outbreaks that have been written about were represented in my data set at all filter levels. However, the 1955 outbreak was only seen when there was a filter of ≤ 20% . This outbreak is the most documented outbreak in the literature. Consequently a 20% filter was used for further analysis applied to the plot-level data.

OUTBREAK calculates the number of outbreaks, average length and maximum reduction of ring width indices for the entire plot based on individual cores. Additional analyses were conducted on the average length between outbreaks, between maximum outbreaks years and the average number of outbreaks per core. Calculations for plot level data with the 20% filter were conducted on the length between outbreaks, length of outbreaks and the number of outbreaks per plot.

STEPWISE LINEAR REGRESSION

In order to determine the influence of environmental variables on outbreaks, I ran a series of stepwise linear regressions on the common period of record among all cores (1944 and 2003). Eight independent variables were used: elevation, latitude, longitude, slope, aspect, AV, curvature (a measure of a convex or concave landscape), and the percent of stems that were monocormic. Slope, aspect and curvature were calculated from a DEM of the study site with a 50 m resolution. AV is conversion of the circular variable aspect to a linear one and indicates the distance that the aspect of a site is away from SW (Cairns 2001). High values represent southwest facing slopes. There were 10 dependent variables: number of outbreaks per plot, average length of outbreaks per core, average length between outbreaks per core, average length between peak outbreaks per core, length of outbreaks by plot, length between outbreaks by plot, average percent growth reduction, average raw ring width, mean sensitivity of ring widths, and autocorrelation of ring widths.

CLUSTER ANALYSIS

A hierarchical cluster analysis was performed to investigate the similarity in timing and magnitude of outbreaks between plots once climate had be removed. Cluster analysis was run in PC-ORD using a Euclidean distance measure and Ward's linking on the percent of cores that expressed outbreaks from the OUTBREAK data set for the common period of 1944-2003. To examine the differences between clusters and the proper number of clusters to analyze a Multi-Response Permutation Procedure (MRPP) was run using a Euclidean distance measure and a weighting factor of $n/\sum n$ (n= number of plots per cluster). MRPP outputs a test statistic (T), the effect size (A), and the p-value of difference amongst the clusters. The test statistic explains the separation between clusters. Greater negativity of the test statistic explains greater separation between clusters (McCune & Grace 2002). The effect size explains within group homogeneity compared to what is expected by chance (McCune & Grace 2002). If groups are completely homogeneous the effect size is one, if they are heterogeneous it is zero.

CHAPTER IV

RESULTS

DENDROCHRONOLOGY

Twenty-one mountain birch (415 cores, 263 trees) and six Scots pine (134 cores, 69 trees) chronologies were developed in this study (Table 7a); 56.7% of the trees were able to be dated from 415 cores (263 dated/464 total trees) (Table 7b). The average mean interseries correlations of mountain birch are 0.613 (0.506-0.710) (Table 7a). This high correlation with the master chronology indicates that there is a common environment influence affecting the trees. The average mean sensitivity is 0.506 (0.389-0.594); this is high enough to be considered sensitive (Fritts 1976; Grissino-Mayer 2001). Sensitive values indicate large changes in ring widths from one year to another (Fritts, 1976). The autocorrelation found in the series ranged from 0.305-0.622 and averaged 0.507. These values are high indicating that there is a large relationship in growth between consecutive rings.

Of the 78 pines 88.4% were able to be cross-dated (Table 7b) and the average interserries correlation is 0.601 (range = 0.570-0.639). The average mean sensitivity for pines is 0.217 (range = 0.191-0.244) which indicate low to intermediate sensitivity to interannual variation. Autocorrelation was high averaging 0.785 (range = 0.757-0.810).

DENDROCLIMATOLOGY

The most positively correlated climatic influences on tree ring development for both mountain birch and Scots pine are June and July temperatures (Tables 8, 9, & 10,

Table 7. Plot statistics for mountain birch and Scots pine. Statistics for plots are the length of chronology (Length), average age of the plot (Avg.Age), number of cores crossdated (# of Cores), number of trees crossdated (# of Trees), number of trees sampled (# Sampled), Interseries correlation (IS Cor), mean ring width (Mean RW), mean sensitivity (Mean MS), Autocorrelation (Autocor), number of absent rings (Absent Rings), and percent of missing rings (% Absent rings).

Birch

Region	Plot	Length	Avg. Age	# of Cores	# of Trees	# Sampled	IS Cor	Mean RW	Mean Sen	Autocor	Absent Rings	% Absent Rings
Kenivuopio	KND	1886-2007	78	20	11	20	0.609	0.575	0.527	0.576	18	1.154
	KNB	1907-2007	65	16	11	20	0.530	0.623	0.514	0.581	8	0.773
	KNA	1858-2006	88	13	9	20	0.576	0.693	0.493	0.622	2	0.176
Jarmara	JAB	1895-2007	73	17	10	20	0.524	0.492	0.480	0.564	2	0.16
	JAA	1923-2007	53	25	16	20	0.690	1.055	0.475	0.441	1	0.075
Tornetrask	ABD	1935-2007	60	21	13	20	0.710	0.724	0.481	0.475	0	0
	ABA	1865-2007	83	28	11	20	0.611	0.499	0.516	0.592	18	0.776
	ABB	1899-2007	66	20	14	20	0.568	0.060	0.560	0.600	7	0.534
Nikkaluokta	NID	1878-2007	50	23	14	20	0.586	0.881	0.594	0.467	17	1.483
	NIE	1882-2007	66	29	17	20	0.668	0.586	0.530	0.520	0	0
Ritsem	GAH	1927-2005	36	20	13	16	0.629	1.474	0.453	0.547	0	0
	GAR	1944-2005	40	21	16	20	0.641	1.069	0.389	0.616	0	0
	GAL	1931-2005	57	20	12	20	0.660	0.699	0.496	0.419	0	0
	RIT1	1917-2003	68	15	13	28	0.630	0.715	0.462	0.573	0	0
	RIT3	1944-2003	59	15	9	16	0.541	1.059	0.499	0.440	0	0
	RIT2	1935-2003	49	28	13	25	0.671	1.158	0.467	0.493	0	0
	VAK	1930-2005	46	14	10	19	0.687	0.906	0.503	0.436	0	0
Kvikkkjokk	SJN	1940-2005	42	27	16	20	0.685	0.710	0.556	0.305	1	0.085
Vuogetjalme	MAD	1915-2005	81	9	7	20	0.506	0.524	0.542	0.373	0	0
	JUA	1876-2005	92	22	17	40	0.636	0.639	0.536	0.503	4	0.197
	STR	1900-2005	79	12	11	40	0.517	0.630	0.546	0.503	0	0
			63.38	415	263	464	0.613	0.751	0.506	0.507	78	0.269

Pines

Region	Plot	Length	Avg. Age	# of Cores	# of Trees	# Sampled	IS Cor	Mean RW	Mean Sen	Autocor	Absent Rings	% Absent Rings
Over Soppero	OSA	1879-2007	105	35	18	20	0.630	1.451	0.207	0.808	0	0
Tornetrask	ABE	1755-2007	157	16	7	7	0.574	0.788	0.244	0.810	0	0
	ABC	1783-2007	132	39	19	20	0.613	1.510	0.208	0.757	0	0
Nikkaluokta	NIB	1648-2007	156	40	21	21	0.570	1.567	0.230	0.800	0	0
Ritsem	KIR	1880-2006	146	13	8	15	0.610	0.962	0.191	0.759	0	0
Vuogetjalme	VOU	1799-2006	110	26	14	15	0.639	1.369	0.220	0.778	0	0
			134.33	134	69	78	0.601	1.239	0.217	0.785		

Table 8. Pearson's correlation between residual tree ring indices for each plot and regional climate variables: temperature (T), precipitation (P), and NAO. Negative symbols represent a significant negative correlation to the climate variable.

CORRELATION FUNCTION

	APR	**MAY**	**JUN**	**JUL**	**AUG**	**SEP**	**OCT**	**NOV**	**DEC**	**jan**	**feb**	**mar**	**apr**	**may**	**jun**	**jul**	**aug**	**sep**	**oct**
KND									T						T	T	NAO		-P
KNB															T				-P
KNA			T							T	P				T, NAO	T, NAO	NAO		
JAB	T													T	T	T			
JAA										-P	-T		-T	-P	T	T, NAO	T		-P
ABD		-P		T, NAO			-P		NAO				-P		-T			T	
ABA			T				-P				-T				T	T		-T	-P, -NAO
ABB			NAO		NAO										T, NAO	T, NAO			-P
NIE															T, NAO	T, -P			-P
NID				T	NAO								NAO		T	T			-P
GAH		T	T				-P									T			
GAR										T					T, NAO	NAO			-NAO
GAL											-T				T, NAO	T, NAO			-P, -NAO
RIT1			T					-T		-NAO	-T				T, NAO	T	T		
RIT3						-P								-P	T, NAO				
RIT2							-P								T, NAO	T, NAO			
VAK										P			-T						
SJN						-P	-NAO								T		NAO		-NAO
MAD		-P													T, -P	T, NAO			-P
JUA														-P	T	T			-P
STR													-P	T			P	T	-P.-NAO
OSA	NAO	T		-T	NAO			NAO	T, NAO				T			T			
ABE	NAO				NAO								T	T	T, NAO	T			
ABC	NAO	T	T, NAO			T		NAO							NAO	T,-P			
NIB	-T		T, NAO												NAO	T, -P			
KIR	-P							NAO								T			
VOU				-T									T	T	T, NAO	T, -P			

Table 9. Response functions between residual tree ring indices for each plot and regional climate variables: temperature (T), precipitation (P), and NAO. Negative symbols represent a significant negative correlation to the climate variable.

RESPONSE FUNCTION

	APR	**MAY**	**JUN**	**JUL**	**AUG**	**SEP**	**OCT**	**NOV**	**DEC**	**jan**	**feb**	**mar**	**apr**	**may**	**jun**	**jul**	**aug**	**sep**	**oct**
KND																T			
KNB																			
KNA											P				T, NAO	T, NAO			T
JAA											P				T	T	T		
JAB												T			T				
ABD				T, NAO							-P								
ABA											-T				T	T		-T	-P,-NAO
ABB	T		NAO		NAO						P				T	T, NAO			-P
NIE															T	T, -P			-P
NID				T						-P			NAO						-P
GAH		T, NAO	T																
GAR									-NAO						T				
GAL											-T				T, NAO	T			-P, -NAO
RIT1								-T		-NAO	-T				T	T			
RIT3						-P					-T				T				
RIT2															T, NAO	T			-P
VAK																	NAO		
SJN						-P									T				
MAD									-T		NAO				T	T			-P
JUA															T	T			-P
STR																		T	-NAO
OSA	NAO			-T	NAO			NAO								T			
ABE	NAO				NAO														
ABC			NAO													T			
NIB	-T		T												NAO	T, -P			
KIR								NAO							-T	T			
VOU				-T									T	T	NAO	T, -P			

Table 10. Percent plots with a correlation or response function to temperature, precipitation, or NAO for the previous and current years.

	Correlation Function						Response Function					
	Temperature (%)		Precipitation (%)		NAO (%)		Temperature (%)		Precipitation (%)		NAO (%)	
Mountain Birch	Positive	Negative	Positive	Negative	Positive	Negative	Positive	Negative	Positive	Negative	Positive	Negative
P Spring	10			10			10				5	
P Summer	29				14		14				14	
P Fall		5		24		5		5		10		
Winter	14	19	10	5	5	5		24	14	10	5	10
Spring	10	10		24	5		5				5	
Summer	81	5	5	10	57		71			5	19	
Fall	10	5		52		24	10	5		38		14
Scots Pine												
P Spring	33	17		17	50			17			33	
P Summer	33	33			67			33			50	
P Fall	17				50						33	
Winter	17				17							
Spring	50						17					
Summer	100			50	67		83	17		33	33	
Fall												

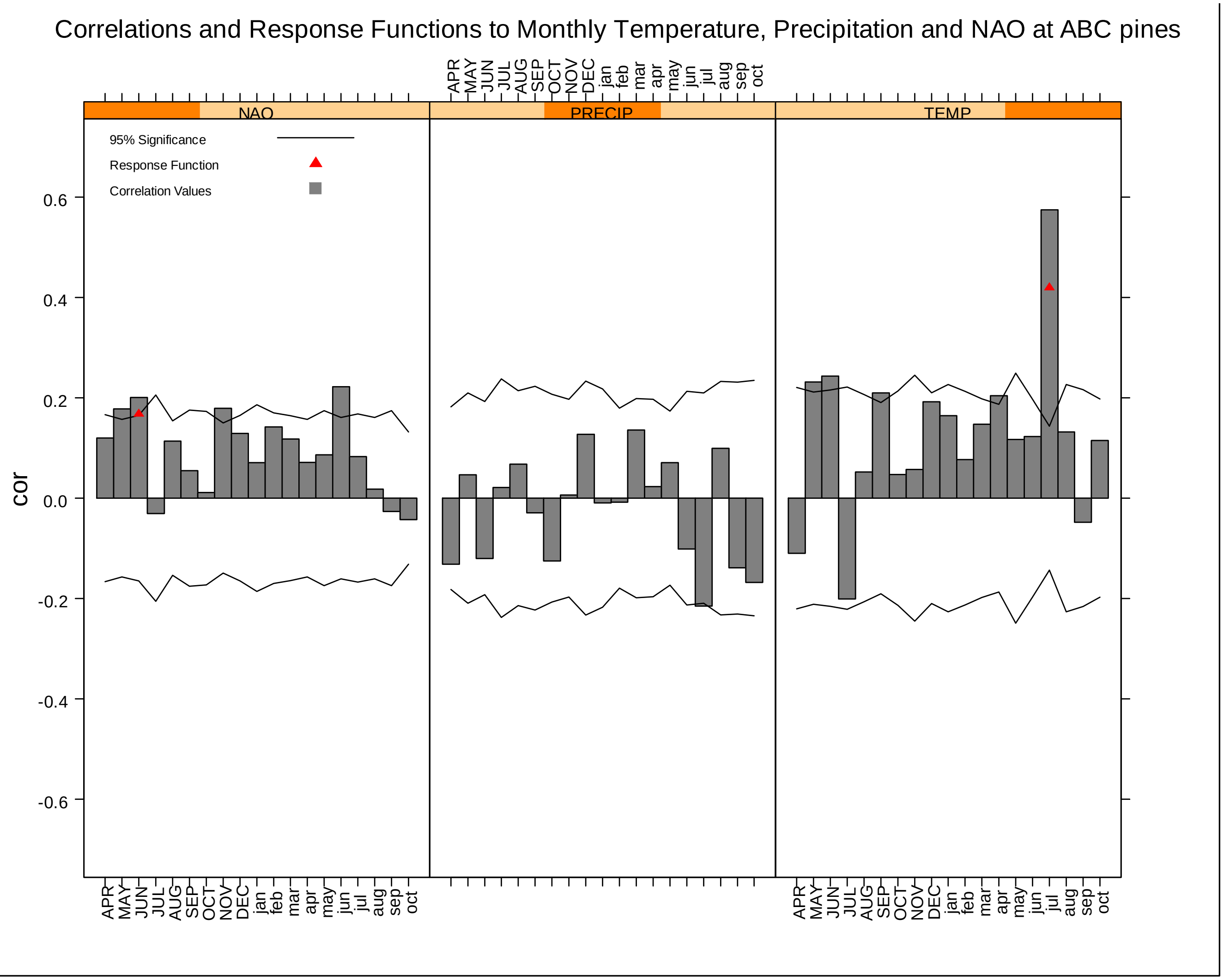


Figure 16 a). Correlation and response functions between the regional climate and NAO series. P-value <0.05. Torneträsk Pines (Example of pine correlations and response).

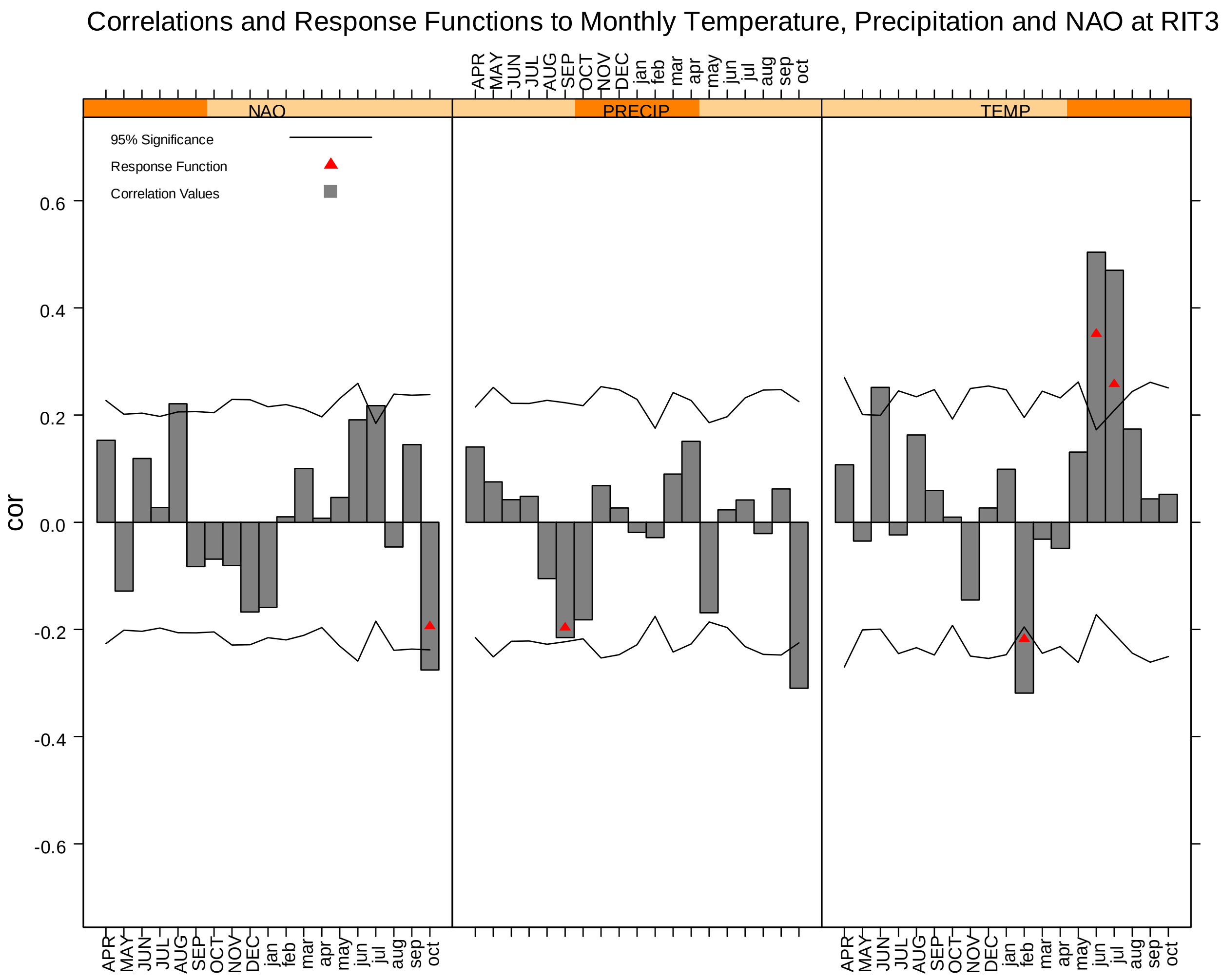


Figure 16 Continued. b). Ritsem Birches (Example of birch correlations and response).

Figure 16). The birches also respond positively to the previous June temperatures but negatively to February temperatures. Precipitations in October of the previous year and current year have negative influences on ring growth.

NAO corresponds similarly to temperature and precipitation and is positive when temperature is positive and negative when precipitation is negative (Tables 8, 9, & 10, Figure 16). NAO responds during the winter for the three pine sites that were located within the continuous forest.

The first PCA axis accounts for 46.2% in the mountain birch and 66.4% in the Scots pines of variation attributed to climate. This axis one represents the response functions that are most influential on tree ring growth. The second and third axes for both species account for indeterminable variation (Table 11).

OUTBREAKS

Figure 17 is example from Vuoggatjålme of the number of outbreaks that occurred per year. The number of outbreaks per year was standardized by dividing the number of cores expressing an outbreak by the total number of cores in the plot for that year (Figures 18). The standardized outbreak record better expresses periods of outbreaks than the raw count data. Background noise from the outbreak record was removed by applying filters of 10, 20, 30, 40, and 50% to the data. The filter removed outbreaks that did not occur in at least 10% (20, 30, 40, 50%) of the cores per year (Figures19 a-e). Filters were first applied to regional data in order to choose a filter strength that best displayed the outbreaks without removing too much information

Table 11. Percent variation of PCA response function axes. In both mountain birch and Scots pine the first axis is the only one that significantly explains variation due to climate.

	Mountain Birch		Scots Pine	
Axis	% of Variance	Cumulative Variance	% of Variance	Cumulative Variance
1	46.155	46.155	66.372	66.372
2	9.112	55.267	11.026	77.398
3	7.137	62.404	9.239	86.637
4	5.5	67.904	6.595	93.232
5	4.976	72.88	4.501	97.734
6	4.473	77.353	2.266	100

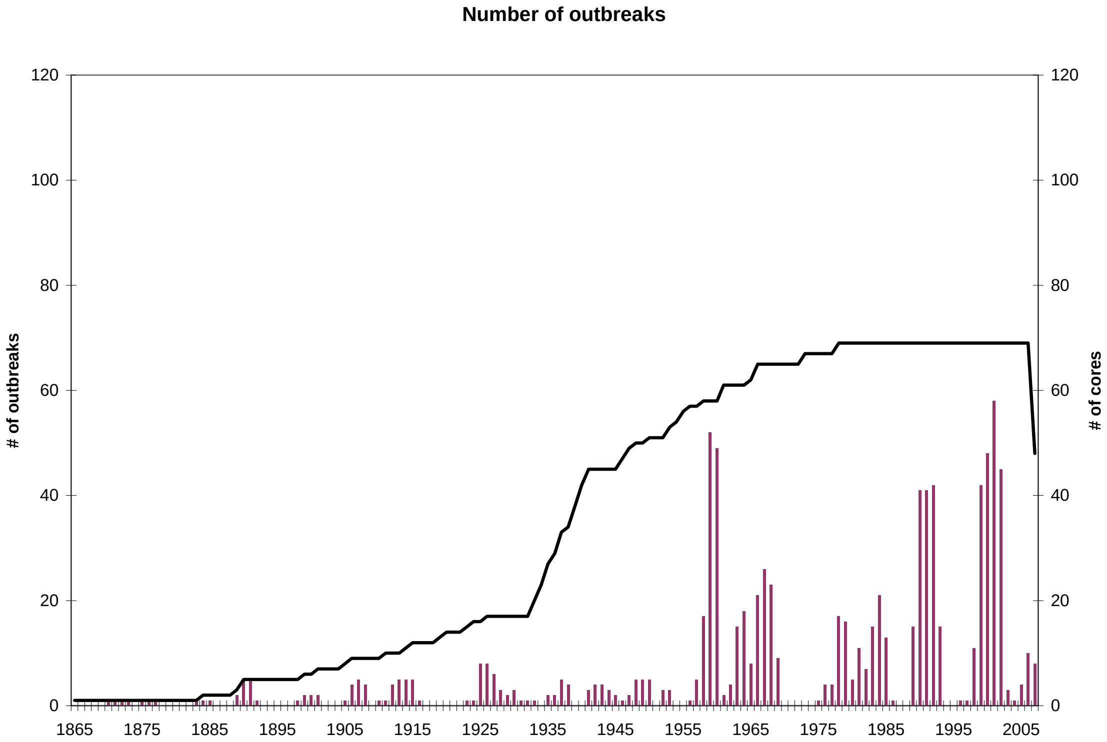


Figure 17. Number of outbreaks recorded per year at Torneträsk. Pink bars represent each outbreak that was counted for all cores. The black line is the number of cores used in the analysis.

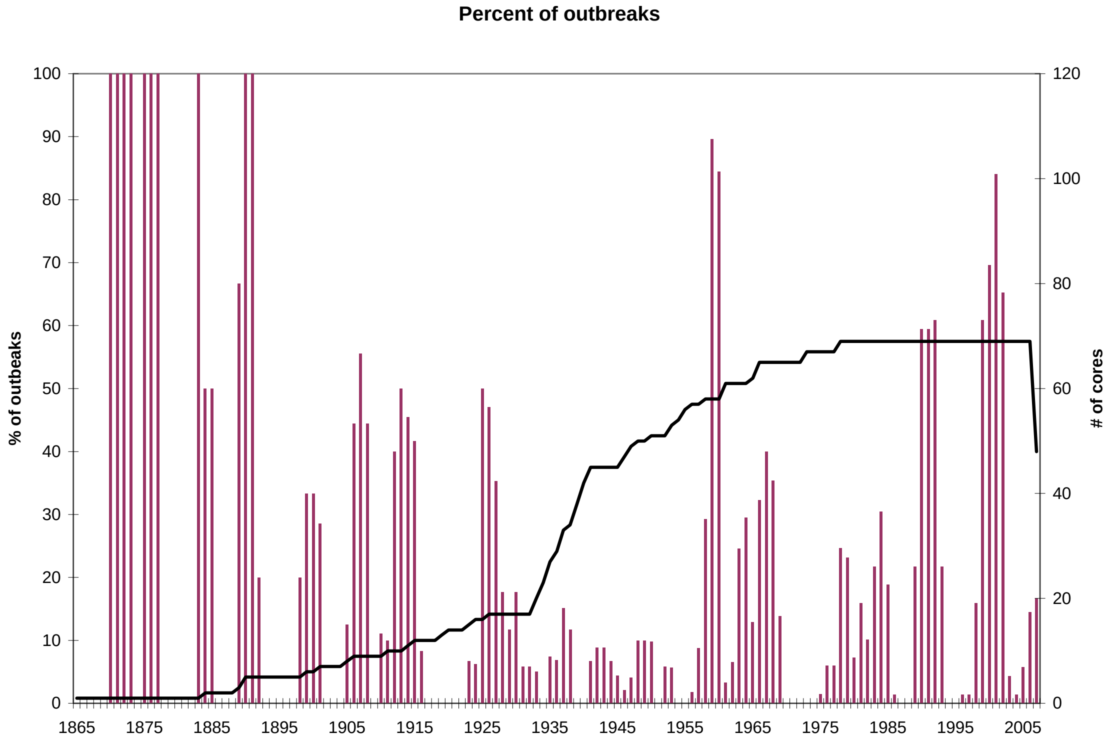


Figure 18. Percent of outbreaks recorded per year at Torneträsk. Pink bars are the number of outbreaks divided by the number of cores. The black line is the number of cores.

a.

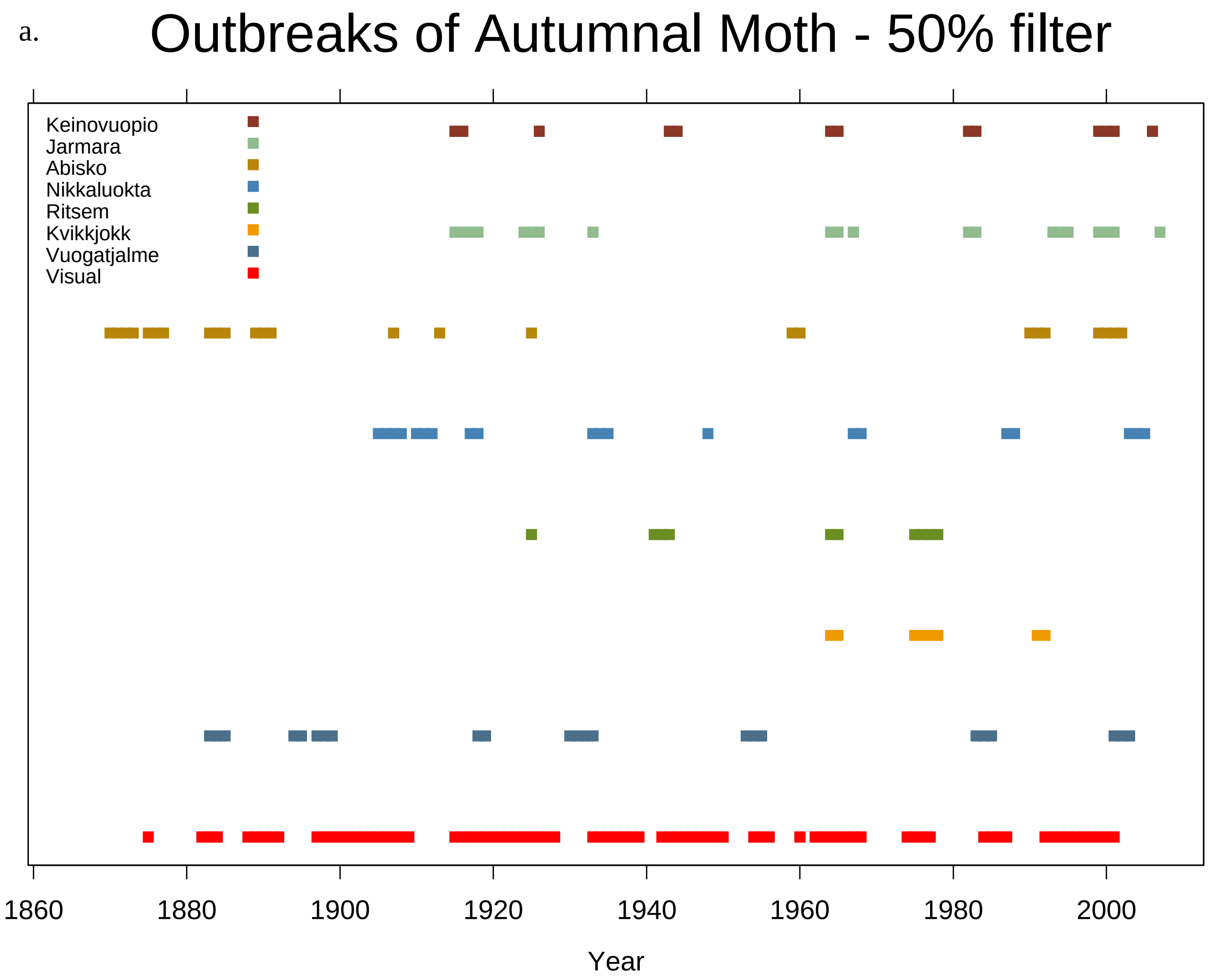


Figure 19. Outbreaks for all regions with 50, 40, 30, 20 and 10% filters. a). 50% filter

b.

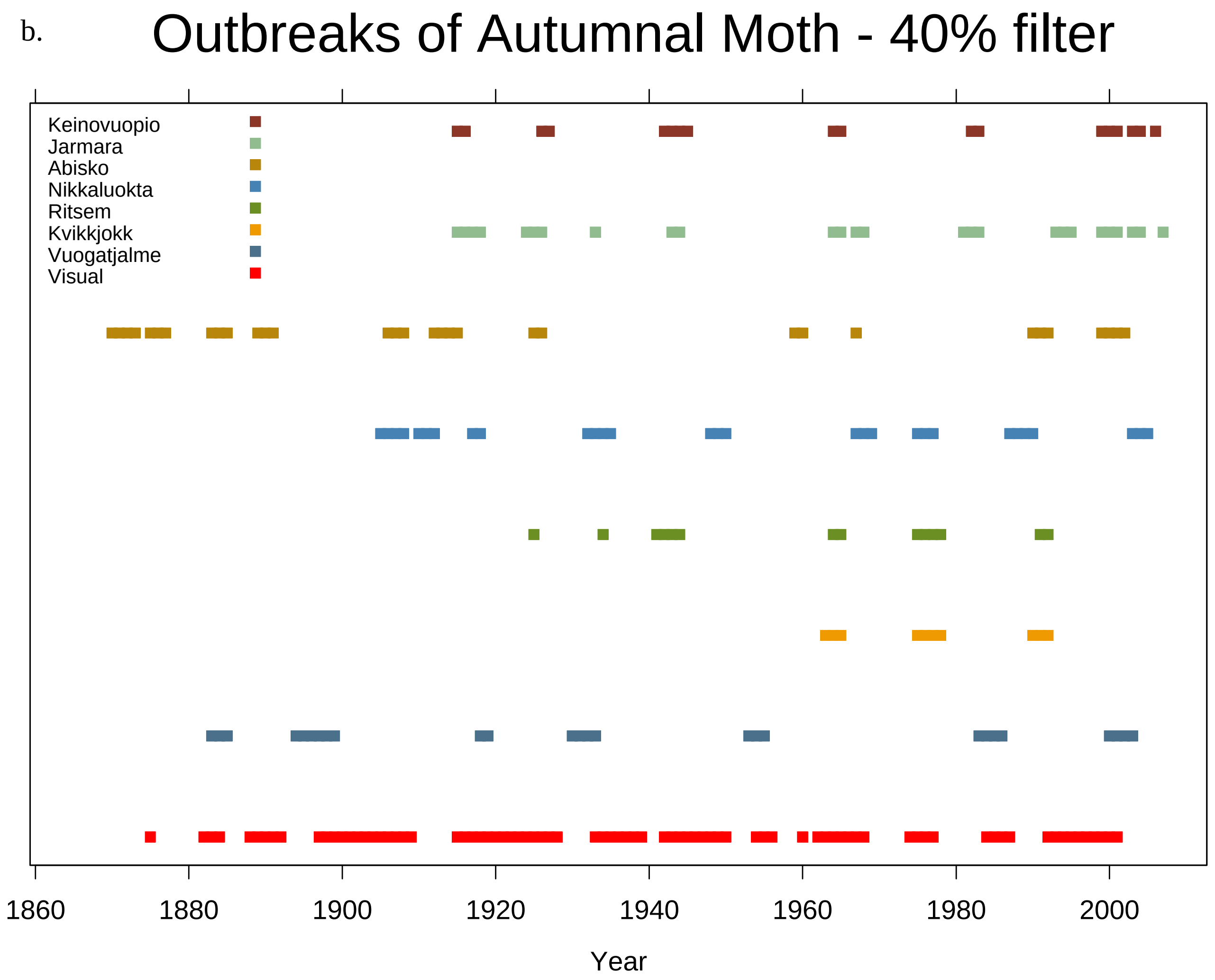


Figure 19 Continued   b). 40% filter.

c.

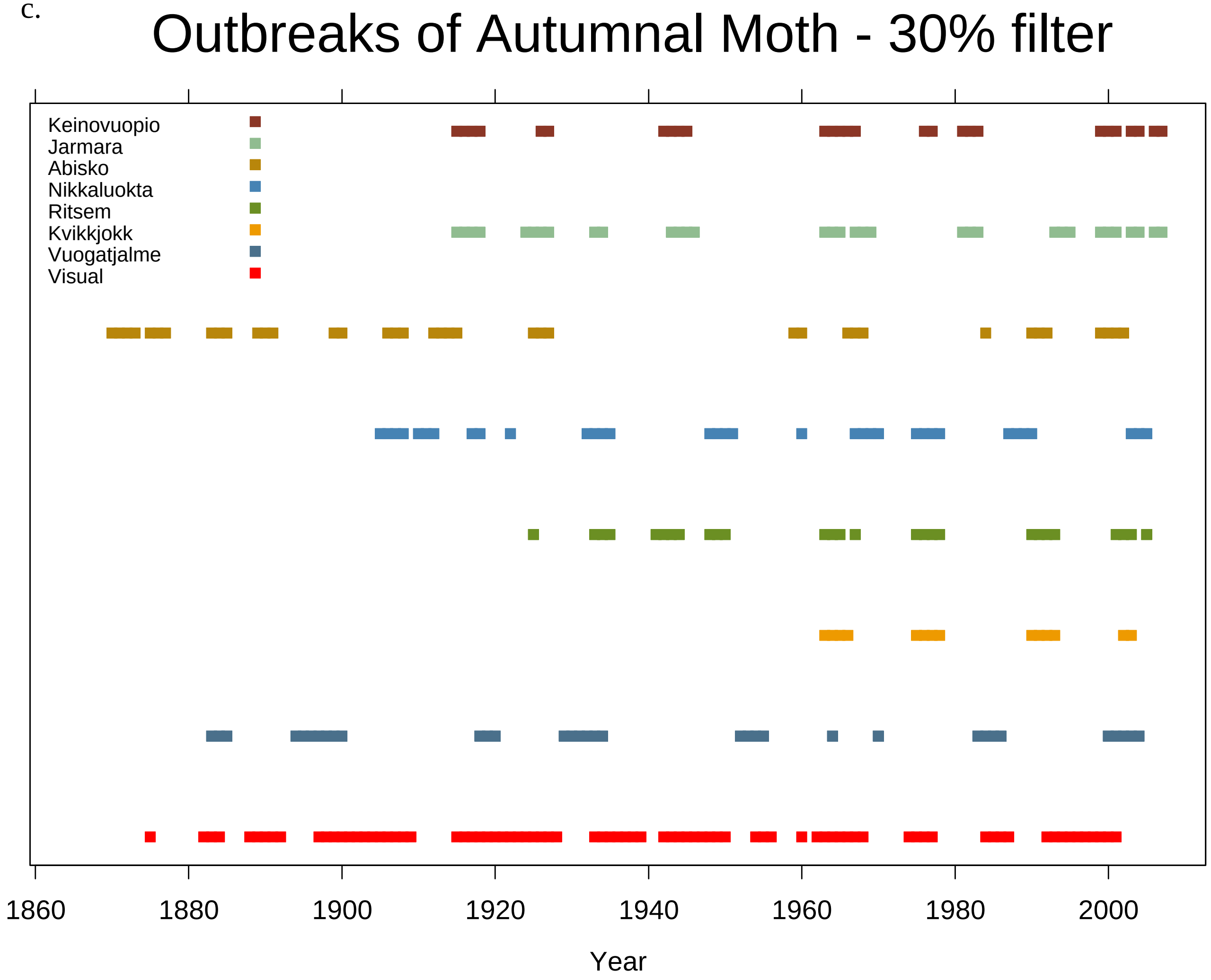


Figure 19 Continued c). 30% filter.

d.

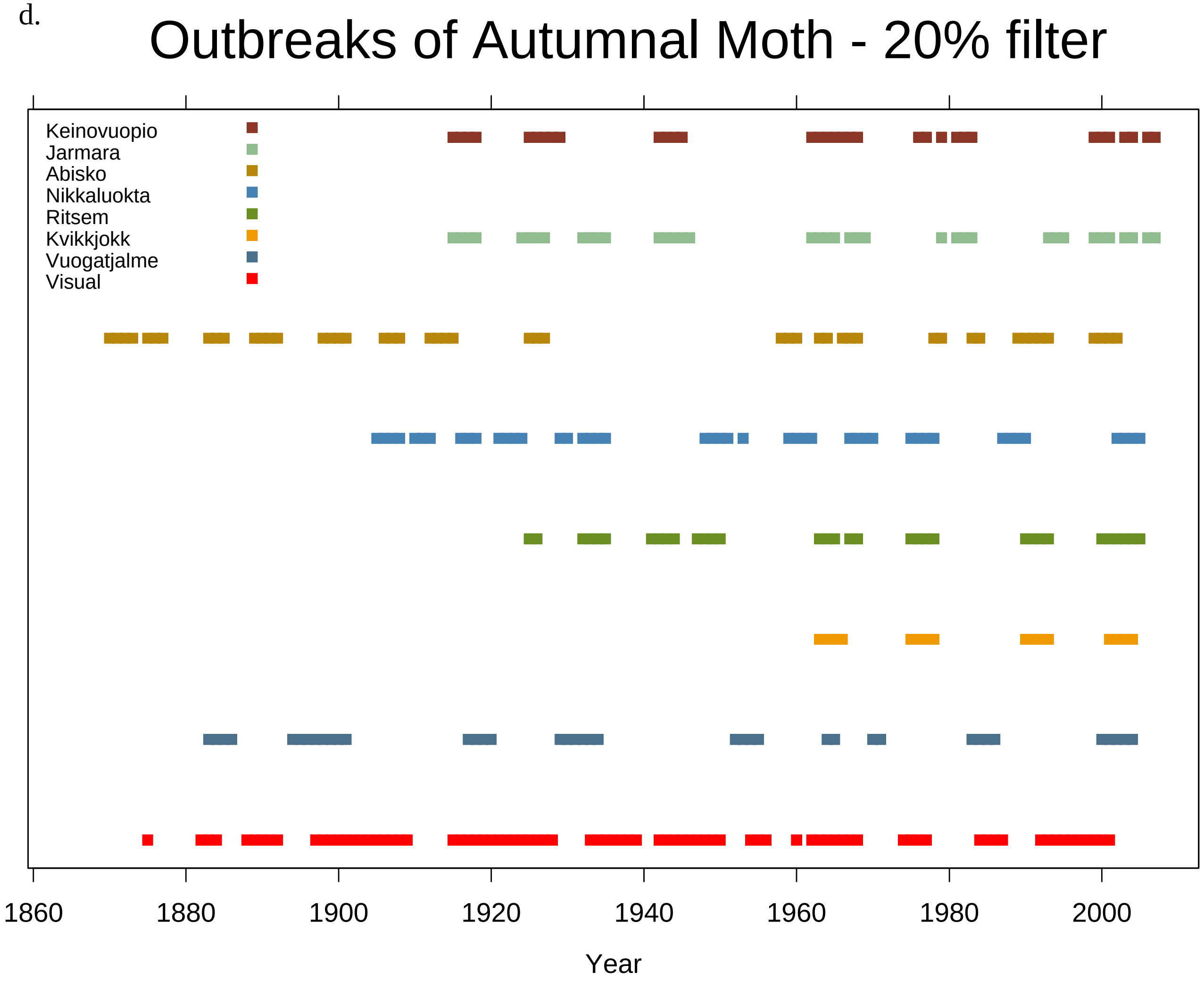


Figure 19 Continued   d). 20% filter.

e.

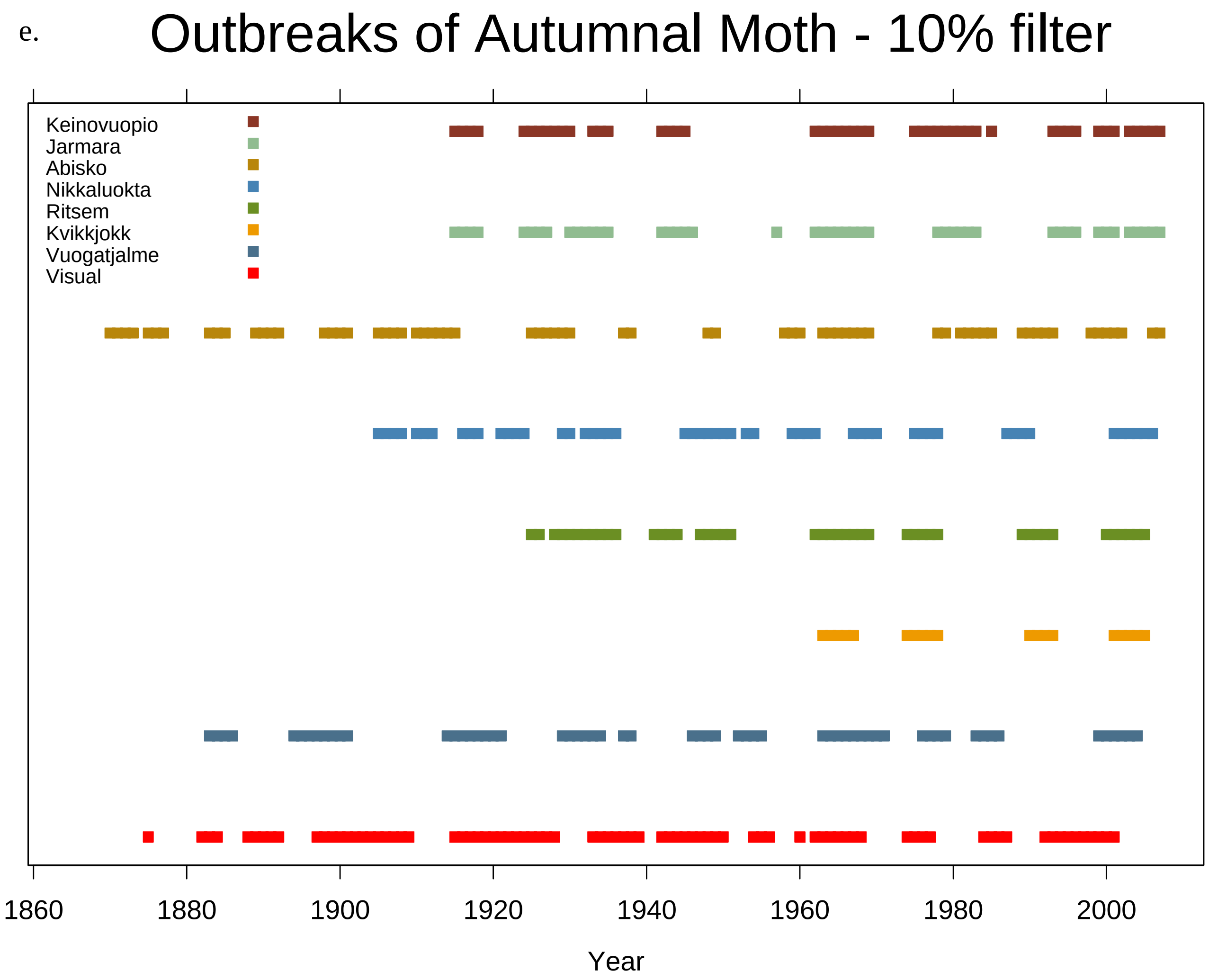


Figure 19 Continued e). 10% filter

Table 12. Number of outbreaks found for the different filters. Outbreaks are the period from when an outbreak is recorded to occur. Max outbreak is the year in which the maximum number of trees recorded an outbreak.

Abisko

10		20		30		40		50	
Outbreak	Max Outbreak	Outbreak	Max Outbreak	Outbreak	Max Outbreak	Outbreak	Max Outbreak	Outbreak	Max Outbreak
1870-1873	1872	1870-1873	1872	1870-1873	1872	1870-1873	1872	1870-1873	1872
1875-1877	1876	1875-1877	1876	1875-1877	1876	1875-1877	1876	1875-1877	1876
1883-1885	1884	1883-1885	1884	1883-1885	1884	1883-1885	1884	1883-1885	1884
1889-1892	1890	1889-1891	1890	1889-1891	1890	1889-1891	1890	1889-1891	1890
1898-1901	1899	1898-1901	1899*	1899-1901	1899*	1906-1908	1907*	1907	1907*
1905-1908	1907	1906-1908	1907	1906-1908	1907	1912-1915	1914	1913	
1910-1915	1914	1912-1915	1914	1912-1915	1914	1925-1926	1925*	1925	1925*
1925-1930	1925	1925-1927	1925	1925-1927	1925*	1959-1960	1959*	1959-1960	1959*
1937-1938	1937	1958-1960	1959	1959-1960	1959*	1967	1967*	1990-1992	1992*
1948-1949	1949*	1963-1964	1964	1966-1968	1967*	1990-1992	1992*	1999-2002	2001
1958-1960	1959	1966-1968	1967	1984	1984*	1999-2002	2001		
1963-1969	1964:1967	1978-1979	1978*	1990-1992	1992				
1978-1979	1978	1983-1984	1984	1999-2002	2001				
1981-1985	1984	1989-1993	1992						
1989-1993	1992	1999-2002	2001						
1998-2002	2001								
2006-2007									

* below filter level

(Table 12). The 20% filter was applied to the plot level data after determining that it best represented known outbreak periods while still removing some background noise (Figure 20).

The number of outbreaks per region ranged from four in Kvikkjokk (SJN) to 15 in Torneträsk (ABA) (Figures 19 d & 20). The frequencies of these outbreaks differ slightly across northern Sweden. The average length between outbreaks is 12.8 years. The shortest occurred in Ritsem (RIT2) 9.2 years and the longest in Vuoggatjåme (MAD) 19.7 years (Table 13). The average length of an outbreak is 3.2 years (range = 2.9-3.6) (Tables 13 & 14). The length of an outbreak may be influenced by the parameter used to determine outbreaks of 2-4 years. The average number of outbreaks on a core ranged from 1.3 in Ritsem (GAH) to 4.9 in Torneträsk (ABA). The lowest average growth reduction was found in Ritsem (79.1%) and highest average growth reduction was in Vuoggatjåme (95.9%) (Table 14).

Lengths between outbreaks and lengths of outbreaks calculated from the 20% filter showed reversed trends. The time between outbreaks showed longest intervals in the southern regions and they also had the shortest outbreak levels. The northern areas had shorter intervals between outbreaks and longer outbreaks (Table 13 & 14). Growth reduction due to outbreaks was high for all plots.

STEPWISE LINEAR REGRESSION

The strongest regression model was for length between outbreaks (R^2= 0.9797). The variables controlling growth reduction are the percent of the plot that is

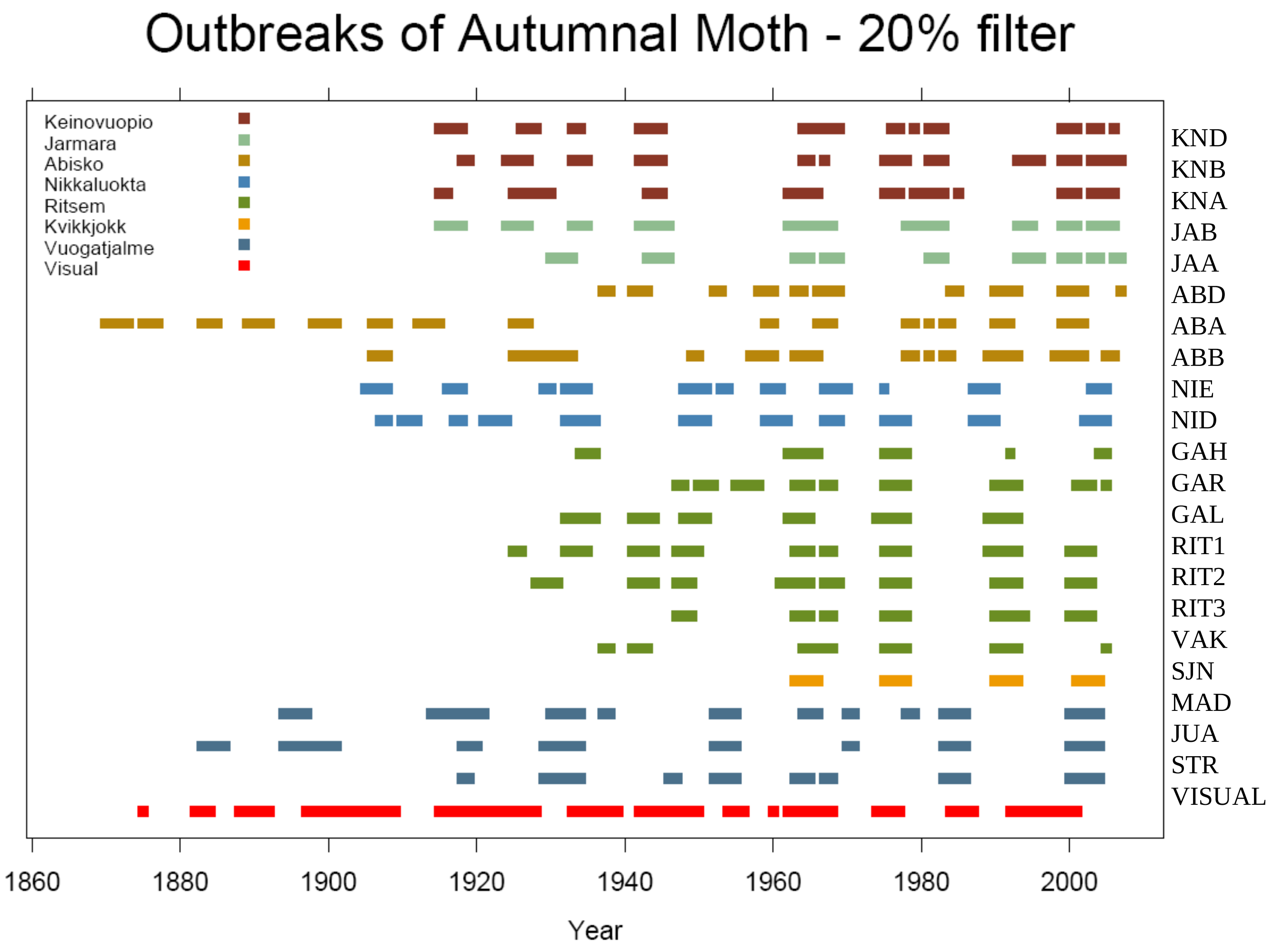


Figure 20. Outbreaks in all plots with a 20% filter compared to the historical outbreak chronology. Plots are displayed from north to south.

Table 13. Regional outbreak statistics. Length out – average length of outbreak per core, GR- average growth reduction in percentage per core, length btw – average length between outbreaks per core, length btw max – average length between peak of outbreaks per core, # per cor – average number of outbreaks per core, length 20% - average length of outbreak per plot with a 20% filter, btw 20% - average length between outbreaks per plot with a 20% filter, # per region – average number of outbreaks per plot.

Region	length out	GR	length btw	length btw max	# per cor	length 20%	btw 20%	# per region
Keinovuopio	3.113	94.26%	13.177	15.459	4.216	5.729	6.367	10.33
Jarmara	2.915	88.76%	10.976	13.057	4.312	5.058	6.438	9.00
Abisko	3.110	92.74%	12.931	15.213	4.087	5.758	5.792	12.00
Nikkaluokta	3.200	94.59%	14.310	16.456	3.512	3.877	6.350	11.00
Ritsem	3.340	89.02%	11.004	13.498	2.371	4.796	7.557	6.57
Kvikkjokk	3.520	95.69%	12.200	15.114	2.259	2.082	8.667	4.00
Vuogetjalme	3.367	95.26%	16.547	18.788	4.365	3.810	10.571	8.33
	3.224	92.90%	13.021	15.369	3.589	4.444	7.392	8.748

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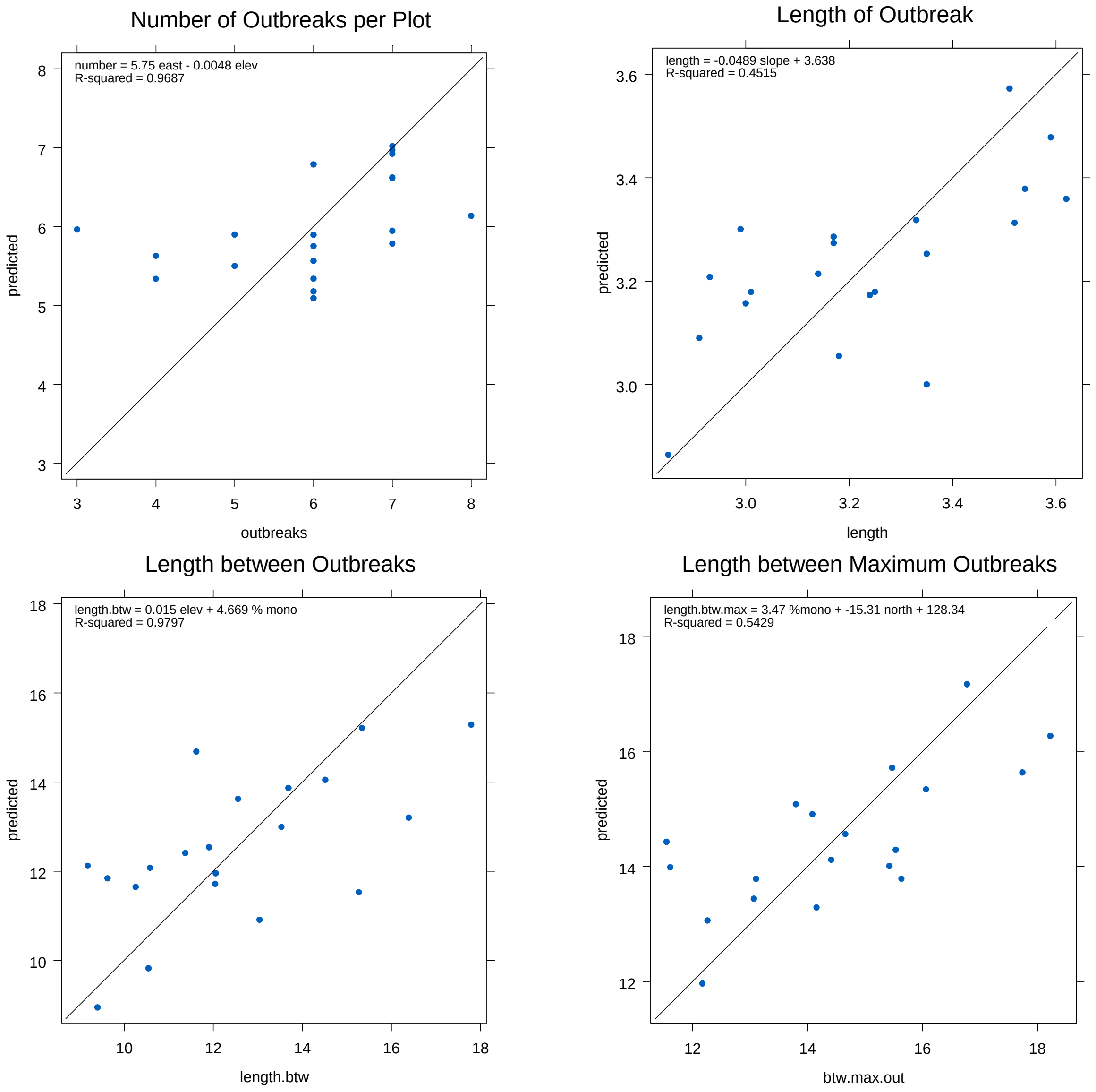
Table 14. Plot outbreak statistics. Length out – average length of outbreak per core, GR- average growth reduction in percentage per core, length btw – average length between outbreaks per core, length btw max – average length between peak of outbreaks per core, # per cor – average number of outbreaks per core, length 20% - average length of outbreak per plot with a 20% filter, btw 20% - average length between outbreaks per plot with a 20% filter, # per region – average number of outbreaks per plot.

Plot	# of Cores	Total # of Out	Length of Out		GR		Length btw Out		Length btw Max Out		# of Out Per Cor		Out w/20%		btw Out w/20%		# Out Per Plot
			mean	stdev	mean	stdev	mean	stdev	mean	stdev	mean	stdev	mean	stdev	mean	stdev	
KND	20	85.00	3.16	0.75	95.4%	8.8%	15.12	11.00	17.54	11.57	4.25	1.45	6.06	1.47	6.10	2.82	11
KNB	16	63.00	3.15	0.80	94.0%	9.5%	12.32	10.68	14.64	10.80	3.94	1.57	5.15	1.17	5.50	3.18	11
KNA	13	58.00	3.03	0.90	93.4%	11.8%	12.09	8.83	14.20	9.15	4.46	2.33	5.98	1.59	7.50	3.56	9
JAB	17	82.00	2.92	0.87	90.4%	12.4%	11.54	8.50	13.60	8.81	4.82	1.19	4.34	1.41	6.63	4.33	9
JAA	25	95.00	2.91	0.86	87.1%	14.4%	10.41	7.03	12.51	7.31	3.80	1.66	5.78	0.78	6.25	3.11	9
ABD	21	76.00	3.01	0.87	92.9%	12.2%	13.27	10.20	15.65	10.15	3.62	0.67	3.98	1.06	4.89	2.70	10
ABA	28	137.00	2.97	0.84	93.0%	10.3%	13.10	10.87	15.18	10.74	4.89	2.17	7.56	0.93	6.29	3.00	15
ABB	20	75.00	3.35	0.83	92.4%	11.0%	12.42	9.86	14.80	10.01	3.75	1.55	5.73	2.25	6.20	3.55	11
NID	23	64.00	3.21	0.76	95.9%	8.6%	15.44	10.82	17.56	11.09	2.78	1.38	4.32	1.04	6.70	3.09	11
NIE	29	123.00	3.19	0.88	93.3%	11.2%	13.18	8.97	15.35	8.98	4.24	1.50	3.43	0.93	6.00	3.55	11
GAH	20	32.00	2.94	0.93	84.1%	21.8%	14.44	7.51	16.69	8.19	1.31	0.87	7.46	1.58	14.25	3.00	5
GAR	21	48.00	3.18	0.83	79.1%	17.6%	10.69	6.34	13.17	6.74	2.29	1.23	3.64	1.05	4.13	2.89	9
GAL	20	61.00	3.52	0.67	95.7%	7.6%	10.81	5.24	13.36	5.35	3.05	1.39	3.32	0.55	7.00	4.50	6
RIT1	14	53.00	3.62	0.71	91.2%	13.6%	12.03	7.78	14.85	7.92	3.79	1.67	3.68	1.01	5.88	3.56	9
RIT3	15	33.00	3.17	0.81	90.9%	13.8%	10.58	5.49	13.11	5.98	2.06	1.12	5.40	2.61	7.25	3.95	5
RIT2	28	61.00	3.54	0.74	89.8%	15.3%	9.18	4.45	11.55	4.59	2.18	0.77	3.33	1.51	4.40	2.19	6
VAK	13	25.00	3.41	0.78	92.4%	10.5%	9.31	5.12	11.77	5.25	1.92	1.19	6.75	1.47	10.00	3.17	6
SJN	27	61.00	3.52	0.84	95.7%	7.9%	12.20	5.67	15.11	6.10	2.26	0.90	2.08	0.00	8.67	4.00	4
MAD	9	34.00	3.42	0.86	94.7%	9.6%	19.72	17.61	21.84	18.17	3.78	1.39	2.86	1.77	11.00	9.51	9
JUA	22	105.00	3.42	0.79	95.9%	8.1%	16.77	10.42	19.19	10.46	4.77	1.88	3.82	1.85	12.29	4.50	8
STR	11	50.00	3.26	0.87	95.2%	9.7%	13.15	9.92	15.33	10.30	4.55	1.13	4.76	1.51	8.43	3.50	8
			3.23		92.01%		12.75		15.10		3.45		4.73		7.40		8.67



Number of Outbreaks per Plot

Length of Outbreak

Length between Outbreaks

Length between Maximum Outbreaks

Figure 21. Stepwise linear regressions of outbreak and ring characteristics compared to dependent variables. Dependent variables are elevation (elev), latitude (north), longitude (east), percent monocormic (% mono), slope, curvature (curv), AV, and aspect.

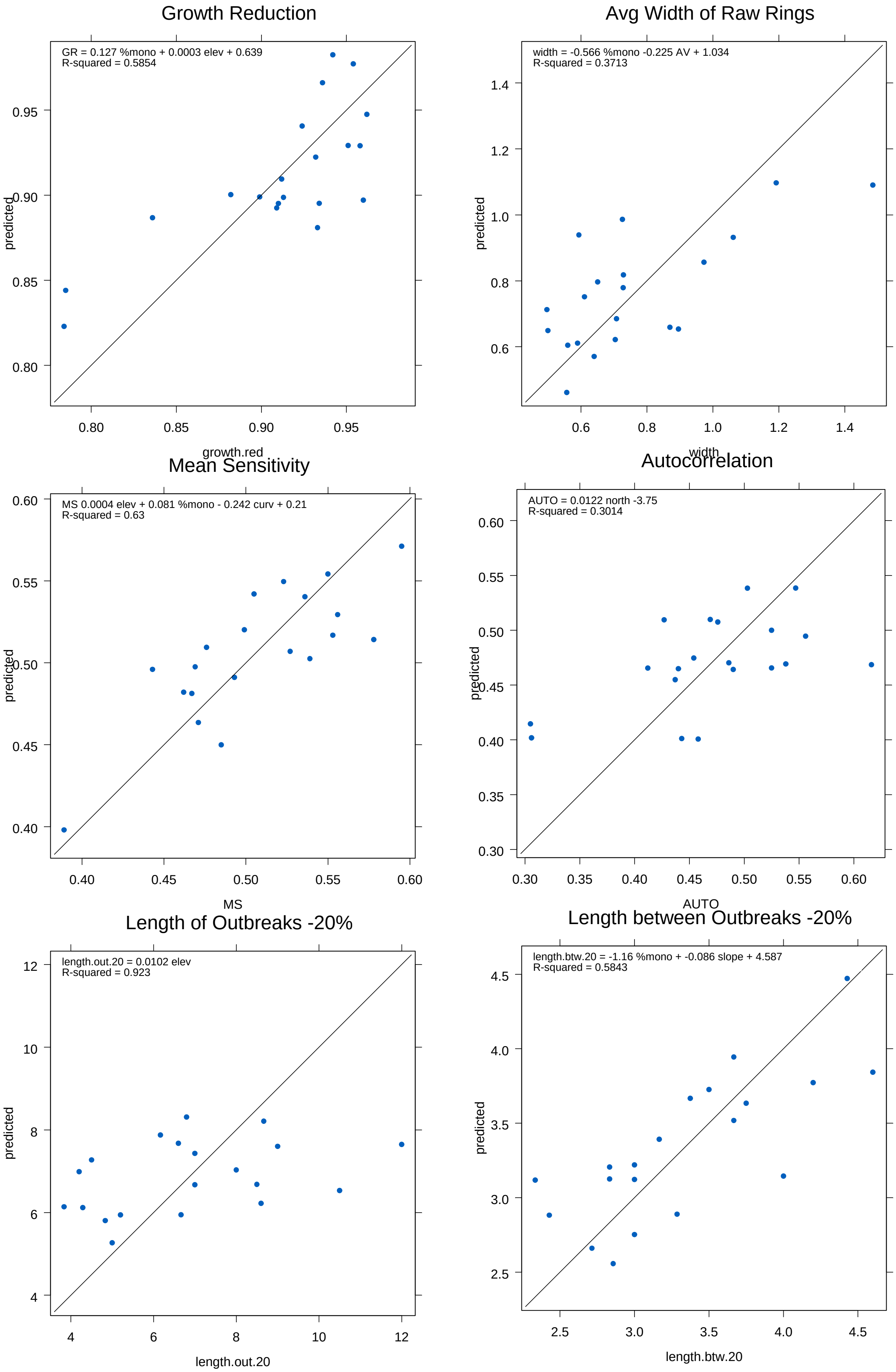


Figure 21. Continued.

Table 15. Stepwise linear regressions of outbreak and ring characteristics compared to dependent variables. Dependent variables are elevation (elev), latitude (north), longitude (east), percent monocormic (% mono), slope, curvature (curv), AV, and aspect.

		Coefficien	t statistic	p.value			
Number of Outbreaks in Plot							
	Elevation	-0.0048	-1.6409	0.118		R-squared	0.9687
	Easting	5.7519	4.6494	<0.001		F stat	278.6
						p.value	<0.001
Length of Outbreaks							
	Intercept	3.6379	32.2076	<0.001		R-squared	0.4515
	Slope	-0.0489	-3.849	0.001		F stat	14.81
						p.value	0.001
Length Between Outbreaks							
	% Mono	4.6693	2.8495	0.011		R-squared	0.9797
	Elevation	0.0154	11.8676	<0.001		F stat	434.3
						p.value	<0.001
Length Between Max Outbreaks							
	Intercept	128.3433	3.8374	0.001		R-squared	0.5429
	% Mono	3.4715	2.7593	0.013		F stat	10.1
	Northing	-15.313	-3.4505	0.003		p.value	0.001
Length of Outbreaks - 20%							
	Elevation	0.0102	15.0902	<0.001		R-squared	0.923
						F stat	227.7
						p.value	<0.001
Length Between Outbreaks - 20%							
	Intercept	4.5869	16.1736	<0.001		R-squared	0.5843
	% Mono	-1.1596	-2.8277	0.012		F stat	11.95
	Slope	-0.0858	-2.6273	0.018		p.value	<0.001
Growth Reduction							
	Intercept	0.6393	8.2876	<0.001		R-squared	0.5854
	% Mono	0.1268	4.0526	<0.001		F stat	12
	Elevation	0.0003	2.8245	0.0117		p.value	<0.001
Avg. Raw Ring Width							
	Intercept	1.0344	9.1858	<0.001		R-squared	0.3713
	% Mono	-0.5657	-2.6216	0.018		F stat	5.021
	AV	-0.2252	-2.875	0.011		p.value	0.019
Mean Sensitivity							
	Intercept	0.2102	2.9178	0.010		R-squared	0.63
	% Mono	0.081	2.7623	0.014		F stat	9.08
	Elevation	0.0004	3.6192	0.002		p.value	<0.001
	Curve	-0.2423	-2.5485	0.022			
Autocorrelation							
	Intercept	-3.7498	-2.4761	0.023		R-squared	0.3014
	Northing	0.5605	2.787	0.012		F stat	7.768
						p.value	0.012

monocormic, elevation and longitude. Three other regression models had R^2 over 0.9 (Figure 21, Table 15). The primary variables controlling the regression models are elevation and the percent of the plot that is monocormic. Only two of the 10 models do not have either of these variables and are two of the weakest models (Table 15).

CLUSTER ANALYSIS

Cluster analysis of the percent outbreaks that occurred from each plot showed distinct clustering into groups. In general, these groups showed that plots from the same valleys were more closely related to each other than to plots in other valleys (Figure 22), thereby indicating some level of regional coherence with regard to the timing and magnitude of the outbreaks. The most negative test statistic from MRPP was -11.2 with an effect size of 0.39 for five clusters (Figure 23). All clusters besides Cluster 1 represent distinctly different areas. Cluster 1 primarily represents the Vuoggatjåme region, however; one plot from Ritsem (VAK) is also included. Cluster 2 includes all of the Ritsem sites except VAK and the Kvikkjokk site. Cluster 3 represents the Nikkaluokta region and Cluster 4 represents the Torneträsk region. Cluster 5 is a combination of the most northerly and continental sites (Järmärä and Keinovuopio).

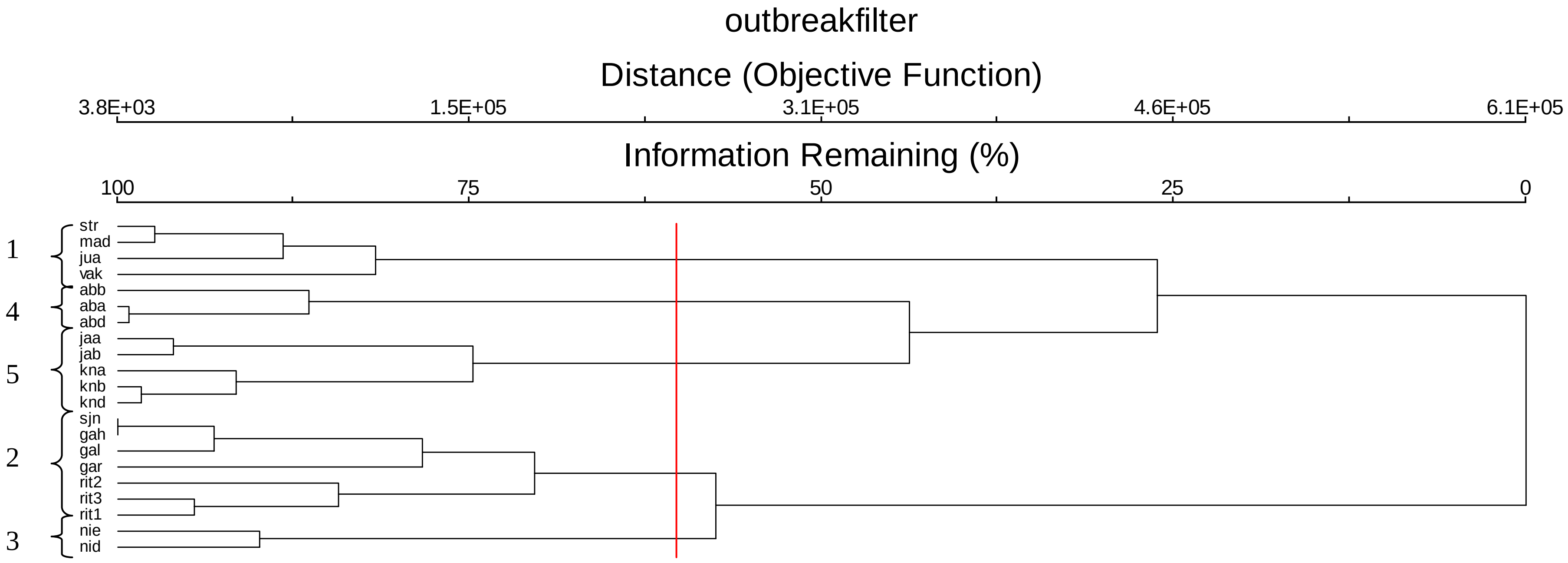


Figure 22. Cluster analysis of percent outbreaks for the common time period of 1944-2003. Red line denotes the cutting point for the optimal number of outbreaks determined by the test statistic from MRPP.

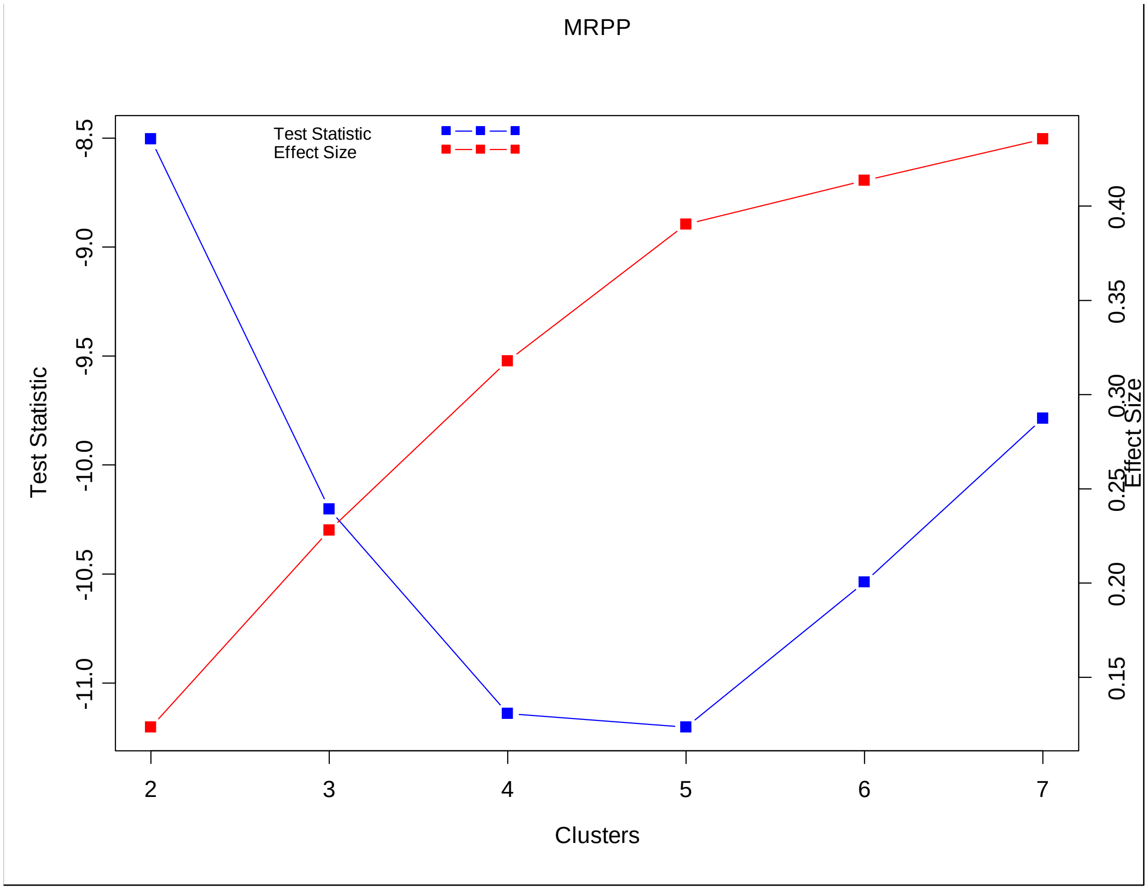


Figure 23. Multi-Response Permutation Procedure. The test statistic represents the differences between groups, the lower the number the more difference. The lowest test statistic is found with 5 clusters.

CHAPTER V

DISCUSSION

CHRONOLOGY AND CLIMATE

The characteristics of tree-ring chronologies vary with location. For example, Fritts (1976) considered the interseries correlation, mean sensitivity, and correlation with climate in relation to location. Typically, interseries correlation, correlations with climate, mean sensitivity, and the number of missing or partial rings will increase the closer one is to the forest boundary. Additionally, ring widths will become smaller and there will be an increased number of days when moisture is a limiting factor (Fritts 1976).

My analysis of mountain birch and Scots pine express similar trends. Both species show a high level of interseries correlation (Table7). Trees growing at the forest border are not limited in growth by competition and are thus more influenced by climatic variation. The climatic analysis showed that the variance attributed to climate and the previous year's growth is 46% and 66% mountain birch and in Scots pine respectively (Table 11).

The mountain birch follow Fritts's model by having a high mean sensitivity indicating there is a high level of interannual variability (Table 7). Scots pine has a low to intermediate level of mean sensitivity. The difference between the two species is due to a number of factors, foremost of which is the physiology between deciduous and coniferous trees. Conifers have an advantage over deciduous trees in that their photosynthetic material is always present; thus if conditions are good they can come out of dormancy and begin photosynthesizing. Deciduous trees have to wait until temperatures are warm enough to set leaves, thereby decreasing their growing season. Additionally, Scots pine is not subjected to cyclical outbreaks of insects that periodically reduce ring widths.

Three of the Scots pine plots are at their physiological limit and the other three are from within the continuous forest. The pines occurring at their physiological limit had a lower mean sensitivity than the mountain birch, which is probably because they are still within the continuous mountain birch forest and have to compete for light, moisture and nutrients. The three pine plots occurring within the pine continuous forest had lower mean sensitivities than those at their physiological limit (Table 7).

Both species show a high level of autocorrelation indicating that growth from the previous year plays a large role in the current year’s development. This is confirmed by the percent of variance that is attributed to the previous year’s growth and climate (Table 11). The first component of the PCA explains more in the pines than it does in the birch.

Temperature

Pearson’s correlation and response functions show that both mountain birch and Scots pine are responsive to climatic variables. Positive values indicate that increases in a climatic variable result in increased growth. Negative values indicate that decreases in a climatic variable result in increased growth. The warmest three months of the year are June, July and August (Figure 1). June and July are the months that birch responds to most positively (Tables 8, 9 & 10; Figure 16). Pines are more responsive to just July temperatures which are the highest during the year (Tables 8, 9 & 10).

Counter intuitively, negative responses to temperature occur in the birch during late winter and spring. Lower winter and spring temperatures keep the trees in a dormant state, delaying budbreak and reducing the risk of frost (Heide 2003; Myking & Heide 1995; Skre *et al.* 2008). Alternatively, the negative response to lower winter temperatures might be an artifact of precipitation and when low temperatures are present moisture falls in the form of snow rather than rain. Rain in the winter can infiltrate the soils and freeze the roots (Fritts 1976). Cold winter temperatures also increase mortality in eggs of the autumnal moth.

Precipitation

Negative response to precipitation is seen in the correlation coefficient for both the previous and current fall, primarily occurring in October (Tables 8, 9 & 10). Less rain in the fall would decrease the potential for moisture to be in the soil when it freezes which could then freeze the roots (Fritts 1976). Moisture due to rain and snow does not seem to be a limiting factor. During the driest months of the year at least 2.5 cm of precipitation falls (Figure 1).

NAO

The high level of correlation between NAO and the climate factors justifies its use as a factor in tree growth (Figure 15). NAO is most significantly correlated with March temperatures which corresponds to other studies in Fennoscandia (Chen & Hellström 1999). The correlation between March temperatures and NAO are hypothesized to correlate with the peak of snow melt (Chen & Hellström 1999). Significant responses between winter precipitation and NAO are also common in the literature and can be explained by a greater difference between the two pressure poles and warm moisture from the Gulf Stream (Chen & Hellström 1999; Hurrell *et al.* 2003; Hurrell 1995; Hurrell & Dickson 2003).

NAO responds at the same time in both mountain birch and Scots pine to temperature and precipitation (Tables 8, 9 & 10). This is an expected trend since NAO is correlated with precipitation and temperature (Figure 15). Summer temperatures and fall rains are two of the most influential factors in mountain birch growth and thus NAO responds similarly to these periods (Table 10).

The response of Scots pine to the NAO index is curious in that there seems to be a differentiation between pines that are from the continuous forest and those that are at their physiological limit (Table 8 & 9). Pines within the continuous forest respond to NAO indices during the growing season while trees at their physiological limits are more responsive to fall and winter NAO indices. This trend parallels other studies on pine that found positive summer responses to NAO indices in maritime climates and in stands at their physiological limits (Lindholm *et al.* 2001). A potential reason for this is that trees at their physiological limits are responding less to competition and more to the climate.

The response of mountain birch to June and July temperatures and fall precipitation in this investigation are comparable to previous studies (Eckstein *et al.* 1991; Karlsson & Weih 2003; Kirchhefer 1996). To my knowledge there have been no previous studies on the influence of NAO on mountain birch. NAO correlations primarily occurred during the summer months which is the same time as Scots pine at their physiological limits responded to NAO (this study; (Lindholm *et al.* 2001)). All the mountain birch plots came from their physiological limits at the treeline. The correlations and responses functions to temperature and precipitation in the Scots pine supports the previous literature that July is the most influential month for Scots pine growth (Helama 2004; Helama *et al.* 2005; Kirchhefer 2001; Linderholm 2001, 2002; Linderholm & Chen 2005; Lindholm *et al.* 1999; Lindholm *et al.* 2000). Variability in response to NAO between physiological limits and continuous forest supports previous work done by Lindholm et al. (2001).

OUTBREAKS

Outbreaks of the autumnal moth have been a constant on the landscape of Fennoscandia since at least the mid 1800's when the first reports were made. This study complements the historical accounts of outbreaks by adding an environmentally recorded time series over the landscape. My data suggest that outbreaks occurred at slightly different time periods than Tenow's (1972) compendium of outbreaks. Some of my study sites have poor representation in Tenow's records thus outbreaks in those regions have not been accounted for in the historical record. Combining these two records together shows a more comprehensive picture of the cyclical behavior of the autumnal moth over the landscape.

Comparison with Historical Record

The most well known outbreak to have occurred in Fennoscandia is the 1955 outbreak, and more specifically, its impacts in the Abisko valley. This outbreak was expected to be seen in cores from the Abisko-Torneträsk region. However, it was barely present in the tree ring records from the area. The only plot to record the outbreak was ABD. This plot is located at lower elevations than the other two plots at the western end of Torneträsk in a large pass between the western and eastern sides of the Scandes. The two other plots are located at treeline on the south side of Torneträsk.

Though the outbreak records do not seem to line up in the Torneträsk area this could be due low levels of defoliation (<50%) that do not appear in the tree ring record (cf. (Hoogesteger & Karlsson 1992)). Perhaps the trees growing at treeline were not significantly affected by the outbreak or were intensively impacted and responded positively to the outbreak. The first of these is more likely the case because, Tenow (1972, 1975) noted that in Abisko valley the trees at treeline were not defoliated. The only region in this study in which the 1955 outbreak was heavily recorded within the tree-ring data was Vuoggatjålme in the south. However, the historical records of the 1955 outbreak are also recorded in the Torneträsk, Nikkoloukta, Ritsem, Kvikkjokk and Vuoggatjålme regions.

A majority of the work on mountain birch growth and impact by autumnal moths has been conducted at lower altitudes. Thus due to the potential climatic and topographic restrictions on treelines they respond differently to outbreaks than forest populations of mountain birch.

Other well document outbreaks had a better response in the tree ring chronologies. In 1927 an extensive outbreak occurred in northern Finland which depressed the treeline up to 1 km in some areas (Kallio & Lehtonen 1973; Lehtonen

1987; Nuorteva 1963; Tenow 1972). This outbreak was recorded in all of the plots from the Keinovuopio and Järmärä regions as well as in the two treeline plots in the Torneträsk region. The one plot in Torneträsk region that was not recorded has more influenced by a maritime climate (ABD) than the other two and thus it did not record the 1927 outbreak.

The 1963-1966 outbreak was recorded throughout Fennoscandia. My tree ring record shows this outbreak in all but Nikkaluokta. The widespread synchrony of this outbreak is impressive (Figure 20). The 1990-2000 outbreak in northern Sweden and Norway is said to have been a wave outbreak moving from east to west in the northern portions of Fennoscandia (Tenow *et al.* 2007). From the tree ring record this outbreak seems to be a moving outbreak from the south to the north which is also from west to east. The difference between the causes of different types of these outbreaks is unclear.

The most recent outbreak comes from Klemola (2008) in northern Norway where the beginnings of an outbreak were monitored from 1999 to 2006 with the peak outbreak occurring in 2002 and 2003. This outbreak was closely followed by an outbreak of winter moth in 2004 and 2005. The occurrence of the winter moth had not previously been recorded in this location. My entire dataset shows an outbreak occurring over the same time period. Both the Järmärä and Keinovuopio areas seem to have had an outbreak in 2004-2005 that was separate from the ones that occurred in 2002 (Figure 24). This is potentially an outbreak of the winter moth.

Periods of extreme weather need to be further researched. The year 1927 was one of the coldest springs on record which was followed by a large outbreak. Similar

Figure 24. A 4-5 year old outbreak of the autumnal moth at Järmärä. Polycormic stems are recovering from the outbreak with basal sprouts.

trends are seen for 1955 and 1966, both also correspond to large synchronous outbreaks. Using local weather data rather than the regional climate data set may help to determine how extreme weather events on the annual and interannual levels control outbreak occurrences.

Outbreak Behavior

The behavior of outbreaks varied across the region. Outbreaks are reported as occurring every 9-13 year throughout the region and lasting 2-4 years when they occur (Bylund 1997; Klemola *et al.* 2006; Tenow 1972). There is a difference between the number of outbreaks that occur within a tree, the stand, and the region. On average there is a shorter length of outbreaks in cores than there is within plots. The interval between outbreaks is almost twice as long in cores as in plots (Tables 13 & 14). The average number of outbreaks per core is approximately a quarter of the outbreaks that are recorded on the plot level (Tables 13 & 14).

The difference in length of time between outbreaks and the number of outbreaks between tree and plot level statistics is interesting. The plot level statistics imply that outbreaks occur about every 7.5 years with about 8.5 outbreaks occurring in each plot. The core level data implies outbreaks occur every 12-15 years with only 2-4 outbreaks per core. During each outbreak that is recorded in plot level data at least 20% of the plot responds to the outbreak meaning potentially 80% of the plot may have been either unaffected by the outbreak or that the level of defoliation was low. This difference between tree and plot level outbreaks exemplifies the reported heterogeneity of outbreaks across a stand (Bylund 1997; Tenow 1975).

Linear Models

I was able to develop 10 models of outbreak characteristics and wood morphology. The strongest models are those that have elevation as one of the independent variables. Elevation is a determining factor in the number of outbreaks that occur in a plot, the growth reduction, the length between outbreak in cores, the length of outbreaks in plots and the mean sensitivity of growth. From Tenow's (1972) collection of the historic documents there are many records where outbreaks did not occur at treeline. It is probable that the extreme conditions at treeline limit the intensity and frequency of outbreaks. The second most influential factor is the percent of plot that is monocormic. Monocormicity influences the length of time between outbreaks, the number of outbreaks in cores, the length of time between outbreaks in the plot, growth reduction, average ring width, and mean sensitivity. Four of the six models that express percent monocormicity as a determining factor have positive coefficients and the two that do not have only slightly negative reductions. This indicates that when a higher percent of a plot is monocormic it takes longer for that stand to recover to a state that has suitable egg deposition locations and foliage. Polycormic stands respond to disturbances quicker than monocormic stands, thus they might be more susceptible to more frequent outbreaks. It was expected that with increased latitude or longitude there would be a change in the cycle of outbreaks, however; based on my data neither are prominent factors in determining outbreaks.

Cluster Analysis

The cluster analysis shows that there is regional coherence of outbreaks between the study sites. There do not seem to be any explicit spatial trends in the data. There are slightly fewer outbreaks on the plot level in the southern plots. Synchrony of larvae densities can be seen up to 700 km (Klemola *et al.* 2006). If we use this measure, all of my study sites fall within 700 km of each other and should be synchronous. However, there are clear separations between the clusters. If we use 60 km, which according to Tenow (2007) is the distance that larvae densities are synchronous, we might be able to explain some of the clustering. The direct line distance between all of the clusters is at or above 60 km. With the exception of the Vuoggatjålme cluster (which has VAK one of the Ritsem sites in it), all of the distances within groups are less than 60 km. Due to this synchrony, the timing and magnitude of outbreaks within clusters may be occurring. There will be variations within these clusters in timing and intensity of outbreaks due to local topography and vegetation.

CHAPTER VI

CONCLUSIONS

Twenty-one mountain birch chronologies were developed during this investigation throughout northern Sweden. This study is the first large scale dendrochronological study of the region for mountain birch. The climate signal found in the mountain birch was consistent across the entire range of this investigation. The main climatic influences on mountain birch annual growth were June and July temperatures which accounted for 46% of the annual growth variation. Negative temperature responses occurred during early spring, potentially as a safety measure to keep trees dormant through periods of potential frost. There was also a negative response to fall precipitation which may come as rain and infiltrate the soils before freezing and disturbing the roots (Fritts 1976).

The six Scots pine chronologies complement previous studies conducted in the region (Kirchhefer 2001; Linderholm 2001; Lindholm *et al.* 2000). July temperature was determined to be the primary influence on growth and accounted for 66% of the annual variation. This study adds to Lindholm's (2001) observation that pines growing at their physiological limit are influenced by summer NAO indices rather than winter indices that have been reported in the continuous pine forests throughout Fennoscandia. Response to winter NAO indices might be due to physiological or competitive mechanisms driving growth at varying forest positions. Mountain birch at treeline responds similarly to summer NAO indices as Scots pine growing at their physiological limit.

Outbreaks of the autumnal moth were detected in all stands of mountain birch. The correspondence between the historical records and my data set indicate that using Scots pine as a non-host species to remove the climate signal from the birch trees is a valid method for detecting outbreaks in mountain birch. Comparing the detected outbreaks to the historic outbreak calibrates and validates this method of detection. This technique helps to determine outbreaks that were not witnessed and helps fill regional gaps where reports of outbreaks had not been gathered.

This investigation shows that there are regional differences in outbreaks by plot temporally and percent occurrence. Heterogeneity of outbreak occurrence within plots is apparent. Increases in elevation tend to increase the length of outbreak in cores and the length between outbreaks in plots. The percent of the plot that is monocormic influences the length between outbreaks in both cores and plots.

Predictions for increased temperatures and precipitation in Northern Europe will affect the growth of mountain birch (Christensen *et al.* 2007; Moberg *et al.* 2005; Serreze *et al.* 2000). Warmer temperatures and precipitation may result in greater moisture infiltration of the soils causing mortality in the roots. Increased winter temperatures will cause lower mortality rates of autumnal moth eggs and increase the potential for large scale outbreaks (Bylund 1997; Ruohomäki *et al.* 1997). Higher winter temperatures may allow mountain birch to be released from dormancy earlier and have a longer growing season at the risk of frost damage during spring. Moth populations may develop into outbreaks due to extremely cold winter weather conditions, thus the warming of winter and spring temperatures might mediate outbreaks. Discovering some of the determining factors of autumnal moth cyclical behavior will help future modeling of where and when outbreaks will occur and how climate change will influence outbreaks dynamics.

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