Section C : Project Description

1. RESULTS FROM PRIOR NSF SUPPORT

D.M. Cairns: NSF Award Number: BCS-9808989. **Amount and Period of Support:** $15,000 subcontract for a $50,000 project; 09/01/98 – 07/31/00. **Project Title:** Coupling field, remote sensing and modeling techniques to examine processes at the deciduous-coniferous ecotone in Great Smoky Mountains National Park. **Summary:** This project was the first stage of developing models and methods useful for investigating ecotone response to climate change with emphasis placed on the deciduous-coniferous ecotone in Great Smoky Mountains National Park. Success was achieved in utilizing remote sensing techniques to perform change vector analysis and investigate the mortality and regeneration of red spruce and Fraser fir at the deciduous-coniferous ecotone. The ATE-BGC model was also successfully modified to incorporate a deciduous canopy. **To date this project has yielded 2 presentations at national and regional conferences, 1 manuscript is in review at Forest Ecology and Management and two others are in preparation.**

2. RESPONSES TO PRIOR REVIEWS

This proposal is a revised version of a proposal previously submitted to NSF. In this proposal the shortcomings of the work identified by the reviewers have been addressed. The primary concern of the panel was the ability to crossdate mountain birch. We have inserted section 5.5.2, “Preliminary dendrochronological analysis of mountain birch” to demonstrate that mountain birch can be crossdated. Specifically, we present a graph showing the standardized ring-width indices for sample cores of mountain birch, and we also provide COFECHA output indicating that the crossdated series display high interseries correlation and high average mean sensitivity. We hope that this will allay reviewer concerns about the ability to use tree-rings to adequately determine establishment dates for mountain birch.

With respect to reviewer concerns about climatic data, we have discovered additional long-term climatic data sets for northern Sweden. Therefore, the proposed analyses no longer rely entirely on the Abisko data set for climate data extending back to the beginning of the 20th century. The temperature data among these sites are highly correlated, indicating that warmer and colder periods occurred in concert across Norrbotten. We also have included an ANOVA analysis in section 5.7.1 to take better advantage of our nested sampling design.

3. INTRODUCTION

The Earth’s climate is expected to change considerably in the near future. Global temperatures are predicted to rise between 1.4 ˚C and 4.4 ˚C over the next century, and precipitation patterns are also expected to be altered (Allen et al. 2000; Boer et al. 2000; Dai et al. 2001). Changes are expected to be greatest near the poles and more moderate in the tropics. Vegetation communities are thought to be in quasi-equilibrium with climate, and as climate changes, so should vegetation communities (Walther et al. 2002). Many vegetation communities may exhibit predictable changes in location, species composition, biomass, and pattern on the landscape. Such changes are expected to be most visible at ecotones between adjacent vegetation types, because at these locations small changes in environmental conditions are more likely to push vegetation communities from one stable state to another (Hansen et al. 1988).

One ecotone of particular interest in this regard is the forest-tundra transition, because it has been shown to be a sensitive bioindicator of climate change (Burga & Perret 2001; Kullman 1998) and it can be viewed as an analog to other zonal biome transitions (Stevens & Fox 1991). Transitions between forest and tundra occur in both Arctic and alpine locations. In both cases, as the thermal climate becomes more severe there is a switch from the arboreal growth forms of a low-latitude or low-elevation forest to short-stature tundra. This transition may be gradual or sharp and may include an intermediate shrub-like growth form of trees in a matrix of tundra.

The treeline is a global phenomenon occurring from the tropics to the Arctic. Both deciduous and coniferous treelines exist. Coniferous treelines are more spatially expansive, but deciduous treelines are of local importance in some areas. Fennoscandian treelines are primarily deciduous and occur at the intersection of both Arctic and alpine conditions.

The last decade has witnessed a dramatic increase in treeline research at various spatial scales, ranging from the individual tree to global treeline patterns (Jobbagy & Jackson 2000; Körner 1998). A wide range of temporal scales have been addressed as well, including treeline response to climate change over millennia, to decadal responses (Burga & Perret 2001; Cuevas 2000; Kullman 1984; Kullman 1989; Meshinev et al. 2000). Most of this work has sought evidence for changes in treeline location or tree growth to demonstrate that treeline is in equilibrium with climate.

For Fennoscandia there is a growing body of literature that indicates that the treeline location is in equilibrium with climate and has responded to both warming (Kullman 1990) and cooling trends through the 20th century (Kullman 1989; Kullman 1993b; Kullman 1998). Observations of the response of the Swedish treeline to climate change are based on the establishment of new trees above the current treeline (Kullman 2002), the increased growth and physiognomic shifts of pre-existing seedlings above the treeline (Kullman 1984), and the reduction in vigor (for treeline retrogression) of isolated trees growing above the treeline (Kullman 1993a). However, Fennoscandian treelines are subject to browsing by semi-domesticated reindeer (*Rangifer tarandus*) and outbreaks of a defoliating moth (*Epirrita (Oporinia) autumnata (Bkh.)*), both of which may have significant effects on the pattern of treeline and its ability to respond to climate change.

Predictions of how treelines will respond to changing climates routinely concentrate on the effects of climate (e.g. Bekker et al. 2001; Cairns & Malanson 1997; Moen et al. 2004) but rarely consider the influence of herbivores. The activity of herbivores in a wide range of environments has been hypothesized to have effects at least as important as climate in the shifting of major ecotones (e.g. Zimov et al. 1995). Niemela et al. (2001) argue that understanding the response of northern forests to climate change can not be achieved without considering the effects of herbivores. Payette et al. (2002) similarly urge that future research should concentrate on finding non-climatic factors that influence treeline migrations. Yet very little is known about how herbivory may limit or augment contemporary treeline response to climate change. **The objective of this research is to discover how herbivore activities interact with climate change to influence the establishment and growth of trees at treeline and thereby contribute to the migration potential of a major ecotone. This will be accomplished by using dendrochronological methods combined with long term high-quality datasets of climate, reindeer populations, and autumnal moth outbreaks in northern Sweden.**

4. BACKGROUND

4.1 CLIMATIC CONTROL OF TREELINE POSITION

The position of the alpine treeline traditionally has been viewed as determined by growth limitations. Growth limitations have been hypothesized to be the result of growing season compression (Havranek & Tranquillini 1995; Tranquillini 1979; Walsh et al. 1994; Wardle 1993) and low productivity during the growing season (Day et al. 1989; DeLucia & Smith 1987; Hadley & Smith 1983; Smith et al. 1984).

More comprehensive treatments of growth limitation at treeline have focused on carbon balance. Stevens & Fox (1991) proposed that treelines were set by carbon balance. This hypothesis has been tested using simulation modeling approaches for the northern Rocky

Mountains, USA and found to work well for predicting the location of the alpine treeline ecotone (Cairns 1998; Cairns & Malanson 1997).

Carbon balance approaches to treeline are however not universally accepted. Tranquillini (1979) noted that treelines in the Swiss Alps did not appear to be controlled by carbon balance. More recently, positive carbon balances for trees at the treeline have been inferred from dendroecological data (Grace & Norton 1990; James et al. 1994; Paulsen et al. 2000) and from measurements of non-structural carbon (Hoch & Körner 2003; Hoch et al. 2002). In cases where a positive carbon balance has been documented at treeline a carbon investment control is hypothesized to explain the presence of a treeline. Specifically, low temperatures act to either restrict or eliminate meristematic activity and thereby constrain tissue formation under otherwise positive carbon balance conditions (Grace et al. 2002; Hoch & Körner 2003; Hoch et al. 2002; Paulsen et al. 2000). The upper limit to tree species survival (at a global scale) is set by thermal conditions (Körner 1998) which are coupled with a regional set of modulatory factors. These modulatory factors can include the tree species of interest and their environmental tolerances (Körner 1998; Sveinbjornsson 2000). With increasing elevation, the trees may still be able to maintain a positive carbon balance but extreme climatic events increase in probability, as do hazards to the survival of a tree (Cairns 2001; Sveinbjornsson 2000; van Gardingen et al. 1991).

Although the upper limit of tree species survival may be set by a simple thermal limitation, alpine treelines are typically spatially complex and do not appear simply as a line on the landscape. Alpine treelines are comprised of some locations where a sharp boundary occurs (Armand 1992), some where subalpine forest forms fingers that extend upslope into the tundra (Bekker et al. 2001; Malanson 2001) and others where tree species exist in a network of patches within a tundra matrix (Benedict 1984; Cairns 1994; Malanson et al. 2001; Marr 1977). Many locations exhibit a combination of these spatial configurations over areas as small as a single hillside.

4.2 TREELINE DYNAMICS UNDER CHANGING CLIMATE

Decadal scale variability in treeline has been documented across the globe using a variety of methods. The most bold examples of treeline change are those where the elevation of the treeline has shifted either upslope or downslope quickly. For example, dramatic increases in the elevation of pine treelines (*Pinus peuce*) in the Central Balkan Mountains have been recorded since 1970 (Meshinev et al. 2000). Treeline elevations there have increased 340 m in a very short time in response to increases in winter temperatures (Meshinev et al. 2000). Such obvious shifts in the elevation of the treeline have led to the conclusion that *Pinus peuce* is a good indicator of environmental changes. Further examples of this type of migration are available in Russia where decadal to century scale changes in the treeline in the boreal zone are evident. Shifts in treeline elevation between 30-80 m have been documented for birch (*Betula* spp.)- and larch (*Larix* spp.)-dominated treelines during the 20th century (Gorchakovsky & Shiyatov 1978).

A less obvious shift in treeline characteristics occurs when the upper elevation of the treeline ecotone does not change, but significant changes occur within the ecotone itself. Changes of this type have been reported at Alaskan Arctic treelines, where Sturm et al. (2001) used repeat photography to document the infilling of a patchy network of spruce in a tundra matrix during a 50-year span. Similar results are reported for krummholz patches at treeline in Glacier National Park, Montana (Klasner & Fagre 2002). Dendroecological data have shown similar patterns (Suarez et al. 1999). Infilling of this type can occur either from the expansion of pre-established tree islands or through the establishment of seedlings. Both processes are evident in the literature. For example, rapid growth in krummholz patches of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea Engelmannii*) at Rocky Mountain National Park, Colorado indicates a potential for the patches to coalesce (Weisberg & Baker 1995a; Weisberg & Baker 1995b). Future infilling of gaps within the treeline ecotone due to the establishment and continued growth of seedlings are noted for a wide variety of sites, including the Snowy Range

(Germino et al. 2002; Moir et al. 1999) and Medicine Bow Mountains (Hattenschwiler & Smith 1999) in Wyoming, the Sierra Nevada (Minnich 1984), and northern Finland (Juntunen et al. 2002).

Incipient treeline migration can be inferred by the presence of a robust cohort of seedlings at and above the current treeline. Typically seedling density is low above treeline (Hattenschwiler & Smith 1999; Srutek et al. 2002; Young 1993). However, in some cases treeline elevation either has increased or is expected to increase dramatically because of seedling establishment above the current treeline. For example, treelines in Scotland have shown remarkable increases in the establishment of seedlings up to and above the regionally climatically controlled treeline subsequent to the reduction of fire frequency and exclusion of herbivores (Bayfield et al. 1998; French et al. 1997). South-facing slopes in the Canadian Rockies have shown extensive upslope establishment of seedlings and a concomitant migration of the treeline (Luckman 1998). Robust seedling cohorts have established upslope of the current pine (*Pinus uncinata*) treelines in the Spanish Pyrenees (Camarero & Gutierrez 1999; Camarero et al. 2000). Some portions of the Alps have also experienced an increase in *Pinus cembra* seedlings at and above the treeline (Didier 2001).

The mountain birch treelines in the southern Swedish Scandes have been shown to be some of the most responsive treelines in the world to climate change. Birch treeline elevations have increased and decreased throughout the 20th century, tracking changes in environmental conditions (Kullman 1998). During the first two decades of the 20th century, birch trees expanded upslope to colonize previously treeless mountain valleys in Fennoscandia. By the 1970s the birch treeline had increased approximately 40 m with most of the advance occurring prior to the 1950s (Kullman 1998). Between the mid-1970s and the mid-1990s approximately 30% of the treeline birch died without being replaced, resulting in fragmentation of the birch belt and the downslope retreat of treeline (Kullman 1990; Kullman 1991; Kullman 1993b; Kullman 1998). This pattern appears to have reversed itself since the mid-1990s and the treeline has advanced 20 m due to the establishment of seedlings above the previous tree limit in the southern Scandes (Kullman 2002). Previous rapid advances of the treeline were attributed to the presence of a persistent bank of seedlings/saplings above treeline (Kullman 1984; Kullman 1989). Dynamics of treelines in northern Sweden and Finland are not as well understood due to the lack of a monitoring network (Kullman 1998).

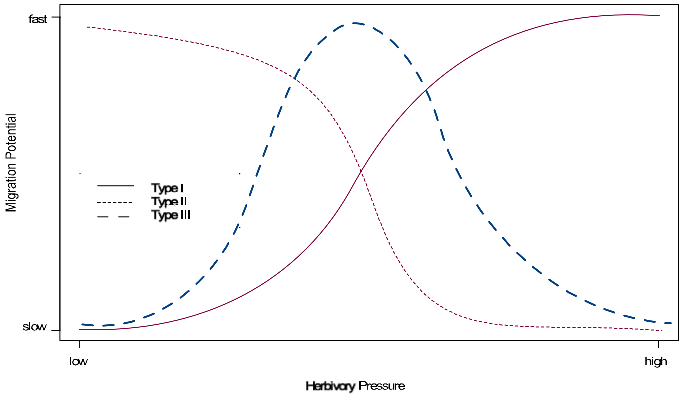
4.3 HERBIVORY AND TREELINE DYNAMICS

It is well-documented that herbivorous mammals may change successional patterns of trees. For instance, deer (*Odocoileus virginianus*) grazing significantly slows down invasion of old fields by trees in the nutrient poor soils of Cedar Creek, Minnesota (Inouye et al. 1994). Moose (*Alces alces*) browsing in the boreal parts of the world also has strong effects on forest succession patterns after fire or clear-cutting by selectively feeding on the early successional deciduous species, thus accelerating the return to coniferous forest (Andrén & Angelstam 1993; Kielland & Bryant 1998; Pastor et al. 1999). Aspen (*Populus tremuloides*) regeneration has been linked to elk (*Cervus elaphus*) populations in western North America (Hessl 2002; Hessl & Graumlich 2002).

Herbivores also may affect tree establishment and growth at treeline. In Fennoscandia, where treelines are formed by mountain birch (*Betula pubescens* ssp. *czerepanovii*), tree saplings usually are found several hundred meters above treeline. However, in alpine areas with high populations of reindeer or sheep, the saplings are browsed and exhibit a coppiced form (Hofgaard 1997; Oksanen et al. 1995). Oksanen et al. (1995) found that browsing influenced the overall treeline structure – treelines exposed to intensive summer browsing were more abrupt than those on sites with less intensive browsing. Reindeer browsing also contributes to the mortality of mountain birch saplings defoliated by the autumnal moth (*Epirrita autumnata*) (Lehtonen & Heikkinen 1995).

Effects of herbivory on treelines are also seen in other parts of the world, including grazing by livestock in the Alps (Ellenberg, 1988), and herbivory by guanaco (*Lama guanicoe*) at *Nothofagus* treelines on Tierra del Fuego (Rebertus et al. 1997). The effects of guanaco are most strongly seen on seedlings where in between 29 and 57% of seedlings in the alpine zone showed signs of grazing, and the grazing pressure was even higher near the treeline where herbivory almost completely inhibited regeneration(Cuevas 2002). It is even suggested that guanaco herbivory prevents an advance of the treeline as a response to higher temperatures (Cuevas 2002).

Figure 1: Theoretical responses of treeline migration potential to herbivory pressure (Cairns & Moen 2004).



Although defoliation is the primary effect of herbivores on trees, animals may also inhibit the migration of treelines through trampling and seed predation. Trampling has been shown to reduce seedling survival in a wide variety of environments as a consequence of damage to the seedlings, as well as compaction of soil (Castro et al. 2004; den Herder et al. 2003; Li et al. 2003). Seed predation reduces the number of potential migrants into the new environment. Seed predation is hypothesized to be a major limitation to regeneration of Scots pine (*Pinus sylvestris*) at Spanish treelines (Castro et al. 1999), and analogs from other ecotones indicate that seed predation is a factor in limiting migration (Garcia 2001; Muñoz & Arroyo 2002)

The negative effects of herbivory on treeline migration, however, are mediated by other potentially positive effects. For example, although trampling by large ungulates may have a negative impact on seedlings in some situations, trampling may also reduce existing vegetation cover and thereby increase soil temperatures and facilitate vascular plant growth (e.g. van der Wal & Brooker 2004). At treelines low soil temperatures are hypothesized to be in part responsible for setting the treeline location world-wide (Körner 1998). Therefore, increased soil temperatures beyond the treeline could result in upslope/poleward treeline migration.

Competition between existing vegetation and invading tree seedlings has been shown to limit the ability of trees to invade beyond the current treeline (Dullinger et al. 2003; Hobbie & Chapin 1998; Moir et al. 1999) and experimental tests have shown that simulated grazing can reduce the intensity of this competition thereby allowing tree seedlings to establish (Castro et al. 2002). Therefore, if the relative palatability of forage is skewed toward the vegetation in the non-woody upslope/poleward matrix the presence of herbivores may be a net positive to tree migration.

Herbivores may also promote upslope/poleward migration at treeline through their role as seed dispersers. Treelines dominated by species that are wind dispersed would not be affected by herbivores in this way, but ecto- and endo-zoochorous species would benefit from herbivore activity. Birds are the primary dispersers of seeds from treeline trees in this regard (Tranquillini 1979).

We have developed a conceptual model (Figure 1) that considers the positive and negative impacts of herbivory on the migration potential of treeline (Cairns & Moen 2004). In this model, three general patterns of treeline response to herbivory pressure are evident. Type I responses are characteristic of systems where the relative palatability of herbaceous and arboreal vegetation is shifted toward herbivores consuming the herbaceous vegetation. Low herbivory pressure in these systems fails to release the invading tree seedlings from competition, and therefore migration rates are low. Type II treelines occur when the foliage of the arboreal vegetation is the preferred forage for the herbivores. Migration rates are highest under low herbivory pressure for Type II treelines. The shapes of response for Types I and II treelines are modified slightly due to the impacts of trampling, seed dispersal, and seed predation. Type III treelines achieve the highest migration rates under moderate herbivory pressure. These treelines occur where the effects of trampling, seed dispersal and seed predation are high relative to the foliage consumption of the two adjacent vegetation types. This type of treeline is most likely to be found where no single herbivore is dominant, but where multiple animal species have a significant impact on the system or where the negative impacts of arboreal foliage consumption are balanced by the positive effects of establishment site preparation due to the consumption of upslope/poleward vegetation.

4.4 HERBIVORY AT TREELINE IN SWEDEN

The two important herbivores active in Swedish treelines are the semi-domesticated reindeer and the autumnal moth. In the late 1990s Sweden had approximately 230,000 reindeer (Bostedt 2001). The great majority was in Norrbotten (Moen & Danell 2003), where this research is planned. Treeline birch populations are affected by reindeer at both the adult and seedling stages. The leaves of mountain birch are a preferred summer food for reindeer (Haukioja & Heino 1974), and reindeer can consume up to 90% of the birch leaves in the 0-130 cm zone (Helle 2001; Helle & Kajala 1992). Seedling mortality is high when reindeer are present (Helle 2001; Lehtonen 1987; Oksanen et al. 1995).

During the mid-summer insect season, reindeer spend their days in snow patches, open and windy fells, and other areas above treeline that are relatively free of insects. They forage in the more productive meadows and birch forests at lower elevations in the evening, when insect harassment is lower. This diurnal pattern of activity results in different levels of leaf biomass consumption between the two elevation zones. Absolute biomass consumption is greater at low elevations, where birch trees are more productive, but a greater proportion of the foliage is consumed at high elevations, where nearly half the birch leaves may be eaten (Helle 2001).

Swedish reindeer herding is an extensive activity involving seasonal migration, a traditional transhumance practice followed for centuries by the indigenous Sami people, who use the reindeer for meat, and ties to culture (Beach 2001). Northern Sweden is divided into 15 reindeer herding districts that contain summer and winter grounds. Reindeer herders split the herd's time between winter grounds near the coast, and summer grounds in the mountains. During summer, the herds are relatively unsupervised, with the exception of the late spring calf-marking period when all reindeer are collected in specific locations. The calf-marking lasts a short time and usually is complete before bud-burst for the birch trees. During summer, the reindeer roam freely within the summer grounds of each herding district (Moen & Danell 2003). The maximum allowable reindeer per herding district is set by government agencies (County Administration Boards) based on forage surveys, and has remained stable for the last few decades (Moen & Danell 2003); the herders have not been able to increase herd numbers significantly.

Outbreaks of the autumnal moth occur on a cycle of approximately 10 years in Scandinavian treeline environments (Hoogesteger & Karlsson 1992; Sonesson & Hoogesteger 1983). These outbreaks usually occur at the beginning of the growing season and can result in severe defoliation of mountain birch. Experimental research has shown that simulated moth defoliation has a significant impact on radial growth of mountain birch (Hoogesteger & Karlsson 1992; Karlsson et al. 2004). Annual ring-width in the year of defoliation is severely reduced, and the reduction continues to be evident for 2-3 years following the defoliation (Hoogesteger & Karlsson 1992). Growth release subsequent to outbreaks is also evident in tree-ring records because of the increased amount of light available to new foliage (Eckstein et al. 1991).

Because carbon balance is important in determining annual growth of trees, any factors that reduce the ability of trees to sequester carbon through photosynthesis should be evident as reduced growth. Annual tree-ring increment in treeline environments is sensitive to a suite of climatic conditions (Innes 1991; Linderholm 2002; Lloyd & Fastie 2002; Lloyd & Graumlich 1997). However, the influence of herbivory on tree growth can be strong (Trotter et al. 2002; Zhang & Alfaro 2002), and must also be considered when interpreting the dynamics of tree growth at treeline.

5. PROPOSED RESEARCH

5.1. OBJECTIVES AND HYPOTHESES

The objective of this research is to investigate whether variations in herbivore populations and climate are related to tree recruitment and growth at treeline in northern Sweden. We will evaluate the following hypotheses:

(1) Contemporary spatial patterns in the density of mountain birch seedlings above the treeline correspond to spatial variations in reindeer populations within the region. The density of seedlings above treeline is a measure of treeline migration potential (sensu Cairns & Moen 2004). Herding districts with higher reindeer densities should have lower seedling densities than districts with less reindeer.

(2) Treelines in which the relative palatability of forage is shifted toward arboreal vegetation (e.g., birch treelines) should exhibit a Type II (sensu Cairns & Moen 2004) response to herbivory pressure.

(3) Temporal variations in tree establishment above treeline have been influenced by both climate and herbivory. Region-wide establishment pulses occurred during periods when favorable climate was coupled with below-average reindeer populations and autumnal moth activity.

(4) Fluctuations in herbivore activity (i.e., reindeer density and autumnal moth outbreaks) influence tree growth. Periods of high herbivore density will be identifiable in tree-ring chronologies as periods of ring-width suppression resulting from foliage consumption.

5.2. OVERVIEW OF THE PROPOSED RESEARCH

5.2.1. The case study. In this research we focus on elevational treelines dominated by mountain birch in northern Sweden. These treelines have been shown to be sensitive to climate change over decadal (Kullman 1998; Kullman 2000) and century long time scales (Kullman 1999). The birch treelines in this area are also subject to high browsing pressure by semi-domesticated reindeer and defoliating insect outbreaks, thereby making them an excellent site for investigating the interplay of herbivory and treeline dynamics. The use of tree-ring data will allow us to derive high annual resolution establishment dates for trees growing above treeline.

5.2.2. Research strategy. The research strategy follows from the four hypotheses above, and is described in detail in sections 5.4 – 5.7. Section 5.8 discusses the specific criteria for evaluating the hypotheses. In this section, we provide a brief overview of the strategy. To test hypothesis 1, sampling sites will be established along a gradient of reindeer population density. Specifically, seedling density will be compared among five herding districts with differing levels of reindeer density. These same data will also allow us to test hypothesis 2. To test hypothesis 3, we will collect tree cores and cross-sections from all five herding districts, and use dendrochronological techniques to estimate region-wide historical variations in birch establishment. Tree establishment history will be analyzed with respect to high-quality historic data on region-wide climate, reindeer density, and moth outbreaks. Hypothesis 4 will be evaluated by measuring the tree-rings from samples collected to test hypothesis 3, and analyzing the ring-width variability with respect to the climatic and herbivore data.

5.2.3. Definitions. Studies of the treeline suffer from a variety of definitions used to explain what particular landscape feature is being studied. Here we define the treeline as the boundary of the continuous forest comprised of upright trees. Other terms that have been applied to this same feature are the forest-limit (Tranquillini 1979) and timber line (Slatyer & Noble 1992). We define the supra-treeline zone as the area immediately above the birch treeline populated by scattered patches of birch trees. This corresponds to Tranquillini's (1979) kampfzone. We adopt this terminology here because in contrast to other treeline environments such as the Rocky Mountains, krummholz or dwarf forms of the dominant tree species are rare in the area.

Establishment is another term that may cause confusion. Mountain birch reproduces both sexually by seed and asexually by sprouting. Both forms of reproduction are evident at treeline (Oksanen et al. 1995). Because advance of the treeline could occur by either method of reproduction, we will not confine our study to either one. Also, in the harsh ecotonal environment, tree seedlings/sprouts may persist for many years with minimal growth, thus maintaining a perpetual seedling/sprout bank (Kullman 1984; Kullman 1989). In order for the treeline to migrate upslope, these sprouts and seedlings must be released from this state and grow to full sized trees. This release of suppressed seedlings/sprouts to form larger trees is the event we refer to as establishment. *Therefore, our analyses of historical patterns in tree establishment will not attempt to determine the date at which mountain birch trees initiate growth (either by sprouting or germination of seed), but rather the date at which they were released from a suppressed state – the establishment date.*

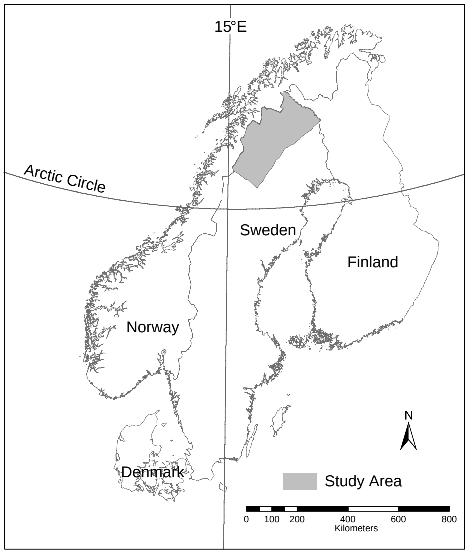
To determine the establishment date for each tree, we will analyze the ring-width chronology of the tree to identify when a sustained growth increase occurred (Copenheaver & Abrams 2003; Frelich 2002; Lafon 2004). For trees in which no such release event is evident (i.e., the tree initiated growth during favorable conditions and did not sustain an initial period of suppressed growth), the year of initiation will be assigned as the establishment date.

5.3 STUDY AREA

This study will be conducted in the Scandes Mountains in the northernmost county of Sweden (Norrbotten) (Figure 2). The Scandes Mountains run along the boundary of Sweden and Norway and extend from above the Arctic Circle down to approximately 62 ° N. The PI (Cairns) has conducted 3 summers of preliminary field reconnaissance in the area with Dr. Jon Moen who will consult on this project.

Treelines in Fennoscandia are dominated by mountain birch (*Betula pubescens* ssp. *czerepanovii).* The width of the birch belt can be between 100 and 150 m. Treeline elevation in the study area occurs between 670 and 700 m. a.s.l. (Sveinbjornsson et al. 1996). Birch trees occur as widely spaced individuals or as clumps within the treeline zone (Sveinbjornsson et al. 1996). Minor species in the birch belt include *Sorbus aucuparia*, *Alnus incana*, and *Populus tremula* (Kullman 1998). Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) also form treelines in the Scandes, but occur 50 and 100 m below those of mountain birch (Kullman 1998) and are found primarily in the southern part of the range. Upslope communities are characterized by heath and dominated by shrubs

Figure 2: Location of study area in Sweden.



including *Betula nana*, *Vaccinium myrtillus*, and *Empetrum nigrum* (Sjörs 1999).

5.4 SAMPLING STRATEGY

5.4.1 Site Selection. To test hypothesis 1 that contemporary herbivory pressure influences treeline migration potential, we propose to establish a gradient in herbivory determined by the reindeer density in different herding districts in Sweden. Herding districts will be categorized along a 5 category gradient. One herding district within each category will be chosen for analysis. Within each herding district three replicate catchments will be identified for tree-ring sampling. Consultations with a local expert (Dr. Jon Moen, Umeå University) will ensure that areas with historically unusual herding histories (e.g. short term enclosures) will be eliminated from the sample and that summer herding grounds will be accurately identified.

Using color infrared photography (CIR) we will classify the land cover in each of the selected catchments according to the scheme proposed by Edenius et al. (2003) for the area near lake Torneträsk in northern Sweden. Edenius et al. (2003) report a ranking of the intensity of reindeer use for each of the six land cover classes in their study. A reindeer use index based on the amount of land cover in each of the six classes and their weighted importance for reindeer use (Edenius et al. 2003) will be calculated for several potential catchments within each herding district. We will choose the three catchments in each herding district to use in our study by minimizing the within-catchment and between-catchment variability in the reindeer use index.

To ensure that the catchments have been accurately categorized with regard to the intensity of reindeer usage, we propose to establish 20 randomly located circular plots (10 m diameter) within the catchments. Each plot will be surveyed for evidence of reindeer usage by way of browse counts on mountain birches and fecal pellet counts. Within each plot, the number of birch trees that exhibit evidence of browsing will be tallied and assigned to browse-level classes to provide an additional measure of browsing intensity. The procedure for fecal pellet counting will be the same as Edenius et al. (2003) whereby a binary categorization is assigned to each plot indicating recent use or lack of use. Quantification of the magnitude of reindeer use for each catchment will be based on the number of plots that exhibit signs of recent reindeer use.

Since the maximum allowable reindeer in herding districts has not changed significantly in recent decades, we assume that the *relative ranking of herding districts with regard to reindeer densities has remained constant*. The practice of letting reindeer graze unsupervised for much of the summer season (Moen & Danell 2003) reduces the influence of human control on reindeer location below the level of the summer herding grounds (i.e. specific valleys or hillsides within the summer herding grounds are not likely highly influenced by human activity).

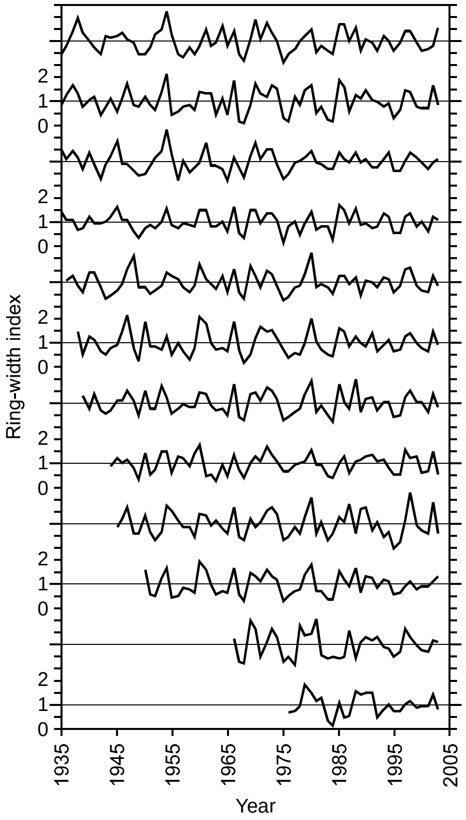
5.4.2 Within site patch selection. Establishment above the current treeline is not homogenous. Patches of trees exist beyond the current treeline. These patches serve as the vanguard of an advancing treeline under changing climate conditions. Within each of the catchments chosen for sampling (5.4.1) we propose to choose 5 patches for measuring establishment. These patches will be chosen to ensure that a variety of slopes, aspects and topographic settings will be incorporated into the study. Potential patches will be identified using color infrared aerial photographs of the study area prior to going into the field. Five primary and 5 alternate patches will be chosen in case particular sites are deemed unsuitable in the field due to either human activities or inaccessibility that was not identifiable from the aerial photos.

5.4.3 Within patch sampling. Within each patch we will sample as many as 40 individual stems. For small patches with less than 40 total stems we will collect cores from every stem > 7.5 cm at the root collar. Stems < 7.5 cm diameter at the root collar will be cut into sections instead of being cored. In large patches, 40 stems will be chosen at random. Collection of cores from 40 stems reduces the probability of missing an age-cohort in the patch to below 10% (Frelich 2002). Two cores will be taken from opposite sides of each stem as close to the root collar as possible and multiple cores will be taken until the core contains the pith. Preliminary data collection indicates that the pith is sampled on the first coring in the majority of cases. These trees are easily cored and cut and data collection proceeds rapidly.

For stems that are too small to be either cored or sectioned (seedlings), we will count all seedlings within the patch and measure diameters. This will allow us to have information on the size of the contemporary seedling bank at each site that was not available by coring or sectioning. Seedling density at these sites is not extremely high and the PI (Cairns) has performed similar seedling censuses at mountain birch sites in the past that have proceeded rapidly.

5.4.4 Collection of Pinus sylvestris cores. Studies of herbivore impacts on trees have often relied on cross-species comparisons between trees that are affected by the herbivore of interest and those that are not (Case & MacDonald 2003; Parish & Antos 2002; Rolland et al. 2001; Simard & Payette 2001). For this study, we will collect tree-ring cores from *Pinus sylvestris* trees growing in the same catchments as our study sites. Scots pine occurs at lower elevation than the birch treeline, but has been used effectively before as a control species for illustrating the impact of herbivores on mountain birch because it is not affected by either reindeer or the autumnal moth (Eckstein et al. 1991). We propose to collect tree-ring cores from approximately 20 trees in each catchment used for this study. Cores will be prepared and dated using the methods described below (5.5) and ring-width indexes will be calculated (5.5). All ring-width series for each catchment will be averaged together to give a single ring-width chronology for each catchment that can then be compared to the birch growth (5.7.5).

Figure 3: Standardized ring widths used for creating a crossdated master chronology for mountain birch in Norrbotten.



5.5 TREE-RING METHODS

5.5.1 Sample preparation and dating. We will mount each core in a standard core mount and use a belt sander to surface each core and cross-section with progressively finer sandpaper (Orvis & Grissino-Mayer 2002; Stokes & Smiley 1968) . To date the samples, we will develop a master chronology (Stokes & Smiley 1968) for each herding district from 10 - 20 of the largest trees, and use significant marker rings to crossdate the remaining samples both visually and using the COFECHA program (Holmes 1986). Preliminary work conducted by the PI demonstrates that the annual growth rings of mountain birch are distinct and can be crossdated without difficulty (Section 5.5.2). We will measure the rings in each sample with a Velmex measuring stage accurate to 0.001 mm, and use COFECHA to verify and refine the calendar dates assigned to individual rings. We will use the ARSTAN program (Cook & Holmes 1986) to remove long-term growth trends and to generate for each study site a residual ring-width chronology with autocorrelation removed.

5.5.2 *Preliminary dendrochronological analyses of mountain birch.* We have developed a preliminary master chronology for the study area (series intercorrelation = 0.651, average mean sensitivity = 0.488) that will be augmented with additional cores collected for this study (Figure 3). Series intercorrelation values above 0.5 and average mean sensitivity values above 0.3 are considered high (Grissino-Mayer 2001). High values, such as those we obtained for treeline birch trees, are typical for stressful environments (cf. Fritts 1976) and are desirable for crossdating.

Preliminary work with the tree-ring series in our master chronology indicates that ring-width index is correlated with climate. We used monthly climate data from Abisko as independent variables in a stepwise linear regression analysis to test the response of mountain birch tree rings to climate. Ring width was influenced by average monthly temperature in March, June, July and November. The resulting model was significant ($F = 25.84$, $p < 0.001$) and had an adjusted $R^2 = 0.60$. Therefore, our own preliminary data, in concert with the number of studies that have utilized crossdated mountain birch chronologies (Eckstein et al. 1991; Hoogesteger & Karlsson 1992; Kirchhefer 1996), give us confidence that we will be able to date our tree-ring series accurately, and suggest that climate is partly responsible for variation in annual growth increment.

5.6 ANCILLARY DATA COLLECTION

5.6.1 Climate data. Climate data are available for a network of sites across the mountainous region of Norrbotten from the Swedish Meteorological and Hydrological Institute (SMHI). Data extending as far back as 1890 are available within the Nordklim dataset (www.smhi.se/hfa_coord/nordklim/) for several stations in the region (Table 1). The data network becomes much more dense throughout the 20th century.

Although the climate stations are not collocated with our study sites, the temperature data among the widely spaced climate stations are highly correlated (average correlations among stations for January 0.89; July 0.85) which indicates that periods of warmer and colder than average temperatures occur in concert across the region. Precipitation is less highly correlated among the sites, but moisture is not limiting in this environment. Therefore, we are confident that with the stations available we can adequately represent important climatic variation over time within the study area.

Table 1: Period of record for climate data at northern Scandinavian meteorological stations.

	Period of Record	
Station	Temp	Precip
Abisko	1913 – 2004	1913 – 2004
Jokkmokk	1890 – 2004	1890 – 2004
Karesuando	1890 – 2004	1890 – 2004
Kvikkjokk	1890 - 2004	1890 – 2004
Sodankylae	1908 - 2004	1980 - 2004

5.6.2 Reindeer population data. Moen & Dannell (2003) have compiled reindeer population data since the mid-nineteenth century for the study area from official reports. The data indicate that there have been periods of high and low reindeer populations throughout the period of record. Peaks in the reindeer population occurred around 1890, 1930, 1955 and 1990. Low reindeer populations were apparent in 1920, 1940 and 1970. Dr. Moen has made these data available to us for this project.

5.6.3 Autumnal moth outbreak data. Historical outbreak data for *Epirrita autumnata* in Sweden between 1860 and 1972 are available from a review written by Tenow (1972). These data are based on annual insect reports sent to the Swedish Forest Service. This review is exceptional in quality in that it provides detailed appendices with information regarding the spatial extent of individual outbreaks along with evaluations of the extent of damage of the outbreaks. For the period after 1972 we plan to supplement the *Epirrita* time series with similar contemporary data. Since 1972 outbreaks have been documented in 1973 (Eckstein et al. 1991), and 1986/7 (Bylund

1997) in the scientific literature. The PI (Cairns) also witnessed a localized outbreak in 2003 near Nikkoluakta.

5.7 DATA ANALYSIS

5.7.1 Contemporary Migration Potential. The number of seedlings at each sample site will be tallied and seedling density will be calculated as the ratio of number of stems to patch area. Mountain birch may remain at the seedling stage for many years and therefore can form a persistent bank of seedlings that will grow into trees under favorable environmental conditions. Supratreeline sites with large numbers of seedlings (regardless of their age) should have the potential to migrate more quickly than sites without large numbers of seedlings. The seedling densities from the 15 patches (5 patches x 3 catchments) in each herding district will be averaged together and correlated with the reindeer densities in the herding districts used for this study. A significant and negative correlation between seedling density and reindeer density will support the hypothesis that contemporary migration potential is influenced by reindeer populations. Additionally, to take advantage of our nested design and to test for variation in seedling response to herbivory at levels below that of the entire region we will perform an analysis of variance (ANOVA) to test for variability within and between herding districts.

The hypothesis that birch treelines represent a Type II treeline with respect to herbivory (5.1 Hypothesis 2) will also be tested using these data. If the conditions at the birch treeline represent Type II conditions, we should expect that the number of seedlings should not only decrease with increasing reindeer densities, but that it should assume a sigmoidal form. We will test this by fitting Weibull functions and Error functions to the data using non-linear regression methods (e.g. Cairns & Waldron 2002). The hypothesis will be accepted if the fitted curve is statistically significant (α=0.05) and the adjusted-R^2 exceeds 0.5.

5.7.2 Identification of historic establishment trends. Age structure diagrams for saplings and trees will be produced by plotting the number of stems established per year for the period of record determined by tree-ring dating. Since the historic reindeer data represent regional conditions, site and catchment level variability in establishment can not be compared to the historic reindeer population data without assuming that reindeer population was evenly distributed over the study area. This is an unrealistic assumption and therefore the establishment data from all sites must be pooled to determine regional-level trends in establishment. Our study sites will be spread across Norrbotten and therefore the pooled establishment data should represent regional conditions adequately.

Static age structures (such as the one created here) are a consequence of establishment as well as survival, hence an apparent lack of establishment for a period actually may reflect high mortality of trees established during the period (Daniels & Veblen 2004; Johnson et al. 1994; Szeicz & MacDonald 1995). Consequently, rather than using seedling number as the predictand for our analyses, we will fit negative exponential and power functions to the frequency *vs*. age data, determine which of these theoretical functions fit the observed data best, and calculate the difference between the actual and theoretical age distribution (Daniels & Veblen 2004; Szeicz & MacDonald 1995). The resultant residuals allow for the identification of periods over the last 150 years where establishment was higher and lower than expected.

5.7.3 Identification of climate variability. Raw climate data will be processed to determine periods of climatic anomalies (periods greater and less than average) for the past 150 years. Anomalies will be calculated relative to the 1961 – 1990 mean (cf. IPCC 2001a). Climatic anomalies for seasonal, monthly, and annual average temperatures will be calculated. Similarly, seasonal and annual total precipitation anomalies will be determined.

The North Atlantic Oscillation (NAO) is another measure of climate variability that we will test as a predictor of mountain birch establishment and growth. The NAO is a major source of interannual climatic variability in Europe. It is particularly influential during the winter (Hurrell 1995). One convenient quantitative representation of the NAO index is proposed by Jones et al. (1997). Positive NAO index values correlate with warm, wet winters in Europe, whereas negative values represent colder air in Europe. The NAO index is calculated at both annual and monthly intervals. Positive NAO index values show a positive correlation with leaf out dates for *Betula pubescens* (Chmielewski & Rotzer 2001; D'Odorico et al. 2002) and therefore may be related to both growth and establishment at treeline in Sweden. The NAO index is also shown to correlate with rate of population change of the autumnal moth (Klemola et al. 2003).

5.7.4 Identification of the climate signal. We will use correlation function and response function analyses (Blasing et al. 1984; Fritts 1976) to evaluate the influence of climate on radial growth of mountain birch at each study site. For correlation function analyses, a series of correlation coefficients will be calculated between the ARSTAN ring-width residual (ring-width index) and a sequence of climatic variables (monthly temperature and precipitation, seasonal temperature, monthly NAO). Although we will include precipitation in our analysis, studies of mountain birch – climate relationships indicate that is not usually a determinant of growth (cf. Karlsson et al. 2004). Correlation analysis investigates possible relationships between growth and climate variables, but does not produce a predictive model. We will will also use response function analysis (Blasing et al. 1984; Fritts 1976) to investigate climate-growth relationships. Response function analysis is a more robust method for uncovering climate – ring-width relationships because it reduces multi-collinearity among the climate variables (Grissino-Mayer & Butler 1993). The response function analyses will use principal components regression to calculate multivariate responses of the ring-width residual to the predictors (Fritts 1976). Separate response function analyses will be conducted for temperature and the NAO index.

The climate variables that are significant in *both* the correlation and response function analyses will then be used as independent variables in a multiple regression analysis to predict ring-width index. The predicted ring-width index will represent the predicted climate signal for each site. Climate signals will be calculated for each catchment to reduce error associated with regional climate variation within the study area.

5.7.5 The herbivory signal. We will obtain the herbivory signal in two ways. First, we will subtract the predicted climate signals from the ring-width index chronologies to produce a chronology of non-climate related signal within the tree-ring data (Lafon & Speer 2002). This series of residuals will represent the potential herbivory signal from the original data. Second, we will use a non-host method to independently determine another estimate of the herbivory signal. Scots pine and mountain birch tend to show similar responses to climate variability in northern Sweden (Hoogesteger & Karlsson 1992). Scots pines are not subjected to herbivory by either the autumnal moth or reindeer and therefore represent an herbivory-free control. Previous studies have relied on the differential response of two species to herbivory pressure to isolate the herbivory signal from a ring-width index chronology (e.g. Hoogesteger & Karlsson 1992; Zhang & Alfaro 2002). We propose to use the method of Hoogesteger & Karlsson (1992) in which the herbivory signal is calculated as the difference between the mountain birch ring-width index chronology and the ring-width index chronology for Scots pine. This procedure will allow us to have two measures of herbivory effects on growth at treeline which can then be compared to herbivore densities.

5.8 HYPOTHESIS TESTING

Hypothesis 1, that the presence and size of a supratreeline seedling bank is related to the local reindeer population, will be evaluated using correlation analysis (5.7.1). A significant and negative correlation between reindeer population and seedling density in the supra-treeline zone will indicate a greater treeline migration potential under low herbivory pressure. **Hypothesis 2**, that birch treelines are a Type II treeline will be evaluated by non-linear regression methods (5.7.1). **Hypothesis 3**, that region-wide historic establishment occurs during periods of favorable climate coupled with below-average reindeer populations and autumnal moth activity will be tested using analysis of covariance (ANCOVA). The establishment residuals (5.7.2) will be the dependent variable and climatic anomalies (5.7.3), and reindeer population will be the independent variables. Insect outbreak periods will be the covariate. If both climate and herbivory variables are significant in the ANCOVA analysis we will accept hypothesis 3. We will only accept the more general hypothesis of reindeer impacting reproduction at treeline if both hypotheses 1 and 3 are supported. This avoids confusing correlation with causation and provides a conservative test of our hypotheses.

We will test **hypothesis 4** that herbivory influences growth of birch trees at treeline by using ANCOVA. We will use the residuals calculated in section 5.7.5 as our dependent variables (each set of residuals will be considered separately), reindeer population data will be our independent variable and autumnal moth outbreak periods will be the covariate. Data for the entire region will be pooled for this analysis. We will accept our hypothesis if the reindeer population has a significant effect on the overall model. We will also be able to test for interaction effects between reindeer populations and autumnal moth outbreaks.

By examining three different modes of treeline response to herbivory and climate (size of the contemporary seedling bank, historic establishment and growth) we will be able to say with some authority how herbivores affect treelines in Scandinavia.

6. SIGNIFICANCE

6.1 Scientific and applied merits

The scientific merits focus on improving understanding of alpine treelines as a diagnostic, though complex system of disturbance (e.g., reindeer browsing) and ongoing climatic change. In most situations, regional treelines have attracted attention (and bias) by mainly investigating disturbance-free locales. This work will directly incorporate climate change and a natural disturbances. Specific benefits of this project include a greater understanding of the spatial constraints of treeline migration within the mountains of Sweden. By concentrating on establishment of trees above the treeline, and the spatial and temporal variability of such establishment, we will be able to understand the spatial complexity of this highly sensitive indicator of climate change at a landscape scale. Plot scale studies of reindeer – mountain birch interaction have been done, but need to now be expanded to the landscape scale. This research will contribute significantly to understanding the interactive effects of reindeer and climate change at a landscape scale at treeline.

6.2 Broad implications

If we can understand the impacts of herbivory on a major ecotone (alpine treeline) in Fennoscandia, then we can share knowledge about the future sustainable development, including economic opportunities, indigenous hunting/herding of reindeer, and tourism for the Far North. The adaptability and resilience we may document in quantifying processes in Fennoscandia could then be extrapolated to other ecotones where herbivory influences ecosystem structure and function (such as treelines in South America, and ecotones in arid western North America where livestock grazing is of paramount importance). Treeline environments are critical to local economies in northern locales and predictions of potential changes in treeline location and structure may allow for more adequate planning for future conditions. This is particularly important considering that rapid upslope migration of mountain birch threatens mid- and high-alpine vegetation in the Scandes (IPCC 2001b).

The involvement of a graduate student and undergraduates with this research will be an integral portion of the work. We anticipate that a master's thesis will result from the contemporary migration potential and historic establishment portions of the work. We will disseminate our research findings through publication in refereed journals and attendance at national and international meetings. We propose to establish a web site that will allow up-to-date summaries of our data to be shared with our collaborators in Sweden as well as with the public in general. In addition, we will submit our chronologies to the International Tree Ring Data Bank (ITDRB), thereby making them available to the scientific community. This will be the first submission of mountain birch chronologies to the ITDRB. Both PIs have a history of supervising graduate and undergraduate students in research activities. Cairns has produced 1 Ph.D. student and is currently supervising 2 Ph.D. and 2 M.S. students; Lafon is supervising 2 Ph.D. students and 1 M.S student. Funding of this project will also allow for the strengthening of ties between the PIs and our Swedish collaborator and students. It will also allow for the training of students in international science.

7. DIVISION OF LABOR AND TIME-TABLE

Dr. David M. Cairns at Texas A&M University will be responsible for field site selection, reindeer use measurement in the field and statistical analysis of the data. He has experience with classification of land types using aerial photographs (Cairns & Waldron 2002) and he will supervise the aerial photography portion of the study. He will coordinate all project activities and supervise a graduate research assistant on the project. He will present the research findings at national and international meetings (AAG, IAVS) and expects to publish 3-5 papers from this project in collaboration with Dr. Lafon, the students working on the project and collaborators abroad.

Dr. Charles W. Lafon will lead the tree-ring analysis portion of the study. He will be responsible for overseeing the preparation and analysis of the tree-ring samples for dating and growth. He will work with Dr. Cairns in the statistical analysis of the tree-rings and comparison with the reindeer population data. He will be the primary supervisor of the undergraduate student and will share graduate student supervision with Dr. Cairns. He will present research findings at selected national and regional scholarly meetings (AAG, SWAAG) and join in publications with Dr. Cairns, students working on the project and collaborators abroad.

Figure 4: Project scheduling and assignment of responsibility.

Major Tasks	Responsibility
Field Site Selection	
Analysis of aerial photographs	Cairns
Identification of supra-treeline patches	Cairns
Field Data Collection	
Quantification of Reindeer Impact	Cairns
Collection of tree-ring cores	Both
Data Analysis	
Core preparation and measurement	Lafon
Statistical analysis	Both