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RECENT TREELINE DYNAMICS IN SUB-ARCTIC
SWEDEN

A MULTI-DISCIPLINARY LANDSCAPE ASSESSMENT

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Abstract

Models project that by the year 2100 the sub-Arctic treeline may shift up to 400 km northwards in flat areas and up to 670 m upslope in mountainous areas in response to projected climate warming. Furthermore, more thermophilic tree species are expected to colonise the treeline ecotone and replace current dominant tree species.

This study aimed to document changes or stability of the treeline in a sub-Arctic alpine model area of 1000 km² over a period of more than 100 years, and particularly to clarify the ambiguity that presently exists about the mechanisms driving treeline dynamics. The study was conducted in the Torneträsk area in northern Sweden where mean annual temperature increased by 2.5 °C in the past century. Mountain birch (*Betula pubescens* ssp. *czerepanovii*) is the dominant tree species and sets the treeline. Multiple techniques were used, including repeat photography, measurements along elevational vegetation transects, and dendrochronological analysis. Overall, we found highly contrasting birch treeline dynamics in our model area: some treeline sites were slowly retreating or had been stationary for at least the past 258 years, as indicated by the oldest recorded birch tree in the world. Only four out of eight treeline sites had advanced and at one site, spanning a distance of more than 10 km, the treeline had retreated 120 m downslope. Moreover, dendrochronological analysis indicated that treeline advance in the past two centuries was most pronounced during the cooler late 1960 and 1970s when reindeer (*Rangifer tarandus*) population numbers reached a record low. A decreased anthropo-zoogenic influence impact since the early 20th century was found to be the main shaping factor of the advancing treeline sites. Also variability in snow depth and geomorphological activity explained the contrasting treeline dynamics of mountain birch. As biotic and abiotic disturbances highly determined the elevational position of the sub-Arctic treeline, both climate-driven model projections of future treeline positions and its use as bio-climatic monitoring should be used with caution. In sharp contrast, more thermophilic tree species such as alder (*Alnus incana*) and particularly aspen (*Populus tremula*) had rapidly expanded during this period. Aspen had become 16 times more abundant over the past hundred years and had successfully colonized the birch treeline ecotone. Tree-sized (>2m) aspen can now be found at the upper birch tree limit, a new phenomenon in the European sub- Arctic. This local geographical range expansion of this thermophilic tree species occurred by increased sexual regeneration, a process promoted by increasing summer temperatures and episodic moth outbreaks on its competitor mountain birch. Whereas 100-year-old birch trees suffered 9.0 years growth reduction due to moth herbivory (predominantly *Epirrita autumnata*), the impact on aspen only amounted to 1.4 years. However, despite recent summer warming, the expansion of subalpine aspen was halted due to an exponentially

increasing moose (*Alces alces*) population since the late 1960s. Herbivory also affected the competition mechanism between pine (*Pinus sylvestris*) and birch; significant growth increases were found in pine following moth outbreaks on birch. Climate reconstructions based on ring width trends in pines sampled in mixed forests could be biased by this mechanism.

Overall, our results indicate that in a scenario of continued warming thermophilic tree species are likely to further expand in the sub-Arctic treeline ecotone, but changing disturbance regimes including future herbivore population dynamics may hamper this process. Therefore, alternating periods of apparent species range stabilities and abrupt non-linear shifts may characterize species migration patterns in the sub-Arctic.

Nederlandstalige samenvatting

Sinds 1880 steeg de gemiddelde temperatuur op aarde met 0,6 °C. In sub-Arctisch Zweden daarentegen bedroeg de temperatuurstijging 2,5 °C. Klimaatsverandering grijpt sneller en drastischer plaats op de noordelijkste breedtegraden gezien de specifieke land-, oceaan- en atmosferische karakteristieken van deze regio. De meest recente klimaatsmodellen verwachten tegen het jaar 2100 een verdere stijging van de gemiddelde jaartemperatuur met 4,5 – 6,0 °C voor de sub-Arctische en Arctische regio en met 2,0 °C voor de globale temperatuur. Een klimaatsopwarming van deze grootteorde zou tegen het jaar 2100 een noordwaartse opschuiving met 400 km van de latitudinale boomgrens kunnen veroorzaken en een hellingopwaartse verschuiving met ruim 660 m voor de sub-Arctisch alpiene boomgrens. Zulk een vegetatiemigratie impliceert drastische veranderingen in de globale koolstofkringloop, permafrost distributie, hydrologie, regionale klimaatdynamiek, alsook migratiepatronen van mens en dier. Ondanks recente vooruitgang in het modelleren van regionale klimaatpatronen, topografie en competitiefactoren, zijn dynamische vegetatiedistributiemodellen voornamelijk nog gebaseerd op enkelvoudige parameters uit de klimatologie en biochemie.

Om een beter inzicht te bekomen in de factoren die de sub-Arctische boomgrensdynamiek reguleren en om na te gaan of de meest recente modellen realistische vegetatiemigraties voorspellen, werd een multidisciplinaire studie aangevat in een modelgebied in sub-Arctisch Zweden (het Torneträskgebied; 68°25' N, 19°00' O). Deze studie werd uitgevoerd op een landschapsschaal (oppervlakte *c.* 1 000 km²) aangezien de grootste kennisleemten wat betreft oorzakelijke boomgrensfactoren en hun modellering zich op deze schaal situeren (Holtmeier and Broll, 2007). Met name grote onduidelijkheid bestaat omtrent verschuivingen in vegetatiecompositie: zullen meer thermofiele boomsoorten de boomgrenszone koloniseren?

De boomgrens in het Torneträskgebied heeft een sub-Arctisch alpien karakter en is gesitueerd op *c.* 700 m boven zeeniveau. In Noord-Europa domineert de lage berk (*Betula pubescens* ssp. *czerepanovii*) de boomgrenszone. Aangezien boomgrensfluctuaties en hun interpretatie sterk afhankelijk zijn van de geografische en temporele schaal van de studie, namen we een ruimtelijk studiekader variërend van een lokale site (0,02 km²), over een individuele berg (*c.* 20 km²), tot een landschap (*c.* 1 000 km²) en een temporele schaal gaande van 30 tot 100 jaar. Hiertoe maakten we gebruik van tijdreeksen van lucht- (1959-2000) en landschapsfoto's (1908-2009), historische boomgrensmetingen die konden gerepliceerd worden (uit 1904 en 1977), alsook van vegetatietransecten en dendrochronologische analyses. Dendrochronologie

bekleedde een sleutelrol in dit proefschrift. Uit de studie van jaarringen kunnen immers klimaat-responscoëfficiënten, leeftijdsdistributies, competitie- en verstoringsfactoren, alsook reproductie en mortaliteit van bosbestanden worden afgeleid. De boomgrens werd gedefinieerd als de gehele zone die zich uitstrekt van de bovengrens van het continue berkenbos (30% bosbedekking werd aangenomen als drempelwaarde) tot aan het hoogst voorkomende individu van een boomsoort onafhankelijk van de stamhoogte. Zulk een ecotonale benadering van de boomgrens bleek het meest geschikt om de complexe overgangszonzone van het sub-Arctische loofbos naar de alpiene toendra te bestuderen. De definitie omvat zowel de veelvoorkomende meerstammige ‘polycorme’ berk alsook de hoogst voorkomende jonge individuen die nog geen boomgrootte (>2 m) hebben bereikt.

Ondanks een temperatuurstijging van 2,5 °C in de voorbije eeuw in het Torneträskgebied, werd geen uniforme boomgrensprogressie waargenomen. Op alle bestudeerde temporele en ruimtelijke schalen werd een zeer heterogene boomgrensdynamiek vastgesteld. Op de landschapsschaal schreed het continue berkenbos gemiddeld 24 m bergopwaarts (effectief hoogteverschil) in de periode 1912-2009. Vier van de acht boomgrenssites bevonden zich in een progressieve fase, drie sites toonden langdurige immobiliteit aan en op één bergflank, die zich uitstreckte over ruim 10 km, was de boomgrens de voorbije eeuw met 120 m gedaald. De vondst van een 258-jarige lage berk, de oudst geregistreerde levende berk ter wereld, toont de langdurige immobiliteit van sommige van de boomgrenssites aan en duidt op voorzichtigheid voor het aanwenden van altitudinale verschuivingen van de boomgrens als hoge-resolutieproxy voor klimaatsverandering. Inderdaad, het was niet de recente klimaatsverandering die de stijging van de vier boomgrenssites had veroorzaakt: perioden waarin belangrijke boomgrensprogressie plaatsvond, kwamen niet overeen met warme perioden. Het jaarlijks aantal opgeschoten berken in de boomgrenszone bleek niet significant ($P > 0,05$) gecorreleerd met temperatuur of neerslag, maar wel met het aantal rendieren in het Torneträskgebied ($r = -0,69$, $P = 0,03$). De sterkste boomgrensstijging vond plaats in de periode 1964-1978, wanneer de rendierpopulatie en het aantal vraatsporen in het berkenhout een historisch dieptepunt bereikten. Vergeleken met de 19^e en begin 20^e eeuw, wanneer de rendierherders de kuddes volgden en hun zomerkampen nabij de boomgrens opsloegen, is de menselijke impact en begrazingsdruk sterk afgenomen en heeft de boomgrenspositie zich grotendeels kunnen herstellen. Historische anthropozoögene invloed en sneeuwdikte waren de twee factoren die significant bijdroegen tot de verklaring van de verandering in boomgrenspositie in de voorbije honderd jaar. Hellingsprocessen en pestuitbraken van de novemberspanner (*Epirrita autumnata*) en de kleine wintervlinder (*Operophtera brumata*) leidden respectievelijk tot boomgrensstagnatie en -terugtrekking

(afdalings).

In sterk contrast met de lage berk, hadden de thermofiele boomsoorten esp (*Populus tremula*) en grauwe els (*Alnus incana*), twee sporadisch voorkomende boomsoorten in het noordelijke berkenwoud, zich snel bergopwaarts uitgebreid in het Torneträskgebied. De distributiegrens van de els was in de periode 1977-2009 met 20 m gestegen en situeerde zich in 2009 c. 100 m lager dan die van de berk. De esp had de berkenboomgrens zelfs gekoloniseerd. Daar waar boomgrote espen (>2 m) in 1904 enkel in het laagland konden gevonden worden, hadden deze in 2009 de berkenboomgrens bereikt. Het gaat om een nieuw verschijnsel in sub-Arctisch Europa: nooit eerder werd zulk een duidelijke verandering in bosstructuur en -compositie gedocumenteerd in het sub-Arctische boomgrensecotoon van Noord-Europa. De expansie van de esp was voornamelijk te wijten aan verhoogde seksuele voortplanting, een proces dat vrij zeldzaam wordt geacht in esp. Onze resultaten toonden aan dat in de voorbije honderd jaar de esp zich minstens zeven maal had voortgeplant via zaailingen. Hoge zomertemperaturen begunstigen zaadvorming en kieming van espenzaailingen. Ook vegetatieve voortplanting werd gestimuleerd door hoge zomertemperaturen. Indien de klimaatsopwarming zich doorzet, is het waarschijnlijk dat de thermofiele esp zich verder zal uitbreiden in het berkenboomgrensecotoon.

Nochtans hangt de uitkomst van het berk-espcompetitieproces sterk af van toekomstige verstoringregimes. Dendrochronologische analyse toonde immers aan dat de espenbosjes in het subalpiene berkenwoud zich het snelst uitbreidden na grootschalige kaalvraat van de berken door motuitbraken. Gemiddeld genomen lijdde honderdjarige berken 9,0 jaar groeireductie door motvraat, daar waar honderdjarige espen slechts 1,4 jaar groeireductie kenden. Toch was door een sterk aangegroeide elandpopulatie (*Alces alces*), die esp verkiest boven berk, de expansie van de subalpiene esp recentelijk sterk afgenomen. De radiale groei in grove den (*Pinus sylvestris*) bleek eveneens beïnvloed door de cyclische motuitbraken op zijn concurrent berk. Deze vaststelling duidt niet alleen op de grote impact van deze kleine invertebrate grazer op het competitieproces tussen de verschillende boomsoorten in het sub-Arctische woud, maar suggereert ook voorzichtigheid met het gebruik van denjaarringen bemonsterd in het sub-Arctische berkenwoud als proxy voor klimaatreconstructie.

Deze studie toonde duidelijk aan dat de dynamiek van de sub-Arctische boomgrens door heel wat meer factoren wordt bepaald dan louter temperatuursveranderingen. Anthropozoogene verstoringen, plant-plantcompetitie en dynamische plant-herbivoorinteracties bleken de positieve effecten van stijgende temperaturen op plantprocessen te overstijgen. Deze complicerende

factoren maken dat de voorspelde boomgrensstijgingen voor ons studiegebied van 233 tot 667 m tegen het jaar 2100 zeer waarschijnlijk niet zullen gerealiseerd worden. Ook de verwachte hernieuwde dominantie van de conifere boomsoorten zoals grove den (*Pinus sylvestris*) en fijnspar (*Picea abies*) ten nadele van de lage berk tegen het einde van de 21^e eeuw contrasteren met de realiteit: voornamelijk thermofiele loofboomsoorten zoals de esp en de els hadden zich uitgebreid in en nabij het berkenboomgrensecotoon. Het is duidelijk dat een tot lijn gereduceerde boomgrenszone of de best overeenstemmende isotherm met de boomgrenspositie ons niet verder helpen in een betere doorgronding en modellering van de noordelijke vegetatiegrenzen. De correlaties bevonden tussen temperatuur en boomgroei over een korte tijdsspanne impliceren niet dat op lange termijn de boomgrens zal stijgen. Plantmigraties worden immers bepaald door veranderingen in voortplantingssucces veeleer dan door de groeivariabiliteit in reeds gevestigde bomen. Het is daarom belangrijk de boomgrens te bestuderen als een populatiedynamiek in een ecotonaal kader over een voldoende lange termijn: verschillende decennia tot meerdere eeuwen. Meer nauwkeurige voorspellingen van de toekomstige boomgrenspositie zullen enkel bekomen worden wanneer de interagerende mechanismen geïdentificeerd in deze landschapsstudie beter geparametriseerd en geïmplementeerd worden in dynamische vegetatiemodellen.

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Chapter 1 Introduction

1.1 Background

1.1.1 Climate change in the North

The sub-Arctic is most commonly defined as the region just South of the 10°-July isotherm and corresponds to the area where the closed boreal forest gradually transforms into the treeless Arctic tundra (Fig. 1).

In the past 20 years the sub-Arctic and the Arctic have attracted a lot of attention because these areas are considered to be most sensitive to global warming (ACIA, 2005, Xue et al., 2010). Indeed, particularly sub-Arctic and Arctic areas have recently warmed: during the past three decades mean annual temperature increased by more than 2.0 °C in the area north of the 60°N-latitude circle (Schiermeier, 2006; Callaghan et al., 2010). For comparison, global mean annual temperature increased by 0.6 °C since 1880 (IPCC, 2007).

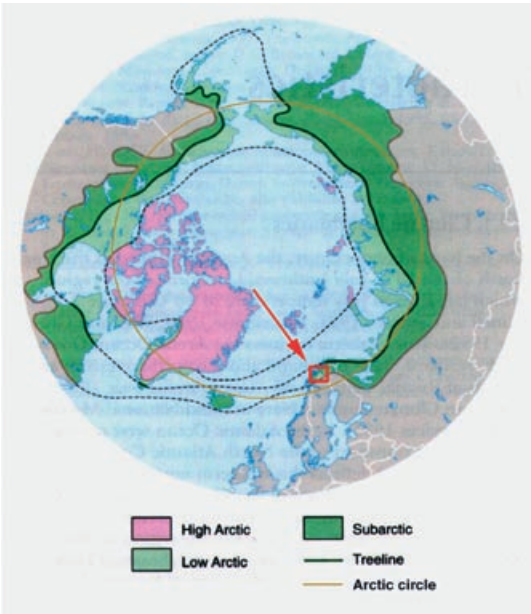


Figure 1. Ecological definition of the sub-Arctic and the Arctic based on the northern boundary line of trees and shrubs respectively. Note the differences in the latitudinal position and areal extent of these biomes across the globe. The location of the study area is indicated by the red box (AMAP, 1998).

The degree of continued warming that is projected for the present century is considerable: up to 4.5 to 6.0 °C north of the 60 °N-latitude circle and even more for the High-Arctic (c. 75°-90° N) by the year 2100 (reference year 1990; ACIA, 2005; IPCC, 2007; Xue et al., 2010). Such warming is expected to stimulate a significant northern and upslope advance of the sub-Arctic treelines (Harsch et al., 2009; Euskirchen et al., 2009; Xue et al., 2010).

1.1.2 Definition of the treeline

Table 1. Overview of the different definitions that exist to delimit the Arctic and sub-Arctic area and their associated biomes. Also different definitions exist to define a tree or the treeline (Callaghan et al., 2002 and references therein).

Term	Definition	Reference
Regions		
Arctic	Area north of the treeline	Hustich (7)
Taiga	A Russian term denoting a marshy, Siberian woodland and often used to denote the circumpolar boreal forest. However, it is also used to describe the ecotone between the boreal forest and the Arctic tundra	Crawford in (32)
Boreal forest	Boreal forest, or taiga, is the world's largest vegetation formation, comprising coniferous forests that stretch around the Northern Hemisphere interrupted only by the North Atlantic Ocean and the Bering Strait. It forms a 1000-2000 km broad zone between the treeless tundra and either broadleaved deciduous forests or dry grasslands and semi-deserts	Vasari in (32)
Tundra	Generally the southern part of the Arctic, with higher vegetation Or Areas with permafrost or areas where the temperature is too low, or precipitation and wind too great for a natural forest vegetation, or where in the time for normal regeneration the area has not recovered from damage by man, fire or animals	Hustich (7)
	The part of the Arctic which bears vegetation on a soil which is frozen, except during the short Summer vegetation period	Rousseau (33)
	In origin from Finnish or Lappish <i>tunturi</i> meaning a treeless hill which has been absorbed via Russian to describe the dwarf shrub, herb and moss vegetation that exists in polar regions too cold to support tree growth	Crawford in (32)
Transition Region		
Tree Tundra	Belt between the treeline and the physionomic forest-line	Hustich (7)
Forest-tundra ecotone	The belt between the timberline and the tree-species-line	Hustich (26)
	The belt between the limit of continuous forest and the treeline	Payette (27)
High subarctic forest-tundra	The landscape mosaic of zonal tree and tundra vegetation composing a transition region lying poleward of the low subarctic open crown forest region and southward of the low arctic tundra region. It is bounded on the south by the southern limit (< 0.1% cover) of upland tundra and to the north by the northern limit (< 0.1% cover) of trees ≥ 3–4 m tall	Timoney et al. (18)

Term	Definition	Reference
Geographical distribution limits		
Treeline	Limit of trees, corresponding to tree individuals characterised by a tree growth-form and a height of 5 m or more	Payette (27)
	Connecting extreme arboreal occurrences of a tree species	Veijola (34)
Tree species-line	The absolute limit of the tree species in question, regardless of growth form	Hustich (26), Payette (27) Veijola (34)
Timberline	The economical or generative forest-line Limit of continuous forest The borderline formed by timber-sized trees	Hustich (26) Payette (27) Hustich (7)
Physiognomic timberline	Boundary of continuous forest	Veijola (34)
Economic timberline	Line within which forest regeneration is regular and forestry is possible	Veijola (34)
Forest-line (H), Forest limit (P)	Limit of the closed forest, regardless of its reproductive capacity	Hustich (26), Payette (27)
	Limit of forest stands	Payette (27)
Historical treeline	Line beyond which no macrofossils or other evidence of past tree cover can be found	Hustich (26), Payette (27)
Historical timberline	The line connecting the extreme arboreal occurrences of a tree species	Veijola (34)
Species growth forms		
Tree	An individual of a species that has a stem and is at least 2 m high (or 3, 4, 5 or 8 m) and reaches above the snow (does not consider polycormic birch of Fennoscandia)	Hustich (7)
Krummholz	Krummholz trees growing at or just beyond the treeline that exhibit a prostrate growth form, pruned by wind and ice-blast. Sometimes this growth form may be genetically determined, while in other cases it may be entirely due to phenotypic plasticity	Calow (35)
Tree Islands	Isolated tree clones far from the present treeline, which might be remnants from a former larger extension of the forest	Hustich (7)

Many attempts have been made to define the treeline (Table 1). Timoney et al. (1992) stated that the treeline has been defined more often than it has been mapped. A uniform definition of the treeline may never be achieved because of the environmental heterogeneity of the global treeline areas and the different tree species that set the treeline (Hustich, 1979; Holtmeier and Broll, 2007). Definitions vary along with authors and their areas of interest. While ecologists define boundaries such as ‘tree species limit’, scientists closely associated with the forestry sector are likely to focus upon ‘forest- or timberlines’ (Heikkinen, 1984; Callaghan et al., 2002). In addition, the treeline concept and its presentation both depend on the spatial and temporal

scale of the study (Callaghan et al., 2002). Currently used treeline definitions range from the continuous forest to the treeless terrain, implying that comparative studies are problematic (Fig. 2 and Table 1).

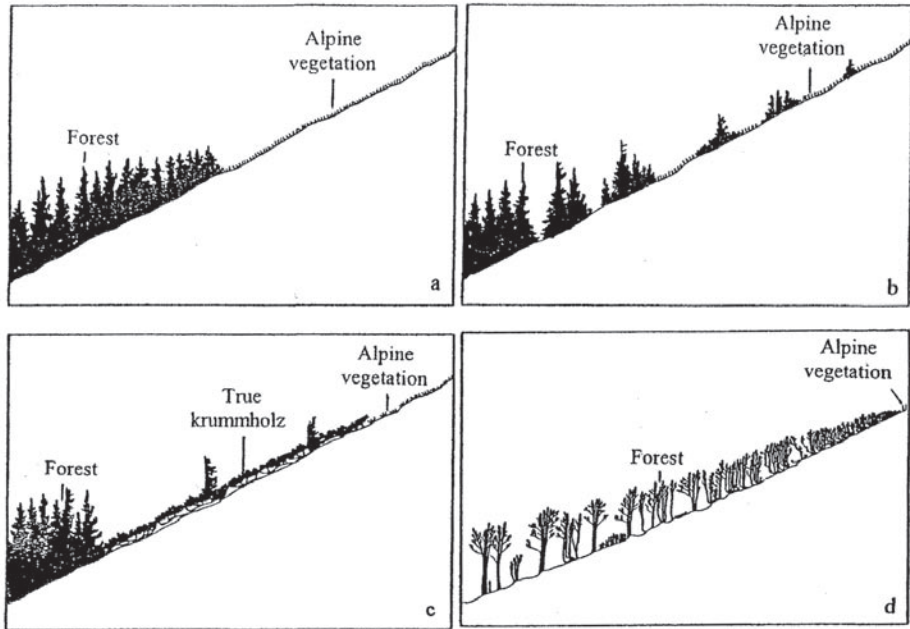


Figure 2. Different types of elevational treelines, suggesting that the delimitation of the treeline by a line appears problematic (Holtmeier, 2003).

The importance of the terminology is often underestimated. In fact, it is the definition setting for the concepts 'tree' and 'treeline' that determines the detection of treeline dynamics. For example, Kullman (1986) considered the spruce (*Picea abies*) treeline in southern Sweden to be rising after some stunted specimen, that had already established during the middle of the 19th century, exceeded 2 m in height (i.e. the threshold height to consider an individual a tree) between 1915 and 1975. Thus, in this case the advance of the treeline is mainly the result of a phenotypic response of the individual trees to more favourable conditions rather than a real advance of trees to a higher elevation (Holtmeier, 2003). Conversely, there is no similar phenotypic response of numerous bristlecone pines (*Pinus longaeva*) that established in the treeline ecotone of the White Mountains (California) between the 1940s and 1970s. Many of them are still smaller than 2 m. If we don't consider these pines as trees, we fail to record the obvious effects of the present climate and if these individuals would never reach 2 m in stem height, they would not even be mapped (Holtmeier, 2003).

1.1.3 Characteristics and importance of the sub-Arctic treeline

The boundary between the boreal forest and the treeless tundra is most easily seen by observing tree distribution, but many other important factors change through this boundary. There are changes in climate, in terms of both temperature and precipitation, and particularly in the depth and duration of the snow cover that determine the length of the growing season for plant species. These climatic changes select to some extent for the species that grow along a north/south or elevational transect through the boundary (Callaghan et al., 2002).

However, the forest and tundra ecosystems *themselves* force the local environment, though in different ways. Tundra ecosystems reflect more incoming radiation than forests and exchange more water and energy with the atmosphere (Callaghan et al., 2002). Conversely, forest ecosystems have a greater primary productivity, catch more carbon (Feddema et al., 2005; Juday et al., 2005), and trap more snow (Sturm et al., 2005).

The plant community structure also varies through the boundary zone. The tree growth form dominates the understorey species to the South or to the subalpine area, whereas dwarf shrubs and graminoids dominate the communities to the North or the alpine area. Therefore, the forest-tundra interface has a large influence on the biodiversity of the animals that are restricted to either zone, or use the two zones at different times and for different purposes. An example is the migration of reindeer (*Rangifer tarandus*) between summer tundra and winter forest pastures.

Changes in commercially useful components of biodiversity (timber, berries, fish, game, reindeer and landscape in terms of wilderness areas and tourist attractions) also affect the use of the forest-tundra-interface by people (Callaghan et al., 2002). Thus, our understanding of this boundary zone should not be constrained by the narrow concept of the species or growth form distributional limit.

Accordingly, northward and upslope shifts of trees as a response to climate warming would significantly alter climate and ecosystem processes (Post et al., 2009; Callaghan et al., 2010). Increasing tree density and spatial expansion of forests will cause a dramatic lowering of the albedo from about 90% for the snow-covered tundra to 11% for the dark evergreens, causing more energy to be absorbed by the ground surface (Juday et al., 2005). This effect is likely to exceed the negative feedback of increased C-sequestration in greater primary productivity

resulting from tundra displacements by forest (Callaghan et al., 2004). Furthermore, forest advance would have drastic consequences for the tundra biota, for instance non-migratory animals as well as vertebrate and invertebrate herbivores would be severely affected. Arctic human societies depending on the sustained use of the Arctic tundra biota, would also be strongly impacted (ACIA, 2005).

As current models project a northern and upslope advance of the sub-Arctic treeline by respectively 400 km and 670 m by the year 2100 depending on the climate scenario used (Kaplan and New, 2006; Euskircher et al., 2009; Xue et al., 2010), the urgency to study this process is high.

1.2. Background of causal factors controlling the sub-Arctic treeline

To model future shifts of the treeline, it is necessary to understand the driving mechanisms of treeline dynamics. In the following, a short introduction is given of the factors that are widely accepted to determine the position of the treeline at high latitudes in the northern hemisphere.

1.2.1 Temperature

Heat deficiency is widely accepted to be the dominant factor controlling the position and dynamics of the treeline at the global scale (Körner, 1998; Grace et al., 2002; Harsch et al., 2009), implying that both elevational (alpine) and latitudinal (polar) treelines occur (Holtmeier and Broll, 2007). Supporting evidence for this universal mechanism includes global relationships between treeline position and temperature isotherms (Körner and Paulsen, 2004) and Holocene fluctuations in the position of this vegetation boundary in accord with past temperature changes (MacDonald et al., 1993; Payette et al., 2002).

1.2.2 Climatic factors other than temperature

Moisture stress is less significant in the northern treeline areas where humidity tends to be high because cold air masses have a lower capacity to hold moisture (Veijola, 1998). However, precipitation may be a restrictive factor for tree growth in continental areas such as central Alaska and central Siberia (Lapenis et al., 2005; Lloyd, 2005). Also, at high-latitudinal treeline areas, soil moisture may be inaccessible to the treeline individuals because of ground frost. In April and May, the ambient air temperature may already exceed 10 °C, but the ground may still

be frozen because of late-lying snow. This process is known as frost drought and may cause severe damage to treeline trees (Holtmeier, 2003). Conversely, paludification is a common phenomenon in the lowlands of northwestern Siberia where the shallow active layer is underlain by permafrost and results in bog development, making the soil unsuitable for tree establishment (Crawford et al., 2003). Further, precipitation is critically important by determining snow depth. In most of the northern ($>60^{\circ}\text{N}$) treeline areas, the ground is covered by snow for more than six months a year (Holtmeier, 2003). Snow insulates young trees from temperature extremes and snow abrasion, whereas in spring it may serve as an important source of water supply (Sveinbjörnsson et al., 2002; Kullman and Öberg, 2009). Heavy snow loads may cause damage to the canopy and stem, particularly to evergreens (Autio and Colpaert, 2005).

1.2.3 Fire

Large parts of the North-American and Russian boreal forest zone are subjected to fire (Juday et al., 2005). Forest fires may cause an abrupt shift in tree species dominance; e.g. in Canada the establishment of a few lodgepole pines (*Pinus contorta*) after a forest fire caused the abrupt shift from a white and black spruce (*Picea glauca* and *P. mariana*) dominated forest to a pine dominated forest (Chapin et al., 2004). Hustich (1966) was of the opinion that the mountain birch (*Betula pubescens* ssp. *czerepanovii*) forest area of Utsjoki in northernmost Finland is the result of a large-scale forest fire where scots pine (*Pinus sylvestris*) has been replaced by birch. However, nowadays forest fires in northern Europe are rare as they are suppressed (Zackrisson, 1985).

1.2.4 Topography

Topography determines soil depth, drainage, and geomorphological activity and therefore exerts a major influence on treeline position and structure (Holtmeier and Broll, 2005; Butler et al., 2007). At the flat terrain of the latitudinal treeline, microtopography is associated with bog formation: well-drained sites will be invaded by trees, whereas sites with poor drainage will remain treeless (Veijola, 1998). Small changes in elevation will determine if a site is wind-exposed and hence the depth of its winter snow cover (Sveinbjörnsson et al., 2002; Dalen and Hofgaard, 2005). At the elevational treelines, soil depth quickly decreases with increasing inclination and seedling establishment becomes difficult (Veijola, 1998). Slopes with an inclination $>35^{\circ}$ are often characterised by snow, rock, and mud avalanches (McClung and Schaerer, 1993; Butler et al., 2007). Further, the annual freeze-thaw cycle and the long duration of the snow cover keep the soil very moist. This regularly causes solifluction that buries seedlings, results in root damage, and inclination of adult treeline individuals (Veijola, 1998).

1.2.5 Soil

Only since the 1990s more attention has been given to the role of soil in treeline dynamics (e.g. Sveinbjörnsson, 1992; Karlsson and Nordell, 1996; Holtmeier, 2003). Soil type, depth, temperature, moisture capacity, and stability determine whether seeds will germinate and whether seedlings will survive (Sveinbjörnsson et al., 2002). Soil type and weathering affect the nutrient pool available to young trees and their survival changes. Carbon limitation has been suggested as a restrictive factor for treeline trees, but a global study by Körner (2003) showed that growth at the treeline does not seem to be limited by carbon supply. Instead carbon allocation in the tree may be of higher importance. Nitrogen is a limiting factor at the treeline, but this factor alone cannot explain treeline position nor the shifts of this boundary (Sveinbjörnsson et al., 1996).

1.2.6 Human impact

Ellenberg (1988) and Haila and Levins (1992) are of the opinion that distinguishing former anthropogenic impacts from previous and current climate variability is one of the most difficult tasks in treeline research. However, according to many authors human impact is one of the major causes of documented treeline dynamics (Hustich, 1966; Emanuelsson, 1987; Holtmeier, 1993; Mattsson, 1995; Hofgaard, 1997; Vlassova, 2002; Juday et al., 2005; Karlsson et al., 2007). For example, in 1864 von Middendorff noted the following during his expedition through northern- and easternmost Siberia: “Carelessly they fell the remotest islands of stunted forests, which would serve as natural shelter against the winds. Man is rapidly promoting the spreading of the tundra” (von Middendorff, 1864). The evaluation of human impact on natural processes is an intensively debated topic and correct estimation requires detailed historical research (Veijola, 1998; Van Bogaert et al., 2007). A major issue is that accurate historical material on this factor is often not available (Hofgaard, 1999; Moen et al., 2008).

1.2.7 Herbivory

Effects of herbivores on the treeline structure and position are seen all over the world (Cairns and Moen, 2004). Ellenberg (1988) showed by pollen analysis that cutting and grazing since the Iron Age has depressed the current treeline position in the Alps more than 200 m below its potential elevation. In northern Europe, the elevational and latitudinal treeline areas are subjected to extensive reindeer (*Rangifer tarandus*) herding. However, since the diet of semi-domesticated reindeer is identical to that of their wild ancestors, it is often argued that reindeer herbivory cannot be a major cause of the recent treeline advance observed in Fennoscandia (Holmgren and Tjus, 1996; Kullman, 2005b). Moreover, some tree species, such as mountain birch, are rather

resilient to browsing and have induced some chemical defense systems (Haukioja and Niemelä, 1976; Danell et al., 1997; Hester et al., 2005). Apart from vertebrate herbivores, invertebrate herbivores are particularly important components in the boreal forest ecosystem (Juday et al., 2005; Van Bogaert et al., 2007). For example, in boreal Canada it is estimated that insect-caused timber losses (i.e. tree death) may be up to 1.3 to 2.0 times greater than the mean annual losses due to forest fires (Volney and Fleming, 2000). The particular insects involved in large-scale boreal outbreaks include defoliating insects (often Lepidoptera-moths and butterflies), bark and wood-boring beetles, and insects that attack roots and cones (Juday et al., 2005). The level of tree mortality caused by insect outbreaks can vary from selective removal of a few percent of dominant trees to the death of the entire forest (Juday et al., 2005).

1.2.8 Tree regeneration process

The reproduction process of a tree species is a factor that should not be overlooked when studying treeline dynamics; e.g. whereas European aspen (*Populus tremula*) and mountain birch (*Betula pubescens* ssp. *czerepanovii*) are able to reproduce vegetatively during suboptimal (cooler) climatic conditions, Scots pine (*Pinus sylvestris*) is not and may therefore have a competitive disadvantage. Seed dispersal depends on the prevalent bird fauna, seed weight, and dispersal capacity of the seeds, whereas germination generally requires favourable nutrient, moisture, and temperature conditions (Karlsson et al., 2005). Also, a tree species may be mono- or di-oecious; for di-oecious species with a fragmented areal distribution, pollination may be problematic.

1.2.9 Plant-plant competition

Growth and survival of tree seedlings at the treeline may be seriously hampered by competition from the prevalent tundra species such as juniper (*Juniper communis*) and black crowberry (*Empetrum nigrum*) (Von Holle et al., 2003; Bekker, 2005). These competitive interactions may be the reason why at some sites tree species do not succeed in colonising the tundra ecotone.

1.2.10 Disease and pathogens

Holtmeier (1974) claimed that high-elevation forest damage in the Alps caused by the fungus *Herpotrichia juniperi* may exceed the afforestation observed in the treeline ecotone as a response to reduced herbivory pressure and climate warming. Lehtonen (1987) reported that the lack of forest recovery after a large-scale outbreak of the autumnal moth (*Eppirita autumnata*) on the mountain birch forests in northern Finland in the mid 1960s, was in the Utsjoki area not caused by reindeer herbivory, but by a rot fungus. The susceptibility of tree species to disease and pathogens varies tremendously; e.g. aspen, a thermophilic tree species found as scattered clones

in northern Europe, is known as very susceptible (Worrell, 1995; Latva-Karjanmaa, 2006).

1.3 Current research gaps

At present, one of the most important gaps and uncertainties in treeline research appears at the intermediate geographical scale: on both regional and landscape levels (Callaghan et al., 2002; Holtmeier and Broll, 2005, 2007). Measurements are frequently made at the point scale and extrapolated directly to the global scale. Consequently, there is often a mismatch between the desired data for model parametrisation and the empirical data available (Skre et al., 2002). The intermediate scale is both important and problematic because it contains considerable heterogeneity and the feedbacks to the climate system are important at this scale (Harding et al., 2002). Furthermore, most treeline studies are short-term studies with a temporal scale ranging from a decade to a few decades (see Payette et al., 2002; Holtmeier and Broll, 2007; Kullman and Öberg, 2009). This is problematic as treeline processes are generally slow and accurate interpretations can only be made over a longer period of time. Therefore, there is a great need for careful field studies on treeline dynamics and its causes based on a complex landscape-ecological approach that also considers the historical aspect (Holmgren and Tjus, 1996; Callaghan et al., 2002; Payette et al., 2002; Sveinbjörnsson et al., 2002; Holtmeier and Broll, 2005, 2007).

1.4 Research objectives and thesis outline

The overall aim of this dissertation is to gain a better understanding of the factors controlling shifts in the *position* and tree *species composition* of the sub-Arctic treeline ecotone at the landscape scale. Particularly the view that continued warming is expected to result in colonisation of the treeline by more thermophilic tree species needs to be examined. To meet our aim, we conducted a multi-disciplinary study in a sub-Arctic model area of c. 1 000 km².

Research Question 1: How well do the causal factors of sub-Arctic treeline dynamics found at the global scale integrate with those identified at the landscape scale? (Chapter 2)

Since most regional to global scale treeline studies cover a very short time span (15 to 40 years) and make use of a single technique such as remote sensing analysis, it is questionable whether the interpretation of the obtained results is indisputable (Holtmeier and Broll, 2007). Therefore, we initiated a multi-disciplinary study that covers a time period of more than a century. We set up an intensive fieldwork campaign using multiple techniques such as repeat photography, field observations along elevational transects, and dendrochronological analysis. The model area in sub-Arctic Sweden (cfr. 1.5 Study Area) is particularly interesting because at present there exist about four different hypotheses on the causal factors of recent treeline dynamics in the area (cfr. Table 1 on page 42). To explore the likelihood of projected treeline dynamics to be realized, we confronted our results with model projections specifically adopted for our study area.

During the fieldwork campaign, an additional research question arose when we found an exceptionally old looking treeline site: how old can mountain birch (*Betula pubescens* ssp. *czerepanovii*) grow?

Research Question 2: Are thermophilic tree species colonising the treeline ecotone in correspondence to model projections ? (Chapter 3)

According to most dynamic vegetation models (e.g. Wolf et al., 2008; Euskircher et al., 2009), thermophilic tree species will colonise the sub-Arctic treeline area in response to climate warming and will have replaced most of the current, less thermophilic, treeline setting species by the year 2100. As climate already warmed by 1-4 °C over the past century in the polar region (IPCC, 2007; Post et al., 2009), including our study area (Callaghan et al., 2010), this process should already be ongoing. In addition to the detection of recent changes in the species composition of the treeline ecotone, we aimed to identify the causal factors of these changes. When revisiting three elevational treeline transects established in 1977, previously unrecorded thermophilic aspen (*Populus tremula*) was found at the birch treeline (Appendix 4, Fig. A5, p. 134). Also thermophilic alder (*Alnus incana*) was recorded in one of the elevational transects in 2006 whereas it was not observed in 1977. To study the scale and the causes of the apparent range expansions of these thermophilic tree species, we initiated this chapter. We focused particularly on aspen; the species that colonised the treeline ecotone.

Research Question 3: How does the competition process work between the rarer more thermophilic treeline species and the current dominant treeline species? (Chapter 4)

Changes in the establishment, survival, and eventual distribution of plant species are one of the major uncertainties of projected impacts of climate warming on ecosystems (Callaghan et al., 2005). The future species composition of the sub-Arctic treeline ecotone can only be accurately modelled if we understand the competition process between the prevalent and invasive tree species by studying the main ecosystem components such as their dominant herbivores. This chapter aims to identify these interacting mechanisms by using multiple techniques.

1.5 Study area

1.5.1 Introduction to the study area

The Torneträsk area is located at the eastern fringe of the Scandes Mountains in sub-Arctic Sweden (68°20'N, 19°00'E) (Fig. 3). Lake Torneträsk is the seventh largest lake of Sweden, being 65 km long and *c.* 6 km wide. The study area has a surface area of *c.* 1 000 km². About 75% of the Torneträsk catchment is alpine terrain (Christensen et al., 2007). The Lake level is situated at 341 m above sea level (a.s.l.) and forms the lowest point of the area, whereas the summits on the southwestern side of the Lake reach up to 1750 m a.s.l. Archaean and Cambro-Silurian bedrocks of hard-shists, granites and amphibolites characterise the area (Holdar, 1957). The soils are dominated by tills and glacio-fluvial sands (Kulling, 1964). Richer soils of weathered calcareous deposits alternate with nutrient-poor soils, creating a mosaic of meadows and heaths respectively (Berglund et al., 1996).

The present climate of the Torneträsk area is slightly oceanic, with an oceanic-continental gradient from West to East. The mean annual temperature for Abisko (388 m a.s.l.), located at the southwestern end of Lake Torneträsk (Fig. 3), is -1.0 °C and mean January and July temperatures are -12.0 °C and +11.0 °C respectively for the normal period 1961–1990 (Alexandersson et al., 1991). Mean annual precipitation amounts to 310 mm for the same period. However, climate has recently changed: mean annual temperature and precipitation increased to +0.6 C and 342 mm for the 10-year period 2000–2009 (Abisko Scientific Research Station meteorological records 1913–2009). Moreover, statistically smoothed trends showed

a 2.5 °C increase in temperature over the period 1913–2006 (Callaghan et al., 2010). Located in the rain shadow of Mount Nuolja, the mean annual precipitation for Abisko is low, thereby contrasting with the surrounding mountain areas in the West that have annual precipitation levels up to 1000 mm and more (Callaghan et al., 2010). Annual precipitation at the northern side of the Lake is c. 600 mm (Sonesson and Hoogesteger, 1983) and mean winter snow depth for Abisko is 52 cm (Kohler et al., 2006).

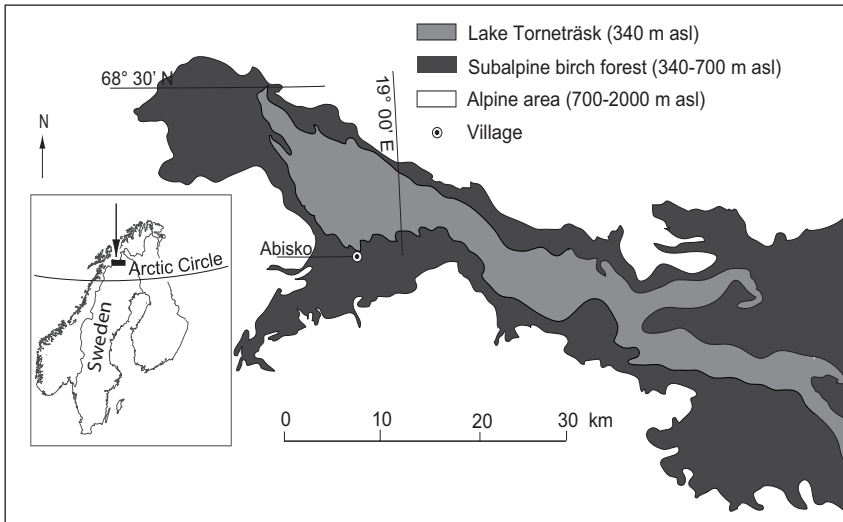


Figure 3. The Torneträsk study area in sub-Arctic Sweden.

The subalpine forest area is dominated by mountain birch (*Betula pubescens* ssp. *czerepanovii*), the species that sets the elevational and latitudinal treeline in Fennoscandia (Hämet-Ahti, 1963) (Fig. 4). The position of the alpine treeline varies around 600 m a.s.l. in the western and around 800 m a.s.l. in the eastern part of Torneträsk (Berglund et al., 1996). Trees of secondary importance in the area are aspen (*Populus tremula*), pine (*Pinus sylvestris*), alder (*Alnus incana*), rowan (*Sorbus aucuparia*), willow (*Salix* spp.), and bird cherry (*Prunus padus*).

1.5.2 Holocene distribution of the different tree species in the Swedish sub-Arctic

Mountain birch forests rapidly colonised vast areas of sub-Arctic Fennoscandia since the deglaciation about 10 000 years ago when summers were more humid and 1.5-2.0 °C warmer than today (Barnekow, 1999). This successful pioneer species coexisted with aspen and alder (Bigler et al., 2002). During the warm and dry mid-Holocene, birch, aspen, and alder were

largely replaced by pine that markedly expanded its range (Barnekow, 1999). About 4 000 years ago a drastic cooling and humidification of the climate occurred, and mountain birch, that relies on an ample snow cover (Kullman, 2005b), again became the dominant subalpine tree species in sub-Arctic Fennoscandia (Barnekow, 1999).



Figure 4. The sub-Arctic Torneträsk area has an elevational treeline (a), although in the southwestern part of the study area the ecotone shows some latitudinal (hemi-Arctic) features where the role of micro-topography becomes important in determining presence or absence of trees (b). The difference in albedo between the snow-covered tundra and the snowpack protruding birches is pronounced.

1.5.3 Mountain birch

In contrast to most other birch forests in northwestern Europe, the Fennoscandian mountain birch forest is a stable forest type and not a transient successional phase (Carlsson et

al., 1999). The total area of subalpine birch forest area in Sweden is c. 22 000 km². Low summer temperature limits the distribution of mountain birch forests with latitude and elevation, but in Fennoscandia the tree species grows at lower summer temperatures than its competitors (Tømmervik et al., 2004). In addition to temperature, precipitation, nitrogen availability, wind velocity, and the length of the growing season determine its areal distribution (Sveinbjörnsson et al., 2002; Tømmervik et al., 2004). At moist nutrient-rich sites with a thick snow cover, mountain birch is commonly single-stemmed or monocormic and up to 12 m tall, while at dry and nutrient-poor sites it is mostly polycormic and about 4-6 m tall (Carlsson et al., 1999). Regeneration from seed is very slow and may easily fail. Therefore, mountain birch forests regenerate almost exclusively by basal stem sprouts and seedlings are rarely found within undisturbed woods (Karlsson et al., 2005).

1.5.4 Aspen

European aspen is the most widely distributed tree species in the world (Worrell, 1995; Latva-Karjanmaa, 2006). The species extends from the Mediterranean area just north of the 35th parallel to the 71st parallel in Europe's sub-Arctic (Lahti and Lampinen, 1999). Aspen seems therefore to be different from most other poplars in that it is able to withstand significant stresses such as drought and cold (Worrell, 1995; Johansson, 2002). Yet, aspen is a more thermophilic tree species than mountain birch (Appendix 4, Fig. A4, p. 134) and is rather rare in northernmost Fennoscandia (Worrell, 1995; Latva-Karjanmaa, 2006). Although aspen is occasionally found above the elevational birch treeline as a prostrate shrub (<1 m tall), it is not considered a likely treeline candidate (Kullman, 1983).

Aspen is thought to reproduce mostly asexually by the production of clonal root suckers (Worrell, 1995). Regeneration from seed is believed to be rare because it requires exacting moisture, temperature, and seed bed quality conditions (Worrell, 1995). Sexual regeneration in aspen is probably related to many local factors such as climate, disturbance events that control competition, soil characteristics, barriers to pollination from scattered male and female stands, and disease.

However, a different control on aspen proliferation could be herbivory. Aspen is a preferred food source of moose (*Alces alces*) (Edenius and Ericsson, 2007) and, in second degree, of mountain hare (*Lepus timidus*) (Latva-Karjanmaa, 2006) and both animals could exert a strong control on its distribution. Reindeer (*Rangifer tarandus*), in contrast, select for

birch rather than aspen (Nieminen and Heiskari, 1987).

1.5.5 Herbivores

Defoliating moths

Two endemic insect herbivores, the autumnal moth (*Epirrita autumnata*) and the winter moth (*Operophtera brumata*), naturally disturb the subalpine mountain birch forests by episodic mass defoliation events (Tenow, 1972; Tenow et al., 2007) (Fig. 5). Both endemic moth species exhibit regular fluctuation patterns with c. 9-11 years between population density peaks (Tenow et al., 2007). Delayed density dependent factors such as natural enemies, disease, and food quality are suggested to drive the cyclic fluctuations in these geometrid moth species (Haukioja and Neuvonen, 1987), but also weather conditions affect the performance and survival rates of the moth's life cycle stages (Bylund, 1999). For example, the eggs of the winter and autumnal moth do not survive winter temperatures below -33 °C and -36 °C respectively (Tenow and Nilssen, 1990). During most population peaks, tree defoliation levels do not exceed 15% (Bylund, 1995). However, about every 60-70 years the moth population peaks reach outbreak densities resulting in a complete defoliation and rejuvenation of the mountain birch forest (Tenow et al., 2005). The monacormic birch form usually dies after such outbreaks (Fig. 6), while the polycormic form can survive by the production of new stems from basal sprouts (Neuvonen et al., 2005).



Figure 5. Caterpillar of the autumnal moth (*Epirrita autumnata*), the main agent of disturbance to the northern mountain birch forests.

The outbreaks of the autumnal moth mainly occur in mature inland forests (Tenow and Bylund, 1989), whereas winter moth outbreaks are restricted to warmer locations along the Norwegian coast or inland south-facing mountain slopes such as on the northern shore of Lake



Figure 6. The birch treeline ecotone on the northern side of the Lake formed by monocormic (single-stemmed) individuals. The uppermost birch stand has become denser, but the major part of the treeline ecotone has been devastated: the upper boundary of the closed forest lowered by 120 m over a distance of more than 10 km because of a severe outbreak by the winter moth in 1964-1965. Upper photo: E. Persson, lower photo: S. Johnsson.

Torneträsk (Tenow et al., 2005). The life cycles in both moth species are similar. The larvae are polyphagous and the eggs are laid on a wide range of trees and bushes, yet mountain birch is

the main host plant in northern Fennoscandia. The females lay their eggs on trunks and twigs in the autumn. The eggs overwinter on the trees and hatch at budburst in the following spring (Bylund, 1999). Both moth species have five larval instars during which the larvae feed on birch leaves (Tenow, 1972; Bylund, 1999).

Reindeer

Reindeer are migratory animals as lichen-rich vegetation (winter) and green forage (summer) are generally found in different places (Helle, 2001). Every summer about 4000 reindeer pass along both shores of Lake Torneträsk on their way to the alpine area. The last wild reindeer in our study area were seen in the early 19th century. Since that time only semi-domesticated reindeer exist: twice a year the herds are gathered by the reindeer herders (Emanuelsson, 1987). However, until the early twentieth century, the reindeer herders (belonging to the Sámi people) were nomadic and followed the herd along their migration route for the entire year (Appendix 3, p. 133). This intensive form of reindeer husbandry disappeared by c. 1920 and nowadays an extensive practice exists whereby the reindeer wander freely (Emanuelsson, 1987; Helle, 2001). Until recently, population dynamics were predominantly regulated by nutrient availability and climate variability, but in recent times market mechanisms and policy have a major impact on population densities (Hofgaard, 1997). During summer, an important part of the reindeer's diet consists of mountain birch leaves, and young treeline birches are particularly vulnerable to reindeer grazing for their easy access, high nitrogen content, and lower stress resistance (Fig. 7; Helle, 2001; Cairns and Moen, 2004). At lower elevation, birch damage caused by reindeer browsing is usually limited (Tenow, 1996).

Moose

The largest animal in boreal and sub-Arctic Fennoscandia is moose (*Alces alces*). Due to low population numbers of its main predators brown bear (*Ursus arctos*) and wolf (*Canis lupus*), and due to changed forestry practices, its population exponentially increased in the second half of the 20th century (Cederlund and Markgren, 1987). Nowadays, its population dynamics are mainly regulated by hunting quota (Ball et al., 1999). Moose mainly feeds on aspen (Fig. 8), willow, birch, pine, and rowan (Persson et al., 2005). To maintain a balanced diet, it tends to over-utilise rarer species such as aspen (Edenius et al., 2007). Many moose migrate between summer and winter home ranges and it has been suggested that moose migration is affected by snow depth and snow quality (Lundmark and Ball, 2008). Moose is a recent immigrant in the Torneträsk area: it arrived in the Abisko area presumably around 1910 (Sonesson, 1970).

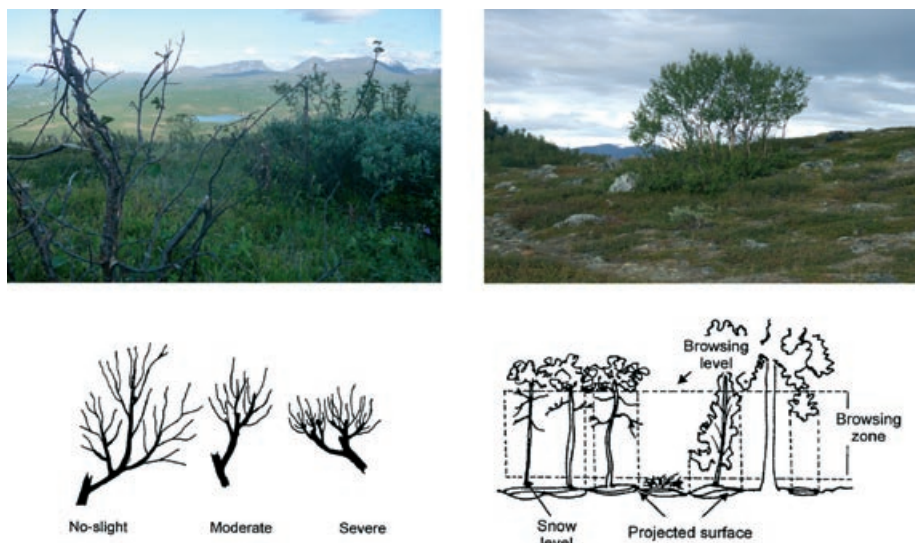


Figure 7. Evaluation of browsing damage, both schematic (Hörnberg, 2001) and in the field.

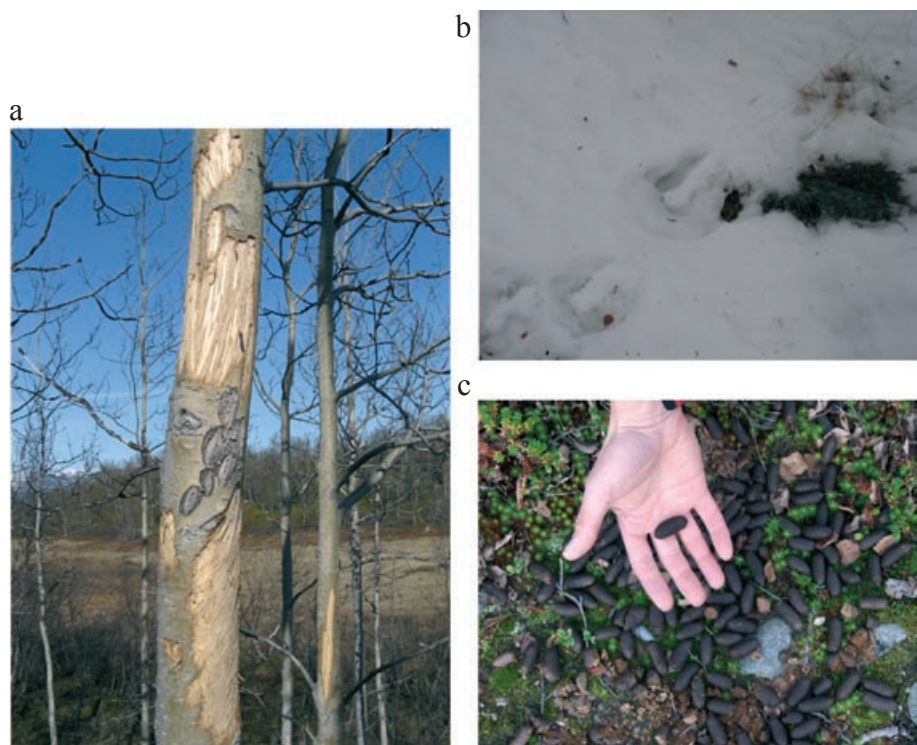


Figure 8. Identification of the herbivore that caused the vegetation damage. Fresh bark stripping of aspen caused by moose in late spring (a). Foot prints of moose inside the aspen stand, mid December (b). Fresh reindeer faeces found in the birch treeline ecotone in July (c).

Other herbivores

Also mountain hare (*Lepus timidus*) and different vole species are important herbivores in the mountain birch forest ecosystem (Karlsson et al., 2005). Mountain hare predominantly feeds on birch and aspen in winter (Danell and Huss-Danell, 1985; Latva-Karjanmaa, 2006), whereas seedling damage by voles may be important during population peaks about every 4-5 years (Henttonen et al., 2001).

1.6 Justification of the study area

The Torneträsk area was chosen as study area for several reasons:

1. The area is located in the sub-Arctic (N 68°25', E 19°00', Fig. 1)
2. The treeline has an alpine character. Although the ecotone has sub-Arctic climate and vegetation features, its position is more controlled by elevation than by latitude. The low elevation (c. 700 m a.s.l.) and relatively narrow areal extent of the treeline ecotone, simplifies its access and the search for causal factors of its dynamics. These conditions allowed for intensive and repeat field measurements and data could be collected over the entire areal extent of the treeline ecotone.
3. The high local variability in topography, climate (mainly precipitation), geology, soil, vegetation, human impact, biotic disturbance regimes, and herbivore population densities make the Torneträsk area an interesting study setting for comparative analyses.
4. The overall present and historical human impact is limited; the Torneträsk area is likely one of the most natural areas in Europe and therefore highly suited to study the mechanisms of treeline dynamics (Emanuelsson, 1987; Hofgaard, 1999).
5. Probably the most important reason is its exceptionally long-term record of environmental, anthropogenic, and biotic data that can serve as a reference and validation of our measurements. Daily temperature and precipitation measurements are available since 1913 (Callaghan et al., 2010), detailed human impact is described since 1600 (Emanuelsson, 1987), reindeer population numbers since 1750 (Ruong, 1937; Emanuelsson, 1987), and moth outbreaks on birch have been reported since 1862 (Tenow, 1972).

1.7 Introduction to methodology

The methodologies that require some further explanation are briefly introduced in this section.

1.7.1 Definition settings for 'tree' and 'treeline'

In Fennoscandia, it is inappropriate to restrict a tree to a woody plant with a single stem because this would exclude polycormic birch, the dominant growth form of mountain birch in large forest areas (Wielgolaski, 2005). Therefore a tree was considered a woody plant species that protrudes through the winter snowpack (>2 m tall) as a full-grown individual. Younger individuals that had not yet reached 2 m stem height were called tree species individuals. The treeline was defined as the ecotone that extends from the closed subalpine forest to the completely treeless alpine tundra, thereby including all tree species individuals irrespective of their stem height.

These definition settings are justified by the ecotonal character of the treeline (Fig. 2) that does not allow a confinement to a boundary line of individuals meeting a minimum stem height. The upper boundary of the treeline ecotone could easily be documented in the field and compared with previous studies. Yet, this definition setting of the treeline immediately rose a detection problem in remote sensing analysis. Therefore, in the case of repeat photograph analysis, we used the lower boundary of this ecotonal transition zone as a main reference for its better distinction compared to the upper boundary. This boundary was set to a 30% tree-canopy cover in convention with most other treeline studies (Rees et al., 2002). Time series of the photographs were scanned at identical resolution, so that pixel per pixel could be compared. A pixel was classified as forest or non-forest area. The 30%-tree-cover isoline was then statistically plotted by using the geographical information system ARCGIS SPATIAL ANALYST 9.2 (ESRI, 2006).

By visiting the position of this 30%-tree-cover isoline *in situ* on the mountain slope (at a location where the boundary line crossed an easily identifiable landmark in the field such as a big boulder, Fig. 9), measurements showed that the trees >2 m tall, detectable on the aerial photograph, had a mean canopy size of 3.5 m in diameter, implying that a 30% tree-cover corresponded to a distance interval of 2.2 m in any direction between the canopy boundaries of different tree individuals. In the field we could now delimit both the upper and lower boundary of the treeline ecotone.

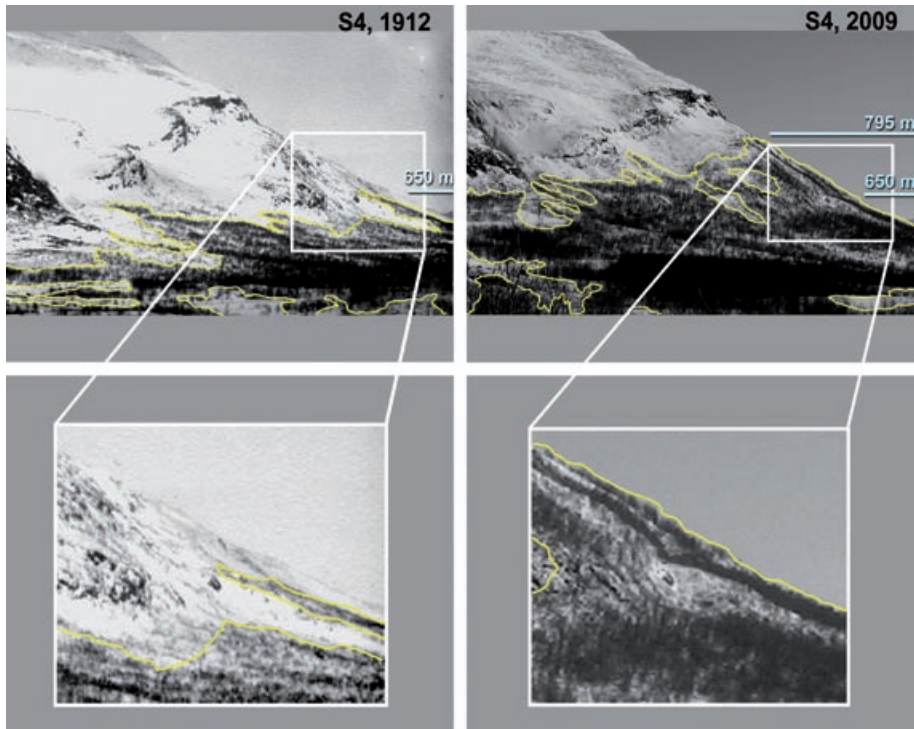


Figure 9. Repeat landscape photography showing the methodology of quantifying the approximate elevational difference in the position of the treeline between the two photographs. In the centre of the inset, a rock outcrop attached to the bedrock can be seen that was positioned near the upper limit of the isoline of 1912. The same landmark is seen on the 2009 photograph and could be recorded in the field with a GPS-device with an aneroid altimeter. As a reference, elevation in metres above sea level is indicated. The yellow lines denote the 30% tree-cover isolines (statistically determined by using the software ArcGIS SPATIAL ANALYST 9.2)

1.7.2 Historical treeline studies and their usability

The oldest studies in sub-Arctic Sweden go back to 1695, when Olof Rudbeck made an initial scientific exploration in the name of the Swedish King Charles XI, shortly followed by the famous floristic expedition of Carl von Linné (Linneus) in 1732. The archive of the Abisko Scientific Research Station contains treeline studies of the Torneträsk area extending back to *c.* 1880, with the first noteworthy studies of Sylvén (1904), Gavelin (1909), and Fries (1913). From that time onwards, treeline studies of the Torneträsk area became more numerous; altogether 15 studies were found and analyzed to their quality. Particularly the study of Fries (1913) appeared potentially valuable; Fries mapped for the first time the elevational position of the treeline (defined as ‘upper forestline’; Fig. 10a) for the entire area of northernmost Sweden, including some parts of northern Norway and Finland. However, this study, similar to most other promising studies, was eventually not suited for an accurate replication. Historical treeline studies often used an ambiguous definition setting of the treeline (Fries, 1913; Persson,

1952; Fig. 10a), or there were uncertainties about the quality of the instruments they used (e.g. Nilsson, 1955) or their calibration: e.g. the topographical map of 1888 used to calibrate Fries' aneroid altimeter had erroneous elevational data points (Fig. 10b).

The most compelling historical treeline study that met all quality conditions was that of Sonesson and Hoogesteger (1983). Four elevational transects extending from the lower subalpine birch forest to the alpine tundra were established in 1977 in different areas across the Torneträsk landscape (Fig. 10c). Three out of four elevational transects were selected for replication; the upper end of the fourth transect near Abisko was located too close to a ski track and therefore not suited for replication. The three transects could be exactly relocated by the assistance of the original researcher and were replicated in autumn 2006 according identical methods of the original study (Chapter 2.1).

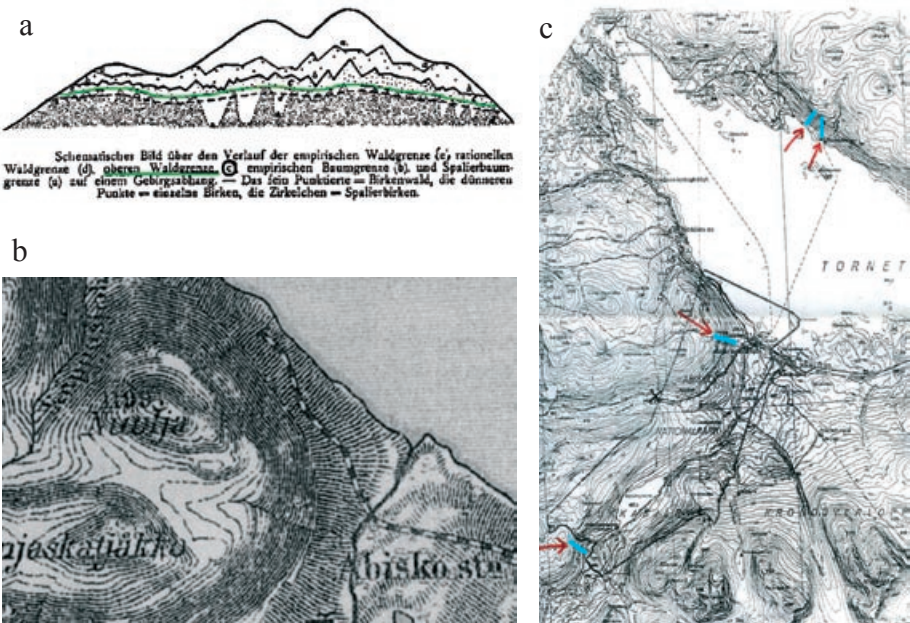


Figure 10. Replication issues when dealing with historical field studies. ‘The upper forestline’ as defined by Fries (1913): the virtual line connecting the uppermost parts of the continuous forest (a). Although the schematic figure suggests that the upper boundary of the continuous forest is easy to determine, many treeline ecotones have a very gradual transition zone making comparable measurements of the elevational position of the treeline (or ‘forestline’) a subjective task. The baseline topographical map produced in 1888 by the Swedish Land Survey used by Fries to calibrate his aneroid altimeter (b). The map is biased by non-linear erroneous elevation measures, preventing replication. The recent map that J Hoogesteger used with the indication of his elevational transects in blue (c). Assistance by the original researcher and his detailed fieldnotes allowed for a proper replication his measurements of 1977 (Sonesson and Hoogesteger, 1983).

1.7.3 Replication of historical landscape photographs

_____The oldest photographs of the Torneträsk treeline we found were taken by a Swedish landscape photographer (Borg Mesch) and dated from the period 1908-1929, an exceptional feature for the sub-Arctic region. Another series of valuable photographs were from E. Persson (1952) who did her MSc thesis on treeline dynamics on the northern side of Lake Torneträsk (Chapter 2.1).

The names of the photo-points were often written on the photographs or mentioned in the accompanying document. If not, the place was usually recognisable since most photographs were made from and of prominent landmarks. To determine the precise location of the photo-point in the field, the principle of parallax was used to find lines of equal perspective and proportionate length between features (e.g. background ridgeline intersections and permanent foreground objects such as big boulders) in the historical photograph and the present landscape (Rogers et al., 1984). Changes in the position or density of the lower treeline boundary were determined via the presence of some prominent landmarks at the position of the historical lower boundary of the treeline ecotone (Fig. 9).

Repeat landscape photographs only provide correct information if the photo point is exactly determined and a similar lens is used. They are powerful unambiguous tools that show the historical position, structure, composition, and vitality of the treeline. Besides, other important information may be shown such as the presence of livestock, human settlement, snow conditions, etc. However, there are also drawbacks to this type of data: (i) photographs usually only show one mountain slope, so their spatial scale is limited; (ii) the original photographer may not have had the same aim as the present researcher and therefore the captured treeline area may only represent a random snap-shot that is not representative at the landscape scale; (iii) even if the original aim was to capture the treeline, the photographer may have specifically selected for some clear examples of treeline shaping processes such as local snow avalanche impacts that are not representative at the landscape scale; (iv) important other photos that belong to the dataset may have been lost or could not be repeated because of poor quality or failure to locate the precise photo-point.

1.7.4 Dendrochronological analysis

Throughout this study, we applied dendrochronological analysis for different purposes: to study (i) the scale and causal mechanisms of elevational range expansions of birch and more thermophilic tree species, and (ii) the competition mechanism between birch and more thermophilic tree species. Dendrochronological analysis is a suitable technique to identify

the site history of the forest: i.e. both environmental and biotic parameters such as age, climate variability, browsing and insect defoliation events, plant-plant competition, geomorphological disturbance, and fire are stored in tree-rings.

Tree-rings are in reality sheaths of cells that appear as concentric rings in a cross-section of the stem. Each ring is usually the result of an annual flush of growth that begins in the spring and ceases in the summer or early autumn, so that one layer is produced every year. A sharp boundary occurs between rings because cells along the inner boundaries of rings (earlywood) are larger and have thinner walls than those along the outer boundaries (latewood) (Fritts, 1976).

However, not all rings are distinct annual increments of growth. Sometimes when factors are highly limiting, growth cannot begin and no ring is produced. At other times, a stress period occurring in the middle of the growing season may cause two or more growth layers to form within a particular year.

Mountain birch is known as a difficult species because of its diffuse porous rings, its irregular growth pattern, light wood colour, and the occurrence of missing rings (Levanič and Eggertsson, 2008). Nevertheless, in open-canopy forests and particularly near its distributional limit such as the elevational treeline, birch has a strong climatic signal and is suited for dendrochronological research (Levanič and Eggertsson, 2008). If the sample number is sufficiently high to distinguish irregular growth patterns from significant growth trends and tree-core preparation is well done, tree-ring analysis has a high potential in this comparatively little-studied tree species. Also alder has rather diffuse-porous rings and is relatively hard for dendrochronological analysis, whereas aspen and pine have large annual increments that are easier to distinguish. Missing or false rings are rare in these tree species (R. Van Bogaert, pers. obs.).

Tree growth, and hence ring width, depends on a range of environmental and biological factors prevailing at the site where the tree grows such as climate, soil, plant-plant competition, and browsing. Careful site and tree selection is critically important to ensure that specific environmental or biotic factors can be studied (Fritts, 1976). Even stem height at which the tree-core or stem disc is taken will affect the outcome of the results (Fig. 11). Tree and site selection depend on the study aim: a steep site with frequent snow avalanches will be suited for the identification of geomorphological disturbance events but is unlikely to be suited for

studying historical climate variability. Undamaged upright monocormic individuals growing at the treeline on a rich soil and with no immediate neighbouring individuals should be selected if one aims to extract the maximum climatic signal from the ring widths of a tree species. However, for herbivory analysis, rather the stunted trees that show the most pronounced browsing wounds may be most suited to identify the herbivore and its impact. If the aim is to study the competition process between two tree species, trees growing in the closed forest at lower elevation or latitude should be aimed for. In reality, however, tree-rings will always be the expression of a combination of environmental and biotic factors; the challenge is to extract the maximum signal of the factor that one is interested for.

Depending on the study aim we either took stem discs or tree-cores. Stem discs were taken from individuals that were too small to core (<2 m) or from dead individuals to identify the cause and the year of tree death (Fig. 11a). In all other cases, tree-cores were taken with a standard increment corer (Fig. 11b). All bore holes with a diameter of 4 mm were filled with wood to reduce the impact on the tree individuals.

Tree-coring, sample preparation, and analysis

If no recruitment analysis was aimed for, tree-cores were taken at standard height (i.e. breast height or 130 cm; Fritts, 1976). The tree-cores were dried, glued into wooden holders and surfaced using a scalpel or razor blade. To make the rings more visible, chalk was rubbed onto the smoothened wood surface so that vessels were filled. We studied the wood anatomical features of the tree-rings with great detail as they generally provide more information on the disturbance event than do statistics of differences in ring widths (Levanič and Eggertsson, 2008). Frost rings, white rings, browsing scars, callus tissue; all point to specific damage patterns (Fig. 12). Wedging rings are seen in a tree individual that experiences high stress or has become too old to invest energy in wood growth over its entire circumference (Fig. 12a). Heavy grazing may cause anomalous wood structures such as wedging rings, small vessels and thin-walled fibers. Large rings after a suppressed period may indicate reduced grazing pressure (Schweingruber, 2007).

At the treeline, frost damage to leaves and needles is frequent (Körner, 1999). Either the formation of ice crystals or high tension in the xylem near the cambial zone causes frost rings, that are characterised by a small zone of collapsed cells, a rather large zone of callus cells, and bent rays (Schweingruber, 2007). The presence of frost rings enables the dendrochronological reconstruction of frost events. Located at the beginning of a ring, they indicate an extremely cold

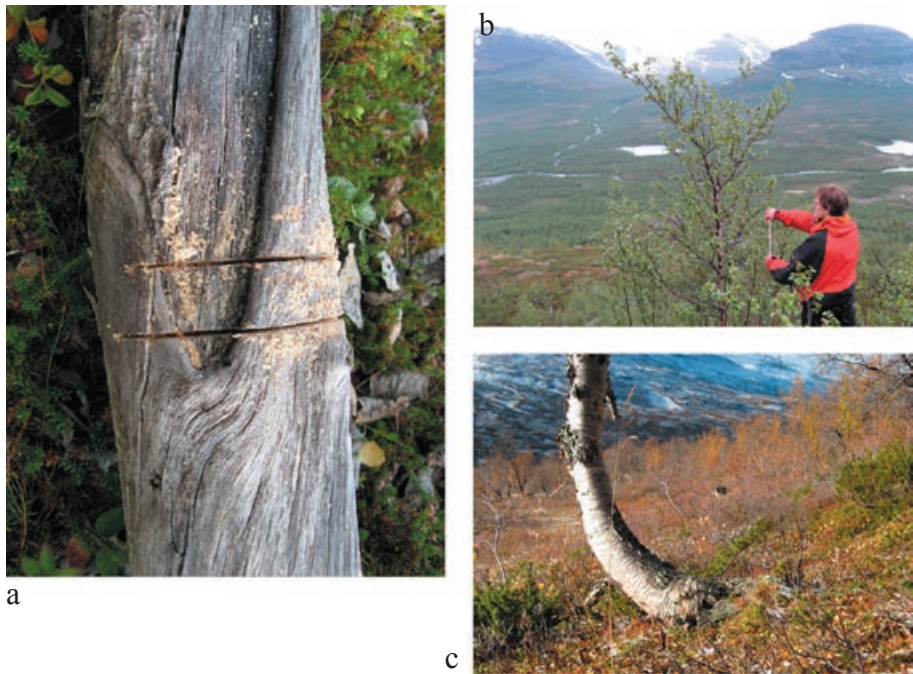


Figure 11. Dendrochronological sampling methodology. Dead stems were cut at the position of the wound to determine the cause of death (a). Coring a mountain birch individual at the treeline in two perpendicular directions at breast height to build a ring width reference chronology (b). Curved basal part of the stem of mountain birch growing on a steep slope (c). This part of the stem should be avoided not to bias the results because of tension wood (Schweingruber, 2007).

period prior to the growing season. Such a phenomenon produces a real frost ring. However, in young trees at the treeline, frost rings may also form in the earlywood and latewood during the growing season, e.g. when a rather long initial warm period is suddenly interrupted by frost that causes high tension in the xylem (Schweingruber, 2007) (Fig. 12b).

Another frequent phenomenon in northern tree species is the occurrence of bright rings, followed by two to four exceptionally narrow rings (Fig. 12d). This usually points to growth damage by insect defoliation. Reduced photosynthetically active leaf area caused by defoliation results in anatomical changes in the xylem. In the first year of the insect attack, the earlywood consists of a few thin-walled tracheids and very few very thin-walled late-wood cells resulting in a light coloured ring. During the following two to four years, wood production is reduced but vital trees generally survive if the prevailing climate conditions are not extreme (Schweingruber, 2007).

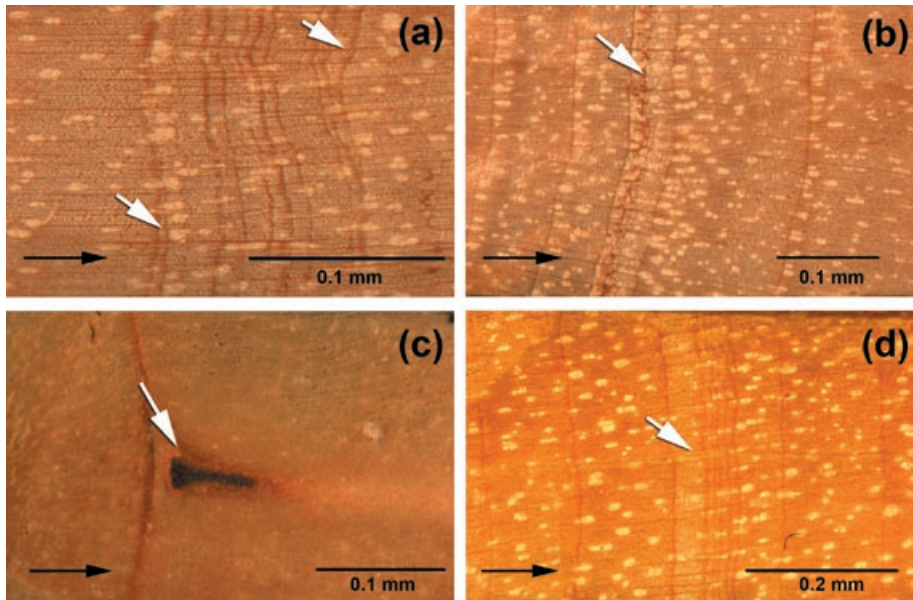


Figure 12. Study of wood anatomical features in mountain birch. The white arrows point to the area of interest, whereas the black arrows show the direction of growth. Birch individuals subjected to biotic or climatic stress regularly show wedging rings (a) that may result in erroneous dating. Pointer years such as the frost ring of 1984 shown in (b) can help in tracing these partly or completely missing rings. A typical frost ring (b) showing damage to the cambium. In June 1984, a 27-day period of warm spring weather with minimum temperatures up to $+11.9^{\circ}\text{C}$ was suddenly interrupted by three days of -1.3°C , recorded at the Abisko meteorological station located 300 m below the treeline. A small scar (c) at 110 cm stem height presumably caused by reindeer browsing in the early summer of 1929. A bright coloured ring followed by four exceptionally narrow rings (d) points to complete tree defoliation by an insect.

Ring width analysis and chronology building

Ring widths were measured to the nearest $1/100$ of a millimetre using standard dendro-chronological equipment. The year-to-year variation in tree-ring width in all individual sample series from each site was cross-matched against all other series from within the same site. This standard procedure in dendrochronology is termed “crossdating” and gives all individual tree-rings a year-datum relative to all other tree-rings at that site (Fritts, 1976). By averaging all data year by year it is then possible to construct a time series of tree-ring data, a chronology. Crossdating is also a method to check the data for missing rings and measurement errors. The quality of the crossdating, as well as a number of statistical properties of the data, was determined by using the software Cofecha (Holmes, 1983). A tree-ring chronology can be absolutely dated as long as there are tree-rings of known age (from living trees) included in the crossdating process.

The age of a tree is one of the main factors affecting its ring width pattern (Fritts, 1976). Generally, ring widths become smaller as a tree grows older. Hence, removing the ‘age-effect’ from tree-ring data is essential when climate is the objective of interest. The common growth trend of a tree species on a particular site can be empirically determined using the Regional Curve Standardization (RCS) approach. In this procedure all ring width series are aligned according cambial age and the mean long-term growth trend should represent the age trend. By subtracting or dividing the annual ring widths by this Regional Curve (RC) the obtained values are relative ring width indices or ‘standardised’ ring widths; i.e. annual growth variability not affected by tree ageing.

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Chapter 2 The mountain birch treeline in the Swedish sub-Arctic

2.1 A century of treeline changes in sub-Arctic Sweden shows local and regional variability and only a minor influence of 20th century climate warming*

Abstract

Models project that climate warming will cause the treeline to move to higher elevations in alpine areas and more northerly latitudes in Arctic environments. We aimed to document changes or stability of the treeline in a sub-Arctic model area at different temporal and spatial scales, and particularly to clarify the ambiguity that currently exists about treeline dynamics and their causes. The study was conducted in the Torneträsk area in northern Sweden where climate warmed by 2.5 °C between 1913 and 2006. Mountain birch (*Betula pubescens* ssp. *czerepanovii*) sets the alpine treeline. We used repeat photography, dendrochronological analysis, field observations along elevational transects and historical documents to study treeline dynamics. Since 1912, only four out of eight treeline sites had advanced: on average the treeline had shifted 24 m upslope (+0.2 m year⁻¹ assuming linear shifts). Maximum treeline advance was +145 m (+1.5 m year⁻¹ in elevation and +2.7 m year⁻¹ in actual distance), whereas maximum retreat was 120 m downslope. Counter-intuitively, treeline advance was most pronounced during the cooler late 1960s and 1970s. Tree establishment and treeline advance were significantly correlated with periods of low reindeer (*Rangifer tarandus*) population numbers. A decreased anthropozoogenic impact since the early 20th century was found to be the main factor shaping the current treeline ecotone and its dynamics. In addition, episodic disturbances by moth outbreaks and geomorphological processes resulted in descent and long-term stability of the treeline position, respectively. In contrast to what is generally stated in the literature, this study shows that in a period of climate warming, disturbance may not only determine when treeline advance will occur but if treeline advance will occur at all. In the case of non-climatic climax treelines, such as those in our study area, both climate-driven model projections of future treeline positions and the use of the treeline position for bioclimatic monitoring should be used with caution.

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Introduction

Mean annual temperatures have risen globally over the past century, with the most pronounced and rapid changes at high elevations and latitudes (ACIA, 2005). As the location of elevational and polar treelines is mainly caused by heat deficiency, in the Northern Hemisphere climate warming is expected to cause treelines to advance to higher elevations and more northerly latitudes (Harsch et al., 2009). Indeed, modern evidence for such relocations exists and these have been explicitly or implicitly related to recent climate warming (Shiyatov et al., 2007; Kullman and Öberg, 2009). However, in many circumpolar and high-elevational areas the position of the treeline has not changed (Masek, 2001; Holtmeier et al., 2003; Payette, 2007; Van Bogaert et al., 2007) or has even retreated (Vlassova, 2002; Dalen and Hofgaard, 2005; Kullman, 2005; Cherosov et al., 2010).

Treeline heterogeneity increases from global to regional, to landscape and to local scales of analysis (Callaghan et al., 2002). Moreover, the factors controlling the position and structure of the treeline are highly scale-dependent and vary from place to place (Sveinbjörnsson et al., 2002). Individual trees and the forest system may respond differently to change; warming may increase tree growth, while at the same time seedling survival may be reduced because of water stress brought about by greater evapotranspiration and drying of the uppermost soil. Furthermore, the time-scale of a study influences outcomes because it determines the processes and responses that can be studied. There are short-term responses (defined as a year or less and reflected in individual tree growth), medium-term responses (some years to a few decades and reflected in changing survival rates of seedlings and altered tree physiognomy) and long-term responses (several decades to centuries and reflected in a general treeline advance or retreat) (Holtmeier and Broll, 2005).

Both experimental and field studies have shown that climate warming might not be the only mechanism leading to recently observed northward and upward movement of vegetation. Changes in disturbance regimes (Holtmeier and Broll, 2010), land use (Hofgaard, 1997), plant–plant interactions (Van Bogaert et al., 2009) and herbivory (Hoogesteger and Karlsson, 1992; Speed et al., 2010; Van Bogaert et al., 2010) may easily override the effect of increasing mean annual temperatures.

On a global scale, heat deficiency may be the dominant factor controlling treeline dynamics, but regional studies have shown that treeline position rarely changes in parallel with the shift of any isotherm (Holtmeier and Broll, 2007). At present, one of the most important gaps and uncertainties in treeline research appears on intermediate (10–10,000 km²) spatial scales (Holtmeier and Broll, 2007; Kullman and Öberg, 2009) at which feedbacks to the climate

system are significant (Harding et al., 2002), yet studies on the causes of treeline dynamics that also consider site history are very rare (Payette et al., 2002).

The main goal of this paper was to identify and explain recent changes in the position and structure of this vegetation boundary. By confronting long-term climatic and environmental records with new dendrochronological measurements, field observations and analysis of repeat photography, we expected to provide new insights into the driving forces behind current treeline dynamics in northern regions. We focused on a Swedish sub-Arctic study area for which multiple previous treeline studies exist. However, these studies presented contradictory results in terms of both the directions and causes of treeline shifts (Table 1). Furthermore, the suggested causal mechanisms behind reported treeline shifts were not supported by convincing evidence. This study differs from previous ones by providing ample evidence of recent treeline dynamics and their causal mechanisms. Here, we focused on different spatial scales, ranging from an individual mountain (*c.* 20 km²) to an entire landscape area (*c.* 1000 km²), and different temporal scales, ranging from a 30-year to a 100-year time period.

Table 1. Previous field studies on observed treeline shifts and their presumed causes in the Torneträsk area of sub-Arctic Sweden.

Reference	Area	Methods	Results	Presumed attribution
Sandberg (1940)	Mount Nuolja	Repeat Observation	Establishment of 0.5 m tall birch saplings during warm 1930s up to 200 m above the upper limit of the closed forest	Climate warming
Persson (1952)	North-Torneträsk	Observations; elevational measurements of treeline ecotone	Contrasting treeline types and age structure	Contrasting site history, climate, geomorphological & biotic processes
Sandberg (1963)	Mount Nuolja	Repeat observations; repeat photography	Forest densification at lower boundary of treeline ecotone. No increased abundance of birch at upper boundary.	Climate warming
Sonesson and Hoogesteger (1983)	West-Torneträsk	Elevational transects; dendrochronology	Elevational advance of treeline ecotone by 20–50 m between 1937–1977	Climate warming
Emanuelsson (1987)	Whole Torneträsk	Ethnographical historical research; aerial and ground observations; interviewing local people; repeat photography	Elevational advance and densification of treeline ecotone since 1900. Significant anthropogenic impact on the treeline in period 1600–1920	Recent decrease in anthropo-zoogenic impact
Holmgren and Tjös (1996)	Mount Nuolja	Field observations; literature review; climate analysis	Elevational advance of the treeline ecotone by c. 40 m between 1930–1996	Climate warming
Lundgren (1999)	Mount Nuolja	Repeat treeline measurements 1971–1998	Elevational advance of upper limit of tree-sized birches (>2 m) by 22–46 m	Climate warming
Hällmarker (2002)	Mount Nuolja	Remote sensing; repeat photography	Elevational advance of lower boundary of treeline ecotone by c. 20 m between 1959–2000	Climate warming, reduced anthropozoogenic impact, moth outbreaks, geomorphology
Cairns and Moen (2004)	Southwest-Torneträsk	Field measurements; herbivory analysis	Differential reindeer grazing impacts cause differential treeline shifts and structure	Differential reindeer grazing pressure
Dalen and Hofgaard (2005)	Southwest-Torneträsk	Dendrochronology; field measurements	Major recruitment phase at upper boundary of treeline ecotone in 1960s; possibly advancing treeline	Moth outbreak of 1955, herbivory, climate warming
Truong et al. (2006)	Southwest-Torneträsk	Field observations; genetic study	Birch seedlings found up to 500 m above the upper limit of the closed forest	Climate warming

Material and methods

Study area

The Torneträsk area is located at the eastern fringe of the Scandes Mountains in sub-Arctic Sweden (68°25' N, 19°00' E) (Fig. 1). The mean annual temperature for Abisko (388 m a.s.l.), located at the south-western end of Lake Torneträsk (Fig. 1), is -1.0 °C and mean annual precipitation amounts to 310 mm for the normal period 1961–90 (Alexandersson et al., 1991). However, climate has recently changed: mean annual temperature and precipitation increased from -1.2 °C and 301 mm, respectively, during the first instrumental decade (1913–22) to +0.6 °C and 342 mm for the 10-year period 2000–09 (Abisko Scientific Research Station meteorological records 1913–2009). Moreover, statistically smoothed trends showed a 2.5 °C increase in temperature over the period 1913–2006 (Callaghan et al., 2010). Lake Torneträsk is surrounded by 1200 km² of subalpine forests dominated by mountain birch (*Betula pubescens* Ehrh. ssp. *czerepanovii* (Orlova) Hämet-Ahti), the species that sets the treeline in Fennoscandia. The position of the alpine treeline varies around 700 m a.s.l. (Dalen and Hofgaard, 2005). Local variability in precipitation, topography, geology and land-use history is substantial (Hofgaard,

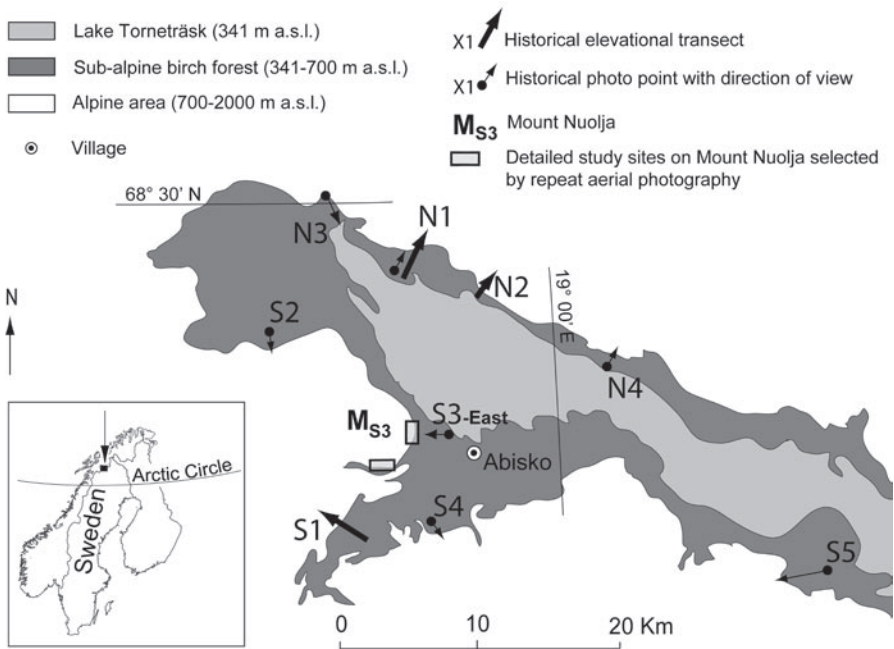


Figure 1. The Torneträsk study area in sub-Arctic Sweden. The locations of the historical transects and photo points that were revisited to study changes in the treeline ecotone are indicated.

1999). Polycormic (multi-stemmed) types of birch forest are found in dry areas with poor soils, whereas monocormic (single-stemmed) birch forests can be found in areas with a deeper snow cover and a more calcareous soil (Sonesson and Hoogesteger, 1983). The dominant agents of disturbance to the birch forest are the more or less cyclic pest outbreaks of the autumnal moth (*Epirrita autumnata* Bkh.) and the winter moth (*Operophtera brumata* L.) (Tenow, 1972). At the treeline, disturbance by reindeer (*Rangifer tarandus* L.) may be significant (Cairns and Moen, 2004).

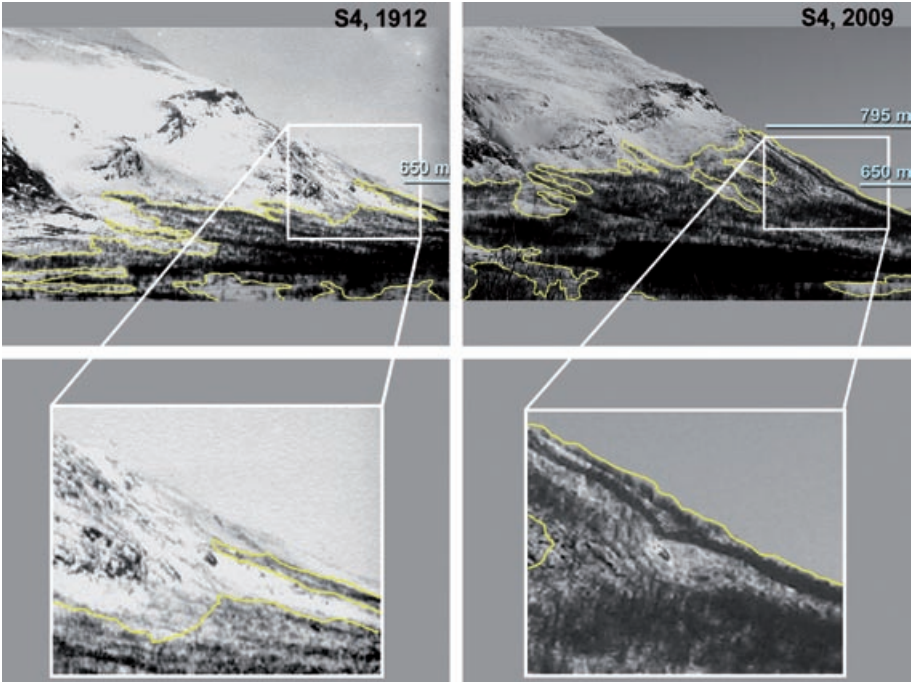


Figure 2. Treeline site S4 on the south side of Lake Torneträsk in sub-Arctic Sweden in 1912 and 2009. The yellow lines denote the 30% tree-cover isolines (statistically determined by using the software ARCGIS SPATIAL ANALYST 9.2). The process of identifying the elevational position of this isoline in the old photographs is illustrated here: in the centre of the inset, a rock outcrop attached to the bedrock can be seen that was positioned near the upper limit of the isoline of 1912. The same landmark is seen on the 2009 photograph and could be recorded in the field with a GPS-device with an aneroid altimeter. As a reference, elevation in metres above sea level is indicated. Left photo, B. Mesch; right photo, R. Van Bogaert.

Definitions and approach

In the present paper the term ‘treeline’ refers to the transition zone extending from the upper limit of the closed subalpine forest to the uppermost birch individual. In repeat photography analysis, we used the lower boundary of this ecotone as a main reference as it is more distinct

than the upper boundary. This boundary was set to 30% tree-cover in a convention used by most other treeline studies (Rees et al., 2002). Time series of photographs were scanned at identical resolution, so that individual pixels could be compared. A pixel was classified as forested or non-forested. The 30% tree-cover isoline was statistically plotted using ArcGIS SPATIAL ANALYST 9.2 (ESRI, Redlands, CA, USA) (Fig. 2).

The boundary line was visited *in situ* at locations where the 30% tree-cover isoline crossed an easily identifiable landmark such as a big boulder (Fig. 2). Field measurements showed that the individual trees at the treeline detectable on the photographs had a mean canopy size of 3.5 m diameter, implying that a 30% tree-cover corresponded to a distance interval of 2.2 m in any direction between the canopy boundaries of different individuals trees. In the field we could now delimit both the upper and lower boundary of the treeline ecotone. Note that the outcome of this study did not depend on the definition setting. A 10% tree-cover analysis (7.0 m between different tree canopy boundaries) produced similar results.

Repeat photographic analysis

Seven ground photographs taken between 1912 and 1952 from different mountain slopes in the Torneträsk area were successfully repeated (Fig. 1). Prominent landmarks were found in the direct vicinity of the historical treeline (Fig. 2). The actual shift in elevational position of the treeline could then be estimated by comparing the old and recent photographs and by recording the elevational difference between the landmark and the present treeline position with a calibrated aneroid altimeter in the field.

Furthermore, repeat aerial photographs from the period 1959–2000 were studied to quantify recent elevational shifts in the boundaries of the treeline ecotone of Mount Nuolja (M_{S3} in Fig. 1). The images were scanned at 1600 dots per inch (d.p.i.) implying a resolution of 0.3 m and were then georeferenced and rectified in the program ORBIT GIS 4.4 (Eurotronics, 2009, Lokeren, Belgium). Maximal geometric distortion between the two photographs amounted to 5 m. To study the driving forces behind treeline dynamics, we looked for contrasting results from the analyses of the aerial photographs. Two areas were selected for further analysis in the field: (1) an area on the east slope of Mount Nuolja characterized by a significant upslope shift of the treeline, and (2) an area on the south slope with no significant change in the position of the treeline.

Repeat transect analysis and field measurements

To study the causal mechanisms and timing of treeline advance, tree sampling and field measurements were carried out at five sites in the wider Torneträsk area in 2006. We sampled

treeline individuals at the two contrasting sites of Mount Nuolja and at the three Sonesson and Hoogesteger transect sites N1, N2 and S1 (Fig. 1). In 1977, these transect sites were randomly selected in treeline areas that differed in climate (dry versus wet), soil (calcareous rich versus poor) and tree growth form (mono- versus polycormic birch forest) (Sonesson and Hoogesteger, 1983). In 2006, we established nine transects through the birch forest: three at sites N1, N2 and S1 corresponding to the original transects of Sonesson and Hoogesteger, and six on Mount Nuolja (three on the east and three on the south slope). The Sonesson and Hoogesteger transects were c. 1200 m long and crossed several contours running from the lake level (341 m a.s.l.) up to the alpine area (c. 700 m a.s.l.). At the upper end of these transects, 40 treeline birches were randomly sampled over a width of 500 m. For Mount Nuolja, a transect set-up of higher resolution was designed to identify the causes of the contrasting treeline dynamics that were found by repeat photographic analysis. The transects were 200 m long and ran along different contours equally spread over the treeline ecotone (see Appendix 1, p. 129). All six transects contained seven plots measuring 10 x 10 m, in which all birch individuals were sampled. The birches were cut off at the root collar (individuals <2 m) or cored as low as possible (individuals >2 m) with an increment corer according standard methods (Fritts, 1976). Twenty-five monocormic erect birch individuals were cored 40 m downslope of all five treeline sites to serve as a reference for the treeline samples. However, because ring growth of these reference individuals may also have been affected by ubiquitous moth herbivory, 30 non-browsed pine (*Pinus sylvestris* L.) individuals were sampled in the Abisko area to construct a birch-minus-pine ring-width chronology that serves as a reference for moth herbivory on birch (Eckstein et al., 1991; Van Bogaert et al., 2009). (For more methodological detail, see Van Bogaert et al., 2009.)

To study the mechanisms behind treeline shifts, the following variables were recorded for all sampled birch individuals: tree height, stem diameter at breast height (130 cm; DBH), growth form (mono- or polycormic), herbivory damage, elevation (m a.s.l.), inclination, aspect and snow depth. Herbivory damage was classified visually as browsed or not browsed, but also statistically by constructing a birch-minus-pine ring-width chronology and anatomically by studying features of wood anatomy (Appendix 2, p. 130). The mean height limit of the epiphytic lichen *Melanelia olivacea* (L.) Essl. on adult birch stems was used as a proxy for mean snow depth (Sonesson et al., 1994). All measurements and dendrochronological analyses have been made with identical methods applied in the original study by Sonesson and Hoogesteger (1983) and with field assistance by one of the original researchers.

Altogether, we studied changes in the elevational position of the treeline ecotone for 10 sites spread over the Torneträsk area (Mount Nuolja M_{ss} had two sites; Fig. 1). In total, 678 tree

cores and 188 stem discs of mountain birch and 30 tree cores of pine were analysed to study site history. (For a detailed description of the dendrochronological analysis, see Appendix 2, p. 130) The samples were also used to cross-reference with the estimated treeline dynamics that we obtained from repeat photography and repeat transect analysis.

Analysis of tree establishment

The year of tree (>2 m) establishment was determined by exact tree-ring dating of the innermost growth ring surrounding the pith. However, the year of establishment is hard to determine when the individual is not cored at the stem–root intersection or the pith is not perfectly hit. Therefore, estimated establishment data were derived from the tree cores after grouping them into 10-year age classes. Tree cores of treeline birches with rotten pith (13%) or with a substantial number of rings missing due to failure to hit the pith (22%) were omitted from this analysis. An annual recruitment analysis was made for the saplings (<2 m) that were cut off at the root collar ($n = 188$) to allow for a more accurate determination of the year of establishment. The presumed annual number of birch recruits was correlated with climatic and biotic factors using Spearman's rank correlation coefficients (r_s).

Historical anthropozoogenic impact

Emanuelsson (1987) produced a map with the locations of the traditional reindeer migration routes and the reindeer herder camps near the treeline (Fig. A2 in Appendix 2, p. 130). These points of relatively intense previous human impact were located in the field and distances to our study sites were recorded by a GARMIN GPSMAP60CSx device.

Long-term records as validation

The Torneträsk area has an exceptionally long-term record of climatic and other environmental data offering a powerful instrument for validation of measurements (Callaghan et al., 2010). Daily temperature and precipitation measurements are available since 1913 (Callaghan et al., 2010), human impact has been described in detail since 1600 (Emanuelsson, 1987), reindeer population numbers since 1750 (Emanuelsson, 1987) and moth outbreaks on birch have been reported since 1862 (Tenow, 1972).

Statistical analyses

Regression analyses with forward selection were used to test which of the environmental and anthropogenic variables best explained the elevational shifts of the treeline ecotone. The sign of relationships and relative importance of the variables that corresponded to elevational

shifts in the treeline position were studied using Pearson correlation coefficients. For further information on the technical details of the correlation of treeline dynamics and compass direction see Dalen and Hofgaard (2005). All statistical analyses were conducted in the program SPSS v. 15.0 (SPSS INC., 2006, Chicago, IL, USA).

Results

Treeline dynamics

At the scale of an individual mountain, analysis of repeat aerial photographs of Mount Nuolja for the period 1959–2000 showed that the upper limit of the closed forest, representing the lower boundary of the treeline ecotone, had increased in elevation by 25 m (rate of +0.6 m

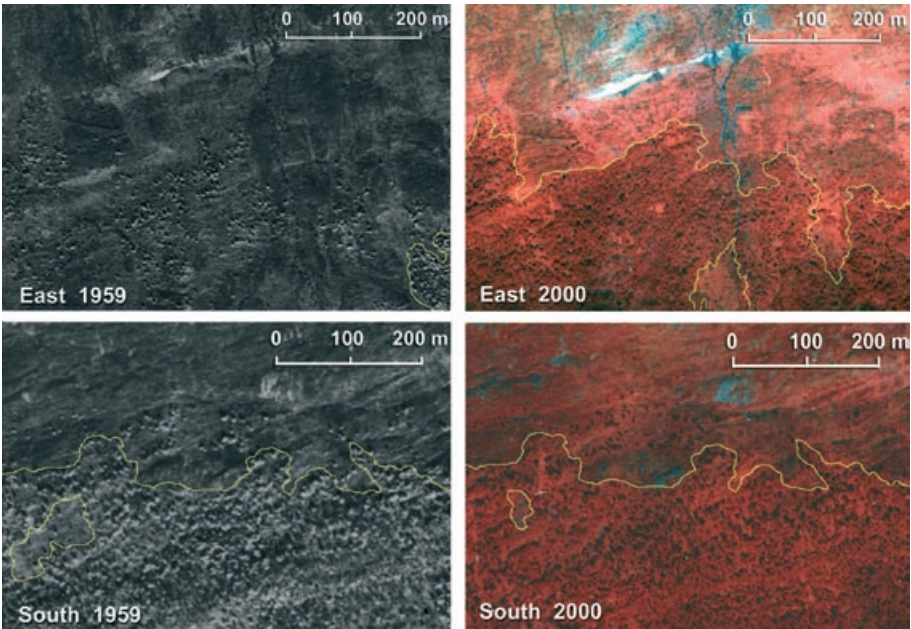


Figure 3. Repeat aerial photograph analysis on Mount Nuolja in sub-Arctic Sweden. Contrasting treeline dynamics are documented for the east- and south-facing slope for the period 1959–2000. The statistically-determined 30% tree-cover isoline is plotted in yellow. Note that due to different camera filters, trees are plotted as white dots in the images on the left, but rather as dark reddish dots in the infrared-images on the right.

year⁻¹ assuming linear advances). However, site variability was high: on the eastfacing slope an area was found where this boundary had increased in elevation by 45 m (+1.1 m year⁻¹) as a result of a dramatic densification of the uppermost tree patches (Fig. 3). In contrast, on the

Table 2. Documented treeline shifts and site conditions for 10 sites studied in the Torneträsk area of sub-Arctic Sweden for the period 1912–2009 (see Fig. 1). Independently obtained results from repeat photography, repeat transect measurements and dendrochronological analysis were cross-referenced to determine the shift of the lower boundary of the treeline ecotone. Browsing damage was classified visually and for five sites also by dendrochronological analysis (the values listed in brackets). So as not to bias the results, Mount Nuolja (site S3), for which the two treeline sites were not randomly selected, was not included in the calculation of the mean elevational shift of the treeline in the Torneträsk area. Pearson correlation coefficients and R^2 -values (the proportion of explained variance in documented treeline shifts) obtained by forward selection of the different variables are listed at the bottom of the table.

Site	Elevational shift of treeline ecotone (m)	Aspect (°)	Inclination (°)	Anthropozoo-genic impact (distance in m from previous camp or railway)	Snow depth (m)	Browsed treeline birches (%)	Polycormic treeline birches (%)
N1	-120 ± 20	220	29	1210	0.5	47 (81)	42
N2	0 ± 10	205	17	720	0.7	35 (73)	24
N3	+50 ± 5	220	26	180	1.2	42	66
N4	0 ± 10	180	41	910	0.3	29	63
S1	+40 ± 15	155	0	490	1.0	51 (64)	52
S2	+50 ± 5	15	27	190	0.9	39	58
S3-East	+60 ± 5	80	26	220	1.2	43 (53)	60
S3-South	0 ± 10	170	10	800	0.3	29 (72)	43
S4	+145 ± 10	200	26	210	1.2	32	68
S5	0 ± 5	50	40	960	0.5	16	74
All except S3	+24 ± 2						
r	All	-0.24	-0.06	-0.46 (0.03)	0.44	0.24	0.44 (0.17)
(P)		(0.45)	(0.87)		(0.04)	(0.48)	
R^2	All	0	0	0.35	0.59	0.59	0.59

south-facing slope a significant area was found where the boundary had remained stationary (Fig. 3). These trends were persistent over a longer period (1912–2009). On the east-facing site, repeat landscape photography showed that the treeline ecotone had advanced 60 m in elevation since 1912 (+0.6 m year⁻¹; Table 2). On the south-facing site, dendrochronological analysis showed long-term immobility: at the upper and lower boundary of the treeline ecotone 8% and 28%, respectively, of the treeline birches had established before 1900 (Table 3).

At the landscape scale, repeat photography and dendrochronological analysis showed that the lower boundary of the treeline ecotone in the Torneträsk area had on average advanced 24 m in elevation over the period 1912–2009 (+0.2 m year⁻¹) (Table 2). However, at this scale also, spatial variability was high: at four out of the eight remaining treeline sites the treeline had moved upslope, at three others it had remained stationary, and at one site the treeline had

Table 3. Treeline shifts in the Swedish Torneträsk area identified by repeat photography analysis (upper part) and compared with dendrochronological analysis (bottom part) for the elevational transects. The geographical scale of the study ranged from an individual mountain (Mount Nuolja, site M₈₃) to the landscape scale (sites N1, N2 and S1). Trees were grouped into three establishment periods: individuals established (1) before 1900; during the peak of intensive reindeer management practices, (2) in the period 1900–63; before the reindeer population reached its long-term minimum, and (3) in the period 1964–2006; the most recent period during which reindeer population numbers were initially very low and subsequently increased again.

		Scale				
		Individual mountain (M ₈₃)		Torneträsk landscape area		
		East Slope	South Slope	N1	N2	S1
Dynamics of treeline ecotone	Elevational shift (m) of the treeline ecotone for the period 1912-2009	+60 ± 5	0 ± 5	-120 ± 5	0 ± 5	+40 ± 5
		Number of individuals (%)	Number of individuals (%)	Number of individuals (%)	Number of individuals (%)	Number of individuals (%)
Age structure of treeline ecotone	Upper transect					
	Before 1900	0 ± 0 (0 ± 0)	3 ± 1 (8 ± 3)	0 ± 0 (0 ± 0)	16 ± 1 (66 ± 4)	0 ± 0 (0 ± 0)
	1900-63	0 ± 1 (0 ± 4)	0 ± 1 (0 ± 3)	5 ± 1 (25 ± 5)	4 ± 1 (17 ± 4)	11 ± 1 (42 ± 4)
	1964-2006	23 ± 1 (100 ± 4)	33 ± 1 (92 ± 3)	15 ± 1 (75 ± 5)	4 ± 1 (17 ± 4)	15 ± 1 (58 ± 4)
	Middle transect					
	Before 1900	0 ± 0 (0 ± 0)	2 ± 1 (10 ± 5)	–	–	–
	1900-63	1 ± 1 (5 ± 5)	1 ± 1 (5 ± 5)	–	–	–
	1964-2006	19 ± 1 (95 ± 5)	17 ± 1 (85 ± 5)	–	–	–
	Lower transect					
	Before 1900	2 ± 1 (6 ± 3)	36 ± 3 (28 ± 3)	–	–	–
	1900-63	1 ± 1 (3 ± 3)	0 ± 3 (0 ± 3)	–	–	–
	1964-2006	30 ± 1 (90 ± 3)	94 ± 3 (72 ± 3)	–	–	–

significantly descended (Table 2).

The treeline ecotone of site S4, located along the reindeer migration route (Appendix 3, p. 133), had shifted 145 m upslope (+1.5 m year⁻¹) or 260 m in actual distance (+2.7 m year⁻¹) over the period 1912–2009 (Fig. 2, Table 2). Moreover, significant forest densification was observed at the treeline and in the lowland (Fig. 2). In sharp contrast, the continuous treeline boundary of site N1 was 120 m lower in elevation in 2009 compared with the years 1912 and 1952 (Fig. 4, Table 2). The retreat was caused by a severe outbreak of the winter moth (*O. brumata*) in 1964–65 and extended over a distance of more than 10 km (Fig. 4). Although in 1977 two young birches were documented at site N1 in the recently created forest gap, these individuals had perished by 2006 (Fig. 5). At treeline site N2 and the area up to 7 km eastwards of this site, both the lower and upper boundaries of the treeline ecotone had remained stationary

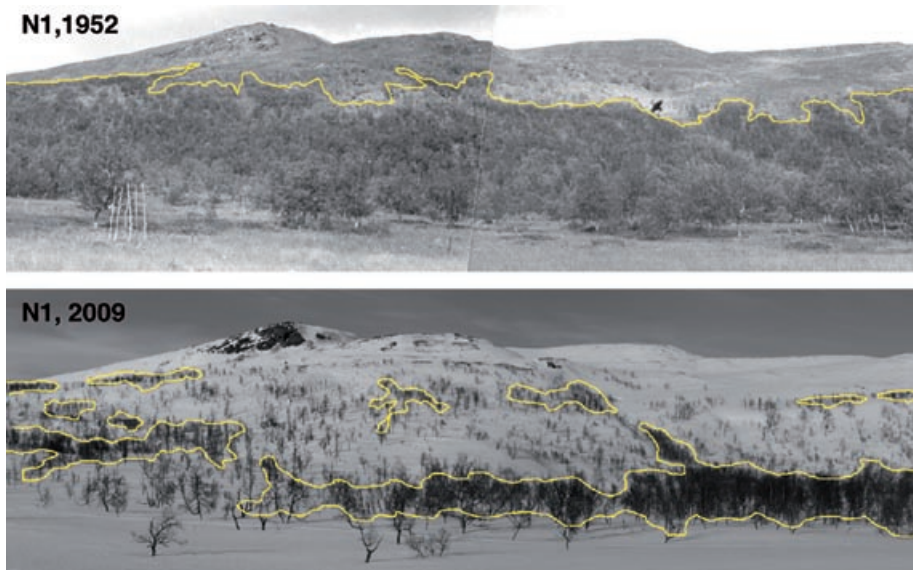


Figure 4. The treeline ecotone near transect N1 on the northern side of Lake Torneträsk in sub-Arctic Sweden in 1952 and 2009. The statistically determined 30%-tree cover isoline is plotted in yellow. Although the 2009 photograph is taken in winter, therefore showing a reduced tree-cover, large forest gaps are seen as a result of a severe moth outbreak in 1964–65. Upper photo: E. Persson, lower photo: R. Van Bogaert.

since at least 1912 (Table 3). The uppermost birch trees (>2 m) were between 110 and 258 years old with little or no recruitment of new trees (>2 m) in the last 100 years (Fig. 5). Most of the smaller birches ($\text{DBH} < 2.5$ cm) recorded at site N2 in 1977 had perished by 2006 (Fig. 5). At site S1 on the southern side of Lake Torneträsk, potential treeline advance was seen (Fig. 5). In contrast, at sites N4 and S5, which were characterized by slope angles $>35^\circ$, immobility of the position of the treeline was documented for the past 60 to 100 years (Fig. 6).

Presumed drivers of treeline dynamics

Sites that were located in the vicinity of previous human activity showed a pronounced advance of the treeline. This was indicated by the significant negative correlation found between the elevational shift of the treeline and the distance to previous campsites of reindeer herders or the railway that was constructed in 1898–1902 ($r = -0.46$; $P = 0.04$; Table 2, Appendix 2, p. 130). Previous anthropogenic impact explained 35% of the variance in documented treeline dynamics (measured by R^2) since 1912. When adding snow depth to the regression, R^2 increased to 59% (Table 2). Visually identified browsing damage of the seedlings was not correlated with documented shifts of the position of the treeline ($r = 0.24$; $P = 0.48$; Table 2). However,

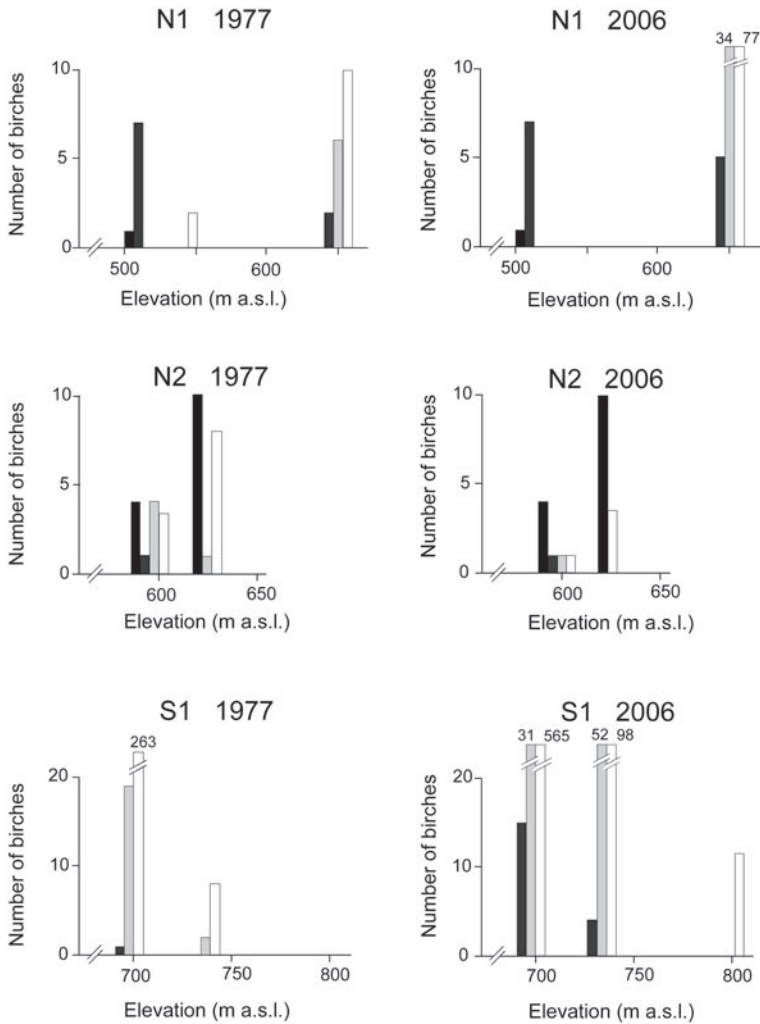


Figure 5. Comparison of the treeline transects N1, N2 and S1 visited in 1977 and 2006. The colours of the bars represent different size classes measured as diameter at breast height (DBH). Black bars denote birch trees that established before 1900, dark grey bars birches with a DBH >7.5 cm that established after 1900, light grey bars birches with a DBH between 2.5 and 7.5 cm, and white bars birch saplings with a DBH <2.5 cm. Note the different scaling of the vertical axis of site S1. (Note that the gap between c. 520 and 640 m a.s.l. at site N1 is due to forest defoliation by invertebrates; see Fig. 4.)

browsing damage to both seedlings and trees (>2 m) identified by dendrochronological analysis showed a significant correlation with documented treeline shifts ($r = -0.82$; $P = 0.03$; Table 2, values in brackets). Adding this parameter to the regression increased R^2 to 68% for these five sites. Polycormicity of treeline birches was positively correlated with advance of the treeline

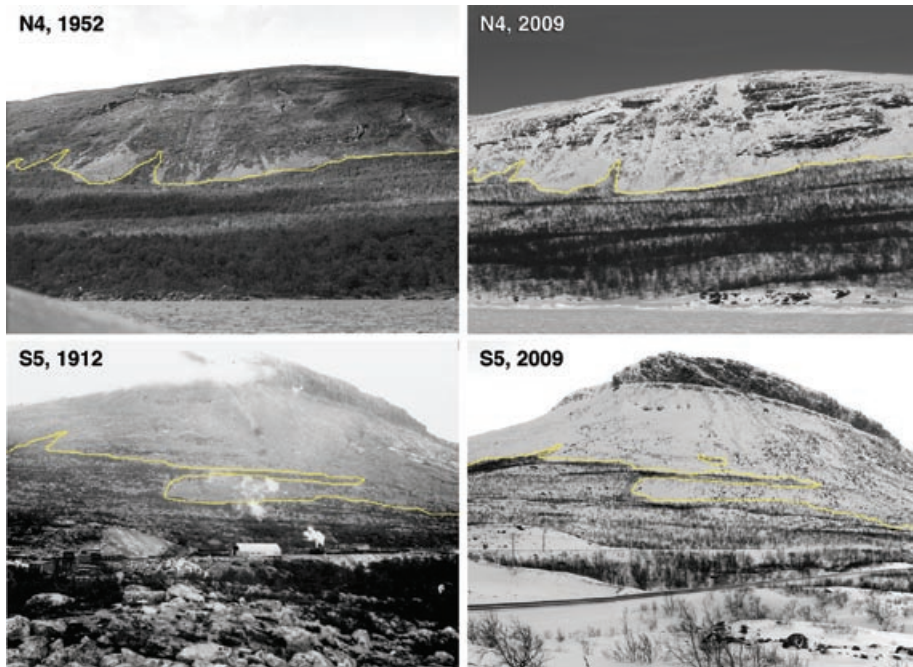


Figure 6. Orographic treeline sites with an inclination $>35^\circ$ showed long-term stability. The statistically determined 30% tree-cover isoline is plotted in yellow. Upper photo on the left, E. Persson; bottom left, B. Mesch; upper and bottom right, R. Van Bogaert.

(Table 2). In contrast, aspect and inclination showed no overall correlation with recorded treeline shifts since 1912.

Annual recruitment of birch saplings (<2 m) at the treeline of Mount Nuolja was not correlated with summer (June–August) or winter (December–February) temperature for the period of measurement 1964–2006 ($r_s = 0.14$, $P = 0.74$ and $r_s = -0.08$, $P = 0.88$, respectively) (Fig. 7). Neither was annual birch recruitment correlated with summer or winter precipitation ($r_s = 0.12$, $P = 0.66$ and $r_s = -0.14$, $P = 0.76$, respectively). Also, no positive correlation ($r_s = -0.21$, $P = 0.20$) was found between summer temperature and tree (>2 m) establishment for the long-term period 1800–2000 (Fig. 8). In contrast, disturbance at the treeline, expressed by the negative birchtreeline-minus-pinesubalpine and birchtreeline-minusbirchsubalpine ring-width indices, was positively correlated with annual birch (<2 m) recruitment ($r_s = 0.54$, $P = 0.06$ and $r_s = 0.47$, $P = 0.10$ respectively) (Fig. 7). Furthermore, a significant negative correlation was found between tree (>2 m) establishment at the treeline and reindeer population numbers for the period 1800–2000 ($r_s = -0.69$; $P = 0.03$). Comparatively low tree establishment numbers were recorded for the warmer 1850s and 1920–30s, when reindeer population numbers were

high, whereas high tree establishment numbers were found for the cool late 19th century and particularly during the cooler late 1960s and 1970s when reindeer population numbers were low (Fig. 8). Even when saplings (<2 m) were included in the analysis, birch establishment at the treeline was highest during the late 1960s and 1970s.

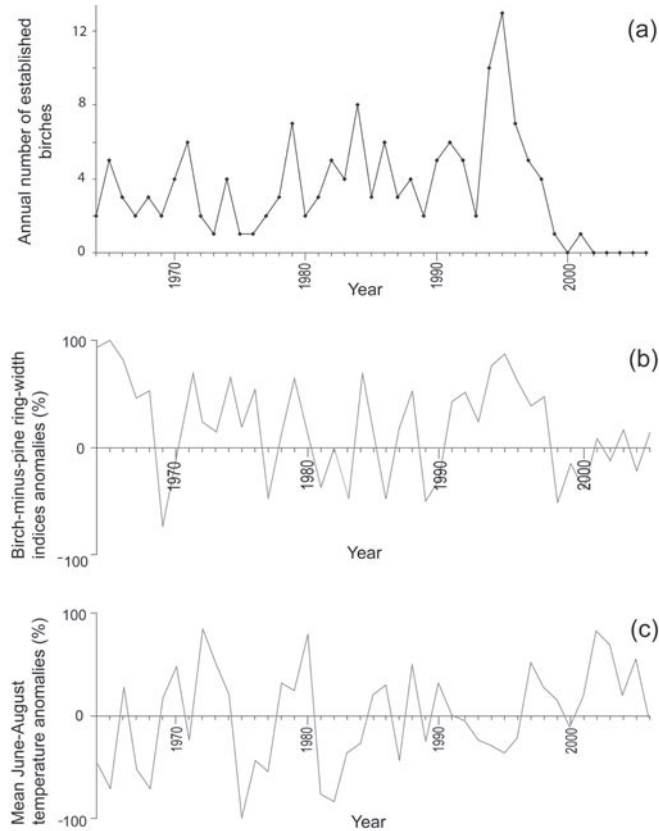


Figure 7. Estimated annual birch recruitment at the treeline of Mount Nuolja, sub-Arctic Sweden (a), in relation to disturbance (b) and summer temperature (c), for the period 1964–2006. Note that birch-minus-pine indices were plotted such that positive values indicate increased moth damage. See text for correlations.

Nevertheless, climate highly determined birch growth at the treeline. Exceptionally cool summers caused significantly ($P < 0.05$) reduced radial growth for 1 year in the subalpine birches, but for 2 years in the birches at the treeline (e.g. 1900–01 and 1975–76, Table 4).

The main biotic disturbance events during the period 1800–2006 that significantly ($P < 0.05$) reduced radial growth in the treeline individuals were, in order of importance, reindeer browsing and moth herbivory (Table 4). Reindeer browsing damage showed local variability,

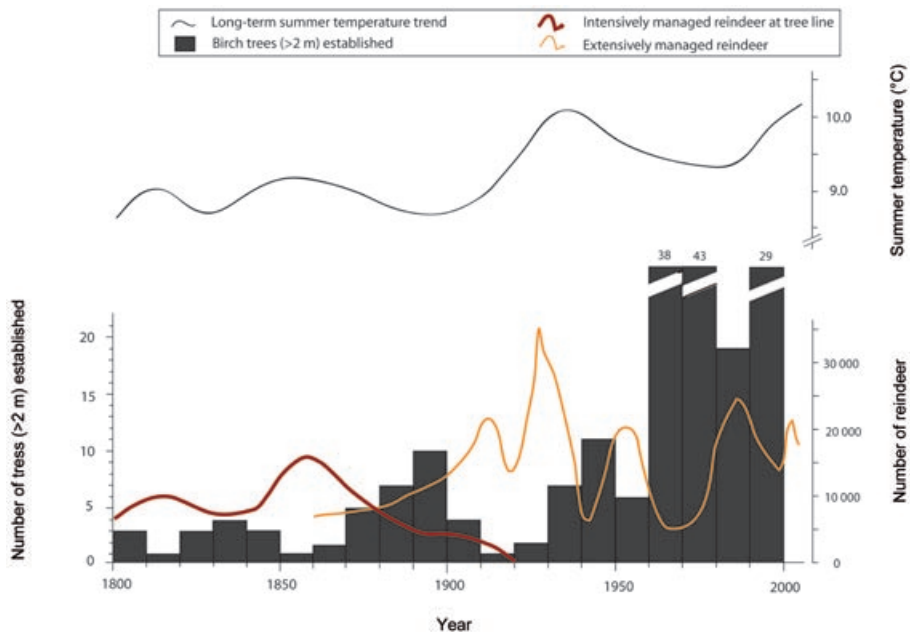


Figure 8. Tree (>2 m) establishment at the Torneträsk treeline versus summer (June–August) temperature and reindeer population numbers for the period 1800–2000. A second-degree polynomial function shows the long-term summer temperature trend. Presumed annual tree establishment numbers were grouped into 10-year classes for five treeline sites: the east and south slope of Mount Nuolja (M_{S3}), and the transect areas N1, N2 and S1 (Fig. 1). Reindeer population numbers for the Torneträsk area were split up into intensively managed reindeer (thick solid red line) that were kept near the treeline and extensively managed reindeer (thin solid orange line) that wander freely (after Emanuelsson, 1987). See text for correlations.

both in timing and intensity. For example, greater damage was seen on the south slope of Mount Nuolja than on the east slope (Table 4). However, if reindeer population numbers were high, browsing damage was ubiquitous on all sites studied: for the years 1863, 1911, 1929, 1979 and 1985 the treeline birches showed browsing scars together with significant growth reductions (Table 4). The most severe and ubiquitous damage in the 20th century caused by browsing was found in the year 1929, when reindeer population numbers reached an absolute peak (Fig. 8). During that year more than 50% of the treeline birches in the Torneträsk area showed a significant growth reduction (Table 4).

Invertebrate herbivory also affected the treeline. During the summers of 1902–03, 1964–65, and to a lesser extent in 1955 and 1994, moth herbivory caused significant growth reductions and, in 1964–65 large-scale mortality (Fig. 4) in the birches constituting the treeline ecotone (Table 4). Local variability in the impact of disturbance was again substantial (Table 4).

Table 4. Significant ($P < 0.05$) disturbance events at the tree line in the Swedish Torneträsk area for the period 1800–2006. The geographical scale of the study ranged from an individual mountain (Mount Nuolja, site M53) to the landscape scale (sites N1, N2 and S1). Ring-width chronologies of birch and pine individuals sampled below the tree line ecotone were used as a reference. Major disturbance events are given in bold and were defined as events that affected 50% or more of the tree line individuals in two or more different sites. The number of replicates is given in brackets. Note that the list of disturbance events is not exhaustive, particularly for the period 1800–1900 for which fewer replicates were available.

Growth reduction period	Scale					Tree-ring anatomical wood features	Validation	
	Tometräsk landscape area							
	Indiv. mountain (M ₅₃)		NI					
	East Slope	South Slope	NI	N2	S1	Presumed event		
1801-11	–	–	–	100% (3)	–	Reindeer browsing 1808	Browsing scar 1808	Peaking reindeer population
1853-59	–	–	–	67% (6)	–	Reindeer browsing 1853, 1857	Browsing scars 1853, 1857	Peaking reindeer population
1863-64	0% (2)	50% (2)	–	50% (6)	–	Reindeer browsing 1863	Browsing scars 1863	Peaking reindeer population
1900-01	50% (2)	50% (2)	–	33% (6)	–	After-effect cold summer 1900	Small ring in old and young individuals 1901	1900: exceptionally cold: 4 °C below long-term mean
1902-04	25% (8)	100% (4)	–	71% (14)	–	Moth defoliation old birches 1902-1903 (N2)	White ring 1902-1903 (N2);	Reported moth outbreak in N-Fennoscandia (Tenow, 1972)
						Reindeer browsing young birches 1903 (M ₅₃)	Browsing scars 1903 (M ₅₃)	Average reindeer population
1909-11	33% (12)	25% (4)	–	71% (14)	–	Reindeer browsing 1909, 1911	Browsing scars 1909, 1911	Peaking reindeer population
1919	50% (12)	0% (10)	–	13% (16)	–	Reindeer browsing 1919	Browsing scars 1919	Average reindeer population
1925	17% (12)	10% (10)	–	13% (16)	0% (2)	Reindeer browsing 1925	Browsing scars 1925	High reindeer population
1929	50% (12)	60% (10)	100% (2)	50% (24)	67% (3)	Reindeer browsing 1929	Browsing scars 1929	Peaking reindeer population
1934-35	14% (14)	10% (10)	100% (2)	0% (24)	25% (4)	Reindeer browsing 1934	Browsing scars 1934	High reindeer population
1955-58	33% (10)	50% (10)	0% (5)	13% (30)	60% (5)	Moth defoliation 1955	White ring 1955	<i>Epirrita autumnata</i> outbreak 1955
1964-68	50% (12)	83% (12)	20% (5)	63% (30)	0% (5)	Moth defoliation 1964 (M ₅₃)	White ring 1964 (M ₅₃)	<i>E. autumnata</i> peak 1964 (M ₅₃)
						Moth defoliation 1965 (N1-N2)	White ring 1965 (N1-N2)	<i>Operophtera brumata</i> outbreak 1965 (N1-N2)
1975-76	33% (18)	18% (18)	10% (20)	15% (32)	10% (10)	After-effect cold summer 1975	Small ring in old and young individuals 1976	1975: exceptionally cold: 3 °C below long-term mean
1979	35% (34)	45% (22)	6% (32)	30% (32)	50% (12)	Reindeer browsing 1979	Browsing scars 1979	High reindeer population
1984	17% (46)	21% (33)	26% (38)	30% (34)	25% (16)	Frost damage	Frost ring 1984	May: 27 days +12 °C; June: 3 days -1.3 °C
1985	9% (46)	21% (33)	21% (38)	30% (36)	29% (14)	Reindeer browsing 1985	Browsing scars 1985	Peaking reindeer population
1991-92	23% (46)	28% (49)	11% (38)	18% (36)	11% (18)	Reindeer browsing 1991-1992	Browsing scars 1991-1992	High reindeer population
1994-96	37% (62)	59% (56)	21% (38)	23% (37)	11% (18)	Moth defoliation 1994 (old birches)	White ring 1994	<i>E. autumnata</i> peak 1994
						Reindeer browsing 1994 (young birches)	Browsing scars 1994	Average reindeer population
1997-98	8% (62)	11% (56)	5% (38)	15% (37)	31% (26)	Reindeer browsing 1997-1998	Browsing scars 1997-1998	Average reindeer population
2005-06	4% (101)	7% (97)	8% (43)	20% (38)	15% (30)	Reindeer browsing 2005-2006	Browsing scars 2005-2006	High reindeer population

Discussion

Trends and presumed causes of treeline dynamics

This study aimed to document changes or stability in the treeline ecotone in the Torneträsk area at different temporal and spatial scales, and particularly to clarify the ambiguity that currently exists about treeline dynamics and the driving processes behind them (Table 1).

In contrast to one of the most widely held expectations of vegetation responses to warming, i.e. that Arctic treelines will move northwards and elevational treelines upslope (Harsch et al., 2009), this study documented highly varying treeline dynamics for the Torneträsk area in sub-Arctic Sweden during a period of multi-decadal climate warming (Callaghan et al., 2010). Contrasting treeline dynamics were recorded at spatial scales ranging from an individual mountain to an entire landscape and at temporal scales ranging from three decades to more than a century (Figs 3 and 5, Table 2). This is surprising because temperature and precipitation, the climatic parameters generally accepted to limit recruitment and growth at the mountain birch treeline (Kullman and Öberg, 2009), both significantly increased since 1913 (see ‘Study area’).

Moreover, dendrochronological analysis indicated that treeline advance in the past two centuries was most pronounced during the cooler late 1960s and 1970s (Fig. 8), contradicting the interpretations of previous studies in the area (Table 1). During this period, reindeer population numbers in the Torneträsk area reached a record low following some severe winters. By the late 1960s the total herd had become three times smaller than in the period 1850–60 when all reindeer were gathered around the treeline by the nomadic herders (Fig. 8; Emanuelsson, 1987). Although reindeer have always been part of the birch ecosystem, their impact on the vegetation should be evaluated in terms of population densities (Helle, 2001). Fenced pastures near the treeline in the 19th and early 20th centuries resulted in higher reindeer population densities in the treeline ecotone than in both earlier and more recent times (Emanuelsson, 1987). Dendrochronological analysis for the five transect sites N1, N2, S1, S3_E and S3_S showed that the impact of reindeer browsing at the treeline gradually decreased after the 1930s (Table 4). From the 1920s onwards, the campsites and pastures have been gradually abandoned, synchronously with most other heavily grazed out-farms in Fennoscandia (Bryn and Daugstad, 2001; Lundh, 2001).

A similar process of reduced human impact was identified at site S2. Repeat landscape photography and dendrochronological analysis showed a remarkable densification and an upslope shift by 50 m of the lower boundary of the treeline ecotone for the period 1912–2009

(Table 2). However, historical reports documented the local clearance of the birch forest at this site between 1898 and 1902, thereby lowering the treeline ecotone by 70 m (Emanuelsson, 1987). Extending the period by 15 years would result in a net balance of a 20 m descent of the treeline for the period 1897–2009. This shows the importance of the temporal scale in treeline research and suggests caution with far-reaching conclusions based on findings such as apparent correlations between temperature and treeline advance obtained from short-term studies.

Reduced anthropozoogenic disturbance (Ellenberg, 1988) compared with the early 20th century best explained the varying treeline shifts recorded in our study area (Table 2). We confirmed the hypothesis of Emanuelsson (1987) and Cairns and Moen (2004) that the impacts of humans and semidomesticated herbivores have significantly determined the elevational shifts of the treeline boundary (Table 1). Distinguishing human impact from natural factors is, however, one of the most difficult tasks in treeline research (Ellenberg, 1988; Hofgaard, 1997). Only accurate historical reports of the anthropozoogenic impact on northern vegetation make a proper evaluation of this factor possible. Unfortunately, this information is often not available (Moen et al., 2008) and is a major weakness in studies dealing with range migrations of plant species. The Torneträsk area has a long history of human occupation, but human impact was presumably not higher than in other areas of northern Eurasia (Von Middendorf, 1864; Veijola, 1998; Hofgaard, 1999; Lundh, 2001; Vlassova, 2002). The major difference from other regions is rather that its anthropozoogenic impact has been well documented since *c.* 1600 (Emanuelsson, 1987).

In addition to reindeer grazing, the mountain birch treeline also suffers from episodic outbreaks of the autumnal and winter moth (Kallio and Lehtonen, 1973). Several studies have shown that the lack of recovery of forests defoliated by moths is the product of an interaction between damage due to moth outbreaks and reindeer grazing (Kallio and Lehtonen, 1973; Helle, 2001; Tenow et al., 2005). In the mid 1960s, caterpillars of the autumnal moth defoliated the birch treeline ecotone in northern Finland over an area of *c.* 5000 km², of which 1200 km² of birch forest did not recover (Seppälä and Rastas, 1980). Exclosure experiments showed that reindeer grazing of birch seedlings was the cause of the lack of forest recovery (Lehtonen and Heikkinen, 1995). This interaction between moth and reindeer herbivory forms the greatest threat to the mountain birch forest, and devastated areas may remain treeless for decades to centuries irrespective of prevailing climatic conditions (Seppälä and Rastas, 1980). At treeline sites N1 and N2 we documented this process. The lack of recent tree (>2 m) establishment and the browsing scars documented in the tree rings indicated that, in addition to moth herbivory, reindeer browsing is still a controlling factor at these sites (Fig. 5, Table 4). This example further stresses the importance of disturbance in regulating recruitment and mortality at the

treeline and masking or even nullifying any beneficial effects of recent climate warming on tree recruitment and treeline shifts (see Fig. 7).

Other factors affecting treeline dynamics

A multitude of environmental conditions affect tree establishment and survival and these factors may differ in space and time (Sveinbjörnsson et al., 2002). Besides anthropozoogenic impacts, snow depth significantly increased the proportion of explained variance in documented treeline dynamics (R^2 increased from 0.35 to 0.59; Table 2). The importance of an ample snow cover for mountain birch, providing insulation in winter and moisture in spring, has been elucidated in previous treeline studies (Dalen and Hofgaard, 2005; Kullman and Öberg, 2009). Nevertheless, winter precipitation was not correlated with tree establishment at the treeline, suggesting that local snow distribution is a more complex factor than just the sum of amounts of winter precipitation (Holtmeier and Broll, 2010).

In contrast to other studies (Danby and Hik, 2007; Kullman and Öberg, 2009), slope aspect and inclination were not correlated with elevational shifts of the treeline ecotone. Possibly, local site conditions and various historical disturbances were of greater importance than relative solar radiation and regional wind exposure. The lack of correlation between inclination and documented treeline shifts resulted from the fact that both flat and very steep slopes experienced immobility of the treeline (Table 2), possibly because of high wind exposure and geomorphological activity, respectively (Holtmeier and Broll, 2010). Polycormicity of treeline birches was positively correlated with documented elevational shifts of the position of the treeline (Table 2). Polycormic birch forests are less prone to disturbance than monocormic forests as they do not rely on hazardous seedling establishment (Tenow et al., 2005). At the polycormic treeline of Mount Nuolja we recorded high birch recruitment during years with increased disturbance (Fig. 7).

Projecting future treeline dynamics

The extreme discrepancy that exists between model projections of the treeline position and *in situ* observations is a world-wide phenomenon (Holtmeier and Broll, 2007; Van Bogaert et al., 2007). In the next 100 years, alpine and polar treelines are projected to shift upslope by 2 to 6 m year⁻¹ (Moen et al., 2004) and northwards by 7.4–20 km year⁻¹ (Kaplan and New, 2006) if climate warming continues. However, the fastest upslope shifts of treelines recorded during 20th century warming are in the range of 1 to 2 m year⁻¹ (Shiyatov et al., 2007; Kullman and Öberg, 2009). Moreover, the fastest northward-migrating treeline replaces tundra by taiga at a rate of 3–10 m year⁻¹ (Kharuk et al., 2006); i.e. 2000 times slower than model projections. For

comparison, the fastest upward and lateral (actual distance) displacements of the treeline in the Torneträsk area were respectively $+1.5 \text{ m year}^{-1}$ and $+2.7 \text{ m year}^{-1}$. A global study by Harsch et al. (2009) showed that only 52% of all 166 global treeline sites had advanced over the past 100 years despite documented amplified climate warming at high-elevation areas and northern latitudes (ACIA, 2005).

Climate scenarios for our study area in northern Fennoscandia project an increase in mean annual temperature of $3.5 \text{ }^{\circ}\text{C}$ by the year 2080 compared to the reference period 1980–2000 (Saelthun and Barkved, 2003) and an upslope shift of the treeline by 233–667 m for the next 100 years (Moen et al., 2004). In such scenarios, mountain birch would be largely replaced by conifer tree species (Wolf et al., 2008a). However, these models almost exclusively operate with positive growth responses, and new findings such as likely increases in birch herbivory in a warming sub-Arctic (Ims et al., 2007; Wolf et al., 2008b) and negative growth responses to increased temperatures (Kirchhefer, 1996) suggest that the modelled treeline advances are unlikely to be fully realized. Indeed, Van Bogaert et al. (2010) showed that not a conifer but deciduous European aspen (*Populus tremula* L.) recently colonized the birch treeline ecotone in our study area. Moreover, topography, being the only relatively constant factor through time, will prevent an upslope shift of orographically controlled treeline areas (inclination $>35^{\circ}$) such as sites N4 and S5 (Fig. 6).

In conclusion, in areas where the number of domesticated herbivores has decreased over the past century, rapid vegetation changes and advances in the treeline may be expected. However, in treeline areas controlled by severe disturbance by moth herbivory or slope processes, treeline advance may not occur. In contrast to Harsch et al. (2009) who concluded that the role of disturbance during recent climate warming is restricted to determining *when* treeline advance will occur, this study shows that disturbance and its after-effects may equally well determine *if* treeline advance will occur at all.

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2.2 Tree-core from the oldest documented birch in the world

At one of the elevational treeline transects on the northern side of Lake Torneträsk (chapter 2.1), the uppermost birch individuals were very old. One monocormic birch stem of 4.6 m tall and a diameter at breast height of 21 cm was particularly old; the tree-core showed 252 distinct annual rings. The pith was hit and the central part of the stem was not rotten. Visual and statistical cross-dating of this ring width series with both the summer temperature record of the Abisko meteorological station and the local pine tree-ring chronology of Grudd et al. (2008) allowed for exact dating of this individual.



Figure 1. The oldest documented birch (*Betula* ssp.) stem in the world found at the sub-Arctic Swedish elevational treeline (N 68°26.984', E 18°53.361').

The tree-core was taken at a stem height of 20 cm and no locally missing rings nor missing outer rings occurred. This apparent high vitality of the tree was confirmed by the width of the two outermost annual rings, i.e. 2007 and 2008. These rings were wider than the mean ring width for the last 50 years, in concert with the positive June-July temperature anomalies of 1.2 °C and 0.4 °C (reference period 1959-2008) recorded for 2007 and 2008 respectively (Abisko Scientific Research Station meteorological record 1913-2009). Further, the individual had no dead branches.

Taken into account the core height and knowing the average time it takes for a monocormic birch tree to grow 20 cm tall at the treeline (4 to 8 years), this individual was presumably 258 years old in 2009 (establishment in the year 1751) with a minimum of 256 years and a maximum of *c.* 262 years. To our knowledge, this is the oldest birch stem ever cored.

Kullman claims to have cored a birch tree that was more than 500 years old (Kullman, 2005), but this was the added sum of one dead stem and another living stem that was not dated according to standard dendrochronological methods (i.e. extrapolation of mean ring width into the past for the inner rotten stem part; see Shigo, 1984).

This finding tells us more about the ecology of mountain birch and the birch species in general. Birch is known as a short-lived species and *Betula pubescens* rarely exceeds the age of 80 years in most of its distributional range (Jónsson, 2004; Forest Service Ireland, 2009), although at its distributional limit individuals of *c.* 200 years have been found (Sonesson and Hoogesteger, 1983).

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Chapter 3 Range expansion of thermophilic tree species in the sub-Arctic Torneträsk area

3.1 European aspen (*Populus tremula*)*

Abstract

In sub-Arctic Sweden, recent decadal colonization and expansion of aspen (*Populus tremula* L.) were recorded. Over the past 100 years, aspen became *c.* 16 times more abundant, mainly as a result of increased sexual regeneration. Moreover, aspen now reach tree-size (>2 m) at the alpine treeline, an ecotone that has been dominated by mountain birch (*Betula pubescens* ssp. *czerepanovii*) for at least the past 4000 years. We found that sexual regeneration in aspen probably occurred seven times or more within the last century. Whereas sexual regeneration occurred during moist years following a year with an exceptionally high June–July temperature, asexual regeneration was favoured by warm and dry summers. Disturbance to the birch forest by cyclic moth population outbreaks was critical in aspen establishment in the subalpine area. At the treeline, aspen colonization was less determined by these moth outbreaks, and was mainly restricted by summer temperature. If summer warming persists, aspen spread may continue in sub-Arctic Sweden, particularly at the treeline. However, changing disturbance regimes, future herbivore population dynamics and the responses of aspen's competitors birch and pine to a changing climate may result in different outcomes.

Introduction

High-latitude ecosystems are considered particularly vulnerable to amplified global climate change, and large vegetation shifts are expected (ACIA, 2005). However, sub-Arctic ecosystem responses to future climate change are likely to be complex both in space and time (Hofgaard, 1997; Chapin et al., 2004; Callaghan et al., 2005; Holtmeier and Broll, 2005; Sitch et al., 2008). Already, there is some evidence of complex changes such as contrasting treeline dynamics, counter-intuitive growth responses, and altered ecosystem processes in response to increased temperatures in high-latitude ecosystems (Myneni et al., 1997; Zhou et al., 2001; Lloyd and

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Fastie, 2002; Dalen and Hofgaard, 2005; Post et al., 2009). While many of the observed responses to increased temperatures show expected northern extensions of species ranges (e.g., Kullman, 2002; Tape et al., 2006), earlier phenology (e.g., Høye et al., 2007), and increased greenness (e.g., Myneni et al., 1997), several studies, both at high-latitude and alpine treeline areas, report long-term vegetation stability or homeostasis despite recent warming (Butler et al., 1994; Masek, 2001; Holtmeier et al., 2003; Payette, 2007; Van Bogaert et al., 2007, 2009) or experimental warming (Grime et al., 2008). Consequently, understanding the mechanisms behind changes in species' ranges remains one of the biggest ecological challenges to predicting changes in the future structure and function of ecosystems and the services they provide (Callaghan et al., 2005; Chapin et al., 2005). Studies that go beyond the plot scale and include high-resolution data of several decades to centuries are critical for a better understanding of recent and likely future vegetation shifts (Manier and Laven, 2002; Callaghan et al., 2002; Kulakowski et al., 2004; Holtmeier and Broll, 2005), but such studies are scarce (Holtmeier and Broll, 2005).

The range extensions of tree species are usually hampered by intense competition from those already established (Davis, 1987). Therefore, in the absence of disturbance, closed forest stands generally respond with time lags in the order of decades to centuries to changing climatic conditions (Wright, 1984; Davis, 1986; Von Holle et al., 2003). In contrast, the more open forests dominated by mountain birch (*Betula pubescens* Ehrh. ssp. *czerepanovii* (Orlova) Hämet-Ahti) in sub-Arctic Europe would be expected to be more susceptible to invasion by more thermophilic tree species in response to increasing temperatures. Although elevated CO₂ levels should be advantageous for slow-growing birch, responses to continued summer warming will probably dominate over responses to elevated CO₂ levels by stimulating the establishment and spread of fast-growing, more thermophilic tree species (Skre, 2001).

In this sub-Arctic forest ecosystem, disturbance to the local 'dominant' mountain birch has been found to be highly important in the competitive interaction with rarer thermophilic European aspen (*Populus tremula* L.) (Van Bogaert et al., 2009). Two insect herbivores, the autumnal moth (*Epirrita autumnata* Bkh.) and the winter moth (*Operophtera brumata* L.), naturally disturb the subalpine mountain birch forests by episodic mass defoliation events (Tenow et al., 2005). Both moth species are endemic to the mountain birch ecosystem and exhibit a population cycle of c. 9–11 years. Sometimes the population peaks reach outbreak densities resulting in a complete defoliation of the forest (Neuvonen et al., 2005; Tenow et al., 2005). The monocormic (i.e. single-stemmed) form usually dies after such outbreaks, whereas the polycormic (i.e. multi-stemmed) form in most cases recovers relatively quickly by producing new stems from the surviving below-ground organs (Tenow et al., 2005). Large-scale birch mortality occurs about

every 60 to 70 years resulting in a rejuvenation of the forest (Tenow et al., 2005). One control of the outbreaks is the temperature threshold of -36°C at which eggs are killed (Nilssen and Tenow, 1990). Currently increasing winter temperatures and climate projections for the area (Saelthun and Barkved, 2003) suggest that this threshold will be exceeded more frequently in the future and that birch forest damage may increase (Neuvonen et al., 2005; Wolf et al., 2008): there is recent evidence from northern Norway indicating that this process is already occurring (Hagen et al., 2007; Jepsen et al., 2008). Whereas in the past recovery of birch forest usually occurred or heath lands with extremely sparse trees were created, current climate change may open possibilities for invasion by other, more thermophilic, species such as aspen.

In contrast to most other birch forests in northwestern Europe, the Scandinavian mountain birch forest is a stable forest type and not a transient successional phase and dominates the higher subalpine forest belt in the Scandes Mountains (Carlsson et al., 1999; Kullman and Öberg, 2009). Mountain birch has rapidly colonised vast areas of sub-Arctic Fennoscandia since the last deglaciation about 10,000 years ago (Wielgolaski, 2005). During the early Holocene when summer temperatures and annual precipitation were markedly higher than today (Barnekow, 1999), aspen, co-existing with birch, was far more abundant (Seppä and Birks, 2001; Bigler et al., 2002; Heinrichs et al., 2005) and may locally have represented 25% of the forest area (J. H. H. Birks, personal communication). During the warm but drier mid-Holocene, birch and aspen were largely replaced by pine (*Pinus sylvestris* L.) that markedly expanded its range (Barnekow, 1999). About 4000 years ago, a drastic cooling occurred and mountain birch again became the dominant subalpine tree species in northern Fennoscandia (Barnekow, 1999). Projected future climate warming is therefore likely to facilitate the spread of more thermophilic species such as aspen and pine, although time lags and periods with co-existence of less thermophilic species such as birch, are likely to occur as in the past (Davis, 1986; Von Holle et al., 2003).

In northernmost Fennoscandia, as elsewhere in Europe, aspen is a rarer component species of the forest, rather than a woodland dominant (Worrell, 1995). Individuals may live for 200–250 years in these northern woodlands (Hedenäs and Ericson, 2008), theoretically allowing stand size reconstructions and dendrochronological analysis back to c. A.D. 1800. Aspen is not a likely treeline candidate, and although this helio- and thermophilic species can be found at the alpine birch treeline, it only occurs as a prostrate shrub seldom exceeding 1 m (Kullman, 1983). Aspen reproduces mostly asexually through the production of vegetative root suckers, and sexual regeneration is believed to be rare as it requires exacting moisture and seed bed conditions (e.g., Johansson, 2002; Latva-Karjanmaa et al., 2003). Establishment from seed is probably related to many local factors such as climate, disturbance events that control competition, herbivory, soil characteristics, barriers to pollination from scattered male and female stands, disease, etc. In

boreal Sweden there are concerns about aspen's longevity because its abundance has drastically declined since the 1950s as a result of logging, changed disturbance regimes, and an increasing moose population (Östlund et al., 1997). However, in aspen's northernmost range in the sub-Arctic, there are no records of recent changes in distribution or abundance.

When revisiting altitudinal transects in sub-Arctic Sweden established by Sonesson and Hoogesteger (1983) to determine decadal dynamics of the alpine birch treeline, previously unrecorded aspen was found. Consequently, a study was initiated to explore the generality of this apparent recent local geographical range expansion of aspen and its probable causes. Specifically, this paper aims to (i) document 20th century changes in European aspen's local geographical range and abundance in both the subalpine forest and alpine treeline area of sub-Arctic Sweden, and (ii) determine the probable mechanisms driving these dynamics in terms of recent changes in climate and species interactions such as herbivory and competition.

Methods

Study area

Lake Torneträsk is the seventh largest lake in Sweden with a surface area of 332 km², and is located at the eastern fringe of the sub-Arctic Scandes Mountains (68°25' N, 19°00' E) (Fig. 1). The lake level is situated at 341 m a.s.l. and forms the lowest point of the area, whereas the summits on the southwestern side of the lake reach up to 1750 m a.s.l. Extensive forests dominated by mountain birch cover about 1200 km² of the subalpine area equaling c. 25% of the Torneträsk catchment. The position of the alpine treeline varies around 650 m a.s.l. in the western part of the catchment where topography and suboceanic climate features quickly increase (Berglund et al., 1996). Trees of secondary importance in the area are aspen, pine (*Pinus sylvestris* L.), rowan (*Sorbus aucuparia* L.), willow (*Salix* ssp.), alder (*Alnus incana* (L.) Moench), and bird cherry (*Prunus padus* L.). On the northern side of the lake, study area N1 (Fig. 1b) was characterized by a southwest-facing slope with a mica-schist marble bedrock. The understory was a lush meadow in a predominantly monocormic birch forest. On the southern side of the lake, both study areas S1 and S2 had a polycormic birch forest on a southeast- (S1) and south- (S2) facing slope aspect. The understory of area S1 was meadow underlain by mica-schist amphibolite, whereas a heath underlain by hard schist characterized area S2.

The mean annual temperature for Abisko (388 m a.s.l.), located at the southwestern end of Lake Torneträsk (Fig. 1b), is -1.0 °C and mean January and July temperatures are -12.0 and +11.0 °C, respectively, for the normal period 1961-1990 (Alexandersson et al., 1991),

but climate has changed recently: i.e. the 0 °C mean annual temperature threshold has been crossed causing multiple cryogenic and ecological impacts (Callaghan et al., 2010). Days with a maximum temperature >25 °C are very exceptional at Abisko (Abisko Scientific Research Station daily climate records, 1913–2009) and possibly nonexistent at the treeline situated 300 m higher up.

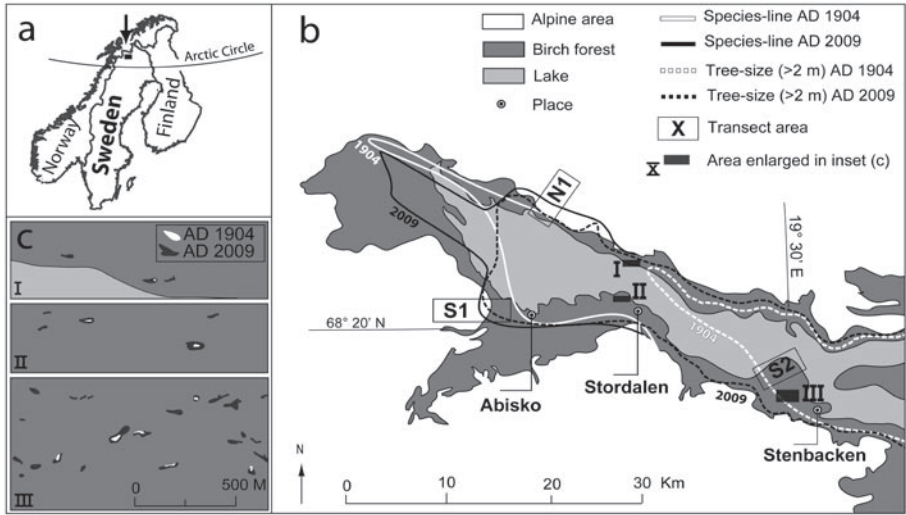


Figure 1. Study area in sub-Arctic Sweden (a) showing aspen dynamics since 1904 (b, c). The figure is based on the studies by Sylvén (1904) and Fries (1913) and dendrochronological analysis. Figure 1b shows the change in position of the western boundary of the species and tree-sized (>2 m) aspen over the period 1904–2009, whereas Figure 1c illustrates the process of infilling and expansion of established stands in the study area for the same period. Note that the distribution lines over the lake are simply to connect the distribution of aspen on the north and south sides of the lake.

Located in the rain shadow of Mount Njulla, the average annual precipitation for Abisko is low and amounts to 304 mm. However, local variation in precipitation is high; i.e. 10 km further north, on the northern shore of Lake Torneträsk, annual precipitation is 600 mm, whereas in Riksgränsen 30 km westwards, annual precipitation is 1000 mm (Alexandersson et al., 1991).

Historical data sources

The Torneträsk area has a rich history of botanical and phytogeographical research extending back to 1880 (Abisko Scientific Research Station library). However, only five studies were useful as they included direct measurements or photographs of the study area; i.e. Sylvén (1904), Fries (1913, 1925), Persson (1952), and Sonesson and Hoogesteger (1983). These studies were used to infer (i) the westernmost position of both aspen and tree-sized (>2 m) aspen, and (ii) the

abundance of aspen in the subalpine forest area and at the treeline.

Tree and stand sampling of aspen

(i) Local geographical range dynamics: recent shifts in the westernmost position of aspen

During the four consecutive field seasons of 2006–2009 the subalpine forest area of western Torneträsk, comprising a total land surface area of c. 450 km², was surveyed (Fig. 1b). Each autumn we climbed to the alpine area to survey the subalpine forest area when aspen leaf colour (bright yellow) highly contrasts with that of birch (orange-brown). Additionally, we used aerial photographs from 2004 to 2006 taken from a helicopter to map the aspen stands in the area. Any recent westward shift in the subalpine range of both aspen and tree-sized (>2 m) aspen individuals, inferred from our comparative study with Sylvén (1904), was verified by dendrochronological analysis. We determined the age of the oldest tree of current aspen stands in the old locations by coring the three thickest, oldest looking individuals at basal stem height (i.e. stem-root intersection) and at a height of 2 m, that conformed with a ‘tree’ identified by Sylvén (1904), with a standard increment corer. By counting the annual rings of these tree cores taken at two different stem heights we could determine the year in which the individual (i) had established and (ii) had reached tree-size (2 m), offering an extra verification of the position of the westernmost aspen and tree-sized aspen stand in 1904. A ‘stand’ was considered an isolated aggregation of aspen individuals in the birch forest; i.e. the distance to the nearest other aspen group was >100 m. The term ‘stand’ was preferred to ‘clone’ because no genetic analysis was performed as verification. The largest aspen stand covered an area of 1.9 ha, but usually the stands were much smaller with a mean size of 0.12 ha for the subalpine area and 0.03 ha near the alpine treeline. It needs to be noted that in most cases the coring at stem-root intersection was difficult and a small part of the upper soil layer needed to be temporarily removed.

(ii) Changes in aspen abundance

To study 20th century changes in aspen abundance in both the (i) subalpine and (ii) alpine treeline area, we randomly selected (i) 40 lowland stands (representing c. 5% of all subalpine aspen stands found in the area) and (ii) 15 treeline stands (representing c. 25% of all aspen stands found at the alpine treeline).

Changes in species abundance may occur via colonization, i.e. new stand establishment, or expansion of existing stands. To record recent aspen colonization, we cored the three oldest looking, usually thickest, individuals of each aspen stand at stem-root intersection to determine

the year of stand establishment by later counting of annual rings in the tree cores. If the oldest looking aspen was a dead individual, we took a sample disc at basal height. However, in 15 out of 55 cases, there were no individuals that were markedly thicker. For those stands, a minimum year of establishment was determined rather than an absolute one by sampling three of the

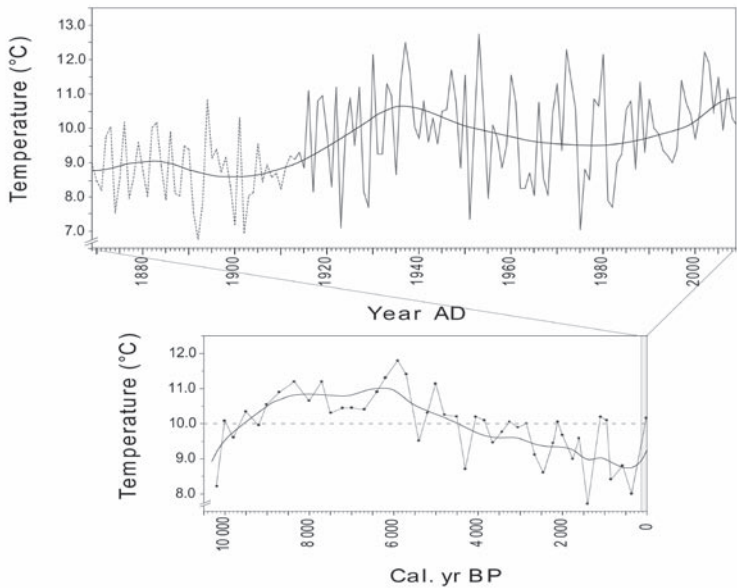


Figure 2. Summer temperature (June–July) trend with low-pass filter for the Torneträsk area since the deglaciation about 10,000 cal. yr BP (modified from Holmgren and Tjus, 1996; Grudd et al., 2002; Hammarlund et al., 2002). Note that the bottom graph shows low-frequency temperature variability. This implies that annual summer temperatures may both have been higher and lower than the values represented by the curve. Instrumental climate records in northernmost Sweden are available since 1869 as shown by the upper graph. The broken line (1869–1912) shows the temperature data extrapolated from four neighboring weather stations to extend the record of the Abisko Scientific Research Station (1913–2009, solid line). Mean June–July temperature for the current period 1913–2009 is shown by the horizontal broken line in the bottom figure.

thickest individuals. In 16 other cases, either the pith was not hit or the center was rotten, making it impossible to identify the exact year of establishment by tree-ring analysis. It should be noted that the individual tree-ring series were not cross-dated adding to the uncertainty of the determination of the exact year of establishment, although the use of pointer years (Schweingruber et al., 1990), abundantly available in highly temperature responsive aspen (Van Bogaert et al., 2009), should have minimized the risk of erroneous dating. Overall, the year of stand establishment could only be determined with high probability for 24 stands. However, for 18 other stands (totaling 42 stands: i.e. 30 subalpine and 12 alpine) the year of establishment

could be classified within one of the following climatic periods: before 1911 (i.e. during the ‘Little Ice Age’), during the 40-yr period 1911–1950 in which mean temperature increased, during the 40-yr period 1951–1990 in which mean temperature decreased, and during the period 1991–2009 characterized by recent warming (see Fig. 2).

To estimate stand expansion rates of aspen we measured basal circumference (BC) of all aspen individuals within a stand and then calculated the land surface areas covered by individuals of a particular BC-class: i.e. age-class (see below). Besides the three thickest aspen individuals that were already sampled per stand (the mean number of individuals per stand was 63), two additional individuals were randomly sampled per stand (i.e. totaling 110 additional aspen individuals) for subsequent age determination to ensure sampling of a wide range of BC-classes to increase the accuracy of the relationship between BC and tree age. Because browsing affects the radial growth rate of a tree, we visibly classified all aspen individuals into browsed and non-browsed so that subsequent analyses using age and BC could be more accurately determined. Regression analysis was used to convert BC’s into age in years. The five individuals sampled in each of the 55 stands were classified into four groups: subalpine browsed, subalpine non-browsed, alpine treeline browsed, and alpine treeline non-browsed. A

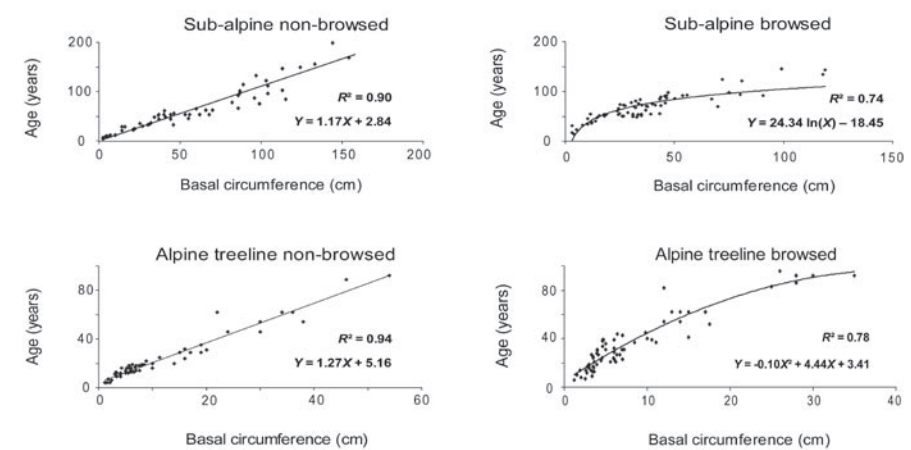


Figure 3. Scatterplot of age versus basal circumference (BC) for the four classes of aspen. Trend lines with equations and R^2 values are plotted. These regressions were used to convert BC into age for all other aspen individuals within the sampled stand. Note that the scaling of the X- and Y-axes varies between the different plots.

significant relationship was found between BC (X) and age (Y) for both subalpine browsed ($Y = 24.34 \ln(X) - 18.45$; $R^2 = 0.74$, $P = 0.05$, $n = 67$) and non-browsed ($Y = 1.17X + 2.84$; $R^2 = 0.90$, $P < 0.01$, $n = 60$). For the aspen individuals growing at the alpine treeline, a slightly different relationship was found for browsed ($Y = -0.10X^2 + 4.44X + 3.41$) and non-browsed ($Y = 1.27X + 5.16$) individuals, but correlation values were similar ($R^2 = 0.78$, $P = 0.04$, $n = 69$, and $R^2 = 0.94$, $P < 0.01$, $n = 58$, respectively). These four regression functions were used to estimate the age of all other aspen individuals in the stands. Even though the BC-age relationships were strong (Fig. 3), likely errors in stand expansion calculations resulting from the use of the regression functions were minimized by grouping the aspen individuals in large BC-classes. We grouped the individuals in four BC-classes corresponding to the earlier stand establishment analysis: i.e. the BC-class corresponding to individuals that established (i) before 1911, (ii) in the period 1911–1950, (iii) in the period 1951–1990, and (iv) in the period 1991–2009. By walking the boundaries of the (preferably non-browsed) aspen individuals of a particular BC-class, and marking a GPS-point every 8 m, we could estimate the stand expansion rates for the three periods. The GPS instrument was a Garmin GPSMap 60 CSx with an aneroid altimeter. The altimeter was regularly calibrated at points with known elevation. Surface areas were calculated using the software ArcGIS 9.0 (ESRI Inc., Redlands, California, 2005).

(iii) Aspen occurrence in relation to the size and mortality of its competitor birch

Three altitudinal transects on the northern side of Lake Torneträsk (area N1) recorded by Sonesson and Hoogesteger (1983) were revisited to determine recent altitudinal aspen (and birch, not presented in this study) spread and its possible causes. The middle altitudinal belt of the predominantly monocormic birch forest in area N1 had usually been disturbed by a winter moth (*Operophtera brumata* L.) outbreak in 1964–1965 that killed the majority of the birch trees, and little or no recovery has occurred since (Tenow et al., 2005). To increase sampling of possible spatial variation, four additional transects were randomly selected in the disturbed landscape to document aspen's recent establishment and spread.

On the southern side of Lake Torneträsk, three altitudinal transects were set up at random in two areas where aspen were found near the alpine birch treeline (S1 and S2; see Fig. 1b). Note that all transects were constrained by having aspen present, as the major objective of the study was to characterize aspen establishment and spread rather than to quantify the abundance of aspen relative to birch. Although the predominantly polycormic birch forest in areas S1 and S2 visibly appeared to be free from recent disturbance, both historical reports

and dendrochronological analysis showed that three outbreaks by the moth *E. autumnata* had disturbed most of these subalpine birch forest areas in the past 60 years (Eckstein et al., 1991; Tenow et al., 2005; Van Bogaert et al., 2009).

The total of 10 transects started from the lake level (341 m a.s.l.) and reached up to the tree species' line (c. 700 m a.s.l.). Each transect was 3 m wide and on average 1200 m long, the first 600 m usually being flat terrain. To study a potential relationship between the occurrence of aspen and the size and mortality of its competitor birch, four tree classes were counted within each transect for every 40 altitudinal meters: the number of aspen, birches <5 m, birches >5 m, and dead birches. Five meters was set as a threshold as mountain birches of this size usually indicate adult individuals with a full-grown canopy (Carlsson et al., 1999) that may affect competition with heliophilic (light demanding) aspen (Worrell, 1995). Any correlation between aspen density and these three categories of birch density was tested using Pearson correlation coefficients. The means of the aspen and birch densities for particular elevations were calculated for the transects on the northern side of the lake representing an open disturbed monocormic birch forest area. These were compared with the means derived from the transects on the southern side of the lake where recent disturbance was masked by rapid polycormic birch recovery. The weighted mean of the northern and southern side of the lake was considered the overall mean of the Torneträsk area.

Sexual regeneration, climate, and disturbance

It was assumed that the oldest individual in an aspen stand had arisen through sexual recruitment since the nearest other group of aspen was >100 m away. This distance was initially determined by our definition of a *stand*, and is a distance that is very unlikely to be bridged by an asexually regenerated root sucker (Schier et al., 1985; Jobling, 1990). We further assumed that the trees within the aspen stand had spread via asexual reproduction, i.e. root suckering (Schier et al., 1985). Three out of the 24 stands for which the probable year of establishment could be identified were not retained for the study of the controlling factors on aspen sexual regeneration as these stands were all found more than 10 km away from the Abisko Meteorological Station (i.e. outside the Abisko Valley) where both climatic and forest disturbance patterns are likely to be very different (Sonesson and Hoogesteger, 1983; Tenow et al., 2005). To relate events of assumed sexual regeneration to climate, anomalies rather than absolute values of the climate variables were used in the regression analysis because local variability in precipitation and temperature is expected to be substantial in a mountainous area.

To identify if years of extensive moth damage to birch (aspen's competitor) were related to years of aspen establishment, correlations were made between the annual index of moth damage to birch and the annual number of aspen recruits. The annual index of moth damage to birch was represented by a birch-minus-pine tree-ring chronology. This established method has proven to be successful to reveal moth outbreaks on birch (Eckstein et al., 1991; Van Bogaert et al., 2009). Because pine is not a host tree for the moth caterpillars and its growth is mainly influenced by summer temperature, the subtraction of the normalized pine ring width indices from those of birch should largely eliminate ring width variance due to climate and hence show reduced birch growth rather caused by disturbance such as defoliation by caterpillar attacks (Eckstein et al., 1991). To produce this birch-minus-pine chronology, 30 monocormic birch and 30 non-browsed pine trees (Fig. 4) located within 2 km distance of the Abisko Meteorological Station were cored according to standard methods (e.g., Fritts, 1976). Multiple regression analysis with forward selection was used to test which climatic and biotic variables best explained the annual variance in the number of aspen stands assumed to have been established from seed.

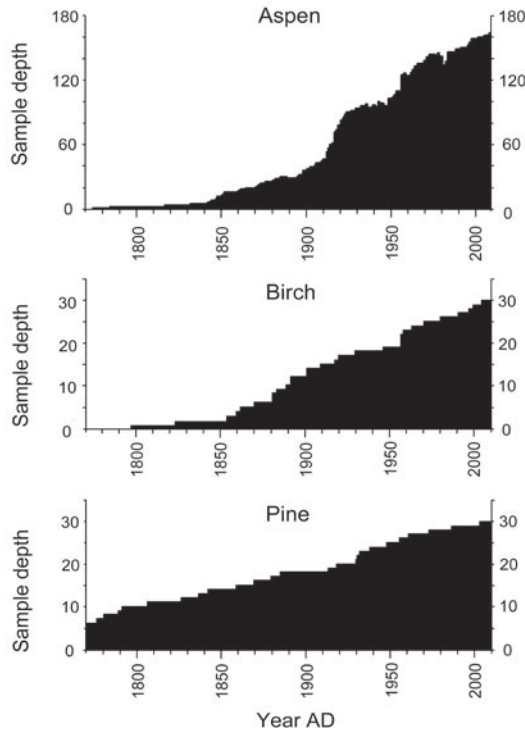


Figure 4. Bar chart of sample depth over time of the sampled tree species. The oldest pine individual that was sampled had established in the year A.D. 1638. Note that the scale of the Y-axes varies between the different plots.

Similar analyses were made for the 110 randomly sampled individuals in the aspen stands that were assumed to have arisen by vegetative root suckering. Although aspen stands in

Table 1. Establishment, expansion, and herbivory features of aspen in the Torneträsk area, sub-Arctic Sweden. Aspen stands in both the sub-alpine birch forest area ($n = 40$) and at the treeline ($n = 15$) have been studied. Establishment and expansion were analyzed for four climatic periods: before 1911 (i.e. during the Little Ice Age), 1911–1950 (i.e. a 40-yr period during which mean temperature increased), 1951–1990 (i.e. a 40-yr period during which mean temperature decreased), and the period 1991–2009 characterized by recent warming (Fig. 6). Standard errors are indicated. Stands that had perished, such as the aspen stand observed in 1904 near the treeline in the northwestern part of the study area (Table 1), were also included. ¹Establishment periods could only be identified for 30 sub-alpine and 12 treeline stands. Used abbreviations: LIA = Little Ice Age; W = a relatively warmer period; C = a relatively cooler period.

	Subalpine ($n = 40$) ¹ (341–500 m a.s.l.)	Alpine treeline ($n = 15$) ¹ (600–700 m a.s.l.)	Total ($n = 55$) ¹ (341–700 m a.s.l.)
ESTABLISHMENT:			
Stands established:			
Before 1911 (LIA)	4 (13%)	1 (9%)	5 (12%)
Period 1911–1950 (W)	10 (33%)	4 (33%)	14 (33%)
Period 1951–1990 (C)	15 (50%)	4 (33%)	24 (45%)
Period 1991–2009 (W)	1 (3%)	3 (25%)	4 (10%)
EXPANSION:			
Land surface area (ha) covered with aspen individuals established:			
Before 1911 (LIA)	0.29 ± 0.02 (6%)	0.03 ± 0.01 (7%)	0.32 ± 0.02 (6%)
Period 1911–1950 (W)	1.30 ± 0.03 (27%)	0.08 ± 0.01 (18%)	1.38 ± 0.02 (26%)
Period 1951–1990 (C)	2.38 ± 0.03 (49%)	0.13 ± 0.01 (30%)	2.51 ± 0.02 (47%)
Period 1991–2009 (W)	0.93 ± 0.03 (19%)	0.20 ± 0.01 (45%)	1.13 ± 0.02 (21%)
Total aspen area in 2009	4.90 ± 0.03 (100%)	0.44 ± 0.01 (100%)	5.34 ± 0.02 (100%)
Mean stand size	0.12 ± 0.27	0.03 ± 0.03	0.09 ± 0.21
BROWSING:			
Individuals browsed per stand:			
Mean	152 ± 42 (16%)	110 ± 32 (76%)	141 ± 36 (24%)
Abisko	1350 ± 152 (61%)	71 ± 22 (66%)	1011 ± 132 (62%)
Stenbacken	62 ± 22 (8%)	33 ± 24 (38%)	54 ± 22 (10%)
Nord side of Lake Torneträsk	70 ± 24 (8%)	278 ± 41 (86%)	350 ± 52 (17%)

¹Establishment periods could only be identified for 30 subalpine and 12 treeline stands.

Fennoscandia are believed to recruit mainly asexually (Latva-Karjanmaa et al., 2003), the potential error by including seedlings could be reduced by eliminating those individuals that had established during years for which sexual regeneration was identified. Also, the youngest (<10 years) aspen were excluded from the analysis so as not to bias the recruitment results because self-thinning was likely still important (Schier et al., 1985; Worrell, 1995). All statistical analyses were performed using the software package SPSS version 15.0 (SPSS Inc., Chicago, Illinois, 2006).

Table 2. Historical and current aspen locations in the Torneträsk area, sub-Arctic Sweden, denoted in Fig. 1.

Study	Area	Historical aspen occurrence	Present aspen occurrence
Sylvén (1904)	North and south side of Lake Torneträsk	10- to 20-cm-tall clonal aspen individuals found at NW border of Torneträsk's birch forest at 560 m a.s.l. (i.e. near the alpine treeline) in 1904.	Perished, no tall aspen found. However, within 2 km distance, three new stands (<20 years) had established.
		Western limit of tree-sized (>2 m) aspen situated near Stenbacken with the tallest individuals measuring 3 m, although most are 1.0–1.5 m tall. At Abisko, tallest aspen measure 0.5 m.	Western boundary of tree-sized (>2 m) aspen moved 30 km westwards (see Fig. 1b). At Stenbacken: >100 aspen stands (c. +20 ha) with trees >10 m. At Abisko: 23 new stands (c. +4.0 ha) with aspen trees up to 13 m.
Fries (1913)	Whole Torneträsk subalpine forest and treeline area	Fries noted: "A rare species that only occurs in tree-form at low elevation."	On the north side of the lake, an aspen stand with 24 individuals up to 7 m tall was found at the alpine birch treeline. Also in areas S1 and S2 seven aspen >2 m were found at the treeline.
Fries (1925)	Area S1: alpine treeline	No aspen observed. Fries went to area S1 about 150 times in the period 1914–1925.	Sixteen aspen stands (c. 0.7 ha) were recorded totaling >1000 individuals; the oldest stand had established in 1948; 90% of the individuals were <20 years old.
Persson (1952)	North side of Lake Torneträsk (including area N1)	No aspen observed at the alpine treeline.	Both tree-sized (up to 7 m tall) and small (over 50,000 individuals 0.1–2.0 m tall) individuals were found.
Sonesson and Hoogesteger (1983)	North (area N1) and south side of Lake Torneträsk	No aspen recorded within any of the three altitudinal transects in 1977.	In 2008, aspen was found within two of the three transects: 24 and 511 individuals, respectively. The individuals had established up to 40 m above the birch treeline. Over 75% of the aspen were <20 years old.

Results

Aspen were found to have become 16 times more abundant in 2009 compared to 1904 in both the subalpine forest (4.90 vs. 0.29 ha) and treeline area (0.44 vs. 0.03 ha) (Table 1). In 1904, the limit of tree-sized (>2 m) aspen, denoted by ring counts of the tree-cores taken at 2m stem height, was found further to the southeast than at present (Fig. 1b). On the northern side of the lake, the boundary has moved 15 km northwestwards, while this shift amounted to nearly 30 km for the southern side. By determining the age of the aspen trees cored at basal height, it was found that the species-line of aspen had been only slightly displaced: it moved about 4 km northwestwards on the southern side of the lake by the establishment of 23 new aspen stands, and had moved about 5 km southwards on the northern side of the lake by the establishment of 3 new stands (Fig. 1b, Table 2). Elsewhere, infilling and expansion of already established aspen stands has been important (Fig. 1c, Table 1). Aspen stands located in the devastated monocormic birch forest on the northern side of the lake were significantly larger than those in the polycormic birch forest (0.14 vs. 0.05 ha, respectively; $P = 0.04$) on the southern side of the lake that had recovered quickly from moth damage. Fifty-four out of the 55 aspen stands were found on a southeast- to southwest-facing slope or ridge.

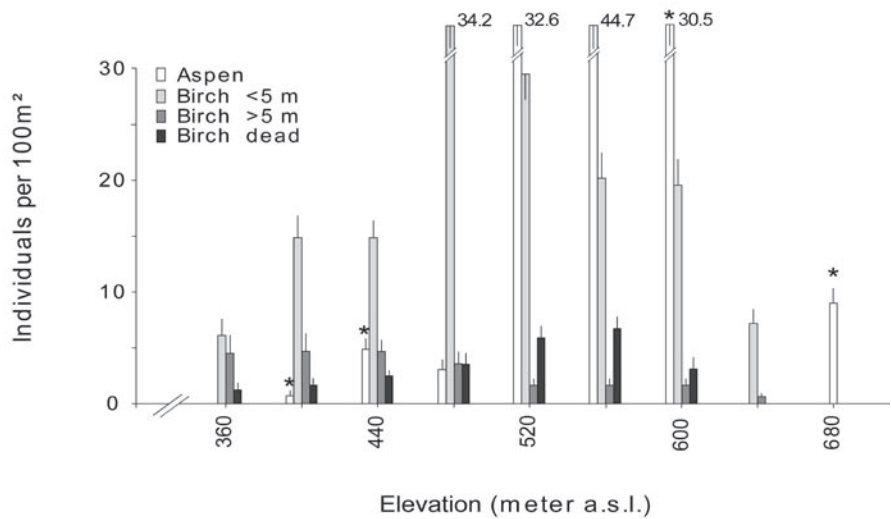


Figure 5. Aspen and birch densities with standard errors along an altitudinal transect in area N1 that experienced a severe moth outbreak in 1964–1965. This transect clearly shows the high abundance of aspen in the disturbed (i.e. high density of dead trees) and still unrecovered monocormic birch forest area. Note, however, that aspen was not restricted to the disturbed area, but also successfully colonised the treeline area. Elevational transects that contained tree-sized (>2 m) aspen individuals are marked with an asterisk.

Whereas in the early 20th century tree-sized (>2 m) aspen stands could only be found in the lower subalpine forest area (Table 2), at present 24 trees up to 7 m tall can be found at the alpine birch treeline at 640 m a.s.l. on the northern side of the lake representing a range expansion of tree-sized aspen by 180 m in elevation or c. 300 m in actual distance (Table 2, Fig. 5)

Seven tree-sized individuals were found at the alpine treeline on the southern side of the lake in areas S1 (up to 2.5 m) and S2 (up to 5.7 m) (Table 2). More than 50,000 smaller (<2 m) individuals were found up to 40 m above the alpine birch treeline in area N1 (Table 2) where aspen densities were usually much higher than those of birch (Fig. 5). Dendrochronological analysis showed that aspen establishment at the treeline increased over the 20th century; i.e. 11 out of 12 stands established after 1910 and 3 out of 12 in the most recent period 1991–2009 (Table 1). In the subalpine forest area, aspen stand establishment also predominantly occurred after 1910 (i.e. 26 out of 30 stands), but establishment in the most recent period was low (i.e. 1 out of 30 stands) (Table 1).

Stand establishment and environmental covariates

A detailed analysis of 21 aspen stands suggested that tree establishment, assumed from seed, took place in years following a year with a high June–July temperature (Table 3a). This parameter explained 32% (using R^2) of the variance in annual numbers of aspen stands established in the subalpine birch forest, while 43% of the variance was explained for the alpine treeline (Table 3b). Annual precipitation anomalies were positively correlated with annual seedling establishment numbers both in the subalpine birch forest and at the treeline, and when adding this parameter R^2 significantly ($P = 0.02$) increased to 46% in the subalpine areas and to 50% at the treeline (Table 3b).

Apart from climatic variables, disturbance to birch (i.e. predominantly moth damage) was also significantly correlated ($r = 0.54$, $P = 0.02$) with the annual variance in assumed seedling establishment of aspen in the subalpine birch forest; i.e. it increased the proportion of explained variance to 69% (Table 3b). This was confirmed by the correlation between aspen and birch densities (Figs. 5 and 6). The four transects on the northern side of the lake that contained subalpine aspen found in an area of birch forest recently disturbed and opened (N1a, N1b, N1e, and N1g), all resulted in a significant correlation between aspen and dead birch density (Fig. 6). Moreover, an overall significantly ($P = 0.04$) negative correlation was found between aspen and tall birch (>5 m) densities (Fig. 6).

Table 3a. Assumed sexual regeneration events in aspen related to climatic and biotic factors for the period 1913-2008. The annual number of stands (total $n = 21$) assumed to have established from seed was related to: (1) summer temperature of the year preceding germination, possibly affecting seed set (mean = 10.0 °C, SE = 0.14); (2) annual precipitation of the current year, possibly affecting germination and seedling survival (mean = 314 mm, SE = 5.99); (3) moth damage to birch during the year of germination, possibly affecting aspen seed bed availability and seedling survival; high positive values point to increased damage (mean = -0.03 birch-minus-pine indices, SE = 0.03). Values that significantly ($P < .05$) differed from the mean are marked with an asterix.

Year	Number of aspen stands established	(1) June–July temperature anomaly of previous year (°C)	(2) Annual precipitation anomaly of current year (mm)	(3) Moth damage anomaly to birch of current year (negative birch-minus-pine indices)
SUBALPINE (340–500 m a.s.l.)				
1919	3	+1.1	+19	+0.66*
1948	3	+1.7	+18	+0.40
1954	7	+2.8*	+32	+0.85*
1961	1	+1.6	+37	–0.01
1973	1	+2.3*	+42	+0.02
2003	1	+2.2*	+81	+0.42
TREELINE (600–700 m a.s.l.)				
1938	2	+2.5*	+45	–0.73*
1948	1	+1.7	+18	+0.40
1973	2	+2.3*	+42	+0.02

Table 3b. Sexual regeneration covariates. Variables that significantly ($P < .05$) explained the annual variance in aspen stands established using forward selection in the regression analysis are given. For both sub-alpine and treeline stands, the cumulative proportion of explained variance (R^2) after adding variable 1 to 3 is shown in the third column. Variables significantly ($P < .05$) correlated with the annual number of aspen stands established are marked with an asterix.

Variable	Elevation	R^2 (variance explained)	Correlation (Spearman's r)	P
(1) June–July temperature anomaly of year preceding germination	Subalpine:	32%	0.459*	<0.001
	Treeline:	43%	0.523*	0.048
(2) Annual precipitation anomaly of year of germination	Subalpine:	46%	0.223*	0.049
	Treeline:	50%	0.281*	0.043
(3) Moth damage to birch, i.e. negative birch-minus-pine ring width index anomaly of year of germination	Subalpine:	69%	0.537*	0.021
	Treeline:	50%	0.033	0.749

In contrast, no effect of disturbance to birch on sexual establishment of aspen at the alpine treeline was seen (Table 3b). Additionally, the transects N1c, N1d, and S1 that only included high-altitudinal aspen showed that aspen density at the treeline was not correlated with the density of dead birch individuals (Fig. 6).

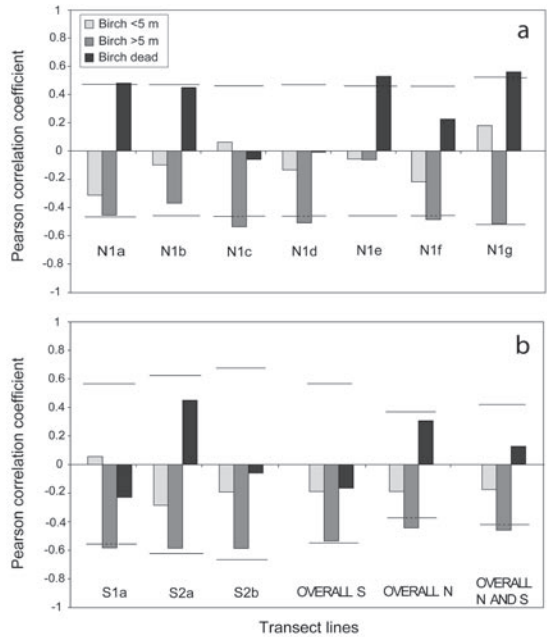


Figure 6. Pearson correlation coefficients quantifying relationships between aspen density and density of three birch classes; i.e. small birches (<5 m), tall birches (>5 m), and dead birches. Part (a) shows the seven altitudinal transects on the northern side of the lake (area N1 in Fig. 1b), and (b) those on the southern side (area S1 and S2 in Fig. 1b) and the means (overall south, overall north, and overall north and south). Significance limits at the $P \leq 0.05$ level are shown by the horizontal lines.

Stand expansion and environmental covariates

Asexual aspen regeneration at the treeline was also positively ($r = 0.67$, $P < 0.001$) affected by a high June–July temperature, explaining 49% of the variance in the annual number of trees assumed to have arisen by asexual reproduction (Table 4b). No such effect was seen for the lower, subalpine aspen. Low precipitation values for June and July were favourable for asexual reproduction, i.e. R^2 was 34% for subalpine and 59% for treeline aspen. Including disturbance

to birch (i.e. moth damage) in the regression significantly ($P = 0.02$) increased R^2 to 68% for subalpine aspen, but did not explain more of the variance in annual asexual recruitment at the treeline (Table 4b). Other monthly temperature and precipitation data were also tested, but neither increased the explained variance in assumed annual seedling establishment numbers nor assumed asexual tree reproduction numbers.

Table 4a. Assumed asexual regeneration numbers in aspen related to climatic and biotic factors for the period 1913–2008. The annual number of trees (total $n = 160$) assumed to have arisen by asexual regeneration was related to: (1) summer temperature (mean = 10.0°C, SE = 0.14); (2) summer precipitation (mean = 84 mm, SE = 3.46); (3) moth damage to birch, possibly affecting aspen asexual reproduction and survival; high positive values point to increased damage (mean = -0.03 birch-minus-pine indices, SE = 0.03). Values that significantly ($P < .05$) differed from the mean are marked with an asterix.

Year	Number of asexually produced aspen	(1) June–July temperature anomaly (°C)	(2) June–July precipitation anomaly (mm)	(3) Moth damage anomaly to birch (negative birch- minus-pine indices)
SUBALPINE (340–500 m a.s.l.)				
1916	6	+1.1	–30	+0.63*
1918	5	+0.8	–4	+0.58*
1945	4	+0.5	–25	+0.37
1950	2	+1.6	–27	–0.46
1955	6	–2.0	–62*	+0.77*
1957	6	+0.4	–37	+0.48
1959	4	–0.5	–23	+0.31
1960	5	+1.6	–3	+0.25
1985	2	+0.6	–9	+0.11
1988	3	+1.4	–48	–0.16
TREELINE (600– 700 m a.s.l.)				
1950	3	+1.6	–27	–0.46
1953	4	+2.8*	–24	–0.34
1960	4	+1.6	–3	+0.25
1972	4	+2.3*	–18	+0.05
1980	4	+2.2*	+3	–0.08
1985	4	+0.6	–9	+0.11
1986	5	+0.8	–39	+0.22
1988	6	+1.4	–25	–0.16
1996	3	–0.6	–15	–0.22
1997	5	+1.4	–32	–0.27

Table 4b. Asexual regeneration covariates. Variables that significantly ($P < .05$) explained the variance in annual number of assumed asexually produced aspen trees using forward selection in the regression analysis are given. For both sub-alpine and treeline stands, the cumulative proportion of explained variance (R^2) after adding variable 1 to 3 is shown in the third column. Variables significantly ($P < .05$) correlated with the annual numbers of aspen stands established are marked with an asterix.

Variable	Elevation	R^2 (variance explained)	Correlation (Spearman's r)	P
(1) June–July temperature anomaly of year preceding germination	Subalpine	0%	0.229	0.209
	Treeline	49%	0.667*	< 0.001
(2) June–July precipitation anomaly of year of germination	Subalpine	34%	−0.467*	0.008
	Treeline	59%	−0.330*	0.037
(3) Moth damage to birch, i.e. negative birch-minus-pine ring width index anomaly of year of germination	Subalpine	68%	0.520*	0.032
	Treeline	59%	0.096	0.350

At the treeline, aspen expansion was high in the most recent, warmer, period of 1991–2009: i.e. 45% of aspen’s current land surface area was colonised during this period (Table 1). In contrast, recent aspen expansion in the subalpine birch forest was relatively small: i.e. the same figure only amounted to 19% (Table 1). Browsing damage, predominantly caused by moose (*Alces alces* L.) and in second degree by snow hare (*Lepus timidus* L.), was high at the treeline with 76% of the individuals browsed. The proportion of browsed individuals was lower in the subalpine forest area, although local variation was high (Table 1).

Discussion

Aspen became 16 times more abundant in the Swedish sub-Arctic compared to the early 20th century, both at the alpine treeline and in the subalpine birch forest area (Table 2). Changes in the local geographical range of aspen were also seen on the northern side of Lake Torneträsk, where aspen had advanced 5 km southwards compared to 1904, and on the southern side of the lake where the westward advance amounted to 4 km (Fig. 1b). The 5 km advance on the northern side of the lake was accomplished by the establishment of 3 new aspen stands, whereas the 4 km advance on the southern side resulted from the establishment of 23 new stands. Although we investigated our extensive study area with the greatest detail, we cannot exclude that we overlooked some aspen stands that may bias the position of the western boundaries of current (2009) and historical (1904) distribution of aspen and tree-sized (>2 m). However, the uniform pattern that was observed of increasing abundance and range expansion of this tree species, is unlikely to be reversed by such potential bias.

Not only have aspen stands expanded, 31 tree-sized (>2 m) aspen individuals can now be found at the alpine treeline indicating a recent shift in the nature of the previously ubiquitous birch treeline. The establishment of tree-sized aspen at the treeline is a new phenomenon in the European sub-Arctic. Although there are many studies reporting changes in the locations of the northern alpine and latitudinal treeline (e.g., Lloyd and Fastie, 2003; Kharuk et al., 2006; Danby and Hik, 2007; Shiyatov et al., 2007; Kullman and Öberg, 2009), and densification of the subalpine forest (e.g., Myneni et al., 1997; Tømmervik et al., 2004; Danby and Hik, 2007), we have found none that provide such compelling evidence of changes in vegetation composition and structure. It can be argued that browsing pressure rather than temperature has previously prevented aspen from reaching tree-size at the treeline (Worrell, 1995). However, this does not explain why aspen individuals have developed to tree-size during a period of significant summer warming (Fig. 2) while its main browser in the area, moose, exponentially increased in population numbers (Sonesson, 1970; Sylvé, 2003; Van Bogaert et al., 2009).



Figure 7. Both sexual and asexual regeneration in subalpine aspen were facilitated by moth disturbance to the birch forest. Here, a young and fast-growing aspen individual can be seen in the vicinity of some dead birch stumps in an open, formerly forested landscape. A severe outbreak by the winter moth (*O. brumata*) during 1964–1965 killed the majority of the monocormic birch trees in this forest area and little or no recovery has occurred since that time. Ongoing aspen dynamics will likely be determined by future frequencies and scales of such events. Photo: area N1, northern side of Lake Torneträsk, sub-Arctic Sweden, 1 September 2007.

The increase in aspen abundance over the 20th century was mainly attributed to colonization of new areas, rather than to the spread of already established aspen stands (Fig. 1c). These new stands were scattered over the study area and had most likely established from seed as they were separated by distances (>100 m) unlikely to be bridged by asexually regenerated root suckers (Schier et al., 1985; Jobling, 1990) (Fig. 1c). Also the mean size of the stands (i.e. 0.09 ha; Table 2) suggested that asexual regeneration was fairly limited, further supporting the view that the infilling and expansion of aspen was mainly attributed to an increase in sexual regeneration. Establishment from seed, as defined by our assumptions, occurred at least seven times during the last 100 years (Table 3a). This degree of sexual regeneration is remarkable because establishment from seed is generally perceived to be very rare (e.g., McDonough, 1985; Kay, 1993; Worrell, 1995; Romme et al., 1997), mainly because of the exacting microclimatic requirements for both germination and seedling survival (McDonough, 1985; Worrell, 1995; Latva-Karjanmaa et al., 2003). Although the frequency of sexual regeneration may be underestimated as suggested by a recent genetic study on European aspen (Suvanto and Latva-Karjanmaa, 2005), widespread sexual regeneration may not have occurred since the early Holocene (10,000–7000 cal. yr BP) when seed set was fairly common in northernmost Fennoscandia (Seppä, 1998; Seppä and Birks, 2001; Bigler et al., 2002; Heinrichs et al., 2005). Therefore, the presumably recent increase in sexual regeneration in aspen's northernmost biome is a noteworthy finding in the light of a potential revival of the tree species (Green and Noakes, 1995). This situation contrasts greatly with boreal Fennoscandia where aspen abundance has declined over the past 60 years mainly as a consequence of the lack of disturbance and changed forestry practices (Östlund et al., 1997).

The presumed increase in sexual regeneration could also have been initiated by a change in the disturbance regime to aspen's competitor, mountain birch. However, the cyclicity and long-term impact of moth damage to the birch forest (i.e. the main disturbance agent in this ecosystem) have so far remained unchanged in our study area; moth population peaks are still observed about every 10 years with high-impact outbreaks every 60 to 70 years (Karlsson et al., 2004; Tenow et al., 2005). Consequently, 20th century warming (Fig. 2) has probably been the main driving force for the observed structural change in the subalpine birch forest: i.e. the increasing abundance, growth, and range expansion of a more thermophilic tree species. The importance of temperature for the functional processes of regeneration in aspen, assuming that the oldest individual of an isolated aspen stand was a seedling and that its neighboring individuals had established through asexual root suckering, was demonstrated by dendrochronological analysis. We found that a high June–July temperature in the previous year significantly explained the variance in annual germination success (Tables 3a and 3b; $P < 0.05$ for both subalpine and

treeline aspen), suggesting that a warm summer promotes seed set in the following year. This finding is supported by other studies from northern areas that showed that seed set in aspen is restricted by summer temperature (Børset, 1960; Kullman, 1983; Worrell et al., 1999). The critical role of temperature in aspen establishment and persistence was also confirmed by its current niche; the aspen stands were almost exclusively found on southeast- to southwest-facing ridges and slope aspects, similarly to the findings of Elliott and Baker (2004) on closely related quaking aspen at the treeline in the San Juan Mountains of Colorado, U.S.A. On the other hand, high temperatures ($>25^{\circ}\text{C}$) sharply lower germination rates in aspen, analogous to low temperatures ($<5^{\circ}\text{C}$) (McDonough, 1985). Whereas numerous studies on quaking aspen in the United States recorded sexual regeneration almost exclusively in cooler years (e.g., McDonough, 1985; Kay, 1993; Romme et al., 1997; Elliott and Baker, 2004), we did not find a negative correlation between annual germination success and summer temperature of the actual year of germination. In contrast, at the alpine treeline, we found a positive correlation between the annual germination number and June temperature (i.e. the month when budburst occurs and germination is expected to take place) ($r = 0.44$, $P = 0.07$). Although June temperature did not significantly increase R^2 , this finding suggests that in the Swedish sub-Arctic failure of seedling establishment due to too low temperatures may be at least as important as failure due to too high temperatures. Because summers are always fairly cool in our high-latitude suboceanic study area (cfr. *Study area*), the risk of germination failure and seedling mortality due to too high temperatures is most likely substantially smaller than in the United States where a warmer and more continental climate confines sexual regeneration to relatively cool summers. Precipitation had a significant ($P = 0.02$) positive effect on aspen germination both at the treeline and in the lower subalpine forest (Tables 3a and 3b), indicating that a sufficient moisture supply is essential for successful seedling establishment (e.g., McDonough, 1985; Worrell, 1995; Latva-Karjanmaa et al., 2003). In contrast to sexual regeneration, asexual regeneration was promoted by dry weather conditions that, if coinciding with high summer temperatures, greatly stimulated root sucker production (Tables 4a and 4b), agreeing with previous studies on quaking aspen (Schier et al., 1985; Elliott and Baker, 2004).

However, if summer warming was the main driver for recent aspen expansion, why was establishment and expansion of subalpine aspen relatively more pronounced during the cooler period of 1951–1990 than during the most recent warming of 1991–2009 (i.e. 6 vs. 2 aspen stands established per decade and 0.63 vs 0.59 ha stand expansion per decade; cfr. Table 1)? We identify two factors that most likely contributed to this finding: (i) the importance of inter-annual temperature variability, and (ii) the occurrence of disturbance to its competitor birch.

Although mean summer temperature decreased over the period 1951–1990, inter-annual

summer temperature variability increased, resulting in a few exceptionally warm summers that stimulated seed set (Table 3a) and asexual expansion of aspen (Table 4a). Taking into account that there are several difficulties associated with reliable estimates of seedling establishment (e.g., high rates of mortality that are often not able to be traced backwards; see Lloyd and Fastie, 2003), the presumably highest number of seedlings was found for the year 1954 (Table 3a), following the year with the highest June–July temperature on record for the period 1913–2009 (i.e. 1953; Fig. 2). Such positive temperature anomalies were not observed in the period 1869–1912 (Fig. 2) and were probably less common during the Little Ice Age, thereby explaining why aspen was rarer at the beginning of the 20th century.

Two important moth outbreaks shortly followed each other and significantly reduced birch growth, eventually causing high stem and tree mortality. On the southern side of the lake, a severe outbreak of the autumnal moth in 1954–1955 resulted in high stem mortality in the polycormic birch forest, but the forest recovered relatively quickly through basal sprouting (Tenow et al., 2005). In 1964–1965, a winter moth outbreak caused high tree mortality in the monocormic birch forest on the northern side of the lake with no or negligible recovery so far (Fig. 7). This event was particularly beneficial for aspen colonization: i.e. mean stand size in the opened monocormic birch forest was 0.14 ha compared to 0.05 ha in the polycormic type. Similar moth disturbance to birch has not occurred during recent decades (Abisko Scientific Research Station records), although defoliation events that did not kill trees have occurred (e.g., 2004).

Disturbance to aspen's competitor mountain birch was critical in both sexual and asexual regeneration of the thermophilic species in its subalpine ecotone (Tables 3 and 4). Continued summer warming without disturbance to the birch forest will therefore likely hamper further aspen expansion in the subalpine birch forest area. This has also been suggested by a paleo-study by Peros et al. (2008) who found that continental-scale expansion of aspen was caused more by the effects of climate change on its competitors, rather than the direct effects of climate on aspen itself. However, at and above the birch treeline, the effect of moth outbreaks on aspen establishment and expansion was not evident (Table 3b), most likely because of low birch tree density. Instead, the effect of summer temperature on aspen establishment and expansion at treeline was more pronounced than at lower elevation, also confirmed by the greater land surface area that was colonised in the most recent, warmer, period (Tables 1, 3b, 4b). Although the lower R^2 found for aspen regeneration at treeline suggest caution as we may have failed to include other important controlling factors in the analysis (e.g., quantification of disturbance caused by grazing (Cairns et al., 2007; Camarero and Gutiérrez, 2007) and geomorphological processes such as snow avalanches), overall, continued summer warming is likely to facilitate aspen

establishment and spread at the treeline. Most global circulation models predict a warmer and wetter Fennoscandian sub-Arctic (e.g., Räisänen and Alexandersson, 2003) that may resemble early Holocene climate conditions when aspen was more common in our study area (Bigler et al., 2002). However, there are several uncertainties in projecting future aspen expansion. It is uncertain if summers will warm to the same extent as winters. So far, winter warming in the area has been more pronounced than summer warming over the past hundred years, i.e. +2.9 °C winter warming versus +1.8 °C summer warming for the period 1913–2009 (Callaghan et al., in press), a process that, if continued, may favour coniferous species such as pine more than aspen or birch by decreasing winter desiccation (Rickebusch et al., 2007; Kullman and Öberg, 2009). Although, future decreased competition from birch caused by increased herbivory (Ims et al., 2007; Jepsen et al., 2008) could continue to facilitate the spread of aspen, the potential recovery of currently fragmented pine in the area could provide a new competitor that may outcompete both aspen and birch in a scenario of continued warming associated with limited precipitation (Kullman and Kjällgren, 2006). Also, probable increased herbivory of aspen itself (Schmölcke and Zachos, 2005) and other factors such as disease may affect future aspen range dynamics.

Overall, therefore, the results of this study demonstrate a new and rare phenomenon of establishment and spread of a thermophilic species in the sub-Arctic subalpine forest belt during 20th century warming, but the continued spread and advance of aspen during future projected warming cannot be assumed because of the complexity of the numerous ecological interactions that have been identified in this ecosystem.

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3.2 Grey alder (*Alnus incana*)

In addition to aspen, we found that alder (*Alnus incana* (L.) Moench) was expanding both its elevational and distributional range in the Torneträsk area. In 2006, alder was recorded inside and just outside the elevational transects N2 and S2 respectively (cfr. Fig.1 in chapter 2.1), whereas the species was not observed in 1977 (Fig. 1). All sampled individuals inside the transects ($n = 11$) and the majority of the sampled individuals outside the transects (24 out of 30 or 80%) had established after 1977. The growth rate of this thermophilic species was much higher than that of birch: tree-cores taken at basal level and at 2 m stem height showed that the average time for grey alder to reach 2 m (i.e. tree-size) in the lowland forest at 360 m elevation was 14 years, compared to 24 years for birch and 13 years for aspen. All these tree species individuals were monocormic, non-browsed, and sampled within 2 ha where climate and soil conditions were similar.



Figure 3.1. Range expansion of thermophilic grey alder -dark green leaf colour- in the Swedish sub-Arctic mountain birch forest -yellow-orange- in the direct vicinity of transect S2 (cfr. Fig. 1 in Chapter 2.1). Alder was not observed at this spot in 1977.

The maximum elevation recorded for alder was 613 m a.s.l. found in the surroundings of transect S2 (Mount Huvkim, southwestern Torneträsk, 68°17.360' N; 18°34.120' E); 100 and 190 m below the respective lower and upper boundary of the birch treeline ecotone. On the northern side of the Lake, maximum elevation for alder was 510 m a.s.l. (68°27.090' N,

18°52.267' E); i.e. 160 and 250 m below the respective lower and upper boundary of the birch treeline ecotone. The individuals representing the uppermost 20 m of the alder stands had all established after 1987 in concert with recent climate warming. About 9 000 years ago during the Early Holocene, when climate was more humid and summer temperatures were about 1.5-2.0 °C higher than today, thermophilic alder was far more abundant in the Torneträsk area (Bigler et al., 2002). Therefore, the expansion of alder during recent climate warming is a noteworthy finding. None-the-less, at present most alder stands were small (mean stand size of 0.10 ha) and confined to moist sites.

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Chapter 4 Competition between mountain birch and thermophilic tree species

4.1 Competitive interaction between aspen and birch moderated by invertebrate and vertebrate herbivores and climate warming*

Abstract

Considerable changes in vegetation structure and distribution are predicted in high latitude ecosystems as a result of amplified climate change. However, some documented plant community changes do not follow model predictions. We compared the growth of and the responses to climate variation by the thermophilic aspen (*Populus tremula*) and its sub-Arctic competitor mountain birch (*Betula pubescens* ssp. *czerepanovii*) over the past 100 years. Repeat photography, high-resolution vegetation transects, dendro-ecological analysis, and local climate record archives were used to study changes in vitality and distributional range of the two tree species in response to climate variability. Aspen grew 45% faster and had seven times higher recruitment numbers than birch. However, no aspen stand expansion was observed, most likely because of browsing by moose (*Alces alces*). Birch, on the other hand, suffered from cyclic outbreaks of the autumnal moth (*Epirrita autumnata*). One-hundred-year-old birch trees experienced on average 9.0 years of reduced growth due to moth herbivory compared to 1.4 years for aspen. Moreover, these moth outbreaks on birch stimulated recruitment of aspen in birch stands. As the sub-Arctic continues to become warmer, the dynamics between aspen and birch in forest ecosystems will likely depend on the number of vertebrate browsers relative to the number of aspen recruits, while major moth outbreaks on birch may facilitate the spread of aspen by reducing competition. Our results suggest that alternating episodes of apparent species range stabilities (homeostasis) and abrupt non-linear shifts may characterise species migration patterns in this ecosystem.

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Introduction

Changes in establishment, survival and eventual distribution of plant species are one of the major uncertainties of projected impacts of climate warming on ecosystems (Callaghan et al., 2005). In the Arctic, climate warming is proceeding faster than elsewhere on Earth (ACIA, 2005), yet there is surprisingly little evidence of large-scale redistribution of species that could affect major ecosystem services such as primary productivity, biodiversity and biotic feedbacks to the climate system (Chapin et al., 2005). Experiments that manipulated the climatic conditions experienced by plant communities in situ for over a decade, have generally recorded changes in the dominance of existing species rather than emigrations and immigrations (Press et al., 1998; Arft et al., 1999; Walker et al., 2006; Sitch et al., 2008). This homeostasis (Grime et al., 2008) contrasts with model projections of major redistributions of vegetation in the twenty-first century (Kaplan et al., 2003; Wolf et al., 2008a) and the contradictions point to an important gap in our understanding of the mechanisms of species' distributional responses to climate change.

In northernmost Europe, the sub-alpine vegetation belt is dominated by extensive mountain birch forests (*Betula pubescens* Ehrh. ssp. *czerepanovii* (Orlova) Hämet-Ahti) (Figure 1) and this species forms the treeline. Aspen (*Populus tremula* L.) is a component species of the boreal forest, rather than a woodland dominant (Worrell, 1995). It is a thermo- and heliophilic tree species (Kullman, 1983) known for its potentially rapid colonisation and strong growth (Worrell, 1995; Johansson, 2002). Whereas the rarer aspen is a highly preferred food source by moose (*Alces alces* L.) (Edenius and Ericsson, 2007), mountain birch suffers from cyclic defoliations by the autumnal moth (*Epirrita autumnata* Bkh.) (Tenow 1972).

Long-term repeat photography of an aspen stand in sub-Arctic Sweden has shown that this stand had remained stable for the past 30 years (Figure 2). This is rather surprising because a significant summer warming has occurred since 1988, increasing the mean June-July temperature from 9.7 °C to 10.5 °C compared with the period 1961-1990, normally used as a baseline, against which recent change in temperature is compared. Since 1996 summer warming has accelerated with 2002-2009 being the warmest period on record (mean July temperature of 12.8 °C (1.8 °C warmer compared with the normal period 1961-1990; Abisko Scientific Research Station data archive). Aspen, being more thermophilic than birch (Kullman, 1983), would be expected to have responded to this warming and expanded into the surrounding birch forest as it did in the early twentieth century as a direct response to the climate warming associated with the end of the Little Ice Age (Van Bogaert et al., in press). Other species in northern Scandinavia have responded to the recent warming. There have been local shifts in shrubs (Hallinger, 2007), treeline (Dalen and Hofgaard, 2005) and forest density (Hållmarker, 2002) in agreement with

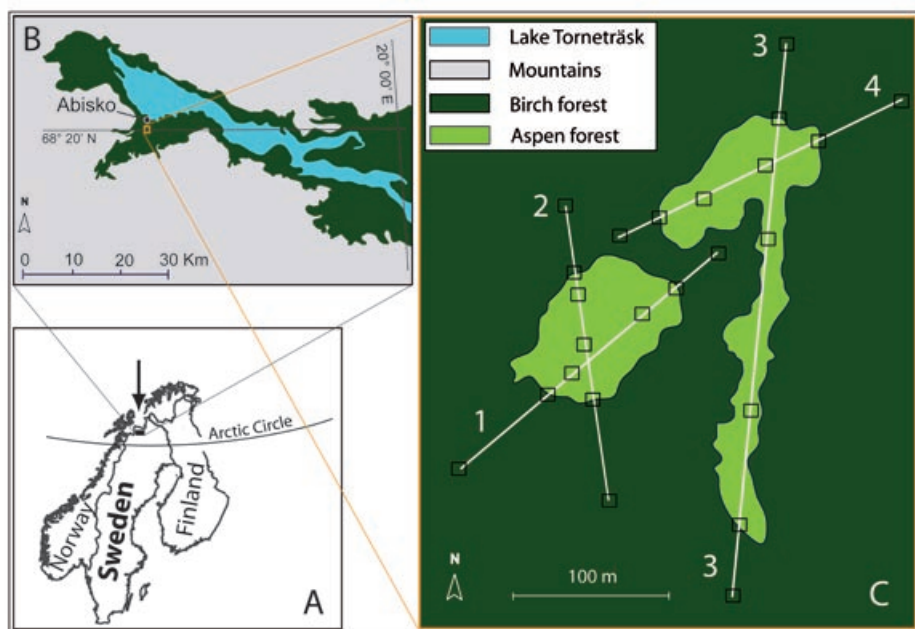


Figure 1. Map of Fennoscandia (A), showing the study region near Lake Torneträsk, Sweden (B), with the transect and plot layout in the aspen-birch forest (C).

Arctic wide shrub expansion and treeline densification (Tape et al., 2006; Van Bogaert et al., 2007)

Chernov (1985) recognised that “the distributional area of a species results from the effects of climate, landscape and biotopical conditions, interrelationships with other closely related taxa, moisture conditions and competition as well as changes in the environment in the past”. Similarly, Callaghan and Johansson (2009) stated that the impacts of climate change on a species cannot be projected without understanding climate change impacts on other, interacting species, such as competitors, facilitators, pests, pathogens, predators and herbivores. For example, Hofgaard (1997) and Olofsson et al. (2009) have shown that vegetation responses to climate warming may be controlled by herbivore activity so that recent documentation of dramatic shrub advance in parts of the Arctic (Tape et al., 2006) might have resulted from changes in herbivore pressure as well as from climate warming.

These concepts of multiple interactions among co-occurring species, each of which might be impacted to a different degree by climate change, are not generally addressed in the major dynamic vegetation models (Sitch et al., 2008; Wolf et al., 2008a). To provide a better conceptual understanding of climate change impacts on plant species as well as a context and empirical data for vegetation modelling, we use a model system of an aspen stand in a



Figure 2. Repeat photography of an aspen stand in northern Sweden. 9 September, 1978 (top); and 9 September, 2008 (bottom). None or only minor expansion is seen despite significant summer warming during this period. Source: Abisko Scientific Research Station archive.

birch forest together with an assessment of vertebrate and invertebrate herbivore activity at a location where climatic data has been collected since 1913, providing a long-term reference for dendro-ecological analysis. We acknowledge that many other interacting factors (e.g. changes in snow depth and precipitation) and organisms (e.g. parasitic fungi) will affect the overall and longer-term outcome of the interactions between the two tree species but here we focus on the following hypotheses:

1. In a warmer climate, the more thermophilic aspen should have a competitive advantage over birch because of its higher growth rate and recruitment levels, whereas during colder conditions birch may be favoured compared to aspen.
2. Climate change will affect the range expansion of a tree species through its competitors and herbivores. Therefore, increased herbivory of birch may result in a competitive advantage to aspen in the sub-Arctic whereas increased herbivory of aspen may favour birch.

Material and methods

Study area

The study was made in a sub-Arctic birch forest surrounding an aspen stand of two clones (each c. 0.7 ha), monitored during the twentieth century. This site is located in the Torneträsk area near the Abisko Scientific Research Station, Sweden (68°21.1' N; 18°48.1' E) (Figure 1). Mean annual temperature for Abisko (388 m above sea level) is -1.0 °C and mean January and July temperatures are -12.0 and + 11.0 °C respectively for the normal period 1961-1990 (Alexandersson et al., 1991). Annual precipitation amounts to 310 mm and mean winter snow depth is 52 cm (Kohler et al., 2006).

Sampling design

Four transects, each 3 m wide, were established in June 2008 through the aspen stand, with origins and ends located in the birch forest either side of the aspen stand; the transects were 240 to 360 m long (Figure 1C). Within these transects, height and diameter at breast height (130 cm from the ground; DBH) were measured for all aspen and birch individuals ($n = 1032$) and 80 aspen and birch individuals ($n = 160$) were selected for coring to build a ring width chronology. The individuals were randomly chosen but in such a way as to ensure that the different DBH classes (i.e. presumed age classes) were equally represented. Tree cores were taken at 130 cm height in two perpendicular directions according to standard methods (Fritts, 1976). In June 2008, the annual ring of 2007 was the most recent completed tree-ring and determined the time range of the study. The number of dead trees was counted and vertebrate herbivory damage was classified visually as (i) no damage, (ii) tip or branch browsed and (iii) bark stripped.

To study recruitment and mortality of the birch and aspen stands, 24 plots of 10 m $\times$ 10 m were established (i) at the origin of each transect, (ii) at every boundary between aspen and birch stands that was crossed, (iii) in the closed aspen stand (two plots) and (iv) at the end of the transect (Figure 1C). Six monocormic individuals were randomly selected per plot for age determination. These aspen and birch individuals were cored at basal level, i.e. at the stem-root intersection, with a small increment corer. In several cases this was difficult and some of the upper soil layer had to be removed (usually not more than the uppermost 10 cm of an area of 0.3 m²). In this way, possible errors of the certainty of age were minimised. From dead individuals, stem discs rather than cores were taken to identify and date lethal disturbance events. Finally, 30 non-browsed Scots pine (*Pinus sylvestris* L.) individuals located within 1 km of the study

were cored to obtain a reference chronology for herbivory analysis on aspen and birch. Scots pine has been shown to be a suitable reference (Eckstein et al., 1991). In total, 160 aspen (192 cores, 48 discs), 144 birch (186 cores, 38 discs) and 30 pine trees (60 cores) were sampled.

A significant ($P < 0.05$) linear relationship between age and DBH was found in both aspen (browsed or bark-stripped individuals needed to be separated from non-affected individuals because dendro-chronological analysis showed that herbivory damage affected DBH: $r = 0.56$, $n = 88$, and $r = 0.87$, $n = 72$) and birch ($r = 0.68$, $n = 144$). The regressions were then used to estimate age for all individuals measured within the transects.

Dendrochronological methods and statistics

To determine tree age, radial growth, impact of climate and the effects of herbivory, tree-rings were measured to the nearest 0.01 mm using a stereo-microscope and a LINTAB measuring stage. TSAP-Win (Time Series Analysis and Presentation for dendrochronology and related applications) software (Rinn, 2003) was used to analyse the tree-ring data. Cross-dating (e.g. Fritts, 1976) was made both visually and statistically (t -value > 4.0 , Gleichlaufigkeit GLK > 60) in the program TSAP-Win, while verification of both cross-dating and missing rings (Sonesson and Hoogesteger, 1983) was made in the program COFECHA (Holmes, 1983).

For the removal of the age trend in the tree-ring series standardisation was applied. All non-browsed individual series were cambial-age aligned to discern a common growth trend. This methodology is known as Regional Curve Standardisation (RCS) in which the age function is defined as an empirical time-independent growth function, controlled by biological age rather than calendar age (Briffa et al., 1992). No biases in the results because of age trend removal are expected since the high sample number over the different age classes resulted in a robust common growth trend function for both birch and aspen. In the case of pine, which had a lower sample number, the established detrending function of Grudd et al. (2002) was used: $A_T^{TRW} = 0.642T^{0.088}e^{-0.0177T} + 0.445$ with A_T^{TRW} being the regional age-related tree-ring width value at cambial age T . Autoregressive standardisation (Cook and Kairiukstis, 1990) was also used to ensure that autocorrelation in the ring-width series had no effect on the results. All tree-ring standardisation was made in the program ARSTAN (Cook, 1985).

Ring width chronologies were built for five different sample categories: 'birch individuals inside birch forest', 'aspen individuals inside aspen stand', 'birch individuals inside aspen stand', 'aspen individuals inside birch forest' and 'pine individuals inside pine forest'. A 'birch individual inside aspen stand' (hereafter referred to as 'birch in aspen') was a birch that grew nearest to an aspen individual in any direction and was separated by at least 15 m from the

nearest other birch individual. ‘An aspen individual inside birch forest’ (hereafter ‘aspen in birch’) was an aspen that grew nearest to a birch individual in any direction and was separated by at least 15 m from the nearest other aspen individual; this horizontal distance of 15 m is greater than the maximum height of any individual tree. Statistical parameters for the different tree categories were compared pair-wise using a two-sided *t*-test with significance limit at $P < 0.05$.

Chronology confidence was determined by using standard threshold values for Rbar and Expressed Population Signal (EPS) (Wigley et al., 1984). The climatic signal of aspen and birch over time was tested using the DENDROCLIM2002 software (Biondi and Waikul, 2004). Temperature response coefficients for the period 1913–2007 were calculated using boot-strapped confidence intervals to ascertain to what degree ring growth was determined by climate.

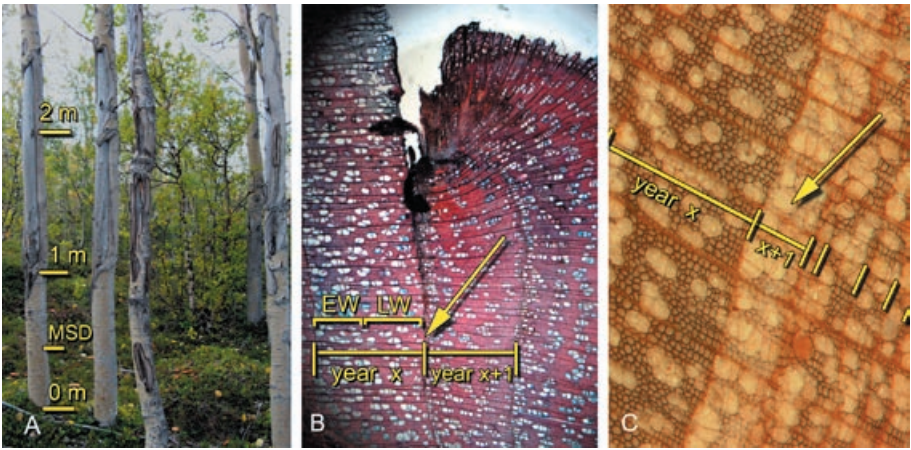


Figure 3. Vertebrate and invertebrate herbivory impacts on aspen and birch. (A) Severe bark damage on aspen caused by moose. Birch in the background is undamaged. (B) Micro-section showing the dating of the moose bark-stripping events. The overgrowth (wound tissue with curved shape) indicates the time of browsing: at the ring-border of year x and year $x + 1$, indicated by the arrow. Late wood formation has completed which indicates that bark stripping occurred during winter. This individual died 2 years after the event. (C) Invertebrate herbivory on aspen is denoted by unusual bright rings (year $x + 1$) of callus tissue. This aspen individual had a growth reduction of 4 years (mean for all sampled individuals = 1.4 years) after the *Epirrita autumnata* outbreak in 1955. Abbreviations: EW, early wood; LW, late wood; MSD, maximum winter snow depth.

Quantifying herbivory impacts

Vertebrate bark-stripping damage to the stem was characterised by the formation of wound tissue that could be dated through the high contrast in ring width, colour, shape and vessel abundance between the undamaged wood and the wound tissue (Figure 3A,B) (Schweingruber, 2007). In aspen, invertebrate herbivory by *Epirrita autumnata* was characterised by unusually

bright narrow rings (Figure 3C). In mountain birch, this detection method failed due to the absence of ring colour contrasts. Instead, a 'birch-minus-pine' chronology was constructed, an approach introduced by Nash et al. (1975) that has proven to be successful to indicate moth outbreaks in species such as mountain birch (Eckstein et al., 1991). Because pine is not a host tree for the moth *E. autumnata* and its growth is mainly influenced by summer temperature, the subtraction of the normalised pine indices from those of birch should largely eliminate ring width variance due to climate and hence show the effect of the caterpillar attacks (Eckstein et al., 1991). However, with this established methodology it is recommended to have a reference of the herbivory events because some of the minima in the resulting chronology may reflect relative growth reductions caused by other factors than herbivory (e.g. fire, fungi or masting). Similarly, an aspen-minus-pine chronology was developed to detect herbivory events in aspen. The direct measure of wound tissue, scars and vessel abundance of the aspen tree-rings was used as a reference. A Tukey's HSD-test showed annual ring width indices that significantly ($P < 0.05$) differed from the mean birch-minus-pine or aspen-minus-pine ring width index and those values were considered growth reduction years due to moth herbivory.

All statistical analyses were made by using the software package SPSS v. 15.0 (SPSS, 2006).

Results

Climate impacts on aspen and birch

Ring growth in aspen and birch was mainly determined by June and July temperatures, respectively, of the current growing season (for aspen: $r = 0.47$ and 0.57 , $P < 0.01$; for birch: $r = 0.24$ and 0.31 , $P < 0.05$). The effect of precipitation on ring growth was insignificant for both species. For aspen, the temperature response coefficient by annual ring width remained constant over the last 100 years (significant value of 0.35). For birch, however, the significant ring growth temperature response coefficient of 0.23 decreased in the period 2001-2007 to 0.10, a value not statistically significant.

The growth of the aspen and birch forest over time is shown by the standardised ring width chronologies (Figure 4). In general, small radial growth was observed at the beginning of the twentieth century when summers were cool, with an increasing trend towards the late 1930s, when summer temperatures markedly increased. In the second half of the century, cooler summers and a decrease in radial growth were observed, but towards the end of the century summers markedly warmed again and radial growth in aspen reached a new peak (Figure

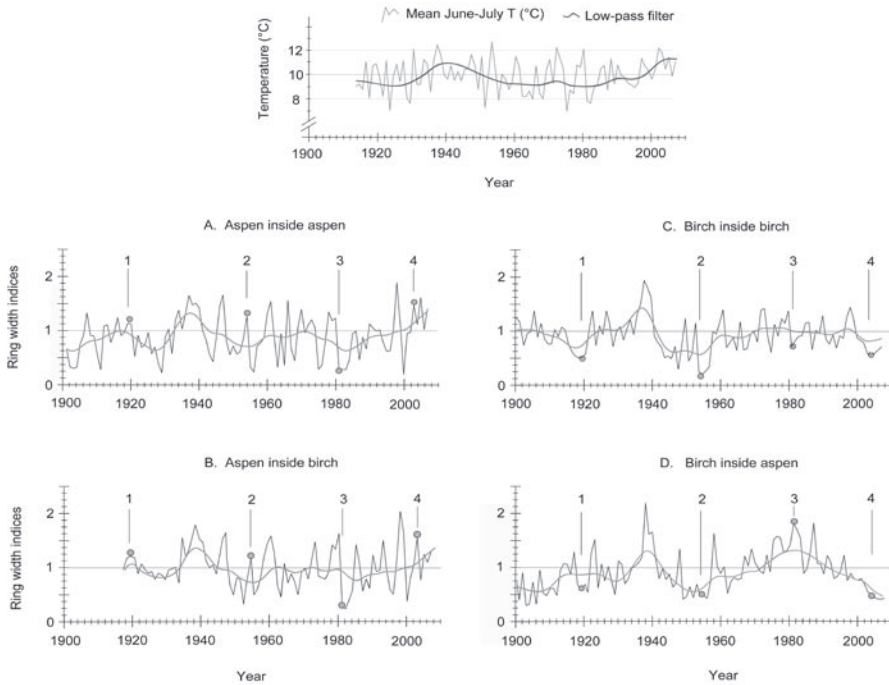


Figure 4. Standardised tree-ring chronologies for aspen and birch at Torneträsk, Sweden for the period 1900-2007. Low-pass filters (second degree polynomial function represented by grey lines) show the long-term trends. Summer temperature for the period is plotted above the chronologies as a reference. Some key years that illustrate the important interactions between the two tree species and their herbivores are marked with circles and are referred to in the discussion section.

4A,B). Both aspen chronologies showed a similar trend over the past century with the highest values in the most recent, warmest years. The birch in birch individuals showed a similar trend to aspen, but the synchrony ceased around 1970; the minimum of the early 1980s was not evident, and instead the most recent years reflected a minimum radial growth (Figure 4C). The chronology of birch in aspen had a similar trend to birch in birch until around 1970. From that time onwards, the radial growth pattern in birch in aspen was opposite to aspen in aspen, i.e. it increased in the 1970s to early 1980s and decreased in the late 1980s up to the present time (Figure 4D).

Annual aspen recruitment was positively correlated ($r = 0.57$, $n = 80$, $P < 0.01$) with mean summer temperature (June-July) over the period 1913-2007, for which recorded temperature data are available, while no correlation was found for birch ($r = 0.12$, $n = 64$, $P = 0.38$).

Competition: stand characteristics, growth, recruitment and mortality

Aspen formed a dense stand with a closed canopy in contrast to the open character of the birch forest; mean aspen density for the 24 plots was 65 individuals per 100 m² compared with 21 birches per 100 m². In the absence of herbivory, aspen grew significantly larger than birch; 80-year-old individuals were on average 4.5 m taller than equally aged birches ($n = 18$, $P = 0.02$). Similarly, annual rings of aspen in aspen were 45% wider than those of birch in birch (Figure 5). Birch trees in the birch forest had 32% wider rings than birch in the aspen stand, but aspen in the aspen stand had 30% smaller rings than aspen in the birch forest (Figure 5). Growth differences between aspen and birch were more pronounced during warmer (1930s and 1990s to 2007) than during cooler periods (1960s to 1980s; Figure 5).

The proportion of young (1-30 years) aspen individuals was significantly higher than the proportion of young birches throughout the study area (Table 1). Within a plot of 100 m², on average there were 23 aspen compared with three birch individuals belonging to the age class < 10 years. Exclusively young (1-30 years) aspen individuals were found in the birch forest up to 50 m away from the closed aspen stand. However, mortality (the proportion of dead trees) of these younger aspen, both in the birch forest and aspen stand, was markedly high too (Table 1). Mortality increased up to age class 31-60 years and then rapidly decreased. For birch, mortality was much lower than that for aspen, both inside the birch forest (7% for birch vs. 49% for aspen) and inside the aspen stand (23% for birch vs. 49% for aspen). The mortality of birch in aspen was significantly higher than that of birch in birch (23% vs. 7%). Inside the aspen stand, birch had no recruitment.

Effects of herbivory

The birch-minus-pine chronology (Figure 6) indicated the moth outbreaks for the period 1860-2007. The most severe moth outbreaks, which caused important birch mortality and a significant growth reduction in the surviving birches were (in order of importance) 1954-1955 and 1917-1918 (Figure 6). These were also the periods with highest aspen recruitment (Table 2). There was a significant correlation ($r = 0.41$, $n = 80$, $P = 0.03$) between the negative birch-minus-pine ring width indices and the annual number of aspen trees established, i.e. the more severe the moth damage on birch was, the higher the recruitment of aspen was.

Since 1860, seven outbreaks by the moth *Epirrita autumnata* have caused radial growth reduction and mortality in birch, while only one outbreak (1955) has affected aspen, causing no mortality. Indeed, the most recent outbreak of 2004 showed a 100% defoliation of birch and none in aspen (Figure 7).

Table 1. Height and age class distributions for aspen and birch. Means and standard errors are given for the four transects. Height classes are based on (1) individuals that are below winter snow cover (50 cm), sapling size (< 2 m), (3) mature tree height up to maximum birch height (9 m) and tallest class for aspen (> 9 m). Age classes were based upon diameter at breast height (DBH) and separated for aspen individuals affected by bark stripping or browsing and those that were not affected. Mortality numbers for aspen reflect mortality that was predominantly caused by moose herbivory, indicated by the severe bark stripping (Figure 3A,B) and continuous removal of the young stem tips (see photographs in Appendix 5). Any potential mortality caused by natural self-thinning was likely masked by the ubiquitous moose damage

	Aspen in aspen (<i>n</i> = 680)		Birch in birch (<i>n</i> = 202)	
	Individuals (%)	Mortality (%)	Individuals (%)	Mortality (%)
-Height class-				
0 - 0.50 m	16.2 ± 2.0	38.9 ± 4.0	8.1 ± 1.3	4.8 ± 2.2
0.51 – 2.00 m	45.2 ± 1.8	65.5 ± 3.7	17.0 ± 0.9	7.2 ± 3.2
2.01 - 9.00 m	27.3 ± 1.7	40.8 ± 3.6	74.9 ± 1.6	7.8 ± 2.0
> 9.00 m	11.3 ± 1.4	11.2 ± 2.4	-	-
-Age class-				
1-30 yrs	59.1 ± 1.3	57.4 ± 3.3	34.1 ± 1.3	5.3 ± 1.8
31-60 yrs	24.7 ± 0.8	66.8 ± 5.3	34.9 ± 2.1	6.6 ± 3.8
61-90 yrs	10.2 ± 2.3	22.6 ± 2.1	20.8 ± 2.3	7.4 ± 4.4
> 90 yrs	6.0 ± 2.1	13.2 ± 6.1	10.2 ± 1.6	11.7 ± 5.3

Table 2. Aspen recruitment (total *n* = 80) in relation to summer temperature and moth herbivory on birch at Torneträsk, Sweden, 1913-1999. The 7 years with highest aspen recruitment are shown. 2000-2009 is not reported here because the process of self-thinning was probably still important for the age class <10 years (Schier et al., 1985). Summer temperature anomalies and moth damage anomalies, i.e. negative birch-minus-pine ring width indices, are presented for this period. Significant (*P* < 0.05), anomalies are marked with an asterix

No. of recruits (<i>n</i> = 80)	Year	June-July temperature anomaly (°C)	Moth damage anomaly (indices)
12	1954	+ 0.8*	+ 0.82*
8	1957	+ 0.5	+ 0.49*
7	1919	+ 0.3	+ 0.73*
6	1997	+ 1.4*	+ 0.25
5	1988	+ 1.1*	+ 0.32
4	1990	+ 1.0*	+ 0.14
4	1960	+ 1.5*	+ 0.07

However, following the outbreak of 1955, aspen showed a significant growth reduction of 1.4 years, although this was lower than the 3.2 years growth reduction observed in birch (Figures 3C and 6). The contrast in moth impact was stronger over a longer period: 100-year-old aspen trees ($n = 35$) experienced on average 1.4 years of reduced growth because of moth herbivory (1955), whereas in 100-year-old birch trees ($n = 38$) the corresponding figure was 9.0 years.

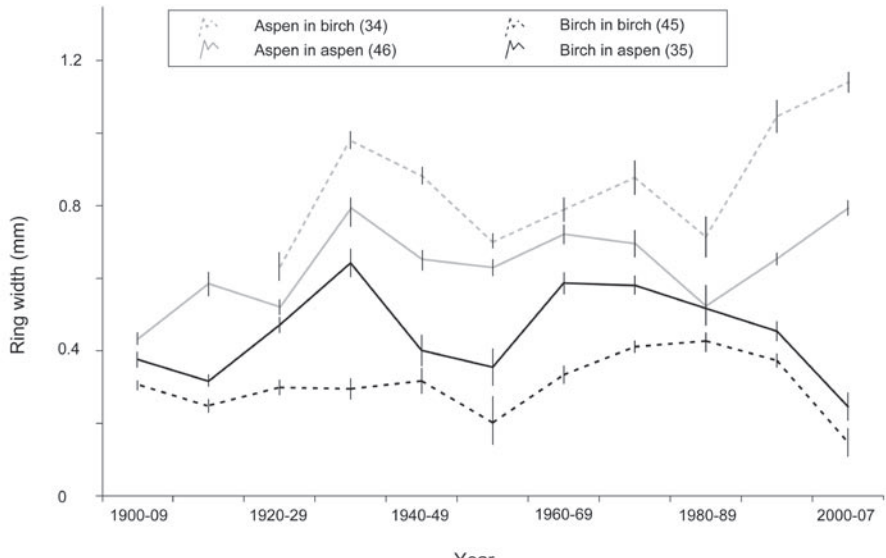


Figure 5. Absolute tree-ring widths of aspen and birch in absence of herbivory at Torneträsk, Sweden for the period 1900-2007. The number of samples included is shown in parentheses and 95%-confidence limits are indicated by bars.

Evidence of vertebrate herbivory damage was also found, but only in aspen (Figure 3A,B). The years with the highest bark stripping damage were, in order of importance, 1980-1983, 1974-1978, 2005-2007 and 1947-1948. Although bark stripping decreased after the peak observed in the mid 1970s to early 1980s, mortality of the youngest aspen (1-30 years) caused by stem damage remained very high (Figure 6). Since 2005 bark stripping increased again causing a relative growth reduction in aspen compared to non-browsed pine individuals (Figure 6). No evidence of large-scale vertebrate herbivory damage was found before 1947. These data correlate well with the aspen-minus-pine chronology (Figure 6). The main vertebrate herbivore was moose, as indicated by wound height (0.9-2.9 m), observed footprints in the snow (R. Van Bogaert pers. obs.), and characteristics of the bark wounds (Figure 3A). Bark stripping and browsing by moose affected 92% (718 out of 780 individuals) and killed 49% (384 out of 780

individuals) of the aspen within the transects. Only the oldest aspen with a thick unpalatable bark and the most recent, smallest recruits not yet discovered by moose were undamaged.

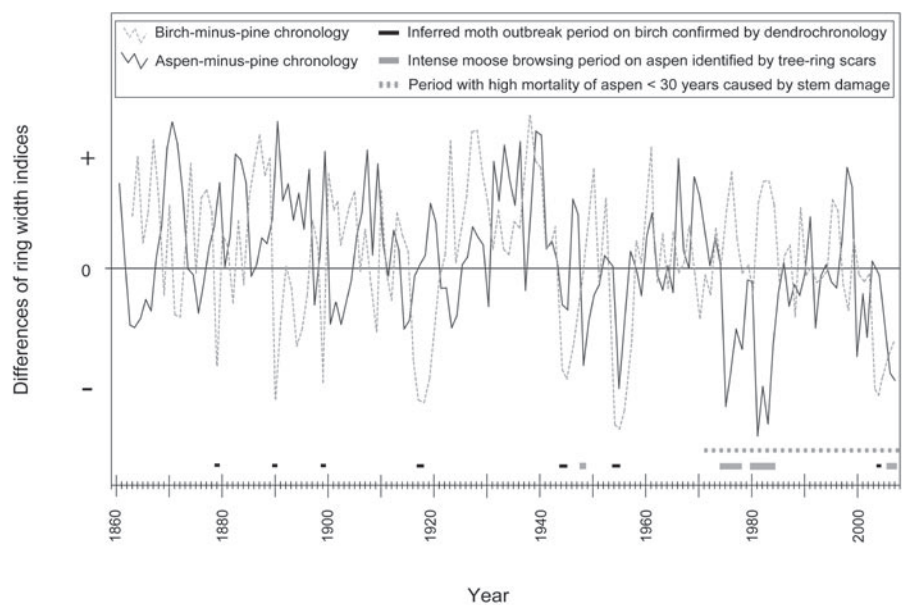


Figure 6. Herbivory impacts on birch and aspen indicated by tree-ring analysis in the Abisko Valley, Torneträsk, sub-Arctic Sweden for the period 1860-2007. The birch-minus-pine chronology shows the herbivory impact on birch, whereas the aspen-minus-pine chronology shows that on aspen. Annual differences between the ring width indices are plotted using non-browsed pine individuals as a reference for its strong climate signal and lack of moth (*Epirrita autumnata*) and moose herbivory. The negative values should indicate years with weak growth in birch (aspen respectively) that are unlikely to have been caused by climate, but rather by factors such as herbivory. The black horizontal bars along the time axis represent moth outbreak periods inferred from various sources (Tenow, 1972; Eckstein et al., 1991; Tenow, 1996) and confirmed by dendrochronological analysis. Grey solid bars represent important moose bark stripping years on aspen, identified by microscopic study of the tree-ring characteristics. Periods with high (>50%) mortality of the younger aspen (1-30 years) due to stem breakage by moose are plotted as broken grey bars.



Figure 7. Contrasting moth herbivory effects on birch (defoliated; brownish colour) and aspen (bright green foliage) at Torneträsk, Sweden, 26 July 2004. The dark spots to the left are isolated pine trees. Source: Abisko Scientific Research Station archive.

Discussion

This study hypothesised that climate change would not only affect species directly, but would also affect each species through competitive interactions and by the activity of herbivores, which might themselves respond to climate change (Callaghan and Johansson, 2009). We have demonstrated that climate affected the growth of birch and aspen (Figures 4, 5) as well as the establishment of aspen (Table 2). The ring growth temperature response coefficient of birch was lower than that of aspen (0.23 vs. 0.35) and rapidly decreased after 2001, during a period of intense warming (mean July temperature increased by 1.8 °C compared with the normal period 1961-1990). Although aspen also grew faster than birch during cooler periods, growth differences were more pronounced during warmer periods (Figure 5), confirming the thermophilic nature of aspen. We showed that the performance of both tree species is further controlled by their herbivores; birch by an invertebrate that periodically reaches outbreak proportions (Tenow, 1972) and aspen by a mammal that has rapidly increased in numbers during the late twentieth century (Cederlund and Markgren, 1987; Sylvén, 2003) as a result of predator reduction and, in more southern areas, also because of forestry practices (Ball et al., 1999).

These complex interactions have resulted in a dynamic balance between birch and aspen. Although aspen has responded to the recent summer warming by increased growth and recruitment, this has not resulted in a net expansion of the stand. This apparent homeostasis agrees with the results from long-term climate manipulation experiments of a grassland ecosystem in England (Grime et al., 2008). What has stopped the spread of this aspen stand under current climate warming?

In the absence of herbivory, aspen grew significantly taller than birch and aspen in birch individuals were not negatively affected by proximity to birch, whereas birch in aspen individuals showed both increased mortality and reduced radial growth (Figure 5; Table 1). Tree-ring analysis of dead aspen indicated that stem damage by moose, a recent immigrant in the study area (Sonesson, 1970), rapidly increased since the late 1940s (Figure 6) and killed the majority (57%) of the youngest age class (Table 1). Although young (1-30 years) aspen were found in the birch forest, high mortality rates since the early 1970s prevented the aspen stand from further expansion (Figure 6). Moreover, these mortality rates may endanger the survival of the aspen stand, a trend that follows a wider Fennoscandian pattern of increasing vegetation impacts in concert with recent high moose population numbers (Persson et al., 2005; Edenius and Ericsson, 2007).

Regional variation in moose population densities (and ungulates in general) is mainly determined by climate through spatial variation in snow depth and quality (Lundmark and

Ball, 2008). Areas with a deeper winter snow cover than the present study area imply increased energy expenditure in locomotion and a higher reach of browse (see Lundmark and Ball, 2008). Ungulate population dynamics over time are also affected by climate (Sæther, 1997; Post and Stenseth, 1999) and a warmer sub-Arctic may cause increased damage to species such as pine and aspen because of a prolonged stay of moose in its winter range (Ball et al., 1999). On the other hand, a higher frequency of rain on snow events that result in an ice crusting of snow may cause increased mortality of moose (Putkonen and Roe, 2003). Overall however, forestry practices and moose hunting policies are likely to overrule the direct effects of climate change on ungulate population dynamics (Mattsson, 1990; Ball et al., 1999; Solberg et al., 1999).

In sharp contrast to aspen, ungulate browsing on birch was not observed in this lowland forest area where reindeer usually just pass through on their way to the alpine tundra (Tenow, 1996). Moose, tends to over-utilise rarer species such as the highly palatable aspen (Edenius et al., 2002 C.Stolter pers. comm.), which may explain why birch was undamaged. However, unlike vertebrate herbivory, invertebrate herbivory on birch was important; cyclic outbreaks of the defoliating moth *Epirrita autumnata* significantly affected the growth and vitality of the forest. One-hundred-year-old birch trees experienced reduced radial growth for 9.0 years because of moth herbivory. Therefore, the recent counter-intuitive decrease in the temperature response coefficient by birch annual ring widths (Figure 4C,D) could have been caused by the moth population growth prior to its outbreak in 2004 that coincided with a period of intense summer warming. Also, there was no positive correlation between temperature and birch recruitment. This was likely to have been cancelled out by the large-scale asexual recruitment during cool summers (e.g. 1955) when moth outbreaks are most lethal to the stems and trigger high regeneration from the surviving organs (Niemelä, 1980; Tenow and Bylund, 2000).

Continued climate warming may not change the frequency of moth outbreaks (Bylund, 1999), but non-outbreak damage on birch may increase by up to 5% by 2080 and affect leaf area index, biomass and net primary productivity (Wolf et al., 2008b). Additionally, northern birch forest areas which were formerly protected from outbreaks by low winter temperatures have recently been affected by the moth (Jepsen et al., 2008). Although aspen is known to be host tree for many invertebrate species (Worrell, 1995), few pest species associated with aspen are currently observed in northernmost Fennoscandia (U. Emanuelsson, pers. comm.) and in our study area we only recorded the defoliating moth *Epirrita autumnata* that occasionally feeds on aspen after all birch leaves have been consumed (e.g. summer 1955). On condition that pathogens and pest species found on aspen in more southern areas do not dramatically shift northwards and reduce aspen vitality, future warming is likely to result in increased moth damage to the birch canopy and ground vegetation that should favour the heliophilic aspen.

Integration of interactions between tree species

The basic tree-tree interactions were punctuated by episodes of invertebrate herbivory and a general increasing pressure of ungulate herbivory together with climatic trends over the past century. Some key years (Figure 4) illustrate important interactions between the two tree species and their herbivores. The years 1919, 1954 and 2004 all had a relatively warm summer (June-July temperature anomaly of +0.8 °C, +1.1 °C and +0.6 °C respectively compared to the long-term mean 1913-2009) and aspen grew well, but birch trees suffered for 3-4 years from the effect of the moth outbreaks in 1917-1918, 1954-1955 and 2004, respectively. The impact of the most recent moth outbreak (2004) on birch in aspen is particularly important and the trees may possibly not recover (note the decline in Figure 4D). The summer of 1981 and the following three summers were cool (June-July temperature anomaly of -1.5 °C) and aspen suffered heavy bark stripping by moose for three consecutive winters (Figure 6). During these years, all aspen and birch in birch showed reduced radial growth, but birch in aspen appeared to benefit from the mortality and stand damage in aspen and experienced four good growing seasons (1981-1984) (Figure 4). In the second half of the 1980s, when summer temperatures increased again, the canopies of the surviving aspen trees started overshadowing the birches causing an important growth reduction in birch in aspen (note the recent decline in Figure 4D). These results confirm our hypothesis that herbivory of the currently more common birch will be beneficial for the rarer aspen, whereas herbivory of aspen will be beneficial for birch. However, because of the site-specific conditions, and both the limited size and presumed limited genetic variance of the aspen stand, to make generalisation of our findings is difficult. Nonetheless, as long-term data series and associated analyses have shown interactions that are important for explaining the observed dynamics for this one site we propose this as a model to explore the generality of the trends elsewhere.

Most global circulation models predict warmer and wetter climate conditions for northernmost Europe (Räisänen and Alexandersson, 2003; Saelthun and Barkved, 2003), comparable to early-Holocene climate conditions (Barnekow, 1999). Palynological studies showed that during this period aspen occupied a much larger part of the northern Fennoscandian forest area (Seppä, 1998; Heinrichs et al., 2005), probably including the Torneträsk area (Bigler et al., 2002). We would therefore expect an expansion of aspen in the future in a scenario of continued summer warming. However, future forest development in a warmer climate might not necessarily follow this pattern as indicated by the aspen stand studied. Moreover, a recent continental-scale study by Peros et al. (2008) on Holocene forest dynamics of closely related quaking aspen (*Populus tremuloides* Michx.) showed that changes in the abundance of aspen were caused more by the

effects of climate change on its competitors than by the direct effects of climate on quaking aspen itself. Altogether, it is clear that we cannot project future range changes of a species without considering the dynamics of its principal interacting species. Our current vegetation models are based upon individual parameters such as climate, topography and biochemistry, but do not usually include such species interactions. Future research should therefore explore how the mechanisms discussed in this paper could be included in a new generation of more realistic models.

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Notes

1. Formally published information is scarce and only grey literature is available. Copies are available in the Abisko Scientific Research Station's library.

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4.2 Birch-pine competition may cause erroneous climate reconstructions

To construct the birch-minus-pine chronologies, we sampled altogether 50 non-browsed Scots pine (*Pinus sylvestris* L.) individuals in the scattered pine stands found in the vast sub-alpine mountain birch forest area of western Torneträsk. To avoid potential competition effects from neighbouring pine or birch individuals, 20 out of 50 pine individuals were sampled at the fringes of the pine stands, i.e. within 5 to 25 m from the nearest birch individual. However, all these samples needed to be removed from further analysis because they showed a uniform, but significantly ($P < 0.05$) deviating, growth pattern from both the other pine ring-width series and summer temperature trend. The part of the ring-width chronology that deviated, i.e. the early 1920s and 1960s, was identical ($GLK > 0.65$ and $t_{bp} > 4.0$) to that of the birch individuals in the surrounding forest (Fig. 1, $n = 128$ birches). These two periods followed the two severest moth outbreaks on birch of the 20th century in the Abisko Valley (i.e. 1917-1918 and 1954-1955, cfr. chapter 4.1) and caused important birch stem mortality, particularly in 1955. Such events stimulate basal sprouting in the below-ground birch organs (Tenow and Bylund, 2000). Reduced competition and a better nutrient supply because of an oversized root system for the young sprouts presumably contribute to the growth peaks observed in mountain birch after severe moth outbreak events (Karlsson et al., 2004). Although pine is not a host tree for the autumnal moth *Epirrita autumnata* Bkh. (Eckstein et al., 1991), the individuals growing at the fringe of the pine stand presumably benefited from the suppression of neighbouring birches and an increased nutrient availability provided by the rotting birch stems. Similar findings come from northern Finland and Norway where pine markedly expanded and grew more vigorously following some severe moth outbreaks on birch (Veijola, 1998). This finding points to an important potential bias in climate reconstruction using pine ring-width series of individuals located in the vicinity of the birch forest. Also other dendrochronological analyses using pine ring-width series such as birch-minus-pine ring width series should take into account this potential bias and remove pine samples that are affected by this competition process. Moreover, since pine trees may live 400 years and longer (chapter 3.1), this underlying competition process may be masked; i.e. 400-year-old pine trees that are currently more than 100 m separated from the nearest birch individual may 350 years ago have been situated at the fringe of the birch forest area. Therefore, the ring-width variability of this pine individual at its juvenile stage may be affected by moth outbreak regimes on its competitor mountain birch.

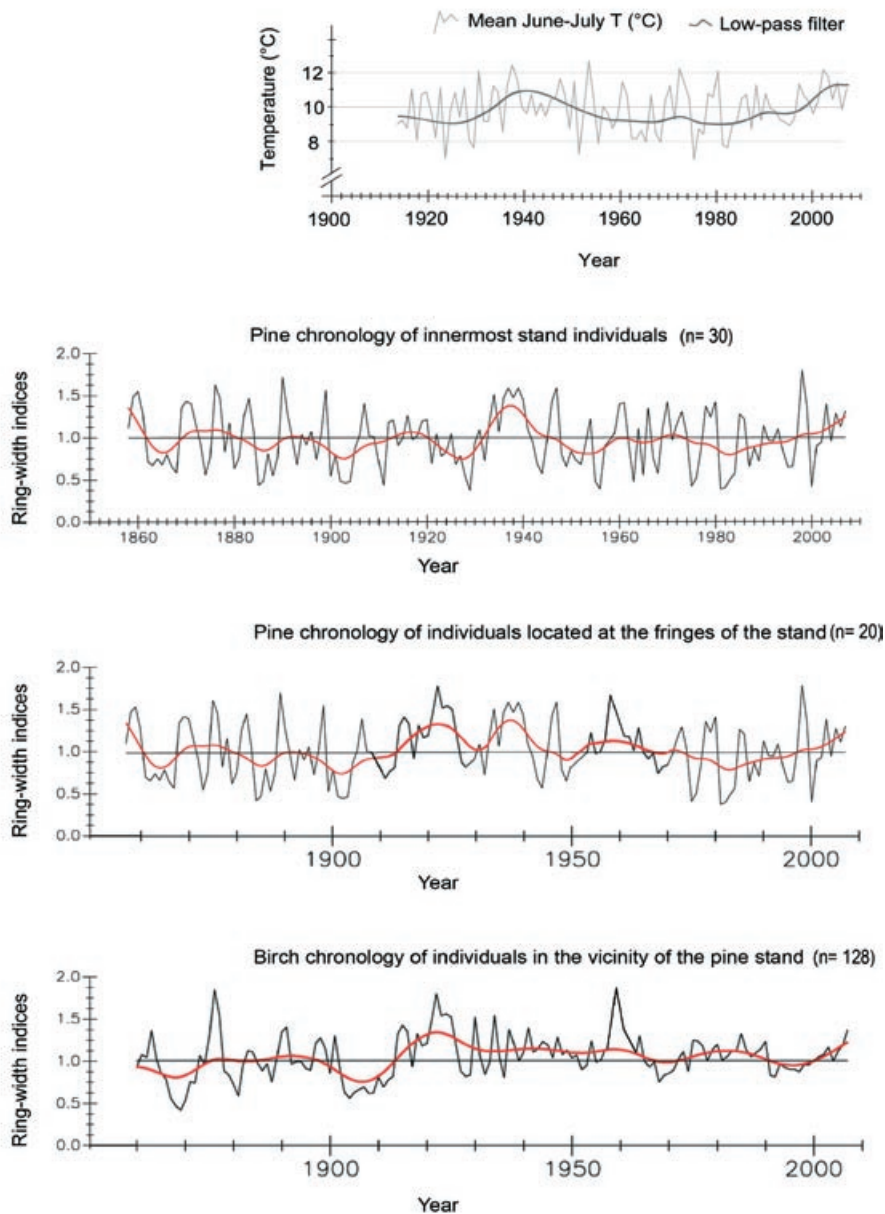


Figure 4.1. Competition effect between pine and birch indicated by the difference in the climatic signal of pine individuals in relation to their distance to birch. Pine individuals located at the fringes of the stand were considered individuals between 5 and 25 m away from the nearest birch (5 m tall) individual. The birch chronology is given as a reference; the most severe moth outbreaks in the past hundred years were documented in 1917-1918 and 1954-1955, causing a strong growth release in the surviving and newly established birch individuals.

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Chapter 5 Conclusions

5.1 General conclusions

This dissertation aimed to identify the causal mechanisms determining shifts in the position and species composition of the sub-Arctic treeline. We focused on the landscape scale and therefore conducted a multi-disciplinary study in a model area. Techniques such as dendrochronological analysis, repeat photography, study of historical documents, and measurements along elevational transects were combined to study the treeline ecotone.

The Torneträsk study area, located in sub-Arctic Sweden (N 68°25', E 19°00'), is characterized by an elevational treeline type set by mountain birch (*Betula pubescens* ssp. *czerepanovii*). Highly contrasting treeline dynamics were recorded despite pronounced 20th century warming by 2.5 °C. Although the birch treeline had on average advanced by 24 m in elevation during the past hundred years, both rapid downslope retreat and centennial-long immobility of the treeline were observed for four out of eight studied sites. The finding that mountain birch may grow as old as 258 years at the sub-Arctic treeline suggests caution with the use of elevational shifts in the treeline position as an accurate bio-climatic proxy. Indeed, not climate warming but a reduced anthropo-zoogenic impact compared to the 19th and early 20th century was found to be the main causal factor for the advancing treeline sites. Since 1920, reindeer (*Rangifer tarandus*) husbandry has changed from an intensive form, whereby the herders lived with their reindeer near the treeline, to an extensive form whereby the reindeer wander freely. Although previously increased mammal herbivory pressure was suggested by dendrochronological analysis of the treeline birches, the availability of accurate documentation on historical human and zoogenic impacts strengthened our study results by providing a reference for validation. Since accurate reports on historical human impacts, including fire dynamics and the introduction of cattle, in sub-Arctic treeline areas are usually not available, the correlation that is often made between rapidly advancing treelines and recent climate warming is not necessarily causal. Previous studies already claimed that anthropo-zoogenic impacts on sub-Arctic treeline areas may be larger than generally believed, and the interpretation of vegetation shifts documented during phases when climate warming coincides with reduced disturbance is particularly difficult. The role of disturbance was found to be critically important in determining treeline dynamics; i.e. irrespective of climate variability,

if disturbance was high, centennial-long treeline stability was observed. Moreover, in the monocormic (single-stemmed) birch forest area high disturbance had resulted in a treeline retreat of 120 m as a consequence of an outbreak of the winter moth (*Operophtera brumata*). The role of disturbance may therefore not be restricted to determining *when* treeline advance will occur in a phase of climate warming, but *if* treeline advance will occur at all.

Whereas the mountain birch treeline showed highly contrasting dynamics in the 20th century, the treelines of thermophilic European aspen (*Populus tremula*) and grey alder (*Alnus incana*) had ubiquitously advanced. Alder had shifted 20 m upslope in the period 1977-2009 and can now be found c. 100 m below the elevational birch treeline. Furthermore, aspen had colonized the birch treeline ecotone and reached elevational positions up to 40 m above the uppermost birch individual. Also tree-sized (>2 m) aspen can now be found at the birch treeline. This finding is a new phenomenon in the European sub-Arctic and presents a rare example of a rapid shift in vegetation composition and structure. The expansion of aspen was mainly attributed to increased sexual regeneration and this process was stimulated by increasing summer temperatures. Therefore, thermophilic aspen is likely to continue its colonisation of the birch treeline ecotone.

However, the outcome of the aspen-birch competition will also depend on future disturbance regimes. Dendrochronological analysis showed that sub-alpine aspen most rapidly expanded after important moth damage to its competitor mountain birch. Whereas 100-year-old birches experienced on average 9.0 years of growth reduction due to moth herbivory, this number only amounted to 1.4 years for similarly aged aspen. On the other hand, aspen suffered severe growth reductions and mortality due to moose (*Alces alces*) browsing, whereas birch was less affected. Also Scots pine (*Pinus sylvestris*) showed increased growth rates when caterpillars of the autumnal moth (*Epirrita autumnata*) moth had defoliated the mountain birch forest. This finding not only further stresses the role of this invertebrate in the competition process between the different tree species in the sub-Arctic Torneträsk area, but also points to a potential bias in summer temperature reconstructions based on pine ring-width chronologies.

Overall, this study showed that sub-Arctic treeline dynamics at the landscape scale are controlled by many interacting factors. These factors attributed to the large discrepancy that exists in our model area between model projections and in situ observations of treeline dynamics. Correlations found between temperature and tree-growth over a short period of time do not imply that the treeline will move upslope. Afterall shifts in plant species distributions depend more on changes in their regeneration success than on changes in growth dynamics of

already established individuals. Hence, the treeline should be studied as the population ecology of plant species on a multi-decadal to centennial time scale. Further, the spatial scale of the study should not be limited to the upper treelimit, but should focus on the entire ecotone extending from the closed forest to the upper- or northernmost tree species individual. Knowledge of the site history such as anthropo-zoogenic disturbances showed to be essential to understand the current position, structure, and species composition of the treeline ecotone. More accurate model projections of the future position of the sub-Arctic treeline can therefore only be obtained if the driving mechanisms identified in this model study will be better incorporated the next generation of dynamic vegetation models.

5.2 Relevance and potential applications

This study brought together unique material such as one-hundred-year-old photographs and treeline measurements, data on anthropo-zoogenic impacts of the past four centuries, and observations along historical elevational transects that have been repeated with one of the original researchers in the field (J. Hoogesteger). This research was undertaken as part of the International Polar Year which had a key aim to provide legacy for future generations of researchers. Most of the presented material would have gone lost if this study would not have been initiated. Through this project we developed a baseline study for future treeline monitoring: i.e. 14 elevational vegetation transects were set up and more than 40 treeline plots have been recorded totalling more than 1 000 treeline individuals distributed over the Torneträsk area (1000 km²).

Although the mountain birch-aspen ecosystem of the Torneträsk area is likely to be very different from other sub-Arctic ecosystems, this process-oriented study identified some important plant-plant and plant-herbivore interactions and should therefore be relevant to several other ecosystems. Factors such as changing disturbance regimes or dynamic competitive interactions between plant species and their respective herbivores are currently not or insufficiently implemented in vegetation models. Our quantification of the differential moth impact on aspen and birch presents a first step in the process of parametrisation and implementation. Also, previous anthropo-zoogenic effects are seldom documented for sub-Arctic areas and present a major weakness in current vegetation models. This study, however, identified the scale and impacts of this disturbance type back to the early 19th century and

provides a unique opportunity to implement these findings in a dynamic vegetation model. Modellers should explore if a new run of the model with the inclusion of anthropo-zoogenic disturbance produce more accurate results of recent (and likely future) treeline dynamics.

Finally, the finding that pine ring growth, a proxy for summer temperature, was positively affected by moth outbreak damage on its competitor mountain birch, is noteworthy and should be taken into account when doing dendrochronological analysis in the sub-Arctic birch forest. Therefore, pine samples with a deviating signal from climate records (if available) and the innermost individuals of the pine stand should be excluded from the climatic analysis.

5.3 Perspectives and suggestions for future research

Several perspectives and new research questions arise from this study that are likely to provide a deeper insight in the controlling factors of sub-Arctic treeline dynamics.

1. Thermophilic alder expanded its elevational and local geographical range in the sub-Arctic Torneträsk area. Although increasing temperatures presumably contributed to this finding, future research should focus on the identification of the causal mechanisms for this range expansion. Since alder appeared to be less affected by herbivory, it may have a competitive advantage.

2. This study showed that mountain birch has a high potential for dendrochronological analysis if sufficient samples are taken from suitable birch stems and tree-cores are well prepared for microscopic analysis. The finding that birch stems may grow as old as 258 years theoretically allows for disturbance events back to 1750. By sampling more birch individuals at this exceptionally old treeline site and conducting a detailed study of wood anatomical features, we could possibly extend the moth outbreak record to the 18th and 19th century and learn more about the cyclicity of these outbreaks and their long-term effects on the sub-Arctic mountain birch forest areas. The dendrochronological methodology introduced in chapter 2.1 may also offer a technique to study approximate local reindeer population dynamics and historical reindeer migration routes.

3. Modelling future disturbance regimes is one of the biggest challenges towards more accurate projections of vegetation migrations. Seen the importance of moth outbreaks on the position

and vigour of the birch treeline, modelling the relationships between egg mortality of the two moth species (*Epirrita autumnata* and *Operophtera brumata*), minimum winter temperatures, and local topography is needed.

4. More circum-Arctic treeline studies are needed that focus on site history by studying historical documents, photographs, and tree-rings. This would increase our understanding of the role of anthropo-zoogenic effects on treeline dynamics at the circum-Arctic scale.

5. Snow was found to play a significant role in birch treeline dynamics in and also affects population dynamics and mobility of vertebrate herbivores (chapters 2.1 and 4.1). Whereas current research generally focuses on the effects of increasing temperatures on vegetation, future studies should concentrate on changes in snow depth, duration, distribution, and physical characteristics such as increased frequency of ice-layer formation in the winter snowpack.

Appendix 1. High-resolution transect design for Mount Nuolja.

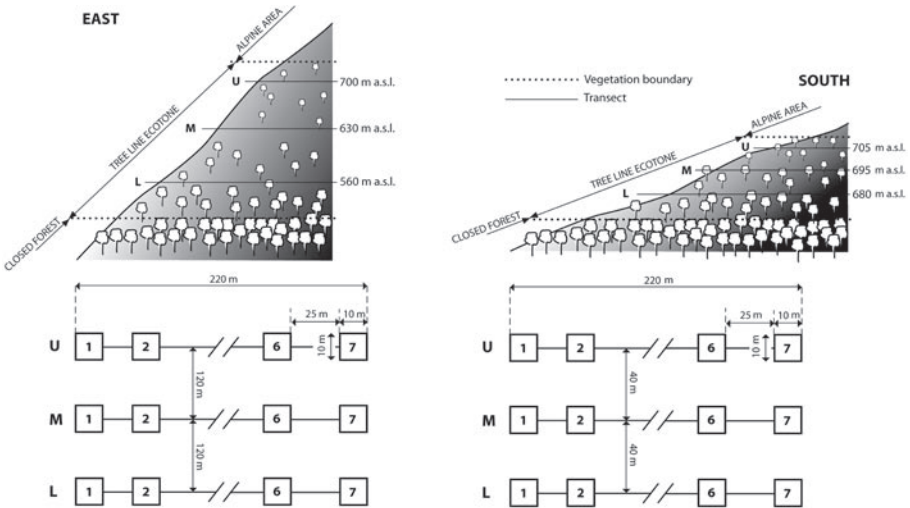


Figure A1. High-resolution transect design for Mount Nuolja. Each transect line had seven plots, numbered from left to right. The spatial intervals refer to actual distances in metres. Abbreviations used: U: Upper transect line; M: Middle transect line; L: Lower transect line.

Appendix 2. Dendrochronological analysis

Tree sampling

Tree cores were taken as low as possible (at *c.* 20 cm stem height), so that the presumed year of establishment could be determined by subsequent tree-ring counting. The mean difference in the number of annual rings counted at the root collar and at 20 cm stem height of the saplings was added to the number of tree-rings counted on the tree cores to make a better estimate of the year of tree establishment. Cores taken at 20 cm stem height or higher are more suitable for the identification of disturbance events (Schweingruber, 2007). Stunted and older individuals were also cored at breast height to avoid tension wood and reduce the number of missing rings that are common at lower stem height (Sonesson & Hoogesteger, 1983).

Ring-width chronology construction

Ring-widths were measured up to 0.01 mm precision using a LINTABTM measuring stage and the dendro software package TSAPWinTM v. 0.53 (Rinn, 2003, Heidelberg, Germany). Ring-width chronologies were built for the reference birches sampled below the tree line ecotone of the five tree line sites located at Mount Nuolja (S3_{East} and S3_{South}) and at the Sonesson and Hoogesteger transects (N1, N2, and S1; Fig. 1). These five birch chronologies, in addition to the pine chronology, served as a ring-width reference for the tree line birches. Chronology building was done in TSAPWinTM using both visual comparisons and well-established statistical parameters. Values of tBP greater than 4.0 and of GLK% ('Gleichläufigkeit'; the degree that trees react with a similar growth increase or decrease compared to the previous growing season) greater than 65% were considered significant in analogy with previous studies (Levanič & Eggertsson, 2008). In this way, missing rings were generally easily identified. Individual ring-width series were standardised in the program ARSTAN (Cook, 1985) using regional curve standardisation (Briffa et al., 1992).

Interpretations of stem cross section anatomy

In addition to a statistical ring-width approach, we performed a meticulous study of the wood anatomical features of the tree line birches. This analysis generally provides more information about the disturbance event than do statistics of differences in ring-widths (Levanič & Eggertsson, 2008). Frost rings, white rings, browsing scars and callus tissue all point to specific damage patterns (Fig. A2).

Narrow rings can be the result of e.g. a cool summer, reindeer (or other mammal) browsing, or moth herbivory. If only young and small (<2 m) tree line individuals show a narrow ring in year 'x', a cool summer is less likely to be the cause of the growth reduction. In this case reindeer browsing is more likely since the browse height of reach for reindeer is limited to *c.* 1.5 m and will therefore mainly affect saplings (Helle, 2001). This hypothesis may later be confirmed if one or more young individuals are found that show a browsing scar for year 'x' (Fig. A2c). If only older individuals (>60 years) show a narrow ring for year 'y', a cool summer is less likely, but defoliation by the autumnal or winter moth, who select for older individuals (Bylund, 1995), is more likely. This hypothesis may later be confirmed if one or more older individuals show a 'white' ring for year 'y', pointing to a defoliation event by an invertebrate (Schweingruber, 2007) (Fig. A2d).

Reindeer mainly strip off the birch leaves, rather than gnawing on the twigs and stems (Haukioja & Heino, 1974). Therefore, a part of the browsing scars observed in the tree-rings may be attributed to moose, voles, and particularly to mountain hare (*Lepidus timidus* L.) that also feed on birch, although predominantly in winter (Danell & Huss-Danell, 1985). However, the most ubiquitous growth reductions accompanied by several small browsing scars were identified for the summer of 1929, the year when reindeer population numbers reached an absolute peak (Fig. 8 and Table 4 in Chapter 2.1). Therefore, we assumed throughout the study that the browsing scars documented in the growing season were attributed to reindeer.

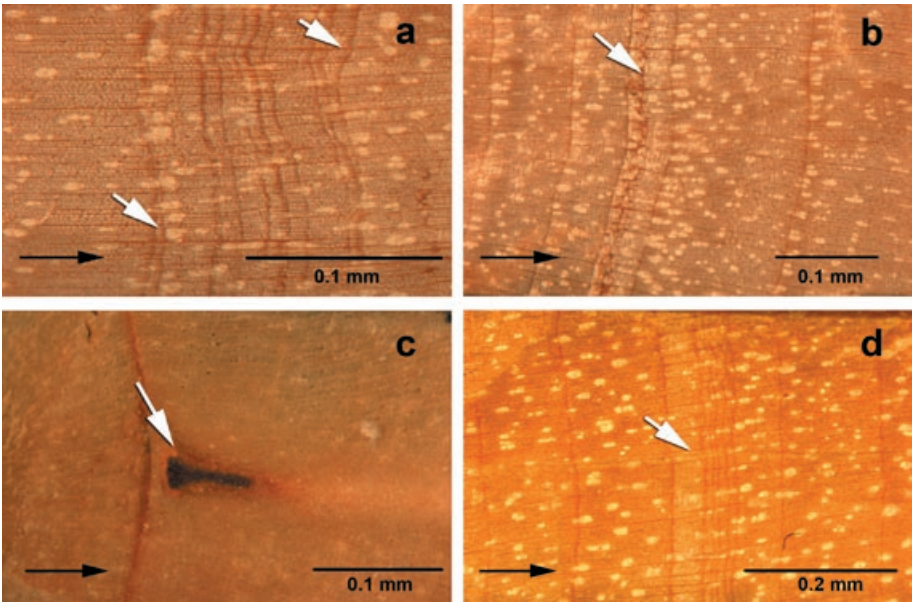


Figure A2. Study of wood anatomical features in mountain birch. The white arrows point to the area of interest, whereas the black arrows show the direction of growth. Birch individuals subjected to biotic or climatic stress regularly show wedging rings (a) that may result in erroneous dating. Pointer years such as the frost ring of 1984 shown in (b) can help in tracing these partly or completely missing rings. A typical frost ring (b) showing damage to the cambium. In June 1984, a 27-day period of warm spring weather with minimum temperatures up to +11.9 °C was suddenly interrupted by three days of -1.3 °C, recorded at the Abisko meteorological station located 300 m below the tree line. A small scar (c) at 110 cm stem height presumably caused by reindeer browsing in the early summer of 1929. A bright coloured ring followed by four exceptionally narrow rings (d) points to complete tree defoliation by an insect.

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Appendix 3. Historical anthropozoogenic impact in the Torneträsk area

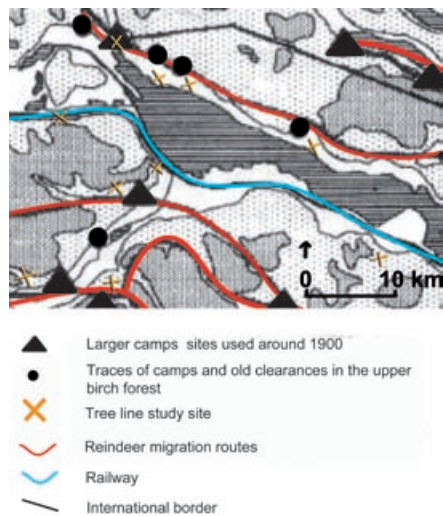


Figure A3. Historical anthropozoogenic impact in the Torneträsk area. The points of relatively intense historical impact identified by Emanuelsson (1987) were relocated in the field and the distances between these points and the studied tree line sites were recorded by a GPS (see Table 2 on page 48).

Appendix 4. Expansion of thermophilic aspen

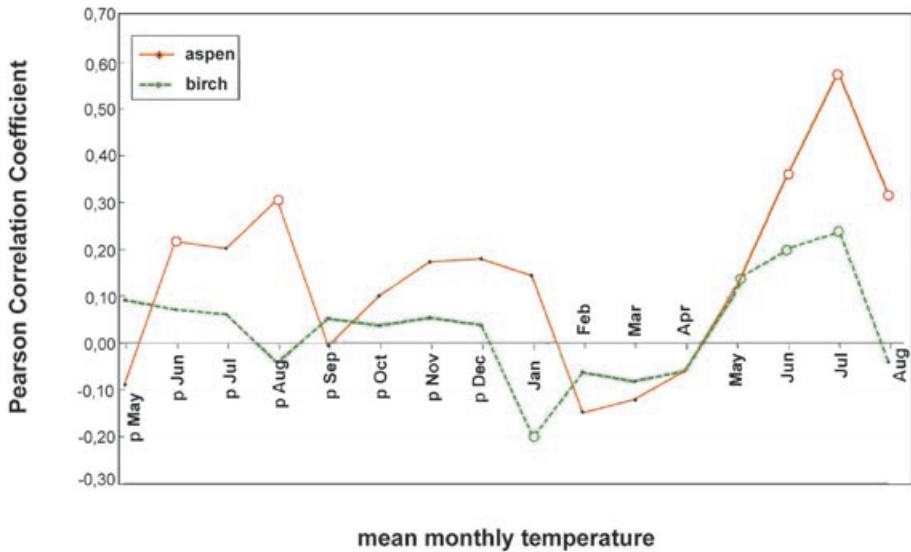


Figure A4. Correlation coefficients between temperature and ring-growth for both sub-alpine aspen and birch. Significant values are marked with a circle. No correlation was found between ring-growth and precipitation. pMay stands for May temperature of the year previous to ring-formation.



Figure A5. Fast-growing 15-year-old aspen individuals 40 m upslope the mountain birch treeline ecotone (individuals 1.5m tall).

Appendix 5. Expansion of thermophilic aspen hampered by moose browsing



Figure A6. Recent aspen recruits in the birch forest showing the potential for aspen expansion. All these recruits, extending up to 50 m from the closed aspen stand, established after 1990 during climate warming. Although most recruits that can be seen here still have some foliage, they have been seriously browsed and there is little chance they will grow to trees.



Figure A7. Young aspen recruits that colonised the birch forest are killed because of browsing (twig stripping and stem breakage) by moose.



Figure A8. Current condition of the aspen stand: severe bark stripping and crown and twig browsing threatens the survival of the stand, particularly since new recruits are systematically removed.

List of publications

Van Bogaert, R., Walker, D., Jia, G.J., Grau, O., Hallinger, M., De Dapper, M., Jonasson, C. and Callaghan, T.V. (2007) Recent changes in vegetation. In: *Arctic Report Card 2007* (ed. J. Richter-Menge). NOAA, 33-40.

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Van Bogaert, R., Jonasson, C., De Dapper, M. and Callaghan, T.V. (2010) Range expansion of thermophilic aspen (*Populus tremula* L.) in sub-Arctic Sweden. *Arctic, Antarctic, and Alpine Research*, 42, 362-375

Van Bogaert, R., Haneca, K., Hoogesteger, J., Hållmarker, M., Jonasson, C., De Dapper, M., and Callaghan, T.V. (2011) A century of treeline changes in sub-Arctic Sweden show local and regional variability and only a minor role of 20th century climate warming. *Journal of Biogeography*, 38, 907-921