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Abstract

In subarctic 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 favored 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 subarctic 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, subarctic 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 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-latitudinal 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 subarctic Europe would be expected to be more susceptible to invasion by more thermophilic tree species in response to increasing temperatures. Although elevated CO_2 levels should be advantageous for slow-growing birch, responses to continued summer warming will probably dominate over responses to elevated CO_2 levels by stimulating the establishment and spread of fast-growing, more thermophilic tree species (Skre, 2001).

In this subarctic 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 colonized vast areas of subarctic 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 (Hedenås 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 subarctic, there are no records of recent changes in distribution or abundance.

When revisiting altitudinal transects in subarctic 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 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 subarctic 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 km^2, and is located at the eastern fringe of the subarctic 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 km^2 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., in press). 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. 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
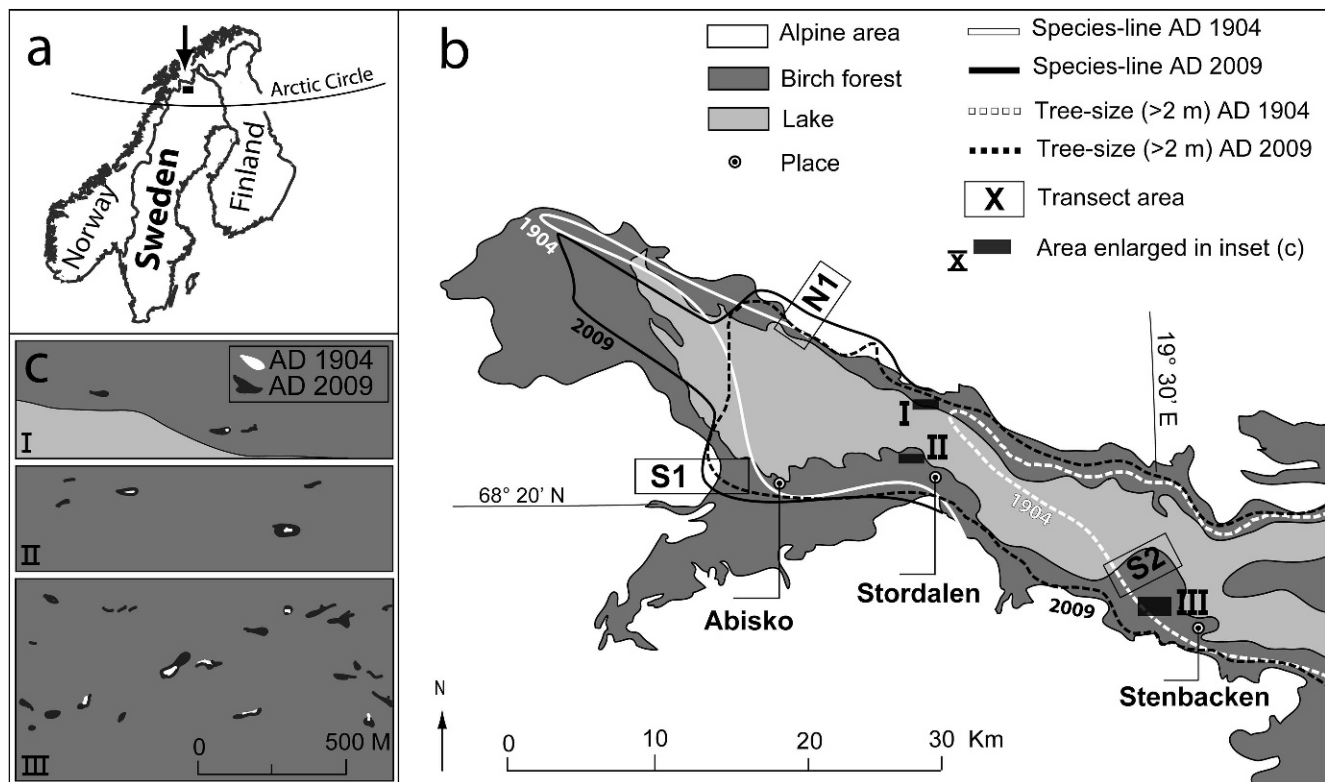
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FIGURE 1. (a) Study area in subarctic Sweden (b, c) showing aspen dynamics since 1904. The figure is based on the studies by Sylvén (1904) and Fries (1913) and dendrochronological analysis. Figure 1b shows the change in position of the western boundary 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.

(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

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 km^2, was surveyed (Fig. 1b). Each autumn we climbed to the alpine area to survey the subalpine forest area when aspen leaf color (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.

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 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
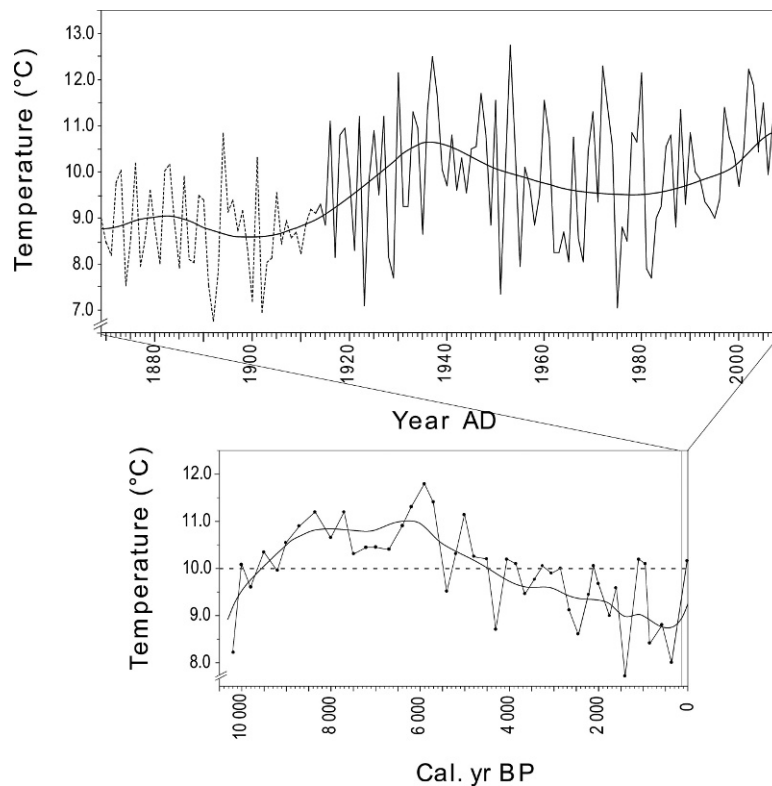
FIGURE 2. Summer temperature (June–July) trend with low-pass filter for the Torneträsk area since the deglaciation about 10,000 cal. yr BP (modified from Holmgren and Tjus, 1996; Grudd et al., 2002; Hammarlund et al., 2002). Note that the bottom graph shows low-frequency temperature variability. This 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.

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 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).

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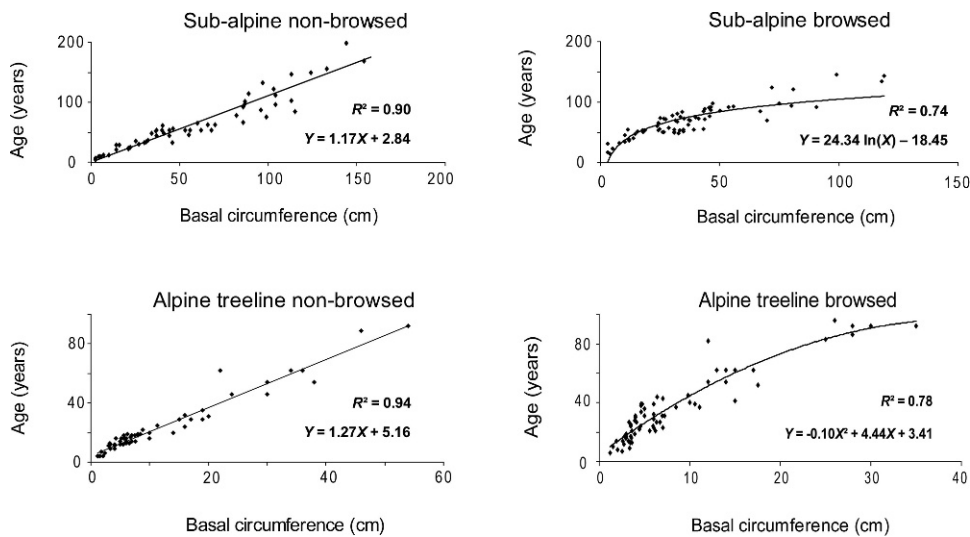
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FIGURE 3. Scatterplot of age versus basal circumference (BC) for the four classes of aspen. Trend lines with equations and R^2 values are plotted. These regressions were used to convert BC into age for all other aspen individuals within the sampled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

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 (Jobling, 1990). We further assumed that the trees within the aspen stand had spread via asexual reproduction, i.e. root suckering (Suvanto and Latva-Karjanmaa, 2005). 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
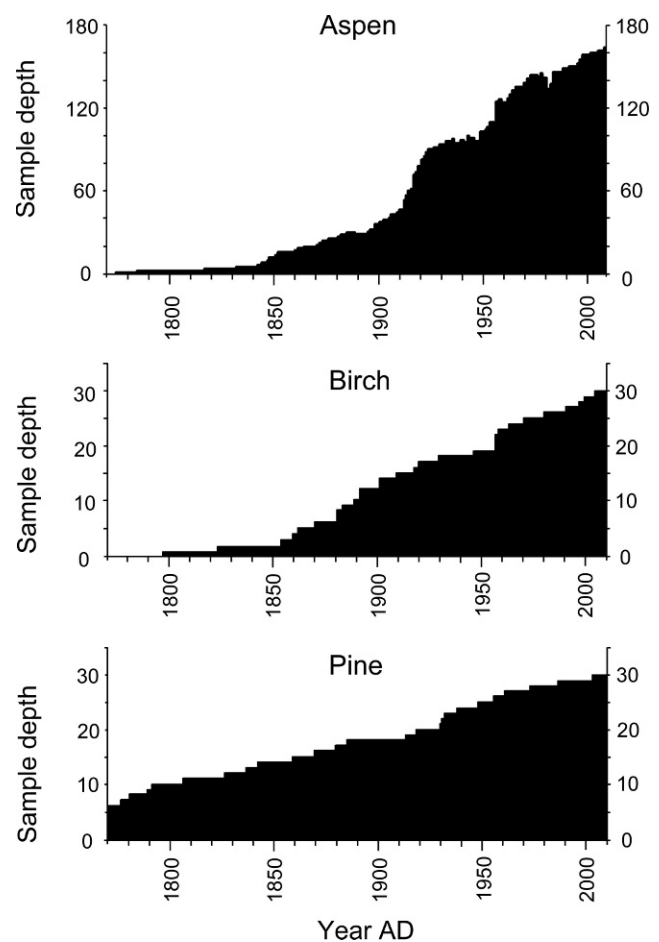

FIGURE 4. Bar chart of sample depth over time of the sampled tree species. The oldest pine individual that was sampled had established in the year A.D. 1638. Note that the scale of the *Y*-axes varies between the different plots.

TABLE 1

Establishment, expansion, and herbivory features of aspen in the Torneträsk area, subarctic Sweden. Aspen stands in both the subalpine 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-year period during which mean temperature increased), 1951–1990 (i.e. a 40-year period during which mean temperature decreased), and the period 1991–2009 characterized by recent warming (Fig. 2). 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 2), were also included. 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%)

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

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.

ASEXUAL REGENERATION ANALYSIS

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 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).

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 2 m 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

TABLE 2

Historical and current aspen locations in the Torneträsk area, subarctic Sweden, denoted in Figure 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.

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.

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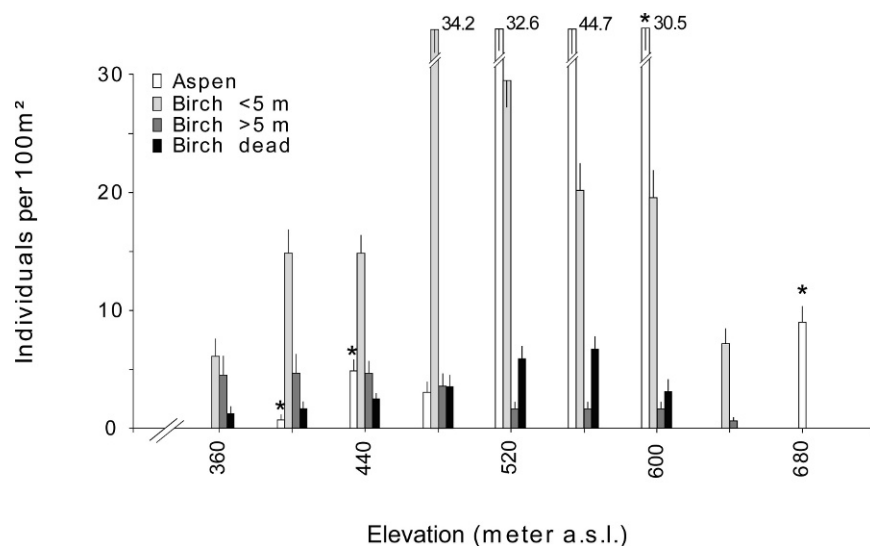
FIGURE 5. Aspen and birch densities with standard errors along an altitudinal transect in area N1 that experienced a severe moth outbreak in 1964–1965. This transect clearly shows the high abundance of aspen in the disturbed (i.e. high density of dead trees) and still unrecovered monocormic birch forest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

TABLE 3A

Assumed sexual regeneration events in aspen related to climatic and biotic factors for the period 1913–2009. 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 negative birch-minus-pine indices, SE = 0.03). Values that significantly ($P \leq 0.05$) differed from the mean are marked with an asterisk.

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	−0.43
1948	1	+1.7	+18	+0.40
1973	2	+2.3*	+42	+0.02

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 three transects on the northern side of the lake that contained subalpine aspen found in an area of birch forest recently disturbed and opened (N1a, 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). 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).

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 favorable for asexual reproduction, i.e. R^2 significantly ($P \leq 0.05$) increased to 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

TABLE 3B

Sexual regeneration covariates. Variables that significantly ($P \leq 0.05$) explained the annual variance in aspen stands established using forward selection in the regression analysis are given. For both subalpine 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 ($P \leq 0.05$) correlated with the annual number of aspen stands established are marked with an asterisk.

| 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

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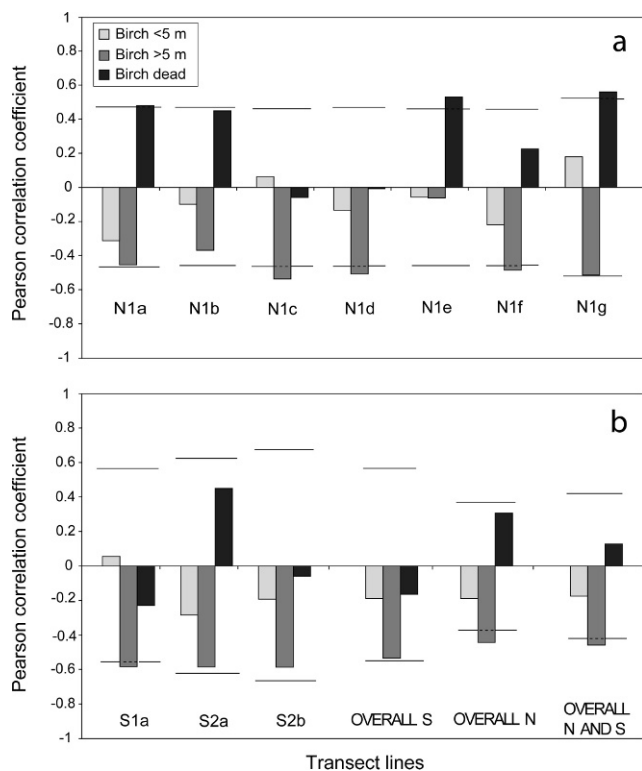
FIGURE 6. Pearson correlation coefficients quantifying relationships between aspen density and density of three birch classes; i.e. small birches (<5 m), tall birches (>5 m), and dead birches. Part (a) shows the seven altitudinal transects on the northern side of the lake (area N1 in Fig. 1b), and (b) 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.

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.

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 colonized 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 mountain 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 subarctic 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) aspen. 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 subarctic. 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; Sylvén, 2003; Van Bogaert et al., 2009).

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 (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., Worrell, 1995; Johansson, 2002), 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).

Assumed asexual regeneration numbers in aspen related to climatic and biotic factors for the period 1913–2009. 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 negative birch-minus-pine indices, SE = 0.03). Values that significantly ($P \leq 0.05$) differed from the mean are marked with an asterisk.

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

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, 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 (*Populus tremuloides* Michx.) at the treeline in the San Juan Mountains of Colorado, U.S.A. On the other hand, high temperatures (>25 °C) sharply lower germination rates in aspen, analogous to low temperatures (<5 °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

TABLE 4B

Asexual regeneration covariates of aspen. Variables that significantly ($P \leq 0.05$) explained the variance in annual number of assumed asexually produced aspen trees using forward selection in the regression analysis are given. For both subalpine 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 ($P \leq 0.05$) correlated with the annual numbers of aspen stands established are marked with an asterisk.

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

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, subarctic Sweden, 1 September 2007.

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 subarctic 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-latitudinal 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, 3B), indicating that a sufficient moisture supply is essential for successful seedling establishment (e.g., 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, 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 occurred per decade; 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 (Fig. 2), 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 colonized 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 subarctic (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 expan-

sion. 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 favor 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 subarctic 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.

Acknowledgments

References Cited

ACIA, 2005, *Arctic Climate Impact Assessment*. Cambridge, U.K.: Cambridge University Press, 1042 pp.

Alexandersson, H., Karlström, C., and Larsson-McCann, S., 1991: Temperature and precipitation in Sweden, 1961–90. Reference normals. *SMHI Reports, Meteorology and Climatology*, 81: 1–87.

Barnekow, L., 1999: Holocene tree-line dynamics and inferred climatic changes in the Abisko area, northern Sweden, based on macrofossil and pollen records. *The Holocene*, 9: 253–265.

Berglund, B. E., Barnekow, L., Hammarlund, D., Sandgren, P., and Snowball, I. F., 1996: Holocene forest dynamics and climate changes in the Abisko area, northern Sweden—The Sonesson model of vegetation history reconsidered and confirmed. *Ecological Bulletins*, 45: 15–30.

Bigler, C., Larocque, I., Peglar, S. M., Birks, H. J. B., and Hall, R. I., 2002: Quantitative multiproxy assessment of long-term patterns of Holocene environmental change from a small lake near Abisko, northern Sweden. *The Holocene*, 12: 481–496.

Børset, O., 1960: Silviculture of aspen. *Scottish Forestry*, 14: 68–80.

Butler, D. R., Malanson, G. P., and Cairns, D. M., 1994: Stability of alpine treeline in Glacier National Park, Montana, U.S.A. *Phytocoenologia*, 22: 485–500.

Cairns, D., Lafon, C., Moen, J., and Young, A., 2007: Influences of animal activity on treeline position and pattern: implications for treeline responses to climate change. *Physical Geography*, 28: 419–433.

Callaghan, T. V., Crawford, R. M. M., Eronen, M., Hofgaard, A., Payette, S., Rees, W. G., Skre, O., Sveinbjornsson, J., Vlassova, T. K., and Werkman, B. R., 2002: The dynamics of the tundra-taiga boundary: an overview and suggested coordinated and integrated approach to research. *Ambio*, 12: 3–5.

Callaghan, T. V., Bjorn, L. O., Chapin, F. I., Chernov, Y., Christensen, T., Huntley, B., and Ims, R., et al. (2005). Chapter 7: Arctic tundra and polar desert ecosystems. *In* Berner, J., Symon, C., Arris, L., and Heal, O. W. (eds.), *ACIA: Arctic Climate Impact Assessment*. Cambridge: Cambridge University Press, 243–352.

Callaghan, T. V., Bergholm, F., Christensen, T. R., Jonasson, C., Kokfelt, U., and Johansson, M., in press: A new climate era in the sub-Arctic: Accelerating climate changes and multiple impacts. *Geophysical Research Letters*.

Camarero, J., and Gutiérrez, E., 2007: Response of *Pinus uncinata* recruitment to climate warming and changes in grazing pressure in an isolated population of the Iberian System (NE Spain). *Arctic, Antarctic, and Alpine Research*, 39: 210–217.

Carlsson, B. Å., Karlsson, P. S., and Svensson, B. M., 1999: Alpine and subalpine vegetation. *In* Sjögren, E. (ed.), *Swedish Plant Geography*. Uppsala: Acta Phytogeographica Suecica, 84: 75–89.

Chapin, F. S. I., Callaghan, T. V., Bergeron, Y., Fukuda, M., Johnstone, J. F., Juday, G., and Zimov, S. A., 2004: Global change and the boreal forest: thresholds, shifting states or gradual change? *Ambio*, 33: 361–365.

Chapin, F. S. I., Berman, M., Callaghan, T. V., Convey, P., Crepin, A.-S., Danell, K., Ducklow, H., Forbes, B., Kofinas, G., McGuire, A. D., Nuttall, M., Virginia, R., Young, O., and Zimov, S., 2005: Polar systems. *In* Hassan, H., Scholes, R., and Ash, N. (eds.), *Millennium Ecosystem Assessment: Ecosystems and Human Well-being: Current State and Trends*. Washington: Island Press, 717–743.

Dalen, L., and Hofgaard, A., 2005: Differential regional treeline dynamics in the Scandes Mountains. *Arctic, Antarctic, and Alpine Research*, 37: 284–296.

Danby, R., and Hik, D., 2007: Evidence of recent treeline dynamics in southwest Yukon from aerial photographs. *Arctic*, 60: 411–420.

Davis, M. B., 1986: Climatic instability, time lags, and community disequilibrium. *In* Diamond, J., and Case, T. J. (eds.), *Community Ecology*. New York: Harper and Row, 269–284.

Davis, M. B., 1987: Invasions of forest communities during the Holocene: beech and hemlock in the Great Lakes region. *In* Gray, A. J., Crawley, M. J., and Edwards, P. J. (eds.), *Colonization, Succession and Stability*. Oxford: Blackwell Scientific Publications, 373–393.

Eckstein, D., Hoogesteger, J., and Holmes, R. L., 1991: Insect-related differences in growth of birch and pine at northern treeline in Swedish Lapland. *Holarctic Ecology*, 14: 18–23.

Elliott, G. P., and Baker, W. L., 2004: Quaking aspen (*Populus tremuloides Michx.*) at treeline: a century of change in the San Juan Mountains, Colorado, USA. *Journal of Biogeography*, 31: 733–745.

ESRI Inc., 2005: ArcGIS 9.0. Redlands, California.

Fries, T. C. E., 1913: *Botanische Untersuchungen im nördlichsten Schweden (Botanical studies in northernmost Sweden)*. PhD thesis. Uppsala University, Uppsala: Flora och Fauna, 361 pp.

Fries, T. C. E., 1925: The vertical distribution of some plants on Nuolja (Torne Lappmark). *Botaniska Notiser*, 126: 207–238.

Fritts, H. C., 1976: *Tree Rings and Climate*. New York: Academic Press, 576 pp.

Green, R. F., and Noakes, D. L., 1995: Is a little bit of sex as good as a lot? *Journal of Theoretical Biology*, 174: 87–96.

Grime, J. P., Fridley, J. D., Askew, A. P., Thompson, K., Hodgson, J. G., and Bennett, C. R., 2008: Long-term resistance to simulated climate change in an infertile grassland. *Proceedings of the National Academy of Sciences*, 105: 10028–10032.

Grudd, H., Briffa, K. R., Karlen, W., Bartholin, T. S., Jones, P. D., and Kromer, B., 2002: A 7400-year tree-ring chronology in northern Swedish Lapland: natural climatic variability expressed on annual to millennial timescales. *The Holocene*, 12: 657–665.

Hagen, S. B., Jepsen, J. U., Ims, R. A., and Yoccoz, N. G., 2007: Shifting altitudinal distribution of outbreak zones of winter moth *Operophtera brumata* in sub-arctic birch forest: a response to recent climate warming? *Ecography*, 30: 299–307.

Hammarlund, D., Barnekow, L., Birks, H. J. B., Buchardt, B., and Edwards, T. W. D., 2002: Holocene changes in atmospheric circulation recorded in the oxygen-isotope stratigraphy of lacustrine carbonates from northern Sweden. *The Holocene*, 12: 339–351.

Hedenås, H., and Ericson, L., 2008: Species occurrences at stand level cannot be understood without considering the landscape context: cyanolichens on aspen in boreal Sweden. *Biological Conservation*, 141: 710–718.

Heinrichs, M. L., Peglar, S. M., Bigler, C., and Birks, H. J. B., 2005: A multi-proxy palaeoecological study of Alanen Laanijärvi, a boreal-forest lake in Swedish Lapland. *Boreas*, 34: 192–206.

Hofgaard, A., 1997: Inter-relationships between treeline position, species diversity, land use and climate change in the central Scandes Mountains of Norway. *Global Ecology and Biogeography Letters*, 6: 419–429.

Holmgren, B., and Tjus, M., 1996: Summer air temperatures and tree-line dynamics at Abisko. *Ecological Bulletins*, 45: 159–169.

Holtmeier, F., Broll, G., Müterthies, A., and Anschlag, K., 2003: Regeneration in the treeline ecotone: northern Finnish Lapland. *Fennia*, 181: 103–128.

Holtmeier, F. K., and Broll, G., 2005: Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global Ecology and Biogeography*, 14: 395–410.

Høye, T. T., Post, E., Meltofte, H., Schmidt, N. M., and Forchhammer, M. C., 2007: Rapid advancement of spring in the High Arctic. *Current Biology*, 17: R449–R451.

Ims, R., Yoccoz, N., Bråthen, K., Fauchald, P., Tveraa, T., and Hausner, V., 2007: Can reindeer overabundance cause a trophic cascade? *Ecosystems*, 10: 607–622.

Jepsen, J. U., Hagen, S. B., Ims, R. A., and Yoccoz, N. G., 2008: Climate change and outbreaks of the geometrids *Operophtera brumata* and *Epirrita autumnata* in subarctic birch forest: evidence of a recent outbreak range expansion. *Journal of Animal Ecology*, 77: 257–264.

Jobling, J., 1990: *Poplars for Wood Production and Amenity*. London: HMSO, 75 pp.

Johansson, T., 2002: Increment and biomass in 26- to 91-year-old European aspen and some practical implications. *Biomass and Bioenergy*, 23: 245–255.

Karlsson, P. S., Tenow, O., Bylund, H., Hoogesteger, J., and Weih, M., 2004: Determinants of mountain birch growth in situ: effects of temperature and herbivory. *Ecography*, 27: 659–667.

Kay, C., 1993: Aspen seedlings in recently burned areas of Grand Teton and Yellowstone National Parks. *Northwest Science*, 67: 94–104.

Kharuk, V. I., Ranson, K. J., Im, S. T., and Naurzbaev, M. M., 2006: Forest-tundra larch forests and climatic trends. *Russian Journal of Ecology*, 37: 291–298.

Kulakowski, D., Veblen, T. T., and Drinkwater, S., 2004: The persistence of quaking aspen (*Populus tremuloides*) in the Grand Mesa area Colorado. *Ecological Applications*, 14: 1603–1614.

Kullman, L., 1983: Past and present tree-lines of different species in the Handölan Valley, central Sweden. *Nordicana*, 47: 25–45.

Kullman, L., 2002: Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology*, 90: 68–77.

Kullman, L., and Kjällgren, L., 2006: Holocene pine tree-line evolution in the Swedish Scandes: Recent tree-line rise and climate change in a long-term perspective. *Boreas*, 35: 159–168.

Kullman, L., and Öberg, L., 2009: Post–Little Ice Age tree line rise and climate warming in the Swedish Scandes: a landscape ecological perspective. *Journal of Ecology*, 97: 415–429.

Latva-Karjanmaa, T. M., Suvanto, L. I., Leinonen, K., and Rita, H., 2003: Emergence and survival of *Populus tremula* seedlings under varying moisture conditions. *Canadian Journal of Forest Research*, 33: 2081–2088.

Lloyd, A. H., and Fastie, C. L., 2002: Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change*, 52: 481–509.

Lloyd, A. H., and Fastie, C. L., 2003: Recent changes in treeline forest distribution and structure in interior Alaska. *Ecoscience*, 10: 176–185.

Manier, D. J., and Laven, R. D., 2002: Changes in landscape patterns associated with the persistence of aspen (*Populus tremuloides* Michx.) on the western slope of the Rocky Mountains, Colorado. *Forest Ecology and Management*, 167: 263–284.

Masek, J. G., 2001: Stability of boreal forest stands during recent climate change: evidence from Landsat satellite imagery. *Journal of Biogeography*, 28: 967–976.

McDonough, W. T., 1985: Sexual reproduction, seeds and seedlings. *In* DeByle, N. V., and Winokur, R. P. (eds.), *Aspen: Ecology and Management in the Western United States*. Fort Collins, Colorado: USDA Forest Service Technical Report, 119: 25–28.

Myneni, R. B., Keeling, C. D., Tucker, C. J., Asrar, G., and Nemani, R. R., 1997: Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, 386: 698–702.

Neuvonen, S., Bylund, H., and Tømmervik, H., 2005: Forest defoliation risks in birch forest by insects under different climate and land use scenarios in northern Europe. *In* Wielgolaski, F. (ed.), *Plant Ecology, Herbivory, and Human Impact in Nordic Mountain Birch Forests*. New York: Springer, 125–138.

Nilssen, A., and Tenow, O., 1990: Diapause, embryo growth and supercooling capacity of *Epirrita autumnata* eggs from northern Fennoscandia. *Entomologia Experimentalis et Applicata*, 57: 39–55.

Östlund, L., Zackrisson, O., and Axelsson, A.-L., 1997: The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forestry Research*, 27: 1198–1206.

Payette, S., 2007: Contrasted dynamics of northern Labrador tree lines caused by climate change and migrational lag. *Ecology*, 88: 770–780.

Peros, M. C., Gajewski, K., and Viau, A. E., 2008: Continental-scale tree population response to rapid climate change, competition and disturbance. *Global Ecology and Biogeography*, 17: 658–669.

Persson, E., 1952: Träd-och skoggränsstudier på nordsidan av Torneträsk (Tree- and forestline studies on the northern side of Lake Torneträsk). M.Sc. thesis. Lund University, 24 pp.

Post, E., Forchhammer, M. C., Bret-Harte, M. S., Callaghan, T. V., Christensen, T. R., Elberling, B., Fox, A. D., Gilg, O., Hik, D. S., Hoye, T. T., Ims, R. A., Jeppesen, E., Klein, D. R., Madsen, J., McGuire, A. D., Rysgaard, S., Schindler, D. E., Stirling, I., Tamstorf, M. P., Tyler, N. J. C., van der Wal, R., Welker, J., Wookey, P. A., Schmidt, N. M., and Aastrup, P., 2009: Ecological dynamics across the Arctic associated with recent climate change. *Science*, 325: 1355–1358.

Räisänen, J., and Alexandersson, H., 2003: A probabilistic view on recent and near future climate change in Sweden. *Tellus*, 55: 113–125.

Rickebusch, S., Lischke, H., Bugmann, H., Guisan, A., and Zimmermann, N. E., 2007: Understanding the low-temperature limitations to forest growth through calibration of a forest dynamics model with tree-ring data. *Forest Ecology and Management*, 246: 251–263.

Romme, W. H., Turner, M. G., Gardner, R. H., Hargrove, W. W., Tuskan, G. A., Despain, D. G., and Renkin, R. A., 1997: A rare episode of sexual reproduction in aspen (*Populus tremuloides* Michx.) following the 1988 Yellowstone fires. *Natural Areas Journal*, 17: 17–25.

Saelthun, N. R., and Barkved, L. J., 2003: *Climate Change Scenarios for the SCANNET Region*. Norwegian Institute for Water Research (NIVA) Rep. SNO 4663.

Schier, G. A., Jones, J. R., and Winokur, R. P., 1985: Vegetative regeneration. *In* DeByle, N. V., and Winokur, R. P. (eds.), *Aspen: Ecology and Management in the Western United States*. Fort Collins, Colorado: USDA Forest Service Technical Report, 119: 29–33.

Schmölcke, U., and Zachos, F. E., 2005: Holocene distribution and extinction of the moose (*Alces alces*, Cervidae) in Central Europe. *Mammalian Biology*, 70: 329–344.

Schweingruber, F., Eckstein, D., Serre-Bachet, F., and Braker, O., 1990: Identification, presentation and interpretation of event years and pointer years in dendrochronology. *Dendrochronologia*, 8: 9–38.

Seppä, H., 1998: Postglacial trends in palynological richness in the northern Fennoscandian tree-line area and their ecological interpretation. *The Holocene*, 8: 43–53.

Seppä, H., and Birks, H. J. B., 2001: July mean temperature and annual precipitation trends during the Holocene in the Fennoscandian tree-line area: pollen-based climate reconstructions. *The Holocene*, 11: 527–539.

Shiyatov, S., Terent'ev, M., Fomin, V., and Zimmermann, N., 2007: Altitudinal and horizontal shifts of the upper boundaries of open and closed forests in the Polar Urals in the 20th century. *Russian Journal of Ecology*, 38: 223–227.

Sitch, S., Huntingford, C., Gedney, N., Levy, P. E., Lomas, M., Piao, S. L., Betts, R., Ciais, P., Cox, P., Friedlingstein, P., Jones, C. D., Prentice, I. C., and Woodward, F. I., 2008: Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). *Global Change Biology*, 14: 2015–2039.

Skre, O., 2001: Climate change impacts on mountain birch ecosystems. *In* Wielgolaski, F. E. (ed.), *Nordic Mountain Birch Ecosystems*. Paris: UNESCO and Carnforth: Parthenon, 343–357.

Sonesson, M., 1970: Studies on mire vegetation in the Torneträsk area, northern Sweden. III. Communities of the poor mires. *Opera Botanica*, 26: 1–122.

Sonesson, M., and Hoogesteger, J., 1983: Recent tree-line dynamics (*Betula pubescens* Ehrh. ssp. *tortuosa* (Ledeb.) Nyman) in northern Sweden. *Nordicana*, 47: 47–54.

SPSS Inc., 2006: SPSS version 15.0. Chicago, Illinois, SPSS Inc.

Suvanto, L. I., and Latva-Karjanmaa, T. B., 2005: Clone identification and clonal structure of the European aspen (*Populus tremula*). *Molecular Ecology*, 14: 2851–2860.

Sylvén, N., 1904: Studier över vegetationen i Torne lappmarks björkregion (Vegetation studies in Torne Lapland's birch woodland area). *Arkiv för Botanik*, 3: 1–28.

Sylvén, S., 2003: Management and regulated harvest of moose (*Alces alces*) in Sweden. PhD thesis. Uppsala University:, 36 pp.

Tape, K., Sturm, M., and Racine, C., 2006: The evidence for shrub expansion in northern Alaska and the Pan-Arctic. *Global Change Biology*, 12: 686–702.

Tenow, O., Bylund, H., Nilssen, A. C., and Karlsson, P. S., 2005: Long-term influence of herbivores on northern birch forests. *In* Wielgolaski, F. E. (ed.), *Plant Ecology, Herbivory, and Human Impact in Nordic Mountain Birch Forests*. Berlin: Springer-Verlag, 166–181.

Tømmervik, H., Johansen, B., Tombre, I., Thannheiser, D., Høgda, K., Gaare, E., and Wielgolaski, F., 2004: Vegetation changes in the Nordic mountain birch forest: the influence of grazing and climate change. *Arctic, Antarctic, and Alpine Research*, 36: 323–332.

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* Richter-Menge, J. (ed.), *Arctic Report Card 2007*. Washington: NOAA, 33–40.

Van Bogaert, R., Jonasson, C., De Dapper, M., and Callaghan, T. V., 2009: Competitive interaction between aspen and birch moderated by invertebrate and vertebrate herbivores and climate warming. *Plant Ecology & Diversity*, 2: 221–232.

Von Holle, B., Delcourt, H. R., Simberloff, D., and Harcombe, P., 2003: The importance of biological inertia in plant community resistance to invasion. *Journal of Vegetation Science*, 14: 425–432.

Wielgolaski, F. E., 2005: History and environment of the Nordic mountain birch. *In* Wielgolaski, F. E. (ed.), *Plant Ecology, Herbivory, and Human Impact in Nordic Mountain Birch Forests*. New York: Springer, 3–18.

Wolf, A., Kozlov, M., and Callaghan, T., 2008: Impact of non-outbreak insect damage on vegetation in northern Europe will be greater than expected during a changing climate. *Climatic Change*, 87: 91–106.

Worrell, R., 1995: European aspen (*Populus tremula* L.): a review with particular reference to Scotland I. Distribution, ecology and genetic variation. *Forestry*, 68: 93–105.

Worrell, R., Gordon, A. G., Lee, R. S., and McInroy, A., 1999: Flowering and seed production of aspen in Scotland during a heavy seed year. *Forestry*, 72: 27–34.

Wright, S., 1984: *Evolution and the Genetics of Populations*. Chicago: University of Chicago Press, 590 pp.

Zhou, L., Tucker, C. J., Kaufmann, R. K., Slayback, D., Shabanov, N. V., Fung, I., and Myneni, R. B., 2001: Variations in northern vegetation activity inferred from satellite data of vegetation index during 1981 to 1999. *Journal of Geophysical Research*, 106: 20069–20083.