

Ingrid Ertshus Mathisen

**Structure, dynamics, and  
regeneration capacity at the  
sub-arctic forest-tundra  
ecotone of northern Norway  
and Kola Peninsula, NW Russia**

Thesis for the degree of Philosophiae Doctor

Trondheim, August 2013

Norwegian University of Science and Technology  
Faculty of Natural Sciences and Technology  
Department of Biology



**NTNU – Trondheim**  
Norwegian University of  
Science and Technology

**NTNU**

Norwegian University of Science and Technology

Thesis for the degree of Philosophiae Doctor

Faculty of Natural Sciences and Technology  
Department of Biology

©Ingrid Ertshus Mathisen

ISBN 978-82-471-4579-1 (printed ver.)  
ISBN 978-82-471-4580-7 (electronic ver.)  
ISSN 1503-8181

Doctoral theses at NTNU, 2013:230

Printed by NTNU-trykk

## **Preface**

During the end of my master studies I remember reading to an exam in plant ecology, thinking “this should I learn more about, I want to be really good at it, I need to do a PhD”. About a year or two later I was sitting in an ice cold office in South Africa, tired of working in savannahs and other dry and to warm environments when I became aware of an available PhD position at the Norwegian Institute for Nature Research (NINA). I pictured sub-arctic mountain landscapes, the smell of fresh heather and normal temperatures, and suppressed the thought of biting bugs and possibilities of snow in July. Luckily the position became mine, and in March 2007 I started on the PhD journey.

The PhD project was part of The PPS Arctic Norway, which was the Norwegian contribution to the IPY (International Polar Year) core project PPS Arctic, it was founded from the Norwegian Research Council through grant no 176065/S30 to Annika Hofgaard.

I am deeply thankful to my supervisors Lars Söderström at Institute for Biology, NTNU and Annika Hofgaard at NINA. A special thanks to Annika for your constructive criticisms and progressive ideas. Your ability to see how things connect, to pick out the essentials; in short; your ecological brain, impresses me. Your inputs have always brought me forward, although sometimes by tiny steps. Thanks to Marianne Evju, Ingeborg Palm Helland, Eirin Bjørkvoll and Sandra Öberg they have all read and commented on various manuscripts.

Thanks to my numerous field colleagues, especially Staffan and Sigrun who not just survived but kept the mood during two summers with hard field work, in mosquito rich environments, staying in various kinds of accommodations. Do you remember the feeling of fortune and happiness in Kirkenes? A cabin with a shower and shopping at Rema was all we demanded.

I would also like to thank colleagues at the terrestrial department at NINA for making my six years here so pleasant, and especially to the group of plant ecologist, you have all been a great source of inspiration. Special thanks to Heidi for sharing office, joys and frustrations, and for helping me with small details whenever it was needed. Sandra, Jens, Mari, Signe, Espen, Arnstein, Ingeborg, Kristine, Camilla, Kristine and Øyvind you have all uplifted my every-day PhD life.

Thanks to my family and friends: Mamma and Pappa, Marius, Lisa, Åsmund, Maria, Trine, Anne Berit, Eirin, Geir, Svein Erik, Mattis, Marit and all the girls from Heimdal. Thank

you for listening to my stories about climate and pines, and for being supportive and encouraging when I needed it. Thanks to Maja and Sigve, the best kids ever, you have always reminded me that there are things in life much more important than a thesis. Thanks to Lars Erik, you have been extremely patient and supportive. The three of you is the most important of all.

Trondheim, May 2013

*Ingrid Ertshus Mathisen*

## **Contents**

List of papers .....	2
Declaration of contributions .....	3
Introduction .....	5
Aims of the thesis .....	7
Study design and study areas .....	7
Sampling.....	11
Major results and discussion .....	11
Conclusions and further prospects.....	15
Literature cited .....	18
INDIVIDUAL PAPERS	

### **List of papers**

- I. Mathisen I. E. and Hofgaard A. 2011. Recent height and diameter growth variation in Scots pine (*Pinus sylvestris* L.) along the Arctic margin: the importance of growing season versus non-growing season climate factors. *Plant Ecology & Diversity* 4, 1-11
- II. Mathisen, I. E., Mikheeva, A., Tutubalina, O. V., Aune, S. and Hofgaard, A. 2013. Fifty years of tree line change in the Khibiny Mountains, Russia. Advantages of combined remote sensing and dendroecological approaches. *Applied Vegetation Science* Doi: 10.1111/avsc.12038
- III. Mathisen I. E., Hofgaard, A. and Söderström L. 2013. Advancing and stationary Scots pine populations, forced by different environmental gradients of the forest-tundra ecotone. *Manuscript*
- IV. Mathisen I.E. 2013. Spatial tree cover variation across environmental gradients at the forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia. *Manuscript*

*The papers are referred in the text by their Roman numerals.*

*Paper I and II are included with permission from the publishers.*

**Declaration of contributions**

The initial idea and design of the PhD project was conceived by Hofgaard. The ideas of paper I and III were conceived and developed jointly by Hofgaard and Mathisen, paper II by Mikheeva, Hofgaard, and Mathisen, and paper IV by Mathisen. The data for all four papers were collected by Mathisen during field work in the summers of 2007 and 2008 with assistance from several co-workers. Sampling followed standard protocols developed by the International Polar Year research group on causes and consequences of changes of the circumpolar forest-tundra ecotone, PPS Arctic, <http://ppsarctic.nina.no>. For paper I, III and IV all analyses were performed by Mathisen. The remote sensing related analyses in paper II were worked out by Mikheeva and Tutubalina. Aune contributed with data for paper II. Mathisen wrote all papers with contributions from the co-authors (papers I-III), in particular Hofgaard.





## Introduction

The location and structure of the boreal-Arctic transition are major determinants for land-atmosphere interactions at the circumpolar scale and for ecological conditions at the local to regional scale (Callaghan *et al.*, 2002; Vlassova, 2002; Hofgaard, 2004; ACIA, 2005). This transition, henceforth the forest-tundra ecotone, covers a large expanse throughout the circum-arctic; with a length of 13,000 km and a width of up to several hundred kilometres. Thus it has a global recognised importance, in terms of vegetation, climate, biodiversity and human settlements (Callaghan *et al.*, 2002).

In the past few decades the sub-arctic and the Arctic have attracted lot of attention due to the areas' high sensitivity to global warming (ACIA, 2005). Since the start of the 20<sup>th</sup> century the mean annual temperature has increased by ca. 1.0 °C in northern Norway (Førland *et al.*, 2009). In comparison, the global mean annual temperature increased by 0.7 °C from 1906–2005 (IPCC, 2007). The degree of continued warming that is projected for the present century is considerable; from 2.5 to 3.5 °C for northern Norway by 2100 (reference year 1990) (Førland *et al.*, 2009). Annual precipitation is predicted to increase with ca. 12 % from 1981–2000 to 2017–2090 in the Arctic (IPCC, 2007). For parts of northern Norway the projected annual precipitation change is 20–30 % from 1961–1990 to 2071–2100 (Førland *et al.*, 2009), with most increase during winter and spring. This warming and increase in precipitation is expected to stimulate a swift northward advance of the sub-arctic forest-tundra ecotones (ACIA, 2005; Kaplan & New, 2006).

The forest-tundra ecotone can extend for several hundreds of altitudinal metres where slopes are relatively gentle, or some tens of meters where the topography is particularly steep. The expanse of the forest-tundra ecotone varies from a very abrupt change from forest to no trees, or gradually less dense forest and more and more scattered trees and saplings (Callaghan *et al.*, 2002). Hence, many different factors are involved in structuring this ecotone on a local to regional scale. Temperature is widely accepted to be the dominant factor controlling the location and structure of the forest-tundra ecotone at the global scale (Körner, 1998; Harsch *et al.*, 2009). Supporting evidence for this universal mechanism includes global relationships between forest-tundra position and temperature isotherms (Körner & Paulsen, 2004), and Holocene fluctuations in the position of the boundary in accordance with past temperature changes (Payette *et al.*, 2002; Jensen & Vorren, 2008). Drought stress has little significance in the northern forest-tundra areas where humidity tends to be high because cold air masses have a lower capacity to hold moisture

(Girardin *et al.*, 2004). However, precipitation may be a restrictive factor for tree growth in continental areas such as central Alaska and central Siberia (Lloyd & Fastie, 2003; Kharuk *et al.*, 2010). Increased precipitation during non-growing season at high latitudes generally creates abundant and long lasting snow packs, which provides protection against browsing and wind abrasion (Sturm *et al.*, 2001; Hofgaard *et al.*, 2009; Holtmeier & Broll, 2010) and supply of early growing season soil moisture (Sveinbjörnsson *et al.*, 2002; Holtmeier & Broll, 2005).

Effects of herbivores on the forest-tundra ecotone structure and position are seen all over the world (Cairns & Moen, 2004). In northern Europe, the forest-tundra ecotone areas are subjected to extensive reindeer herding. In lichen dominated locations the tramping and grazing of reindeer may change the forest cover by opening gaps where Mountain birch (*Betula pubescence* Ehrh. ssp. *tortuosa* (Ledeb.) Nyman) can germinate and sprout (Tømmervik *et al.*, 2004). On the other hand can reindeer prevent uphill/northward movement of the forest-tundra ecotone at summer grazing sites by browsing birch seedlings, shoots, and leaves (Olofsson *et al.*, 2009). Scots pine (*Pinus sylvestris* L.) saplings are vulnerable to winter browsing by moose (*Alces alces* L.), as Scots pine is an important food source during winter for moose (Edenius *et al.*, 1993; Månsson, 2009), and to snow blight (*Phacidium infestans* P. Karst.), a fungal infestation that spreads between Scots pine. Both factors hinder saplings to reach tree size, resulting in no or very slow advancement rates (Stöcklin & Körner, 1999).

Remote sensing of the forest-tundra ecotone has great potential for analyses of change rates at the ecotone (Rees, 2007). High spatial resolution remote sensing products can provide detailed information on changes in structure and location during specific time periods (Heiskanen, 2006), and to some extent at the tree species level (Næsset *et al.*, 2004). This information can be used to calibrate and validate coarser-resolution global remote sensing products to give standardised and precise estimates of forest cover change at regional to circumpolar scale (Stow *et al.*, 2004; Montesano *et al.*, 2009; McManus *et al.*, 2012). However, a prevailing characteristic of the ecotone is a considerable time lag between tree establishment and the ability of remote sensing to detect small saplings and trees (Dalen & Hofgaard, 2005; Heiskanen, 2008). Combined remote sensing and ground based analyses can therefore assist in the calculation of climate-driven change rates, as the ground based data will give information on on-going changes or potential for change.

### **Aims of the thesis**

This thesis deals with the dynamics and potential response to climate change of Scots pine and to some extent Mountain birch of the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia. The dynamics and potential change are investigated along three major environmental gradients; between regions dominated by air masses of different origin, i.e. moist Atlantic vs. dry Arctic, between coast and inland, and along the altitudinal gradients of the forest-tundra ecotone. Present trees and saplings of the ecotone constitute the basis for further development of the ecotone. Hence, special attention is given to changes in tree recruitment capacity across the environmental gradients.

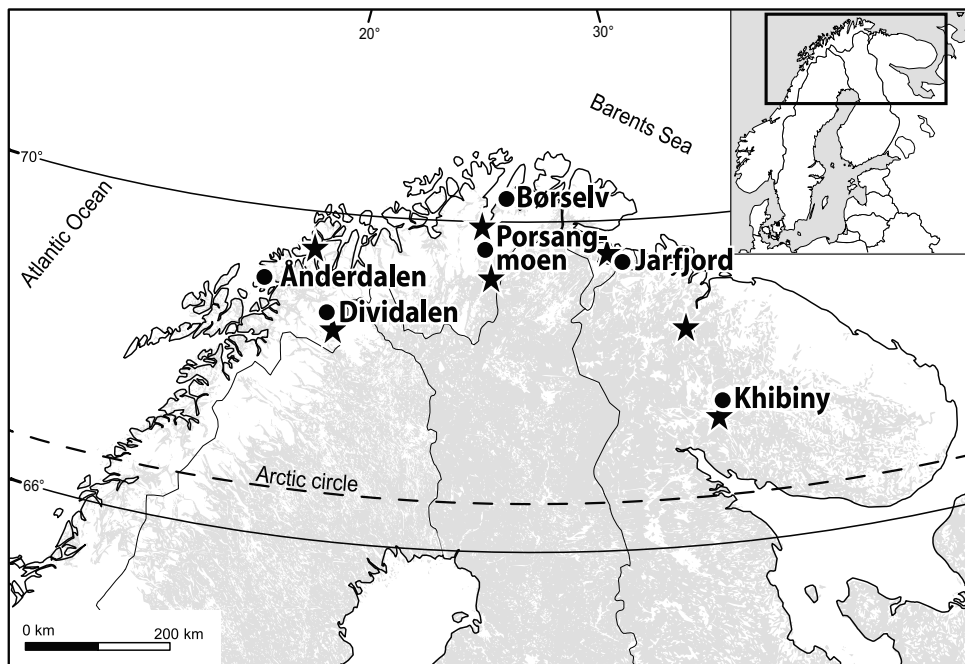
The specific aims of the thesis are:

1. To analyse how the structure of the forest-tundra ecotone change along spatial and temporal scales (paper II & III, paper IV only spatial)
2. To analyse if there are significant differences in growth, structure, and locations present across the environmental gradients, and if so elucidate main environmental forces (paper I, III & IV)
3. To explore evidence for correlation between growth, regeneration, and climate across the forest-tundra ecotone and through time (paper I-III)
4. Explore the possible advantages of joint use of remote sensing and dendroecology in understanding tree line changes (Paper II)

### **Study design and study areas**

The different studies took place along a climatic gradient characterised by decreasing impact of Atlantic air masses from western Troms County in northern Norway to an increasing Arctic impact in the Kola Peninsula in north-western Russia (Fig. 1). The study areas were located in three regions along this climatic gradient, one western (in Troms County), one central region (in Finnmark County) and one eastern region (Finnmark County and Kola Peninsula). In each of the three regions, one area representing coastal and one area representing inland conditions were designated. The studies of paper I, III, and IV were conducted in all areas, while the study of paper II only took place at the Khibiny Mountains at Kola Peninsula. In two studies (paper III and IV) three sites were located along an altitudinal gradient within each area. The frequency of Scots pine decreases with altitude across the forest-tundra ecotone, and the lowermost site was

located at the forest line, i.e. the upper boundary of the closed pine forest, the middle site in the tree line zone, as defined by the uppermost > 2 m trees, and the uppermost site in the krummholz zone above the tree line where Scots pines are < 2 m in height.



**Figure 1.** The location of the study areas; Ånderdalen, Dividalen, Børselv, Porsangmoen, Jarfjord, and Khibiny (circles) and used meteorological stations (stars) in northern Norway and north-western Russia. Grey shaded areas indicate forest.

In the western region, the coastal area Ånderdalen is situated at the island of Senja and is characterised by a rather rugged mountain terrain, while the inland area Dividalen is situated in a slightly gentler mountain terrain. Ånderdalen has a coastal climate characterised by moist mild winters and cool summers and Dividalen a continental climate with cold, relatively dry winters and warm summers (Table 1). In the central region, the coastal area Børselv is situated close to the Porsanger fjord in a gentle terrain, while the inland area Porsangmoen is situated in a more mountainous and less gentle terrain. Børselv has warmer winters but colder summers than Porsangmoen, while precipitation levels are more or less similar between the two areas. In the eastern region, the coastal area Jarfjord is situated in a gentle landscape with small hills close to

the Barents Sea, and the inland area Khibiny is situated in the largest mountain massif on the Kola Peninsula with rather rugged mountains. Both Jarfjord and Khibiny have relatively cold winters, but summers are warmer at Khibiny and precipitation is much higher at Khibiny than Jarfjord (Table 1). All study areas are normally snow covered from October to May, and the coldest month is January and the warmest July. Climate data for each study area refer to the nearest meteorological stations, which are located in a similar landscape as the study areas they represent (Federal Service for Hydrometeorology and Environmental Monitoring, 2008; Norwegian Meteorological Institute, 2011). Ten-year running means for annual, summer, and winter temperatures show a warming trend over the last century with peaks in the 1930s, and from the 1980s and until today, the exception being Khibiny, where no temperature trend is recorded.

**Table 1.** Climate data refer to the meteorological normal period 1961-1990 (Norwegian Meteorological Institute, 2011). Data from the Yukspor station refer to the period 1881-1980 (Bulygina & Razyvaev, 2008). Summer refers to June, July and August. Winter refers to December, January, and February. Continentiality sections are according to Moen (1999): O1 slightly oceanic, OC indifferent, C1 slightly continental.

Study area	Ånderdalen	Dividalen	Børselv	Porsangmoen	Jarfjord	Khibiny
<i>Location</i>						
Latitude	69°12'N	68°51'N	70°17'N	69°57'N	69°39'N	67°42'N
Longitude	17°20'E	19°36'E	25°32'E	25°09'E	30°15'E	33°14'E
Altitudinal range of study area (m a.s.l.)	125-290	360-560	40-250	95-270	75	325-380
<i>Climate data and source</i>						
Meteorological station	Tromsø	Dividalen	Banak	Karasjok	Kirkenes	Yukspor
Distance and direction from study area	82 km, NE	11 km, SE	28km, SW	50 km, S	16 km, NW	30 km, E
Altitude (m a.s.l.)	100	228	5	130	89	910
Continentiality section	O1	C1	OC	C1	OC	C1
<i>Temperature (°C)</i>						
annual average	2.5	0.8	0.6	-2.4	-0.6	-3.7
summer average	10.6	11.3	11.1	11.3	10.4	7.0
winter average	-3.4	-8.5	-9.0	-15.9	-10.9	-11.7
<i>Precipitation (mm)</i>						
annual sum	1031	282	345	366	430	1066
summer sum	207	132	146	171	163	297
winter sum	283	44	59	48	88	219

## **Sampling**

All field work was accomplished during July and August in 2007 and 2008. Annual height growth and diameter growth of Scots pine were collected at open woodlands with mesic soil conditions at all six study sites (paper I). The height growth was measured as the distance between annual branching nodes along the stem of Scots pine saplings using a ruler. To record diameter growth, adult trees were cored at breast height, and ring widths were measured according to standard dendrochronological methods (Fritts, 1976; Cook *et al.*, 1990) (paper I).

For paper II and III all Scots pine individuals within sample plots located across the altitudinal gradient were sampled (for paper II the tree line and krummholz sites were investigated, while for paper III all three sites were used). Height, basal stem diameter, and diameter at breast height of each individual were measured and crown area was calculated using two perpendicular diameter measures. Scots pine and birch age at ground level was sampled by taking cores or cutting the individuals. A dissecting microscope (6 – 40 x) was used for counting the tree rings and determine establishment year (paper II and III), and to measure ring width (paper I).

In paper II changes in the tree line ecotone of the Khibiny Mountains were mapped for two sites (Scots pine and birch) using air photos and satellite images. The tree line position was contoured on high resolution images from 1958 (air photos) and 2006/2008 (satellite images). The contouring was done by hand by applying a connection line between the uppermost trees along the slopes. To enable analysis of elevation changes of the contoured tree lines, digital elevation models for both sites were produced.

In paper IV, the stand density and hemispherical photographs were sampled at all sites. At each site, 50 meter long lines were located perpendicular to the main gradient from the forest to the tundra. Three hemispherical photographs were taken at 25 m intervals along each line. The hemispherical photographs have a 3872 x 2048 resolution and were captured from the ground facing upward using a Nikon D80 camera equipped with a fisheye lens placed in the field vegetation on a stable board. Stand density was measured with a relascope.

## **Major results and discussion**

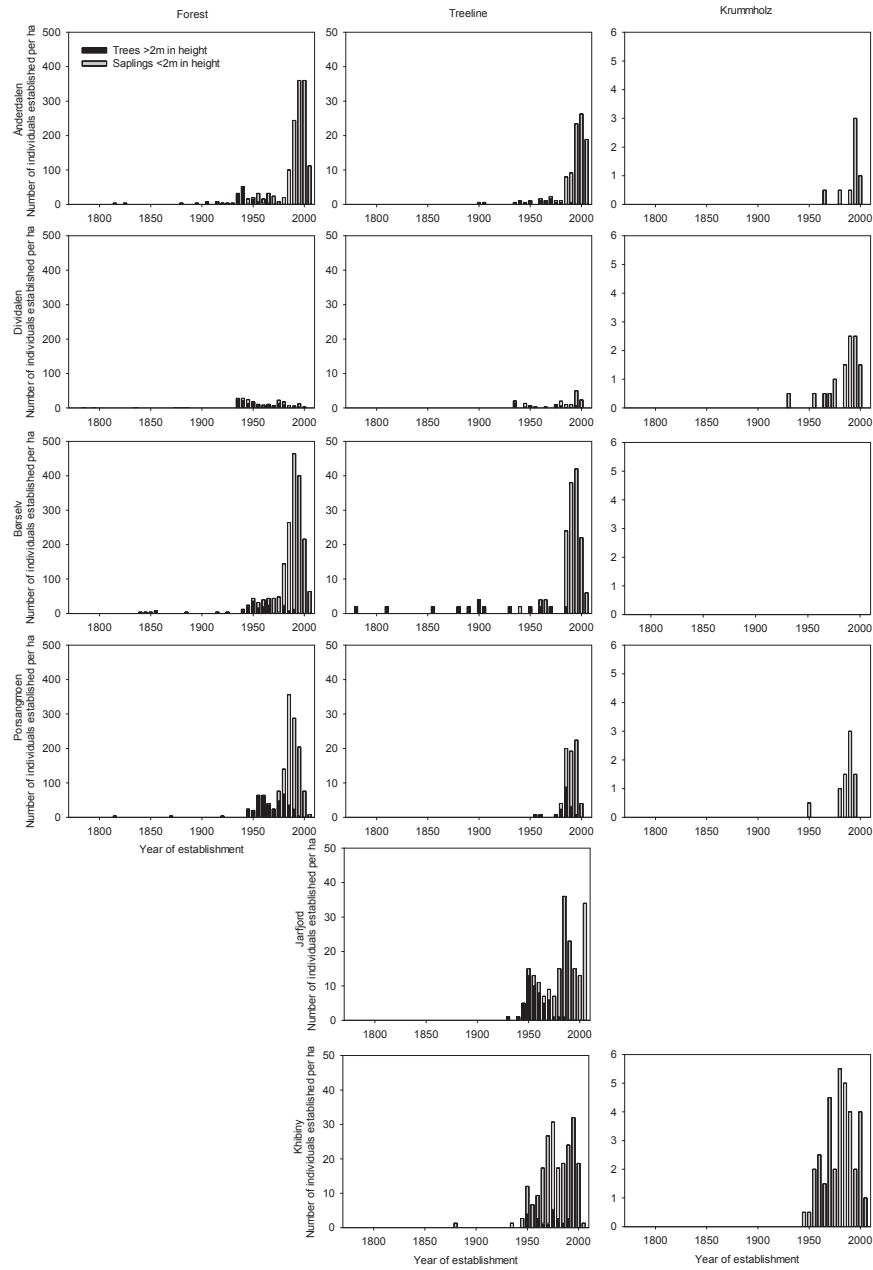
Summer temperature is generally considered to be the main driver of location and structure at the forest-tundra ecotone (Junttila & Heide, 1981; Körner, 1998; Kullman, 2002; Salminen &

Jalkanen, 2005). The recent longer and warmer summers in the western and central study regions (Førland *et al.*, 2009) seems to be less limiting for growth and establishment (paper I and III) (Linderholm *et al.*, 2010) as non-growing season precipitation was found to have a strong influence on structuring and shaping of the forest tundra ecotone (paper I–IV). The non-growing season precipitation, i.e. snow cover, is regarded as a facilitative mechanism (Kjällgren & Kullman, 1998; Smith *et al.*, 2003; Batllori *et al.*, 2009), as the snow protects from wind abrasion and winter browsing (Sturm *et al.*, 2001; Sveinbjörnsson *et al.*, 2002; Holtmeier & Broll, 2010). In addition, it contributes to soil moisture in spring (Baumeister & Callaway, 2006), and the higher soil temperatures during winter favour nutrient uptake the following summer (Weih & Karlsson, 2002). The drawback of increasing snow cover is a shortening of the growing season (Vaganov *et al.*, 1999). The forest-tundra ecotone of regions that today are considered as snow rich will thus probably suffer from increased precipitation, while more continental regions may experience increased seedling survival and sapling growth.

Strong among-area correlations of annual height growth (paper I) across the climatic gradients of sub-arctic northern Norway and Kola Peninsula suggest summer temperature to be the common environmental driver of height growth across the regions studied. In contrast, diameter growth of Scots pine lacks a common climate–growth relationship across the climatic gradients (paper I). Also for age structures and tree cover, a substantial heterogeneity is found across the studied regions (paper III and IV). This implies non-homogenous climatic regions in terms of variables related to diameter growth, establishment, and survival (Fig. 2) and tree cover changes. The climatic differences between study regions and choice of Scots pine variables are thus deterministic for the degree of variation in spatiotemporal establishment and growth patterns (Linderholm *et al.*, 2003; Aune *et al.*, 2011). It is also suggested that variations in spatial patterns of the forest-tundra ecotone across large regions and the potential factors affecting establishment within the ecotone are site specific (Harper *et al.*, 2011). However, correlation between establishment at the coastal areas and gridded winter precipitation over a regional scale suggests that the age structures are regionally representative (paper III). Especially the age structure that originates from Børselv had a large geographical representativity both west- and eastwards from the sample area, probably explained by the location, influenced by both Atlantic and Arctic dominated air masses forming a Scots pine population that thus is representative over large regions.



In contrast to the general assumption of rapidly advancing forest-tundra ecotones due to climate change (ACIA, 2005; Kaplan & New, 2006), the studied ecotones showed a response pattern with evidence of both potential Scots pine population advancement and stationary populations (paper II and III). The models used for predicting the above mentioned rapid northward movement assume that vegetation is in equilibrium with current climate and do not include other mediating factors.



**Figure 2.** Age structure given as trees and saplings per hectare. The data is aggregated to 5-year age classes for each study site. Note that the scaling of the y-axes varies between the altitudinal gradients.

Pine species establish at specific microsites that in general consist of sparsely vegetated gaps, bare soil, gravel, or litter, and that have a protective element (Batllori *et al.*, 2009). Further, growth into the tree layer must overcome increased stress related to exposure when protruding above the snow layer, mainly controlled by wind damages (paper III). Advancing tree lines is often dominated by an infilling process at the local scale (paper II) (Tømmervik *et al.*, 2004) where additional establishment occurs in areas of pre-established populations of scattered trees and saplings. A forest-tundra ecotone advance is thus facilitated by pre-established seedlings and saplings. This is evident in the Khibiny age structure (Fig. 2) (paper II). However, it should be stressed that this infilling process changes and shapes the forest-tundra ecotone (Danby & Hik, 2007), but do not necessary cause an advance of the ecotone.

Implications for a forest-tundra ecotone shift consider both alterations in climate and biodiversity (Callaghan *et al.*, 2002; Hofgaard *et al.*, 2012). Changes in forest cover and tundra encroachment would change both the albedo and energy exchange between the atmosphere and the biosphere, especially at high latitudes and altitudes that are snow covered part of the year (Harding *et al.*, 2002; Chapin *et al.*, 2005; Bala *et al.*, 2007). The carbon uptake of the forest contributes significantly to the land carbon sink and hence causes climate cooling (Betts, 2000). However, this effect will be offset by radiative forcing effects of a decrease in the land surface albedo. Chapin *et al.* (2005) concluded that the warming albedo effect of increasing forest cover was almost 2–7 times stronger than the cooling effect of carbon uptake. Accordingly, a northward shift of the forest-tundra ecotone as a response to climate warming would significantly alter climate and ecosystem processes (Callaghan *et al.*, 2002). Furthermore, forest advance would have drastic consequences for the tundra biota; arctic plant species restricted beyond the ecotone would experience severe habitat fragmentation and reduction, resulting in an increased risk of regional extinction and reduction in beta-diversity (Engler *et al.*, 2011; Miller & Smith, 2012). A northward movement of the forest-tundra ecotone will also have significant impact for animal biodiversity within and beyond the forest-tundra ecotone (Hofgaard *et al.*, 2012). Arctic human societies depend on the sustained use of the Arctic tundra biota, and would also be strongly impacted (ACIA, 2005).

### **Conclusions and further prospects**

The location, dynamics, and environmental drivers at regional and circumpolar levels of the forest-tundra ecotone are not fully understood, and will probably never be, but the scientific

community has made a large progress recently. To be able to more precisely predict the effect of future climate changes and feedbacks from the system, profound knowledge on how the location is changing in response to a range of abiotic and biotic forces is still needed. Refined techniques for the detection of spatial shift of the ecotone for large spatial scales are necessary to develop further. At present, one of the most important gaps and uncertainties in forest-tundra research appears at the intermediate regional geographic scale (Callaghan *et al.*, 2002; Holtmeier & Broll, 2005, 2007). Regional differences in establishment and size structure imply different responses to the same environmental factors as focal predictors for the forest-tundra zone response (Harsch & Bader, 2011). As suggested by Harper *et al.* (2011), the positive feedback will act differently at different locations dependent on specific underlying factors, and thus increase the variation of the shaping and structuring of the forest-tundra ecotone. Therefore must site-specific, species-specific, and time-specific patterns be carefully deciphered when local scale data are used to interpret changes of the forest-tundra ecotone on a regional or ecotonal scale (Hofgaard *et al.*, 2013). Studies combining remote sensing and ecological approaches can be utilised to merge local scale studies, but are generally not feasible over larger spatial scales (due to cost and labour demands). However, a balance between remote sensing and ecological approaches is useful for production of high quality information valid for large regions, such as the sub-arctic forest-tundra ecotone (paper II). The regional 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 forest-tundra studies are short-term studies with a temporal scale ranging from a decade to a few decades (Payette *et al.*, 2002; Holtmeier & Broll, 2007; Kullman & Öberg, 2009). This is problematic as forest-tundra processes are generally slow and accurate interpretations should be made over long time periods. Therefore, there is a great need for careful field studies on forest-tundra dynamics and its causes based on a complex ecological approach (Callaghan *et al.*, 2002; Payette *et al.*, 2002; Sveinbjörnsson *et al.*, 2002; Holtmeier & Broll, 2005, 2007).

The thesis encompassed a large geographical and climatically varied region of the circumpolar north, to be able to address cause-response forces of the changing forest-tundra ecotone. Both short and longer time periods and the use of growth variables and age structures can assist in improving scenarios for forest cover changes in sub-arctic regions. But the forest-tundra ecotone is a highly dynamic system and thus any study of it will be challenging. Until

today, documented changes are only a part of the changes likely to have occurred. Additional changes are expected in the coming decades, emphasising the need for further research that will enhance the knowledge of the local and regional variation in the causes of the status and dynamics at the forest-tundra ecotone.

## Literature cited

- ACIA (2005) *Arctic Climate Impact Assessment* Cambridge University Press, New York, US.
- Aune, S., Hofgaard, A. & Söderström, L. (2011) Contrasting climate- and land-use-driven tree encroachment patterns of subarctic tundra in northern Norway and the Kola Peninsula. *Canadian Journal of Forest Research*, **41**, 437-449.
- Bala, G., Caldeira, K., Wickett, M., Phillips, T.J., Lobell, D.B., Delire, C. & Mirin, A. (2007) Combined climate and carbon-cycle effects of large-scale deforestation. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 6550-6555.
- Batliori, E., Camarero, J.J., Ninot, J.M. & Gutiérrez, E. (2009) Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* tree line ecotones. Implications and potential responses to climate warming. *Global Ecology and Biogeography*, **18**, 460-472.
- Baumeister, D. & Callaway, R.M. (2006) Facilitation by *Pinus flexilis* during succession: A hierarchy of mechanisms benefits other plant species. *Ecology*, **87**, 1816-1830.
- Betts, R.A. (2000) Offset of the potential carbon sink from boreal forestation by decreases in surface albedo. *Nature*, **408**, 187-190.
- Bulygina, O.N. & Razyvaev, V.N. (2008) *Opisanie massiva dannukh sutochnoy temperatury vozdukhha I kolichestva osadkov na 223 meteorologicheskikh stantsiyakh na territorii byvshego SSSR (TTTR) [Description of the TTTR data array of daily temperature and precipitation for 223 meteorological stations at the territory of the former USSR]*. Available at: URL: <http://www.meteo.ru/climate/descrip1> (accessed September 2008)
- Cairns, D.M. & Moen, J. (2004) Herbivory influences tree lines. *Journal of Ecology*, **92**, 1019-1024.
- Callaghan, T.V., Werkman, B.R. & Crawford, R.M.M. (2002) The tundra-taiga interface and its dynamics: Concepts and applications. *Ambio Special Report*, **12**, 6-14.
- Chapin, F.S., Sturm, M., Serreze, M.C., McFadden, J.P., Key, J.R., Lloyd, A.H., McGuire, A.D., Rupp, T.S., Lynch, A.H., Schimel, J.P., Beringer, J., Chapman, W.L., Epstein, H.E., Euskirchen, E.S., Hinzman, L.D., Jia, G., Ping, C.L., Tape, K.D., Thompson, C.D.C., Walker, D.A. & Welker, J.M. (2005) Role of land-surface changes in Arctic summer warming. *Science*, **310**, 657-660.
- Cook, E.R., Briffa, K.R., Shiyatov, S. & Mazepa, V. (1990) Tree-Ring Standardization and Growth-Trend Estimation. *Methods of Dendrochronology: applications in the environmental science* (ed. by E.R. Cook and L.A. Kairiukstis), pp. 104-123. Kluwer Academic Publishers, Dordrecht.
- Dalen, L. & Hofgaard, A. (2005) Differential regional treeline dynamics in the Scandes Mountains. *Arctic, Antarctic, and Alpine Research*, **37**, 284-296.
- Danby, R.K. & Hik, D.S. (2007) Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. *Journal of Ecology*, **95**, 352-363.

- Edenius, L., Danell, K. & Bergström, R. (1993) Impact of Herbivory and Competition on Compensatory Growth in Woody Plants: Winter Browsing by Moose on Scots Pine. *Oikos*, **66**, 286-292.
- Engler, R., Randin, C.F., Thuiller, W., Dullinger, S., Zimmermann, N.E., Araujo, M.B., Pearman, P.B., Le Lay, G., Piedallu, C., Albert, C.H., Choler, P., Coldea, G., De Lamo, X., Dirnbock, T., Gegout, J.C., Gomez-Garcia, D., Grytnes, J.A., Heegaard, E., Hoistad, F., Nogues-Bravo, D., Normand, S., Puscas, M., Sebastia, M.T., Stanisci, A., Theurillat, J.P., Trivedi, M.R., Vittoz, P. & Guisan, A. (2011) 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology*, **17**, 2330-2341.
- Federal Service for Hydrometeorology and Environmental Monitoring [Federalnaya sluzhba Rossii po gidrometeorologii i monitoringu okruzhajuschei spedy] (2008). Roshydromet, Moscow, RU.
- Fritts, H.C. (1976) *Tree Rings and Climate*. Academic Press, London, UK.
- Førland, E.J., Benestad, R.E., Flatøy, F., Hanssen-Bauer, J., Haugen, J.E., Isaksen, K., Sorteberg, A. & Ådlandsvik, B. (2009) Climate development in North Norway and the Svalbard region during 1900-2100. *Report no. 128, Norwegian Polar Institute* (ed. E.J. Førland), p. 43 p. Report series Report no. 128, Tromsø, NO.
- Girardin, M.P., Tardif, J., Flannigan, M.D. & Bergeron, Y. (2004) Multicentury reconstruction of the Canadian Drought Code from eastern Canada and its relationship with paleoclimatic indices of atmospheric circulation. *Climate Dynamics*, **23**, 99-115.
- Harding, R., Kuhry, P., Christensen, T.R., Sykes, M.T., Dankers, R. & van der Linden, S. (2002) Climate feedbacks at the tundra-taiga interface. *Ambio Special Report*, **12**, 47-55.
- Harper, K.A., Danby, R.K., De Fields, D.L., Lewis, K.P., Trant, A.J., Starzomski, B.M., Savidge, R. & Hermanutz, L. (2011) Tree spatial pattern within the forest-tundra ecotone: a comparison of sites across Canada. *Canadian Journal of Forest Research*, **41**, 479-489.
- Harsch, M.A. & Bader, M.Y. (2011) Treeline form - a potential key to understanding treeline dynamics. *Global Ecology and Biogeography*, **20**, 582-596.
- Harsch, M.A., Hulme, P.E., McGlone, M.S. & Duncan, R.P. (2009) Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, **12**, 1040-1049.
- Heiskanen, J. (2006) Tree cover and height estimation in the Fennoscandian tundra-taiga transition zone using multiangular MISR data. *Remote Sensing of Environment*, **103**, 97-114.
- Heiskanen, J. (2008) Evaluation of global land cover data sets over the tundra-taiga transition zone in northernmost Finland. *International Journal of Remote Sensing*, **29**, 3727-3751.
- Hofgaard, A. (2004) Feedbacks between Northern Terrestrial Systems and Climate. *Arctic Climate Feedback Mechanisms* (ed by S. Gerland and B. Njåstad), pp. 23-25. Tromsø.

- Hofgaard, A., Dalen, L. & Hytteborn, H. (2009) Tree recruitment above the treeline and potential for climate-driven treeline change. *Journal of Vegetation Science*, **20**, 1133-1144.
- Hofgaard, A., Harper, K.A. & Golubeva, E. (2012) The role of the circumarctic forest–tundra ecotone for arctic biodiversity. *Biodiversity*, **13**, 174-181.
- Hofgaard, A., Tømmervik, H., Rees, G. & Hanssen, F. (2013) Latitudinal forest advance in northernmost Norway since the early 20th century. *Journal of Biogeography*, **40**, 938-949.
- Holtmeier, F.K. & 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.
- Holtmeier, F.K. & Broll, G. (2007) Treeline advance -driving processes and adverse factors. *Landscape online*, **1**, 1-33.
- Holtmeier, F.K. & Broll, G. (2010) Wind as an Ecological Agent at Treelines in North America, the Alps, and the European Subarctic. *Physical Geography*, **31**, 203-233.
- IPCC (2007) Climate Change 2007. Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. *IPCC assessment reports*, pp. 104. Cambridge University Press, Geneva, CH.
- Jensen, C. & Vorren, K.-D. (2008) Holocene vegetation and climate dynamics of the boreal alpine ecotone of northwestern Fennoscandia. *Journal of Quaternary Science*, **23**, 719-743.
- Junttila, O. & Heide, O.M. (1981) *Shoot and Needle Growth in Pinus sylvestris as Related to Temperature in Northern Fennoscandia*. *Forest Science*, **27**, 423-430.
- Kaplan, J.O. & New, M. (2006) Arctic climate change with a 2 degrees C global warming: Timing, climate patterns and vegetation change. *Climatic Change*, **79**, 213-241.
- Kharuk, V.I., Ranson, K.J., Im, S.T. & Vdovin, A.S. (2010) Spatial distribution and temporal dynamics of high-elevation forest stands in southern Siberia. *Global Ecology and Biogeography*, **19**, 822-830.
- Kjällgren, L. & Kullman, L. (1998) Spatial patterns and structure of the mountain birch tree-limit in the southern Swedish Scandes - A regional perspective. *Geografiska Annaler Series a-Physical Geography*, **80A**, 1-16.
- 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. & 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.
- Körner, C. (1998) A re-assessment of high elevation treeline positions and their explanation. *Oecologia*, **115**, 445-459.



- Körner, C. & Paulsen, J. (2004) A world-wide study of high altitude treeline temperatures. *Journal of Biogeography*, **31**, 713-732.
- Linderholm, H.W., Solberg, B.O. & Lindholm, M. (2003) Tree-ring records from central Fennoscandia: the relationship between tree growth and climate along a west-east transect. *Holocene*, **13**, 887-895.
- Linderholm, H.W., Björklund, J.A., Seftigen, K., Gunnarson, B.E., Grudd, H., Jeong, J.H., Drobyshev, I. & Liu, Y. (2010) Dendroclimatology in Fennoscandia - from past accomplishments to future potential. *Climate of the Past*, **6**, 93-114.
- Lloyd, A.H. & Fastie, C.L. (2003) Recent changes in treeline forest distribution and structure in interior Alaska. *Ecoscience*, **10**, 176-185.
- McManus, K.M., Morton, D.C., Masek, J.G., Wang, D.D., Sexton, J.O., Nagol, J.R., Ropars, P. & Boudreau, S. (2012) Satellite-based evidence for shrub and graminoid tundra expansion in northern Quebec from 1986 to 2010. *Global Change Biology*, **18**, 2313-2323.
- Miller, P.A. & Smith, B. (2012) Modelling Tundra Vegetation Response to Recent Arctic Warming. *Ambio*, **41**, 281-291.
- Moen, A. (1999) *National Atlas of Norway: Vegetation*. Norwegian Mapping Authority, Hønefoss, NO.
- Montesano, P.M., Nelson, R., Sun, G., Margolis, H., Kerber, A. & Ranson, K.J. (2009) MODIS tree cover validation for the circumpolar taiga-tundra transition zone. *Remote Sensing of Environment*, **113**, 2130-2141.
- Månsson, J. (2009) Environmental variation and moose *Alces alces* density as determinants of spatio-temporal heterogeneity in browsing. *Ecography*, **32**, 601-612.
- Norwegian Meteorological Institute (2011) [www.eklima.no](http://www.eklima.no).
- Næsset, E., Gobakken, T., Holmgren, J., Hyypä, H., Hyypä, J., Maltamo, M., Nilsson, M., Olsson, H., Persson, A. & Söderman, U. (2004) Laser scanning of forest resources: The Nordic experience. *Scandinavian Journal of Forest Research*, **19**, 482-499.
- Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P.E., Oksanen, T. & Suominen, O. (2009) Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology*, **15**, 2681-2693.
- Payette, S., Eronen, M. & Jasinski, J.J.P. (2002) The Circumboreal Tundra-Taiga Interface: Late Pleistocene and Holocene Changes. *Ambio Special Report*, **12**, 15-22.
- Rees, W.G. (2007) Characterisation of Arctic treelines by LiDAR and multispectral imagery. *Polar Record*, **43**, 345-352.
- Salminen, H. & Jalkanen, R. (2005) Modelling the effect of temperature on height increment of Scots pine at high latitudes. *Silva Fennica*, **39**, 497-508.

- Smith, W.K., Germino, M.J., Hancock, T.E. & Johnson, D.M. (2003) Another perspective on altitudinal limits of alpine timberlines. *Tree Physiology*, **23**, 1101-1112.
- Stow, D.A., Hope, A., McGuire, D., Verbyla, D., Gamon, J., Huemmrich, F., Houston, S., Racine, C., Sturm, M., Tape, K., Hinzman, L., Yoshikawa, K., Tweedie, C., Noyle, B., Silapaswan, C., Douglas, D., Griffith, B., Jia, G., Epstein, H., Walker, D., Daeschner, S., Petersen, A., Zhou, L.M. & Myneni, R. (2004) Remote sensing of vegetation and land-cover change in Arctic Tundra Ecosystems. *Remote Sensing of Environment*, **89**, 281-308.
- Sturm, M., McFadden, J.P., Liston, G.E., Chapin, F.S., Racine, C.H. & Holmgren, J. (2001) Snow-shrub interactions in Arctic tundra: A hypothesis with climatic implications. *Journal of Climate*, **14**, 336-344.
- Stöcklin, J. & Körner, C. (1999) Recruitment and mortality of *Pinus sylvestris* near the nordic treeline: the role of climatic change and herbivory. *Ecological Bulletins*, **47**, 168-177.
- Sveinbjörnsson, J., Hofgaard, A. & Lloyd, A. (2002) Natural causes of the tundra-taiga boundary. *Ambio Special Report*, **12**, 23-29.
- Tømmervik, H., Johansen, B., Tombre, I., Thannheiser, D., Høgda, K.A., Gaare, E. & Wielgolaski, F.E. (2004) Vegetation changes in the Nordic mountain birch forest: The influence of grazing and climate change. *Arctic Antarctic and Alpine Research*, **36**, 323-332.
- Vaganov, E.A., Hughes, M.K., Kirilyanov, A.V., Schweingruber, F.H. & Silkin, P.P. (1999) Influence of snowfall and melt timing on tree growth in subarctic Eurasia. *Nature*, **400**, 149-151.
- Vlassova, T.K. (2002) Human impacts on the tundra-taiga zone dynamics: The case of the Russian lesotundra. *Ambio Special Report*, **12**, 30-36.
- Weih, M. & Karlsson, P.S. (2002) Low winter soil temperature affects summertime nutrient uptake capacity and growth rate of mountain birch seedlings in the subarctic, Swedish lapland. *Arctic Antarctic and Alpine Research*, **34**, 434-439.

# Paper I



## Recent height and diameter growth variation in Scots pine (*Pinus sylvestris* L.) along the Arctic margin: the importance of growing season versus non-growing season climate factors

Ingrid E. Mathisen and Annika Hofgaard\*

Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway

(Received 25 October 2010; final version received 4 March 2011)

**Background:** High-latitude forests are controlled by climate and as temperature increases, a northward extension in distribution and more vigorous tree growth are expected. The replacement of tundra by forest involves changes in carbon sequestration, land–atmosphere energy balance and ecosystems. The understanding of climate-related height and diameter growth patterns across geographical regions is therefore important.

**Aim:** To analyse recent within- and between-region variations in climate–growth relationships for Scots pine at the forest–tundra ecotone (northern Norway, Kola Peninsula).

**Methods:** Six pine (*Pinus sylvestris*) woodland sites, representing different climate regions along the forest–tundra zone, were sampled for annual height growth (saplings) and diameter growth (adult trees) and the analyses were related to local climate data.

**Results:** Height growth was strongly similar among all sites and climate regions, but not diameter growth. Although summer temperature was the most important factor, non-growing season climate showed significant importance for both diameter and height growth across regions.

**Conclusions:** The results highlight the importance of factors that are often overlooked, specifically, non-growing season factors for tree growth at high latitudes, and the role of short-term climate variation. Future climate scenarios predict moister and milder winters for large areas of high-latitude regions. Thus, detailed analyses of region-specific climate–growth relations that focus on growing season vs. non-growing season effects are essential in the evaluation of future forest cover response to climate change.

**Keywords:** climate gradients; forest–tundra ecotone; height increment; Kola Peninsula; northern Norway; *Pinus sylvestris*; radial growth

### Introduction

High-latitude regions are recognised for their sensitivity to climate change (ACIA 2005). The growth of trees and forests at or close to the Arctic forest–tundra boundary are strongly affected by climate, both from a short- and long-term perspective (Callaghan et al. 2002). In the short-term, changes in the climate cause shifts or alterations in tree growth rate, tree vitality, stand structure and forest cover, and over the long-term, displacement of the forest–tundra boundary (Payette et al. 2001; Kapralov et al. 2006; Danby and Hik 2007; Kullman 2007; Moen et al. 2008). Changes in forest location and in forest cover (density) throughout the circumpolar north will alter regional CO<sub>2</sub> sequestration, water/energy balance and albedo (Harding et al. 2002; Hyvönen et al. 2007). Increased conifer tree cover can decrease regional albedo and may offset expected negative radiative forcings (Hyvönen et al. 2007; IPCC 2007).

There are large regional differences in forest responses to climate changes throughout the forest–tundra zone, including evidence of both advance and the lack of it (Harsch et al. 2009), and large differences between specific time periods (Lloyd and Fastie 2002). The climate warming after the end of the Little Ice Age, around 1850,

improved tree vitality, caused an increase in stand density and advanced distribution limits of marginal stands in northern Europe (Hofgaard et al. 1991; MacDonald et al. 2008; Kullman and Öberg 2009). However, the response to warming did not follow a uniform pattern: a warming during the 1930s resulted in increased tree growth, while warming since the late 1980s has not shown a similar response pattern (Solberg et al. 2002; Tuovinen et al. 2009). This divergence between time periods is important to consider when modelling tree growth (Linderholm et al. 2010).

Summer temperature is the primary determinant of both height and diameter growth for dominant trees in the northern boreal zone. However, non-growing season temperatures and precipitation are also known to be of significant importance (Grace and Norton 1990; Mäkinen et al. 2000; Fagre et al. 2003; Kullman 2007; Huang et al. 2010; Aune et al. 2011). In addition, the seasonal timing of height and diameter growth responses to climate differs within and among species. These factors, along with differences in sensitivity to climate variation, including the shifting relative importance of previous and current growing seasons, need considering when growth or growth rate

\*Corresponding author. Email: annika.hofgaard@nina.no

is used to predict forest cover responses to climate change (Jalkanen and Tuovinen 2001; Gamache and Payette 2004).

Climate scenarios for the north European sub-Arctic region indicate an increase in both annual temperature and precipitation, and thus tree growth enhancement is expected (IPCC 2007). In northern Norway and the western Kola Peninsula, Russia, Scots pine (*Pinus sylvestris* L.) forms the northern conifer stands. Height and diameter growth variation in these stands can thus provide essential information on climate-related growth responses that are fundamental for constructing growth, sink and feedback scenarios (Goodale and Davidson 2002). In the light of both recent climate changes and predicted scenarios for rapid climate change (IPCC 2007), a focus on recent growth responses (recent decades) is needed along with how growth responses vary within and across climatic regions. Hypothetically, contrasting response patterns between coastal and inland localities and between regions dominated by air masses of different origin, e.g. moist Atlantic vs. dry Arctic, will cause significantly different landscape level responses regarding changes in forest cover and carbon sequestration.

In this paper, we focus on decadal between-region (Atlantic vs. Arctic), within-region (coast vs. inland) and growing season variation vs. non-growing season variation in climate–growth relations for Scots pine at its northern distribution limit in northern Norway and the Kola Peninsula. The following questions are addressed. (1) How have height and diameter growth of Scots pine at its northern distribution margin responded to climate variability during recent years? (2) Are growth responses consistent within and between climatic regions?

## Methods

### Study sites

Areas in the north-western part of Eurasia, northern Norway and north-western Russia are exposed to climatic influence from both the North Atlantic Ocean and the Arctic. Study sites for collection of height and diameter growth data were located in three regions (west, central, east) along the main climatic gradient characterised by decreasing impact of Atlantic air masses (and increasing Arctic impact) from western Troms County in northern Norway to the Kola Peninsula in north-western Russia. In each of the three regions, two sites representing coastal (1) and inland (2) conditions were selected (Figure 1, Table 1).

A coastal climate is generally characterised by moist mild winters and cool summers, and an inland climate by cold and relatively dry winters and warm summers. However, in these high-latitude sub-Arctic regions, this is only pronounced in the west (Moen 1999). In the eastern region, the inland climate is both warmer and moister than at the coast (Table 1, Figure 2). All study sites are normally snow-covered from October to May, while the coldest month is January and the warmest is July (Figure 2). Climate data for each study site refer to the nearest meteorological station. The meteorological normal period of 1961–1990 (Federal Service for Hydrometeorology and Environmental Monitoring 2008; Norwegian Meteorological Institute 2008) was used for all stations except Ukspor, where only mean data for the standard Russian normal period 1881–1980 were available (Science and applied guide to the climate of the USSR

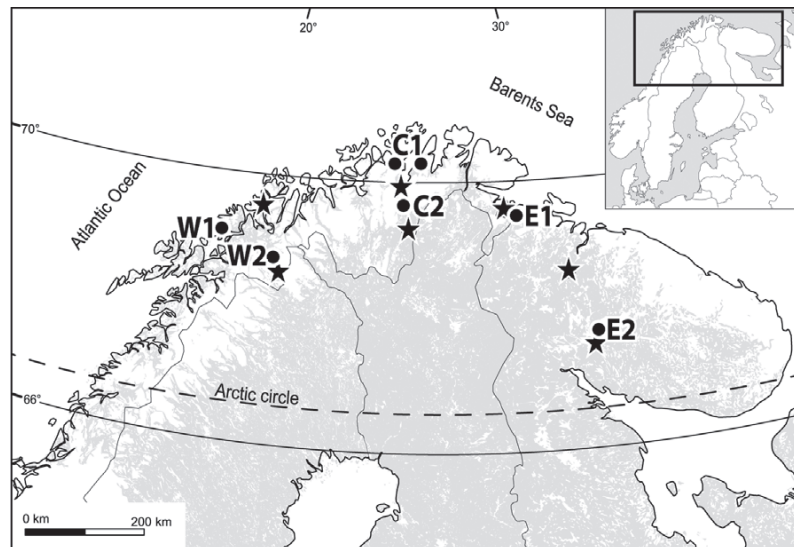


Figure 1. The location of the study sites (circles) and meteorological stations (stars) in northern Norway and north-western Russia (see Table 1 for the names of study sites and meteorological stations). Grey shaded areas indicate forest.

Table 1. Site characteristics and summary information on sampling material. Continentality classification according to Moen (1999): O-1 slightly oceanic; O-C indifferent; C-1 slightly continental. Temperature and precipitation data for Norwegian sites refer to the meteorological normal period 1961–1990 (Norwegian Meteorological Institute 2008). Data for the Russian site refer to the period 1881–1980 (Science and Applied Guide to the Climate of the USSR 1988).

Study site	W1	W2	C1	C1	C2	E1	E2
<i>Location</i>							
Name	Ånderdalen	Dividalen	Stabbursdalen	Børselv	Porsangmoen	Jarfjord	Khibiny
Latitude	69° 12' N	68° 51' N	70° 10' N	70° 17' N	69° 57' N	69° 39' N	67° 42' N
Longitude	17° 20' E	19° 36' E	24° 47' E	25° 32' E	25° 09' E	30° 15' E	33° 14' E
Altitude (m a.s.l.)	115	360	50	40	100	50	340
<i>Climate data and source</i>							
Continentality class	O-1	C-1	O-C	O-C	C-1	O-C	C-1
Meteorological station	Tromsø	Dividalen	Banak	Banak	Karasjok	Kirkenes	Murmansk
Distance and direction from study site	82 km, NE	11 km, SE	12 km, SE	28 km, SW	50 km, S	16 km, NW	140 km, N
Altitude (m a.s.l.)	100	228	5		130	89	57
Temperature (°C)							
Annual average	2.5	0.8	0.6		-2.4	-0.6	0.2
Decadal change <sup>2</sup> , annual	0.18	0.22	0.45		0.24	0.07	0.20
Decadal change <sup>2</sup> , JJA	0.15	0.19	0.14		0.20	0.05	0.05
Precipitation (mm)							
Annual sum	1031	282	345		366	430	488
Decadal change <sup>2</sup> %, annual	3.44	6.50	8.32		0.93	1.56	3.72
Decadal change <sup>2</sup> %, JJA	1.43	2.54	-2.48		-0.36	4.52	2.42
<i>Sampling</i>							
Diameter growth							
No. trees	22	29	30		27	21	23
Cores ( <i>n</i> )	37	49	50		51	28	33
Mean ring width (mm)	0.63	0.87	0.9		1.05	0.68	0.42
Height growth							
Saplings ( <i>n</i> )	92	71		67	50	49	49
Mean height growth (cm)	5.54	5.46		8.05	7.63	8.15	8.76
Uksport <sup>1</sup>							20 km, S
							910
							-3.7
							1066

<sup>1</sup>No monthly data available.

<sup>2</sup>Based on regression line for last 50 years (1956–2006). JJA: June, July, August.

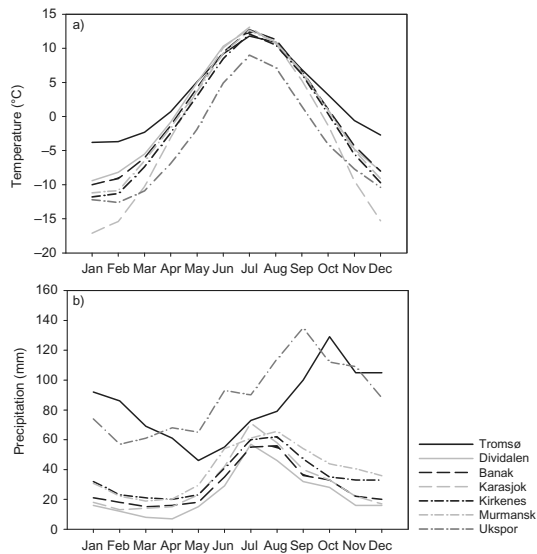


Figure 2. Normal period temperature (a) and precipitation (b) data for the meteorological stations representing each study site (see Figure 1 for locations). The data are based on the period 1961–1990 for all stations except Ukspor, where only mean data for the standard Russian normal period 1881–1980 were available. Coastal sites are shown with black lines and inland sites with grey lines.

1988). Selected meteorological stations were located in a similar landscape to the study site they are meant to represent (Figure 1, Table 1). Temperature data representing

individual sites showed a similar annual pattern with common summer peak temperatures for all but Ukspor (representing E2; i.e. eastern inland in Figure 1), but with somewhat more deviation in winter temperature lows, with Karasjok (C2) as the coldest and Tromsø (W1) the mildest (Figure 2). Precipitation showed a similar pattern for all but the western coastal site and the eastern inland site. At these sites, the annual precipitation was between two and three times higher than at the other sites and precipitation peaks during the late growing season or autumn compared to summer for other sites (Figure 2). The period 1992–2006 was selected for all analyses, and was the period for which height and diameter growth data for all sites were collected (see below). For the Khibiny site (E2), data from the Murmansk climate station were used as the closest station, because Ukspor did not have monthly data available (Table 1). Summer (June, July, August) temperature anomalies for the 1992–2006 period showed a general increase of 1.5 degrees among all sites, but with apparent variations between years (Figure 3). Annual temperature anomalies showed a weak increasing trend, with variations among years. Summer precipitation anomalies showed considerable year-to-year variation, but no trend. Annual precipitation anomalies showed less variation among years and a weak increasing trend (Figure 3). During the last 50 years (1956–2006), the decadal increase in annual and summer temperatures among the meteorological stations ranged from 0.07 to 0.45 degrees and from 0.05 to 0.2 degrees per decade, respectively. Precipitation change ranged from 0.93% to 8.32% for annual values and  $-2.48\%$  to  $-0.36\%$  for summer values (Table 1).

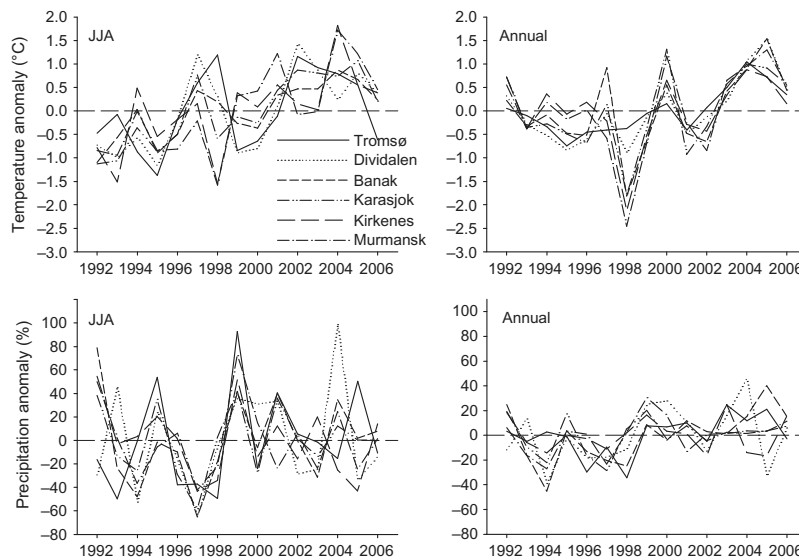


Figure 3. Growing season (June–August) and annual temperature and precipitation anomalies compared to the mean of the analysed period, 1992–2006. Data from the Norwegian Meteorological Institute (2008) and the (Russian) Federal Service for Hydrometeorology and Environmental Monitoring (2008).





Figure 4. Typical sapling (a) and tree (b) individuals of Scots pine sampled in mesic open woodland sites along the northern distribution limit of the species in northern Norway and the Kola Peninsula (see Figure 1).

All sites were open woodlands with mesic soil conditions, dominated by Scots pine in a sparse matrix with mountain birch (*Betula pubescens* ssp. *czerepanovii* (Ledeb.) Nyman) in the tree layer, and *Vaccinium vitis-idaea* L., *V. myrtillus* L., *V. uliginosum* L. and *Empetrum nigrum* L. in the field layer. The stand structure of the study sites has not been affected by forest fire, but some selective logging has occurred at all sites. However, the logging has not had an important impact on the general stand structure.

#### Sampling and preparation

The height and diameter growth data were collected during July and August 2007 and 2008. To emphasise climate-growth correlations we used saplings (height 50–200 cm; Figure 4(a)) for the height growth analyses, and adult trees (Figure 4(b)) for diameter growth analyses (Fritts 1976; Lanner 1976). For height growth, a minimum of 45 healthy and non-browsed saplings were selected at each study site. Annual height growth, measured as distance between annual branching nodes along the stem, was recorded with a ruler to the nearest 0.5 cm. To be selected, saplings had to provide data for at least the last four years. For diameter growth, measured as the annual tree ring width, a minimum of 20 adult trees were cored at each site. Two cores were taken from each tree at breast height (130 cm above the ground) in opposite horizontal directions. The cores were mounted on wooden supports, dried and brought to the laboratory, where they were planed with a scalpel. Zinc ointment was applied, when needed, to increase the contrast between early and late wood in the tree rings. Ring

widths were measured to an accuracy of 0.01 mm using a LINTAB measuring system and a dissecting microscope with a magnification of 6–40 $\times$ .

#### Chronology construction

The ring-width series of the individual cores were visually and statistically cross-dated by comparison of cores within trees, between trees and with the site chronology. COFECHA 6.06P and TSAP-win software were used for the statistical correlation analyses (Holmes 1994; Rinn 2003). Cores showing low correlation ( $r < 0.5$ ) with the mean site chronology were excluded from further analyses. To increase the climate signal in the constructed chronologies, trees that showed signs of senescence were excluded (i.e.  $a < 0.4$  mm average ring width over the last 15 years was used as the cut-off level). At E2, where trees were generally slow growing, 0.15 mm was set as the lower limit. This selection and exclusion process resulted in chronologies ranging from 33 to 51 cores per site (Table 1).

In order to strengthen a common high-frequency signal in both the height and diameter growth data and to remove low-frequency variation, the height and diameter growth series (from height increment and ring-width series, respectively) from each study site were standardised to create indexed chronologies. These chronologies generally have a better correlation with yearly climate variation (Cook and Kairiukstis 1990). For this standardisation the unprocessed annual height and diameter growth records for each individual were divided by the individual's mean annual growth. To allow for a variable number of recordings

the resulting values were summed up by year and divided by the number of individuals/cores representing each year in each chronology, thus forming two (height and diameter) indexed chronologies per site. Height and diameter growth relations within and between sites were examined with Pearson's correlation analyses (R Development Core Team 2008).

#### Climate-growth analysis

As the period with tree growth data varied among sites with sampling year and sampling time, we used the common period of 1996–2006 in the analyses. The period was based on a minimum of 15 height and diameter growth samples as the cut-off level over the whole period. Climate-growth relationships were examined by correlation- and response-function analyses, and bootstrapped confidence intervals, which estimate the significance of correlation and response-function coefficients, by the software program DendroClim 2002 (Biondi and Waikul 2004). A 16-month period was analysed, encompassing May of the year prior to growth ( $May_{t-1}$ ) to August of the year of growth ( $August_t$ ), with the indexed chronologies as dependent variables and monthly mean temperature and monthly total precipitation values as predictors. Details for the response-function results are not presented, since the number of predictors was too few to give statistically reliable results. However, when tested, significant response-function values were indicated for the same climate variables as significant correlation-function indications.

## Results

#### Growth pattern and height-diameter relations

Height growth correlated strongly ( $P < 0.01$ ) among all sites (Table 2), while diameter growth only showed significant correlation between a limited number of site combinations (Table 2). There was a general low and non-significant

correlation between height growth of saplings and diameter growth of adult trees at most sites. The exceptions were the eastern inland site, which showed a strong positive within-site correlation, and the western coastal site, which showed a significant negative within-site correlation (Table 2.)

An inter-annual pattern with common growth peaks (index values) among sites was evident for both height and diameter (Figure 5). Height growth peaked in 2005 at all sites, and was at its lowest level in 1996 at the western and central sites and in 1993 at the eastern sites. Diameter growth showed high values for 1993 at all sites except at the eastern inland site. The year 2000 showed increased diameter growth at all sites, with the most pronounced peaks at the two eastern sites (Figure 5).

#### Height growth and climate

Height growth was significantly and positively correlated with  $July_{t-1}$  temperature at all sites (Figure 6). The temperature during the current growing season was of minor importance except in the east, where above-average  $June_t$  temperature had a positive effect on growth. Precipitation had no significant effect except in the western coastal site, where above-average precipitation in  $June_t$  was significantly and positively correlated (Figure 6).

During the late non-growing season, above-average  $April_t$  temperatures had a significant positive effect on height growth at all sites except site E1 (Figure 6). In the winter months, above-average temperatures in  $February_t$  in the west, in  $December_{t-1}$  at the central sites and in  $November_{t-1}$  and  $December_{t-1}$  in the east had an apparent positive effect on height growth. In contrast, above-average late winter temperatures ( $March_t$ ) had a negative effect in the east. Higher than average precipitation in  $February_{t-1}$  caused increased growth at W1 but had a negative effect in the east. Above-average  $April_t$  precipitation had a negative effect on growth in the west, while  $May_t$  precipitation above

Table 2. Pearson's product-moment correlation for height and diameter growth chronologies among sites, and height versus diameter growth within sites for the period of analysis of 1996–2006.

	W1	W2	C1	C2	E1	E2
Height growth						
W1						
W2	0.854**					
C1	0.960**	0.755**				
C2	0.911**	0.852**	0.946**			
E1	0.870**	0.751**	0.922**	0.934**		
E2	0.812**	0.886**	0.796**	0.883**	0.869**	
Diameter growth						
W1						
W2	-0.233					
C1	0.357	-0.001				
C2	-0.336	0.656*	0.429			
E1	-0.305	0.228	0.371	0.686*		
E2	-0.283	0.243	0.075	0.445	0.844**	
Height vs. diameter	-0.671*	0.166	-0.294	0.038	0.512	0.739**

\*  $P < 0.05$ ; \*\*  $P < 0.01$ .

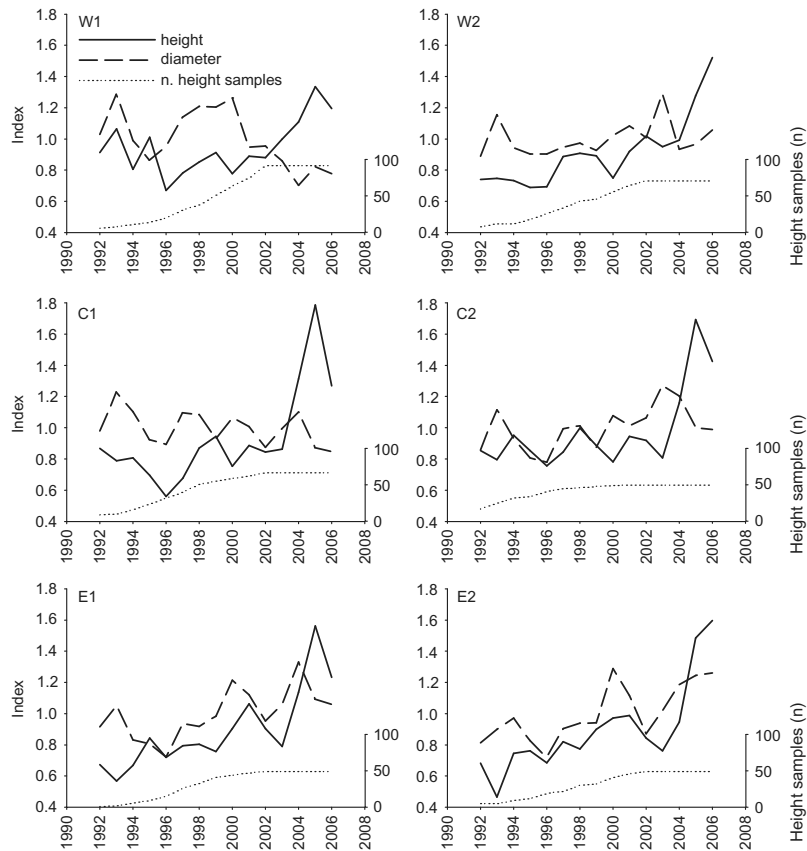


Figure 5. Indexed chronologies for the six study sites. Height growth values are shown by solid lines, diameter growth is shown by dashed lines and the number of individuals included in height growth chronologies by dotted lines (the latter refers to the right-hand y-axis). The number of diameter growth values was constant over time and are given in Table 1.

average was favourable to height growth at the two central sites. These late non-growing season months showed no significant importance in height growth in the east (Figure 6).

#### Diameter growth and climate

Above-average  $July_{t-1}$  temperatures had a significant positive effect on diameter growth at the two eastern sites, and  $July_t$  temperature had a positive effect at the two central sites and E1 (Figure 7). Diameter growth showed limited correlation with June temperatures ( $June_t$  was positive at E2 and negative at C1). In the west, current growing season temperatures had no significant effect on diameter growth, and current growing season precipitation was of no significant importance at any of the sites. However, moist  $July_{t-1}$  had a positive effect at the central and eastern inland sites.

For the late non-growing season, above-average April temperatures were positively related to diameter growth at

the eastern inland site, while the effect was negative at W1 (Figure 7). In May, (late non-growing/early growing season), temperature was of significant positive importance at all inland sites and E1 (and  $May_{t-1}$  at W2 and C2). W1 showed a deviating pattern, with above-average temperature in both  $May_{t-1}$  and  $May_t$  having a significant negative impact on diameter growth. During the early winter (October–December $_{t-1}$ ), temperatures above average had a positive effect in the east but were of no importance at other sites. A mild midwinter ( $February_t$ ) in the west had a negative effect at the coast but had a positive effect inland. Growth responses to non-growing season precipitation showed only a few common signals, but a moist  $February_t$  had a negative effect both at W1 and at the two eastern sites, and  $March_t$  precipitation had a positive effect at the western inland and eastern coastal sites. At the central sites, precipitation during the non-growing season was of no significant importance (Figure 7).

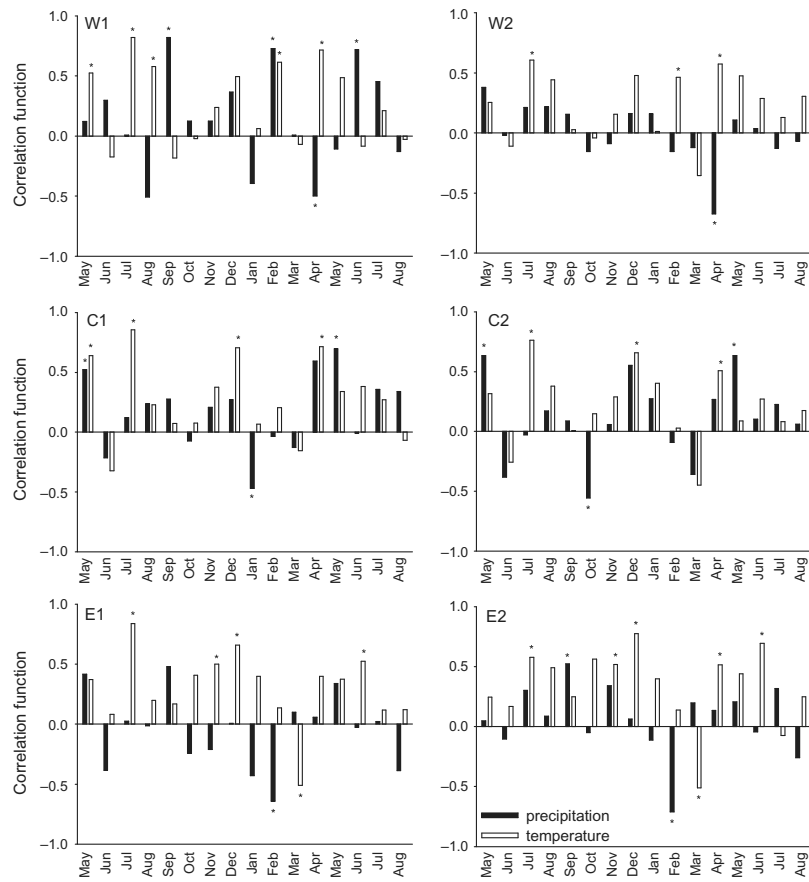


Figure 6. Height growth bootstrap correlation functions, based on indexed chronologies, showing the effect of monthly precipitation (filled bars) and monthly mean temperature (open bars) on height increment for the period 1996–2006. Data are shown for  $\text{May}_{t-1}$  to  $\text{August}_t$ . An asterisk above or below the bars indicates significant bootstrap correlation elements. See Figure 1 for site location and Table 1 for site characteristics.

### Discussion

Growth conditions at the forest-tundra transition with cool summers and short growing seasons are marginal. Warmer than normal summers are thus associated with increased photosynthetic activity and hence increased tree growth rates (Grace et al. 2002). The strong among-site correlations for height growth demonstrated here indicate a common environmental driver across the regions studied, from the north-western coast of Norway to the inland Kola Peninsula, with July temperature the year prior to growth as the most likely factor of importance. This is in accordance with the general pattern for climate–tree height growth relations at high latitudes (Junttila and Heide 1981; Salminen and Jalkanen 2005), and is related to the time period when the following year's buds are initiated (Lanner 1976). Most climate scenarios predict increased annual temperatures for European sub-Arctic regions, including warmer summer

conditions (ACIA 2005; IPCC 2007; Førland et al. 2009), and increased tree growth rates and northward forest expansion into the current tundra are generally expected (ACIA 2005; IPCC 2007). It follows, therefore, that an alteration in mean July temperature would have a perceptible impact on height growth and subsequently cause forest cover/density change. However, in contrast to height growth, diameter growth lacked a strong common climate–growth relationship. This implies non-homogenous climatic regions in terms of variables related to diameter growth, and thus lessens the support for summer temperature as the dominant driver for forest cover change. The climate difference between study regions, and choice of measured growth variables will hence be deterministic in the degree of detected homogeneity in the spatio-temporal growth pattern (Linderholm et al. 2003; Macias et al. 2004).

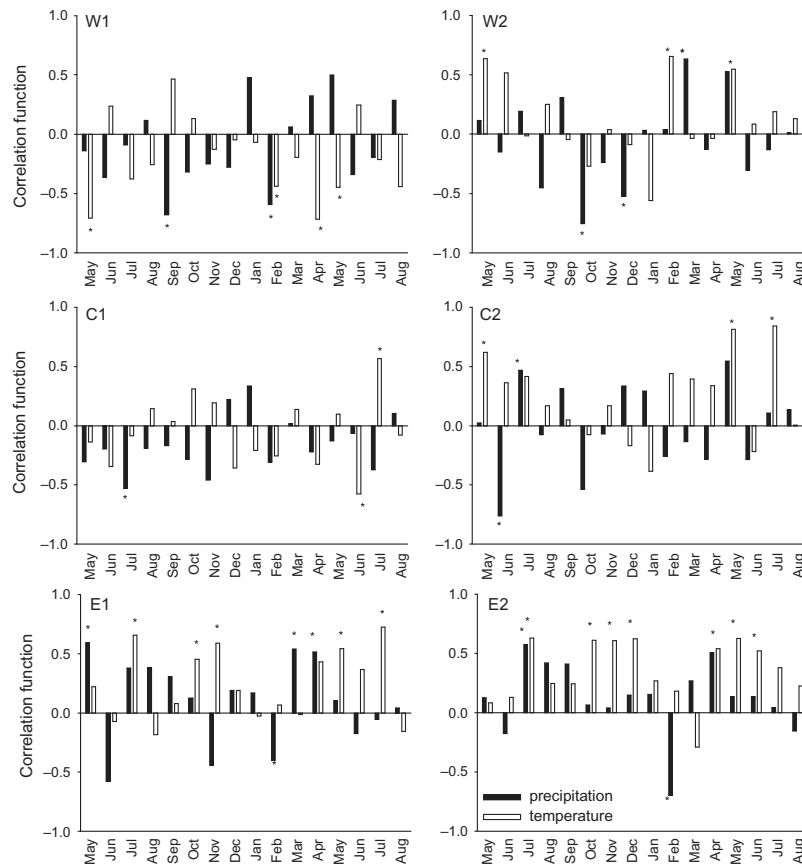


Figure 7. Diameter growth bootstrap correlation functions, based on indexed chronologies, showing the effect of monthly precipitation and monthly mean temperature on diameter increment growth for the period 1996–2006. Data are shown for  $\text{May}_{t-1}$  to  $\text{August}_t$ . An asterisk above or below the bars indicates significant bootstrap correlation elements. See Figure 1 for site location and Table 1 for site characteristics.

The reduced importance of current summer temperature for both height and diameter growth towards the west coincides with an increase in decadal summer temperature in the western and central regions (Table 1). These recent longer and warmer growing seasons in the Atlantic-influenced west have lessened the dependence on July temperature, as also has been shown for coastal areas further south in the boreal zone (Linderholm et al. 2003). Furthermore, the limited correlation between growing season precipitation and growth is a common pattern at high latitudes (Linderholm et al. 2010). However, in the central region where the growing season has become drier over the last 50 years (Table 1), May precipitation was of significant importance for height growth. This implies that growing season precipitation, even at high northern latitudes where growth generally is limited by temperature, can be a temporarily important growth-limiting factor (Kirchhefer 2001). Thus, the increased temperatures can result in reduced tree growth rates, if not accompanied

by an increase in precipitation (Lloyd and Fastie 2002; McGuire et al. 2010).

One of the main features in climate scenarios for the north European sub-Arctic region is an increase in winter and late non-growing season temperatures and precipitation (ACIA 2005; IPCC 2007; Førland et al. 2009). These climate factors had significant effect on tree growth in the subsequent growing season in the studied regions, although diameter growth showed no effects in the central region. The effects are mediated by a complex set of interactions of both direct and indirect climate factors. The general pattern of increased precipitation and long-lasting snow cover appeared to hamper early-season tree growth in snow-rich regions, but improved early-season growth in dry regions through melt water supply (Vaganov et al. 1999; Kirchhefer 2001; Bekker 2005). An exception to this general pattern was the positive height growth relation to late winter temperature and precipitation at the snow-rich western coastal site, where growing season length has

increased during recent years (Karlsen et al. 2007, 2009). Such a growing season increase likely counteracted the negative effect of snow accumulation in the region. In contrast, in the Arctic-dominated east, growing season length has decreased during the last few decades, on average starting 1–2 weeks later (Karlsen et al. 2007, 2009). The shortened season and delayed start have strengthened the dependency on late non-growing/early growing season conditions in the region. The location of the central region between the Atlantic and Arctic-dominated west and east is likely to be the reason for the limited response to winter climate that was shown in this region. Hypothetically, snow accumulation during the winter in this region provides favourable early growing season soil-moisture conditions without delaying the start of the growing season (Vaganov et al. 1999; Bekker 2005).

When short climate-growth periods are analysed, response patterns deviating from the long-term mean pattern may arise because of short-term climate variations. A general increase in summer temperature, as was found during the period analysed, could be a key factor promoting tree growth and hence forest cover change if prolonged, but this increase would be of little importance if representing a short-term episode. Similarly, a shortening of the growing season, as recorded during the most recent decades in the eastern part of the regions studied (Karlsen et al. 2007, 2009) would have a negative effect on forest cover if prolonged, and would involve a more dominant role for the non-growing season climate in tree growth (Linderholm and Chen 2005). The importance of winter climate is generally overlooked in scenarios for tree growth responses to climate change, since growing season temperature is the dominant factor when longer periods are analysed (Briffa et al. 1988; Kirchhefer 2001; Linderholm and Chen 2005). Consequently, the use of long-term mean data could lead to over-estimation of the rate of climate-mediated tree growth change if counteracting non-growing season effects are not considered. Trees from high-latitude regions have shown decreased sensitivity to growing season temperature towards the end of the twentieth century (Briffa et al. 1998; D'Arrigo et al. 2008; McGuire et al. 2010). This divergence between tree growth and temperature increase could be linked to a stronger relation between tree growth and non-growing season climate during recent decades (Vaganov et al. 1999; D'Arrigo et al. 2008; Linderholm et al. 2010). As most climate scenarios predict increased oceanicity, i.e. moister and warmer winters, throughout the regions studied (IPCC 2007; Førland et al. 2009), in addition to annual and summer temperature increases, the importance and effects of mild winters would accordingly be amplified (Linderholm and Chen 2005). Climate difference between study regions and the importance of growing vs. non-growing season variables vary through time, due to temporal variations in individual climate variables. Detailed analyses of short time periods and the use of more growth variables can thus assist in improving scenarios for forest cover changes in sub-Arctic regions.

## Acknowledgements

We thank three anonymous reviewers for their constructive comments on the initial manuscript, and Nancy Bazilchuk who helped to improve the language of the manuscript. We would also like to thank Sigrun Aune, Jorunn Eriksen, Maria Golubeva, Ksenia Kozlova and Erin Sandberg for help in the field, Staffan Dovårn for his help both in the field and the lab, Kari Sivertsen for help with Figure 1, and Mikhail Zimin and Yurate Plyushkiavichyute for help with Russian climate data. This paper was produced under the International Polar Year (IPY) core project *PPS Arctic* (<http://ppsarctic.nina.no>) and was financially supported by the Research Council of Norway through grant no. 176065/S30 to AH.

## Notes on contributors

Ingrid E. Mathisen is a Ph.D. student, whose main research interests lie in vegetation ecology in sub-Arctic, alpine and savannah ecosystems.

Annika Hofgaard is a senior scientist/professor in vegetation ecology, with her main interests in processes across ecotones, in particular the forest–tundra transition zone. She is the leader of the IPY project *PPS Arctic*, which has a focus on this theme in the circumpolar north.

## References

- ACIA. 2005. Arctic climate impact assessment. New York: Cambridge University Press. p. 1042.
- Annual review Roshydromet. 2008. Federal Service for Hydrometeorology and Environmental Monitoring [Federalnaya sluzhba Rossii po gidrometeorologii i monitoringu okruzhajuschei sredy]. Moscow: Roshydromet.
- Aune S, Hofgaard A, Söderström L. 2011. Contrasting climate- and land-use-driven tree encroachment pattern of sub-arctic tundra in Northern Norway and Kola Peninsula. *Canadian Journal of Forest Research* 41:437–449.
- Bekker MF. 2005. Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier National Park, Montana, USA. *Arctic Antarctic and Alpine Research* 37:97–107.
- Biondi F, Waikul K. 2004. DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. *Computers & Geoscience* 30:303–311.
- Briffa KR, Jones PD, Pilcher JR, Hughes MK. 1988. Reconstructing summer temperatures in northern Fennoscandia back to AD 1700 using tree-ring data from Scots pine. *Arctic and Alpine Research* 20:385–394.
- Briffa KR, Schweingruber FH, Jones PD, Osborn TJ, Shiyatov SG, Vaganov EA. 1998. Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. *Nature* 391:678–682.
- Callaghan TV, Werkman BR, Crawford RMM. 2002. The tundra-taiga interface and its dynamics: concepts and applications. *Ambio Special Report* 12:6–14.
- Cook ER, Kairiukstis LA, editors. 1990. *Methods of dendrochronology: applications in the environmental sciences*. Dordrecht: Kluwer Academic Publishers.
- Danby RK, Hik DS. 2007. Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. *Journal of Ecology* 95:352–363.
- D'Arrigo R, Wilson R, Liepert B, Cherubini P. 2008. On the 'Divergence Problem' in Northern Forests: a review of the tree-ring evidence and possible causes. *Global and Planetary Change* 60:289–305.
- Fagre DB, Peterson DL, Hessl AE. 2003. Taking the pulse of mountains: ecosystem responses to climatic variability. *Climatic Change* 59:263–282.

- Førland EJ, Benestad RE, Flatøy F, Hanssen-Bauer J, Haugen JE, Isaksen K, et al. 2009. Climate development in North Norway and the Svalbard region during 1900–2100. Tromsø: Norsk Polarinstittutt 128; p. 45.
- Fritts HC. 1976. Tree rings and climate. London: Academic Press.
- Gamache I, Payette S. 2004. Height growth response of tree line black spruce to recent climate warming across the forest-tundra of eastern Canada. *Journal of Ecology* 92:835–845.
- Goodale CL, Davidson EA. 2002. Carbon cycle: uncertain sinks in the shrubs. *Nature* 418:593–594.
- Grace J, Berninger F, Nagy L. 2002. Impacts of climate change on the tree line. *Annals of Botany* 90:537–544.
- Grace J, Norton DA. 1990. Climate and growth of *Pinus sylvestris* at its upper altitudinal limit in Scotland – evidence from tree growth-rings. *Journal of Ecology* 78:601–610.
- Harding R, Kuhry P, Christensen TR, Sykes MT, Dankers R, van der Linden S. 2002. Climate feedbacks at the tundra-taiga interface. *Ambio Special Report* 12:47–55.
- Harsch MA, Hulme PE, McGlone MS, Duncan RP. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters* 12:1040–1049.
- Hofgaard A, Kullman L, Alexandersson H. 1991. Response of old-growth montane *Picea abies* (L.) Karst. forest to climatic variability in northern Sweden. *New Phytologist* 119:585–594.
- Holmes RL. 1994. Dendrochronology program library. User's manual. Tucson (AZ): Laboratory of Tree-Ring Research, University of Arizona.
- Huang JG, Tardif JC, Bergeron Y, Denneler B, Berninger F, Girardin MP. 2010. Radial growth response of four dominant boreal tree species to climate along a latitudinal gradient in the eastern Canadian boreal forest. *Global Change Biology* 16:711–731.
- Hyvönen R, Ågren GI, Linder S, Persson T, Cotrufo MF, Ekblad A, Freeman M, Grelle A, Janssens IA, Jarvis PG. 2007. The likely impact of elevated [CO<sub>2</sub>], nitrogen deposition, increased temperature and management on carbon sequestration in temperate and boreal forest ecosystems: a literature review. *New Phytologist* 173:463–480.
- IPCC. 2007. Climate change 2007. Synthesis report. Geneva: Cambridge University Press. p. 104.
- Jalkanen R, Tuovinen M. 2001. Annual needle production and height growth: better climate predictors than radial growth at treeline? *Dendrochronologia* 19:39–44.
- Junttila O, Heide OM. 1981. Shoot and needle growth in *Pinus sylvestris* as related to temperature in northern Fennoscandia. *Forest Science* 27:423–430.
- Kapralov DS, Shiyatov SG, Moiseev PA, Fomin VV. 2006. Changes in the composition, structure, and altitudinal distribution of low forests at the upper limit of their growth in the Northern Ural Mountains. *Russian Journal of Ecology* 37:367–372.
- Karlsen SR, Høgda KA, Wielgolaski FE, Tolvanen A, Tømmervik H, Poikolainen J, Kubin E. 2009. Growing-season trends in Fennoscandia 1982–2006, determined from satellite and phenology data. *Climate Research* 39:275–286.
- Karlsen SR, Solheim I, Beck PSA, Høgda KA, Wielgolaski FE, Tømmervik H. 2007. Variability of the start of the growing season in Fennoscandia, 1982–2002. *International Journal of Biometeorology* 51:513–524.
- Kirchhefer AJ. 2001. Reconstruction of summer temperatures from tree-rings of Scots pine (*Pinus sylvestris* L.) in coastal northern Norway. *Holocene* 11:41–52.
- Kullman L. 2007. Tree line population monitoring of *Pinus sylvestris* in the Swedish Scandes, 1973–2005: implications for tree line theory and climate change ecology. *Journal of Ecology* 95:41–52.
- Kullman L, 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.
- Lanner RM. 1976. Three physiology and yield improvement. London: Academic Press Inc. London Ltd. Patterns of shoot development in *Pinus* and their relationship to growth potential; p. 223–243.
- Linderholm HW, Björklund JA, Seftigen K, Gunnarson BE, Grudd H, Jeong JH, Drobyshchev I, Liu Y. 2010. Dendroclimatology in Fennoscandia - from past accomplishments to future potential. *Climate of the Past* 6:93–114.
- Linderholm HW, Chen HYH. 2005. Central Scandinavian winter precipitation variability during the past five centuries reconstructed from *Pinus sylvestris* tree rings. *Boreas* 34:43–52.
- Linderholm HW, Solberg BO, Lindholm M. 2003. Tree-ring records from central Fennoscandia: the relationship between tree growth and climate along a west-east transect. *Holocene* 13:887–895.
- Lloyd AH, Fastie CL. 2002. Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change* 52:481–509.
- MacDonald GM, Kremenetski KV, Beilman DW. 2008. Climate change and the northern Russian treeline zone. *Philosophical Transactions of the Royal Society Biological Sciences* 363:2285–2299.
- Macias M, Timonen M, Kirchhefer AJ, Lindholm M, Eronen M, Gutierrez E. 2004. Growth variability of Scots pine (*Pinus sylvestris*) along a west-east gradient across northern Fennoscandia: a dendroclimatic approach. *Arctic Antarctic and Alpine Research* 36:565–574.
- Mäkinen H, Nöjd P, Mielikäinen K. 2000. Climatic signal in annual growth variation of Norway spruce (*Picea abies*) along a transect from central Finland to the Arctic timberline. *Canadian Journal of Forest Research* 30:769–777.
- McGuire AD, Ruess RW, Lloyd A, Yarie J, Clein JS, Juday GP. 2010. Vulnerability of white spruce tree growth in interior Alaska in response to climate variability: dendrochronological, demographic, and experimental perspectives. *Canadian Journal of Forest Research* 40:1197–1209.
- Moen A. 1999. National atlas of Norway: vegetation. Hønefoss: Norwegian Mapping Authority.
- Moen J, Cairns DM, Lafon CW. 2008. Factors structuring the treeline ecotone in Fennoscandia. *Plant Ecology & Diversity* 1:77–87.
- Norwegian Meteorological Institute. eKlima. 2008. Available from <http://www.eklima.no>.
- Payette S, Fortin MJ, Gamache I. 2001. The subarctic forest-tundra: the structure of a biome in a changing climate. *Bioscience* 51:709–718.
- R Development Core Team. 2008. R: a language and environment for statistical computing. Vienna, Austria.
- Rinn F. 2003. TSAP-Win 0.53. Heidelberg: Rinntech.
- Salminen H, Jalkanen R. 2005. Modelling the effect of temperature on height increment of Scots pine at high latitudes. *Silva Fennica* 39:497–508.
- Science and Applied Guide to the Climate of USSR [Nauchno-prikladnoy spravochnik po klimatu SSSR]. 1988. Leningrad: Gidrometeoizdat.
- Solberg BO, Hofgaard A, Hytteborn H. 2002. Shifts in radial growth responses of coastal *Picea abies* induced by climatic change during the 20th century, central Norway. *Ecoscience* 9:79–88.
- Tuovinen M, McCarroll D, Grudd H, Jalkanen R, Los S. 2009. Spatial and temporal stability of the climatic signal in northern Fennoscandian pine tree-ring width and maximum density. *Boreas* 38:1–12.
- Vaganov EA, Hughes MK, Kirilyanov AV, Schweingruber FH, Silkin PP. 1999. Influence of snowfall and melt timing on tree growth in subarctic Eurasia. *Nature* 400:149–151.





# Paper II





## Fifty years of tree line change in the Khibiny Mountains, Russia: advantages of combined remote sensing and dendroecological approaches

Ingrid E. Mathisen, Anna Mikheeva, Olga V. Tutubalina, Sigrun Aune & Annika Hofgaard

### Keywords

Age structure; *Betula pubescens*; Climate change; Climate–establishment relation; Infilling; *Pinus sylvestris*; Sub-arctic; Tree line change rate

### Nomenclature

Plant nomenclature: Lid & Lid (2005)

Received 2 September 2011

Accepted 14 March 2013

Co-ordinating Editor: Duccio Rocchini

**Hofgaard, A.** (corresponding author, annika.hofgaard@nina.no) & **Mathisen, I.E.** (ingrid.mathisen@nina.no): Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway

**Mikheeva, A.** (arvin2@yandex.ru) & **Tutubalina, O.V.** (ovt20@cam.ac.uk): Faculty of Geography, M.V. Lomonosov Moscow State University, Moscow, Russian Federation

**Aune, S.** (sigrun.aune@bioforsk.no): Norwegian Institute for Agricultural and Environmental Research, NO-7512 Stjørdal, Norway

### Abstract

**Questions:** Tree line ecotone regions are expected to respond swiftly to climate changes. In this paper, remote sensing- and ground-based tree population data are used to examine past and on-going changes of the tree line ecotone in a sub-arctic region characterized by precipitation increase. Questions addressed are: (1) at what rate has the tree line ecotone changed since the mid-20th century; (2) can specific temporal dynamics be identified; and (3) do combined remote sensing and tree population analyses add essential knowledge for the interpretation of tree line changes?

**Location:** Khibiny Mountains, Kola Peninsula, northwest Russia.

**Methods:** Aerial photos from 1958, high-resolution satellite imagery from 2006/2008 and age structure data for dominant tree line species (birch and pine) were used to analyse rate of change and temporal and species-specific tree line recruitment patterns. This was accomplished using digital elevation models, resolution-merging procedures, visual interpretation and dendroecological methods.

**Results:** Mean tree line advance for birch and pine was recorded as 29 and 27 altitudinal metres ( $0.6$  and  $0.5$   $\text{m}\cdot\text{yr}^{-1}$ ), respectively. The advance was accompanied by an apparent infilling of pre-established tree populations and by recruitment beyond the tree line. Evident increased recruitment occurred in the late 1980s for birch and in the 1970s and 1990s for pine. Establishment showed no strong correlations with climate variables, but the importance of non-growing season variables was indicated.

**Conclusions:** The recorded tree line advance is modest compared to global model predictions for advance at high latitudes, but in accordance with results from a number of high-latitude areas. Concomitantly, the apparent increased recruitment is indicative of a more rapidly advancing tree line zone. Studies combining remote sensing and ground-based data minimize the risk of under- or overestimating potential tree line advance. Low detectability of small seedlings and saplings by remote sensing can cause underestimation of the current potential, while ground-based data used alone can overestimate potential advance. A balance between the two approaches is beneficial and enhances quality in production of change scenarios related to high latitudinal tree line areas at local to large regional scales.

### Introduction

The location of the northern tree line ecotone, which links the boreal forest to the south with the treeless tundra to the north, is considered a sensitive bioclimatic indicator of both

climate changes and landscape changes (Holtmeier & Broll 2005). Tree recruitment, forest cover density and tree growth forms across the ecotone are structured by inter-laced climate, topography and land-use-related latitudinal and altitudinal gradients (Callaghan et al. 2002; Moen

et al. 2008; Aune et al. 2011). The ecotone therefore has area- or region-specific characteristics determined by multiple variables (Hofgaard et al. 2012), dominated by temperature, precipitation, wind and herbivory (Sveinbjörnsson et al. 2002; Cairns & Moen 2004; Holtmeier & Broll 2005). Micro-topographical shelters and presence of tree cover alter the impact of these abiotic and biotic factors through the creation of relatively benign local environments in terms of wind, radiation, temperature, snow cover and soil moisture (Hofgaard et al. 2009; Batllori et al. 2010; Holtmeier & Broll 2010). These microhabitat conditions are essential to recruitment, survival and growth of new seedlings, and thus essential to both relocation and structural change (e.g. infilling) of the ecotone (Danby & Hik 2007; Batllori & Gutiérrez 2008; Kullman & Öberg 2009). A change in the regeneration capacity in the tree line ecotone has caused its main features, forest line (limit of continuous forest), tree line (limit of uppermost > 2-m tall trees) and species line (limit of tree saplings and seedlings), to move back and forth over time in accordance with long- and short-term climate changes (Hofgaard 1997a; Dalen & Hofgaard 2005; Payette 2007; Shiyatov et al. 2007). The history and climate sensitivity of the ecotone has led to the assumption of swift advance and spatially extensive response to the on-going global warming (ACIA 2005; Kaplan & New 2006). In a short-term perspective, an advancing tree line ecotone would cause locally altered stand structure and forest cover, while in a long-term perspective forest encroachment onto the tundra would cause large-scale changes of the current sub-arctic and low-arctic regions (Payette et al. 2001; Kapralov et al. 2006; Danby & Hik 2007; Moen et al. 2008). At the circumpolar scale, northward forest advance would decrease the regional albedo and thus amplify global warming (ACIA 2005; Chapin et al. 2005; Bala et al. 2007).

Remote sensing of the tree line ecotone has great potential for analyses of rates of change (Rees 2007). Using high spatial resolution airborne and Earth-orbiting tools, such as QuickBird and WorldView satellite images, detailed information can be acquired on changes in position and structure during specific periods (Heiskanen 2006), and to some extent at the tree species level (Næsset et al. 2004). This information can thus be used to calibrate and validate coarser-resolution global remote sensing products for standardized and precise characterization of change in forest cover at regional to circumpolar scale (Stow et al. 2004; Montesano et al. 2009; McManus et al. 2012). However, a prevailing characteristic of the ecotone is a considerable time lag between tree establishment and the ability of remote sensing to detect small saplings and trees (Dalen & Hofgaard 2005; Heiskanen 2008). Combined remote sensing and age structure analyses can therefore assist in the calculation of climate-driven rates of change. Age struc-

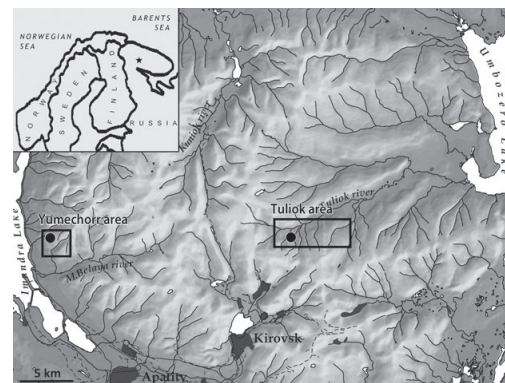
tures of tree line tree communities show the combined outcome of recruitment and survival and how it has varied through time (Lavoie & Payette 1992; Villalba & Veblen 1998; Aune et al. 2011). The resulting establishment pattern can thus be used to elucidate ecotonal responses to changed climate conditions (Elliot 2012).

In the present study, we analyse changes of the tree line ecotone in the Khibiny Mountains, Kola Peninsula, Russia, for the period from 1958 to 2008, by combining remote sensing techniques with analysis of tree population age structures. The following questions are addressed: (1) at what rate has the tree line ecotone changed since mid-20th century; (2) can specific temporal dynamics be identified; and (3) do combined remote sensing and tree population analyses add essential knowledge for the interpretation of tree line changes?

## Methods

### Description of study area

Two study areas situated in the Khibiny Mountains are used for the analyses. The Khibiny Mountains form an approximately 2500-km<sup>2</sup> massif in the central Kola Peninsula in northwest Russia (Fig. 1). The highest peaks lie between 900–1200 m a.s.l., and the geology consists of crystalline bedrock covered mainly by Quaternary glacial till (Kononov et al. 2009). The Khibiny region is characterized by slightly continental climate (Moen 1999), and is generally snow-covered from October to May. The region has an average annual temperature and total precipitation of around  $-3.7$  °C and 1070 mm, respectively. The average temperature of the warmest month (July) is 9.0 °C and for the coldest (February)  $-12.6$  °C. February

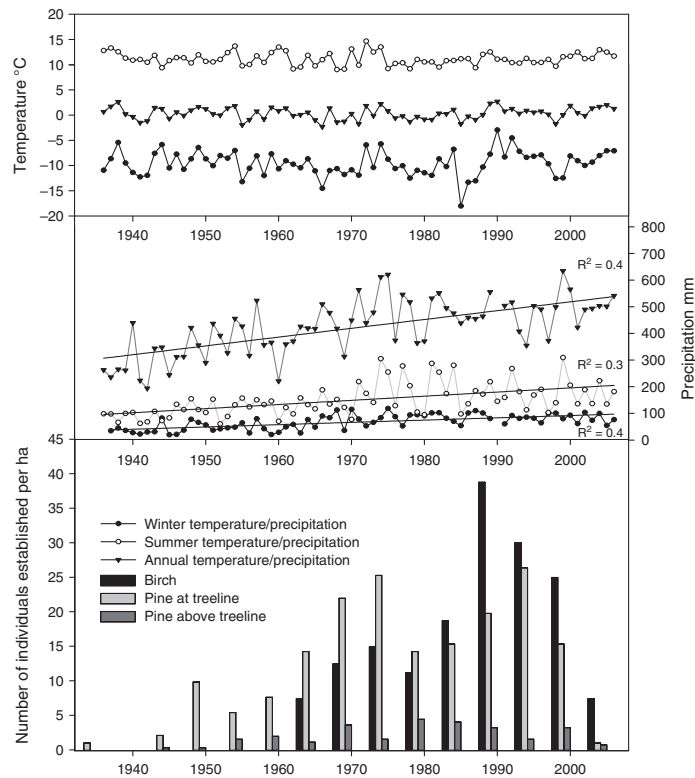


**Fig. 1.** Map of the Khibiny Mountains study region in the Kola Peninsula, northwest Russia (star on inset map), and the two sampling areas, Tuliook and Yumechorr (indicated by squares on the map). Filled circles show field study sites within the areas.

is also the driest month, with on average 57 mm precipitation, and September the wettest month with 135 mm. The climate data refer to the Russian normal period 1881–1980, and the Yukspor meteorological station, in the central Khibiny Mountains (910 m a.s.l.; Vlasenko 1988). In the analysis, climate data from Murmansk meteorological station (54 m a.s.l and 140 km north of the Khibiny Mountains) are used (Bulygina & Razyvaev 2008). This is the closest station to the study sites, which has daily data recordings. Monthly normal period temperature and precipitation values for the Murmansk and Yukspor meteorological stations are strongly correlated ( $r = 0.991$  and  $r = 0.796$ , respectively, both at  $P < 0.005$ ). The daily data available for the Murmansk meteorological station are, however, restricted to the period 1936–2006. Over this period, precipitation shows a significant increasing trend but no temperature trend was

registered (Fig. 2, upper sections). Cumulative sum plot analyses (data not shown) revealed that the increase in precipitation began around the 1960s and persisted until the end of the period. No significant temporal autocorrelation was detected for the climate data.

The dominant species in the tree layer are Scots pine (*Pinus sylvestris*) and mountain birch (*Betula pubescens* subsp. *tortuosa*) together with some scattered aspen (*Populus tremula*), and the shrub layer is dominated by juniper (*Juniperus communis*) and dwarf birch (*Betula nana*). The mountain area has a low grazing/browsing pressure from moose (*Alces alces* L.), hare (*Lepus timidus* L.), grouse (*Lagopus* spp.), voles (*Microtus* spp., *Clethrionomys* spp.) and lemmings (*Lemmus lemmus* L.), and has had low or no human land-use impact throughout the 20th century and until the present time (Myagkova 1988; O.V. Tutubalina pers. com.).



**Fig. 2.** Temperature and precipitation data (upper sections; trend lines shown when significant) from the Murmansk meteorological station for the period 1936–2006 (Bulygina & Razyvaev 2008), and age structures of birch and pine (lower section). Age structures are given as individuals per ha in the period 1931–2005 for birch above the birch tree line ( $n = 133$ ) and for pine at ( $n = 164$ ) and above ( $n = 70$ ) the pine tree line. One pine established in 1878 (tree line sub-site) is not included in the graph. Individuals are merged into 5-yr age classes. Note missing values for winter precipitation and annual precipitation in 1990 and the use of three y-axes.

### Field surveys

Tree population data were collected during the summer of 2008 at the two sites, Tuliok and Yumechorr, in central and western Khibiny Mountains, respectively (Fig. 1). The Tuliok site is located on a north-facing slope (67°42'N 33°46'E) at 500–600 m a.s.l. The study species is mountain birch, and the birch tree line (as defined by the uppermost > 2 m trees) runs on average at 535 m a.s.l. The Yumechorr site is located on a southwest-facing slope (67°42'N, 33°14'E) at 330–470 m a.s.l. The study species at this site is Scots pine, and the pine tree line runs at ca. 400 m a.s.l.

The data from Tuliok and Yumechorr originate from two different field surveys that were part of the international *PPS Arctic* research programme (see: <http://ppsarctic.nina.no>), and were collected to individually fit the design of these studies (i.e. Aune et al. 2011; I.E. Mathisen et al. unpublished data). Consequently, the layout of the sampled area differs between the two study sites, but common criteria were gentle topographic slopes, with no signs of forest fire, logging or other human land use. At Tuliok, 133 birch seedlings (<15 cm in height) and saplings (>15 cm–2 m in height) were sampled (details given below) within two sampling bands, covering 0.66 ha in total, stretching from the local tree line and 80 and 50 altitudinal metres into the tundra, respectively. In the analyses, the two bands are merged to one data set. At altitudes beyond the bands, birch is increasingly more scattered. In addition to the sampling within the bands, the altitude of the most advanced birch specimen was recorded. At Yumechorr 234 pine seedlings, saplings and trees (>2 m) were collected at two sampling sub-sites, one at the tree line ( $n = 164$ ) and one above it ( $n = 70$ ). The tree line sub-site covered 0.75 ha, and the above tree line sub-site covered 2 ha. Scattered pine seedlings occurred also at altitudes above the tree line sub-site, but the uppermost specimen was not recorded. The difference in total area analysed at the birch and pine site/sub-sites was due to the requirements to sample at least 100 focal tree species individuals per site/sub-site in the original studies. This was, however, not fully met at the pine sub-site above the tree line due to low pine density. Birch and pine seedlings <5 cm in height are difficult to locate and could consequently be underrepresented in the data sets. Height, age and location were recorded for all seedlings, saplings and tree individuals of the site-specific study species represented in the sampling bands and sub-sites. The height was measured with a ruler (resolution 1 cm) and age determined by coring (individuals with a stem diameter >3.5 cm) or cutting (stem diameter <3.5 cm) at the stem base (i.e. at ground level). Location coordinates were recorded with a hand-held GPS (WGS84 datum, horizontal accuracy 10 m or better). The

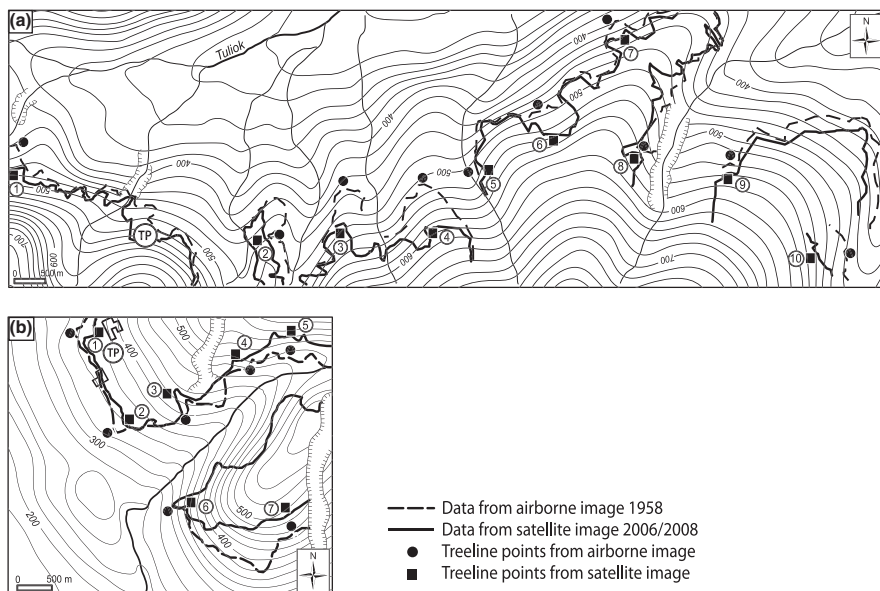
cores were mounted on wooden supports, and all age samples (cores and basal stem sections) were dried and planed. A dissecting microscope (6–40×) was used for counting tree rings and determining the year of establishment. Ground level samples give high quality data for the year of establishment, but an uncertainty of ca. 0–3 yr can be expected due to possible variations in the exact coring height.

### Remote sensing data and processing

Changes in the tree line ecotone were mapped for the two areas where the two field surveys were conducted by contouring the tree line positions on high-resolution images from 1958 and 2006/2008. The contouring was done by hand, by drawing a continuous line between the uppermost trees (>2 m, judging from their shadow in the image) along the slopes. The 1958 images covered both areas and had a 2-m resolution (black-and-white air photos from 14 August 1958). For 2006/2008, two image dates were used: a multispectral and panchromatic QuickBird satellite image from 28 June 2006 (resolution 0.6 m) for Tuliok, and a panchromatic WorldView satellite image from 29 July 2008 (resolution 0.5 m) for Yumechorr. The selection of satellite images was based on availability, correspondence to peak growing season in the study area, minimal cloud coverage and maximization of the period between airborne and satellite images.

To enable analyses of elevation changes in the tree line contours digital elevation models (DEMs) were produced for both sites. For Tuliok, a stereopair of GeoEye panchromatic satellite images from 2009 was used, and for Yumechorr overlapping black-and-white airborne images from 1958, with a scanned 1:50 000 topographic map as the elevation data source were used (details of this process are given in Appendix S1). Airborne images from 1958 were then orthorectified (geo-referencing with terrain correction) using these DEMs, and satellite images (2006/2008) were geo-referenced to the orthorectified 1958 airborne images using image transformation with a second-order polynomial equation (Leica Geosystems Geospatial Imaging, Norcross, US), which provided positioning accuracy better than 10 m. Additionally, the images were visually quality checked to make local adjustments and achieve image co-registration accurate at the individual tree level.

Tree line points containing the uppermost, scattered trees of birch and pine were selected for tree elevation recordings along the contoured tree lines (Fig. 3). These points were horizontally separated by at least 500 m to avoid local dependencies and to include a variety of microclimatic and microtopographic locations. The distance of 500 m was empirically selected for the Khibiny Mountains, where significant changes in topography and soil



**Fig. 3.** Altitudinal tree line contour lines representing 1958 (broken line) and 2006/2008 (solid line) for (a) birch (Tuliok area) and (b) pine (Yumechorr area) as derived from airborne and satellite images. Encircled numbers indicate the selected tree line point locations that were analysed along the lines. Field-based sampling locations for tree population data are marked with TP in (a), and with TP and plot shapes in (b). Gaps in the tree line contour lines are caused by shadows and clouds in the used images. Encircled tree line point numbers are congruent with numbers in Table 1, and area locations are indicated in Fig. 1.

conditions occur at much shorter distances (field-based observations). For the Tuliok site, an approximately 13 km horizontal stretch along the tree line ecotone was used for the selection. As a first step in the selection procedure, ten points along the 2006 tree line contour were selected (visual-based selection on the geo-referenced QuickBird image). Second, on the airborne image of 1958, we selected the closest birch trees that were situated directly downhill from the ten 2006 points. In this second step we used, in addition, trees that had existed throughout the period or other terrain features for precise spatial reference. In each selected 1958 and 2006 point, ten trees (>2 m, judging from their shadow in the image) were identified, their elevation was extracted from the DEM and averaged per point to represent the elevation of the points along each individual time-specific tree line contour. At the Yumechorr site, seven points along a 5-km horizontal stretch containing the uppermost pine trees were selected, and the same process as for the Tuliok site was repeated. The smaller number of points at the Yumechorr site was due to cloud and terrain shadow limitations of the airborne image.

The interpretations of airborne and space-borne images were performed after applying a 'resolution merge' proce-

dure in the ERDAS Imagine 9.1 software (Leica Geosystems Geospatial Imaging). This procedure enables combination of spectral information and spatial detail from multispectral and panchromatic images. To test if the calculated altitudinal tree line positions in 1958 and 2006/2008 were significantly different from one other, a non-parametric Wilcoxon rank sum test was performed using R (R Foundation for Statistical Computing, Vienna, AT).

#### Age structure construction and climate-establishment analysis

To enable comparisons between the sites, the seedling, sapling and tree data were calculated to represent the number of individuals per hectare by dividing the number of birch/pine per site/sub-site by the size of the site/sub-site. The birch establishment data covered the period 1960–2008 and the pine data 1878–2008 (only a few individuals originate from the period prior to 1960). The data from 1960 onwards were divided into two periods, 1960–1984 and 1985–2008, for temporal comparison of establishment rates (i.e. given as mean number of individuals·ha<sup>-1</sup>·yr<sup>-1</sup>).

Daily climatic data from the Murmansk station were used to calculate monthly, seasonal and annual climate



data. The calculations included correction of precipitation data recordings for the period 1947–1966 (due to change of instruments) according to instructions from the All-Russian Research Institute of Hydrometeorological Information. The winter period was set as December–February, spring as March–May, summer as June–August and autumn as September–November. The relationship between establishment and mean monthly, seasonal and annual temperature and precipitation was examined using Pearson's correlation analysis, with Bonferroni adjustment of the significance level ( $\alpha = 0.005/\text{number of comparisons}$ ; Rice 1989). Due to possible error in exact determination of the establishment year, the establishment data and climate data were analysed both on a 1-yr basis and a merged 5-yr class basis. The period 1960–2004 was used in the analysis to suit uniform 5-yr classes.

## Results

For the remotely sensed birch and pine tree lines, the mean advance between 1958 and 2006/2008 was 29 and 27 altitudinal metres, respectively (Table 1). Based on this, the upward tree line migration rate was approximated to  $0.6 \text{ m}\cdot\text{yr}^{-1}$  for birch and  $0.5 \text{ m}\cdot\text{yr}^{-1}$  for pine. The Wilcoxon rank sum test revealed non-significant differences between the average altitudes of the species-specific tree lines (Table 1). Individual differences between the tree line points selected in the airborne (1958) and the satellite images (2006/2008), respectively, ranged from  $-4 \text{ m}$  to  $69 \text{ m}$  for birch and from  $1 \text{ m}$  to  $53 \text{ m}$  for pine (Table 1). At the location of the tree population data collection sites, the calculated advance was within these ranges and amounted to  $36 \text{ m}$  for birch and  $2 \text{ m}$  for pine over the 50-yr period.

In accordance with the change detected by the remotely sensed data, a range expansion was also apparent in the tree population data (Figs 4 and 5). The establishment (i.e. as represented by surviving individuals) of birch was initiated in the 1960s and had a colonization peak in the late 1980s (Fig. 2). From 1960 to 1984, birch seedlings were established along the entire analysed altitudinal range, with a mean establishment rate of  $3.1 \pm 2.1$  (mean  $\pm$  SD)  $\text{individuals}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ . In the period between 1985 and 2008, birch establishment continued along the entire studied altitudinal range (Fig. 4), but with a higher mean establishment rate,  $5.2 \pm 4.4$   $\text{individuals}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ . The birch specimen with most advanced altitudinal position was found at 398 altitudinal metres above the current tree line, and had reached a height of 28 cm since it established in 1968.

The earliest establishment of pine originates from the time before 1960, both at and above the tree line (Figs 2 and 5). After 1960, new individuals filled in between already established individuals (Fig. 5), with establishment

**Table 1.** Altitudinal tree line position (m a.s.l.) in 1958 and 2006/2008 and calculated changes over the period for birch and pine, as retrieved from airborne and satellite images.

	Point	1958	2006/2008	Change	P-value
Birch	1	419	452	32	0.186
	2	482	495	13	
	3	451	520	69	
	4	545	577	32	
	5	521	517	-4	
	6	489	525	36	
	7	409	422	13	
	8	537	554	17	
	9	533	554	21	
	10	477	534	57	
	Average	486	515	<b>29</b>	0.186
	<i>TP</i>	494	530	36	
Pine	1	364	395	31	0.535
	2	322	331	9	
	3	385	407	22	
	4	498	531	33	
	5	491	544	53	
	6	300	301	1	
	7	444	484	40	
		Average	401	428	
	<i>TP</i>	346	348	2	

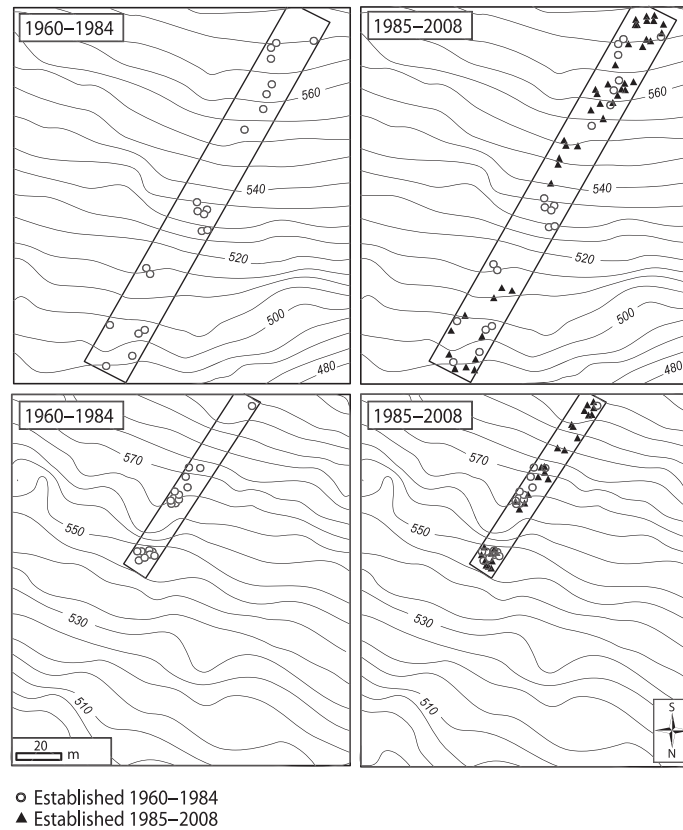
Values are given for individual points (for location see Fig. 1) and total average per species. P-values are based on Wilcoxon rank sum tests. The field-based tree population data (TP) given in italics are not included in the calculated average change (bold).

peaks at the tree line in the 1970s and 1990s (Fig. 2). Above the tree line, there were no evident peak periods, but the mean establishment rate for the two periods of comparison varied somewhat, with  $0.8 \pm 0.8$   $\text{individuals}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$  during 1960–1984 and  $0.4 \pm 0.5$   $\text{individuals}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$  during the 1985–2008 time period. At the tree line, pine establishment was more abundant than above the tree line, but similarly decreased slightly over time (Fig. 2):  $4.4 \pm 2.5$   $\text{individuals}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$  during 1960–1984, and  $3.3 \pm 2.9$   $\text{individuals}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$  between 1985 and 2008. No strong correlations were found between monthly, seasonal or annual climate variables and establishment, and there was no indication of growing season restrictions on establishment. The 1-yr values for birch establishment indicated a weak association with March temperature, and a similarly weak association was indicated for pine establishment with annual precipitation (Appendix S2). The 5-yr-based values indicated no correlation with climate for either birch or pine (Appendix S2). When Bonferroni adjusted, none of the correlations was significant.

## Discussion

The recorded tree line advance in the Khibiny Mountains during the 1958 to 2006/2008 period is modest when





**Fig. 4.** Temporal and spatial recruitment distribution of birch individuals present above the birch tree line at the Tuliok site in July 2008 (location of the site is indicated in Fig. 1). The panels show two sampling bands running from the local tree line uphill into the tundra. The band viewed in the upper panels is 20-m wide and spans 80 altitudinal metres, while the band in the lower panels is 10-m wide and spans 50 altitudinal metres.

compared to global climate model-based predictions for forest advance at high latitudes (ACIA 2005; IPCC 2007). These predictions correspond to advance rates at the scale of kilometres per year (ACIA 2005; Kaplan & New 2006), which however remain to be empirically shown (Van Bogaert et al. 2011; Hofgaard et al. 2013). Upward migration rates similar to those found in the Khibiny Mountains are recorded for a number of areas in the circumpolar north (i.e. 0.5–1.5 m·yr<sup>-1</sup>; Lloyd & Fastie 2003; Shiyatov et al. 2007; Kullman & Öberg 2009; Van Bogaert et al. 2011). Even if latitudinal and altitudinal advance are not directly comparable, the implications of these much slower advance rates, compared to current model-based assumptions, has to be recognized (Van Bogaert et al. 2011; Hofgaard et al. 2013).

Slow rates of change are challenging when monitoring large areas, such as regional to circum-arctic tree line

ecotones, is required (Rees 2007; Montesano et al. 2009; McManus et al. 2012). Even if the biological response to a changing climate is immediate at tree level (Mathisen & Hofgaard 2011), it might not be detectable remotely at larger spatial scales (Montesano et al. 2009). The recorded advance of both birch and pine occurred through both tree encroachment of non-treed areas and additional establishment in areas of pre-established populations of scattered trees and saplings. This infilling process changes and shapes the ecotone (Danby & Hik 2007), but does not necessarily cause an apparent advance of the ecotone or advanced location of the outermost tree-sized individuals (tree line markers). Instead, the slow advance characterizing the Khibiny Mountains study sites is accompanied by an apparent infilling and densification of the treed part of the ecotone (i.e. as shown for the pine site). This change in land cover is a more prominent climate driver than tree



**Fig. 5.** Temporal and spatial recruitment distribution of pine individuals present at the two sub-sites at the Yumechorr site in July 2008 (site location is indicated in Fig. 1). Upper panel shows the above-tree line sub-site (eight merged 50 × 50-m squares) and the lower panels the tree line sub-site (three merged 50 × 50-m squares).

line change *per se* through its stronger link to surface radiation and albedo (Harding et al. 2002; Chapin et al. 2005; Bala et al. 2007; Hyvönen et al. 2007), and can be more efficiently monitored through remote sensing than changes in tree line location, due to its lesser demand on resolution (Rees 2007).

An infilling process promotes both continued recruitment and survival within protective microhabitats of taller individuals during both growing and non-growing seasons (Bekker 2005; Batllori et al. 2009; Holtmeier & Broll 2010). However, to reach tree size, establishing individuals must overcome exposure-related increased abiotic stress, both when establishing in non-sheltered environments and when protruding above sheltered environments (Batllori et al. 2009; Hofgaard et al. 2009; Olofsson et al. 2009). In the Khibiny Mountains, and despite generally increased abiotic stress at higher elevation, both species revealed a clear potential for upward migration of the

ecotone through the abundance of seedlings and saplings beyond the tree line. In addition, the age structures showing increased establishment of both birch and pine saplings indicate progressive recruitment typical for advancing tree lines (Dalen & Hofgaard 2005; Aune et al. 2011). The survival and height growth success of this recruitment pool will be deterministic to tree line advance (Sveinbjörnsson et al. 2002).

In contrast to many other high-latitude and altitude areas of Europe, where an advancement of the tree line can be explained as a combination of declines in human land use and climate changes (Hofgaard 1997b; Cairns & Moen 2004; Gehrig-Fasel et al. 2007; Batllori & Gutiérrez 2008; Aune et al. 2011), the tree line ecotones of the Khibiny Mountains have been insignificantly affected by human land use throughout the 20th century and until the present time (Myagkova 1988; O.V. Tutubalina pers. com.). Although establishment showed no clear relation to

any climate variables, the recorded climate change in the region (doubling of seasonal and annual precipitation over the study period; Førland et al. 2009) is a plausible underlying cause of the ecotonal change in the region (Aune et al. 2011). The lack of significant evidence for climate-controlled ecotonal change in our data is likely related to both climate data quality (long distance to the meteorological station with daily data) and the uncertainty associated with age determination of trees and saplings by coring and cutting at ground level (Gutsell & Johnson 2002). Increased precipitation during, for example, the growing season, if not accompanied by increased temperature, generally causes fewer and less severe summer drought events (Girardin et al. 2004). In addition, at high latitudes and altitudes, increased precipitation during the non-growing season usually generates thicker and longer-lasting snow packs, which provides protection against browsing and wind abrasion (Sturm et al. 2001; Hofgaard et al. 2009; Holtmeier & Broll 2010), and supply of soil moisture early in the growing season (Sveinbjörnsson et al. 2002; Holtmeier & Broll 2005). These season-related processes, taken individually or combined, would favour survival and growth of establishing tree species individuals, and thus promote advancement of the tree line ecotone (Danby & Hik 2007; Batllori & Gutiérrez 2008; Elliott 2011). Increased precipitation, particularly during the non-growing season, is one of the main features in climate scenarios for the north European sub-arctic region (Førland et al. 2009). Consequently, a plausible response scenario for tree line ecotones of the studied region would be continued advance, characterized and accompanied by a precipitation-driven infilling process.

Remotely sensed data alone provide valuable information on past changes of the main ecotone features, such as forest cover and distribution of larger trees, but no information about on-going changes or potential for change. Through combining remote sensing and dendroecological studies, the risk of over- or underestimating potential tree line advance can be minimized. When tree population data alone are used, the occurrence of abundant seedlings and saplings above the current tree line may be interpreted as a sign of rapidly advancing tree lines, although combined and partly counteracting abiotic and biotic drivers may generate a deviating response pattern (i.e. stationary or retreating; Dalen & Hofgaard 2005; Aune et al. 2011). Contrary to this plausible overestimation of the potential tree line advance, remote sensing data alone may underestimate the current potential due to the low or non-existent detectability of small seedlings and saplings (but see Næsset & Nelson (2007)). As a consequence, remote sensing-based change rates, as recorded for the studied region, give a very restricted view regarding change potential. The tree line ecotone is a highly dynamic system and thus any study of

its changes will be challenging. Studies combining remote sensing and ecological approaches are advantageous to avoid misinterpretations, but generally not feasible over larger spatial scales (due to cost and labour demands). However, a balance between the two approaches is needed for the production of high-quality information valid for large regions, such as the high-latitude tree line ecotone.

### Acknowledgements

The project is part of the 'Benefits' collaboration network between Norway and Russia, and the IPY core project PPS Arctic (<http://ppsarctic.nina.no>), both financially supported by the Research Council of Norway (grants 185023/S50 and 176065/S30, to A. Hofgaard). In addition, O.V. Tutubalina and A. Mikheeva received support from the Russian Leading Science Schools Programme, project HIII-3405.2010.5, and from the Russian Scientific Educational Centres Programme, project 14.740.11.0200. We thank K. Sivertsen for help with Figures 3–5, Y.A. Plyushkiyavichyute and M.V. Zimin for help with Russian climate data, and Gareth Rees for language improvement. Brad Case and three anonymous referees are thanked for their constructive comments on earlier versions of the manuscript.

### References

- ACIA 2005. *Arctic climate impact assessment*. pp. 1042. Cambridge University Press, New York, US.
- Aune, S., Hofgaard, A. & Söderström, L. 2011. Contrasting climate- and land-use-driven tree encroachment patterns of subarctic tundra in northern Norway and the Kola Peninsula. *Canadian Journal of Forest Research* 41: 437–449.
- Bala, G., Caldeira, K., Wickett, M., Phillips, T.J., Lobell, D.B., Delire, C. & Mirin, A. 2007. Combined climate and carbon-cycle effects of large-scale deforestation. *Proceedings of the National Academy of Sciences of the United States of America* 104: 6550–6555.
- Batllori, E. & Gutiérrez, E. 2008. Regional tree line dynamics in response to global change in the Pyrenees. *Journal of Ecology* 96: 1275–1288.
- Batllori, E., Camarero, J.J., Ninot, J.M. & Gutiérrez, E. 2009. Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* tree line ecotones. Implications and potential responses to climate warming. *Global Ecology and Biogeography* 18: 460–472.
- Batllori, E., Camarero, J.J. & Gutiérrez, E. 2010. Current regeneration patterns at the tree line in the Pyrenees indicate similar recruitment processes irrespective of the past disturbance regime. *Journal of Biogeography* 37: 1938–1950.
- Bekker, M.F. 2005. Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier National Park, Montana, USA. *Arctic, Antarctic, and Alpine Research* 37: 97–107.

- Bulygina, O.N. & Razyvaev, V.N. 2008. Opisaniye massiva danukh sutochnoy temperatury vozdukha I kolichestva osadkov na 223 meteorologicheskikh stantsiyakh na territorii byvshego SSSR (TTTR) [Description of the TTTR data array of daily temperature and precipitation for 223 meteorological stations at the territory of the former USSR]. Retrieved September 2008, URL: <http://www.meteo.ru/climate/descrip1>.
- Cairns, D.M. & Moen, J. 2004. Herbivory influences tree lines. *Journal of Ecology* 92: 1019–1024.
- Callaghan, T.V., Werkman, B.R. & Crawford, R.M.M. 2002. The tundra–taiga interface and its dynamics: concepts and applications. *Ambio Special Report* 12: 6–14.
- Chapin, F.S., Sturm, M., Serreze, M.C., McFadden, J.P., Key, J.R., Lloyd, A.H., McGuire, A.D., Rupp, T.S., Lynch, A.H., Schimel, J.P., Beringer, J., Chapman, W.L., Epstein, H.E., Euskirchen, E.S., Hinzman, L.D., Jia, G., Ping, C.L., Tape, K.D., Thompson, C.D.C., Walker, D.A. & Welker, J.M. 2005. Role of land-surface changes in Arctic summer warming. *Science* 310: 657–660.
- Dalen, L. & Hofgaard, A. 2005. Differential regional treeline dynamics in the Scandes Mountains. *Arctic, Antarctic, and Alpine Research* 37: 284–296.
- Danby, R.K. & Hik, D.S. 2007. Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. *Journal of Ecology* 95: 352–363.
- Elliot, G.P. 2012. Extrinsic regime shifts drive abrupt changes in regeneration dynamics at upper treeline in the Rocky Mountains, USA. *Ecology* 93: 1614–1625.
- Elliott, G.P. 2011. Influences of 20th-century warming at the upper tree line contingent on local-scale interactions: evidence from a latitudinal gradient in the Rocky Mountains, USA. *Global Ecology and Biogeography* 20: 46–57.
- Førland, E.J., Benestad, R.E., Flatøy, F., Hanssen-Bauer, J., Haugen, J.E., Isaksen, K., Sorteberg, A. & Adlandsvik, B. 2009. Climate development in North Norway and the Svalbard region during 1900–2100 [report no. 128], Norwegian Polar Institute, Tromsø, NO.
- Gehrig-Fasel, J., Guisan, A. & Zimmermann, N.E. 2007. Tree line shifts in the Swiss Alps: climate change or land abandonment? *Journal of Vegetation Science* 18: 571–582.
- Girardin, M.P., Tardif, J., Flannigan, M.D. & Bergeron, Y. 2004. Multicentury reconstruction of the Canadian Drought Code from eastern Canada and its relationship with paleoclimatic indices of atmospheric circulation. *Climate Dynamics* 23: 99–115.
- Gutsell, S.L. & Johnson, E.A. 2002. Accurately ageing trees and examining their height-growth rates: implications for interpreting forest dynamics. *Journal of Ecology* 90: 153–166.
- Harding, R., Kuhry, P., Christensen, T.R., Sykes, M.T., Dankers, R. & Van der Linden, S. 2002. Climate feedbacks at the tundra–taiga interface. *Ambio Special Report* 12: 47–55.
- Heiskanen, J. 2006. Tree cover and height estimation in the Fennoscandian tundra–taiga transition zone using multiangular MISR data. *Remote Sensing of Environment* 103: 97–114.
- Heiskanen, J. 2008. Evaluation of global land cover data sets over the tundra–taiga transition zone in northernmost Finland. *International Journal of Remote Sensing* 29: 3727–3751.
- Hofgaard, A. 1997a. Structural changes in the forest–tundra ecotone: a dynamic process. In: Huntley, B., Cramer, W., Morgan, A.V., Prentice, H.C. & Allen, J.R.M. (eds.) *Past and future rapid environmental changes: the spatial and evolutionary responses of terrestrial biota*, pp. 255–263. NATO ASI series, Vol. 147. Springer, Berlin, DE.
- Hofgaard, A. 1997b. 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.
- Hofgaard, A., Dalen, L. & Hytteborn, H. 2009. Tree recruitment above the treeline and potential for climate-driven tree line change. *Journal of Vegetation Science* 20: 1133–1144.
- Hofgaard, A., Harper, K.A. & Golubeva, E. 2012. The role of the circumarctic forest–tundra ecotone for arctic biodiversity. *Biodiversity* 13: 174–181.
- Hofgaard, A., Tømmervik, H., Rees, G. & Hanssen, F. 2013. Latitudinal forest advance in northernmost Norway since the early 20th century. *Journal of Biogeography*, 40: 938–949.
- Holtmeier, F.K. & 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.
- Holtmeier, F.K. & Broll, G. 2010. Wind as an Ecological Agent at Treelines in North America, the Alps, and the European Subarctic. *Physical Geography* 31: 203–233.
- Hyvönen, R., Ågren, G.I., Linder, S., Persson, T., Cotrufo, M.F., Ekblad, A., Freeman, M., Grelle, A., Janssens, I.A., Jarvis, P.G., Kellomäki, S., Lindroth, A., Loustau, D., Lundmark, T., Norby, R.J., Oren, R., Pilegaard, K., Ryan, M.G., Sigurdsson, B.D., Strömgren, M., Van Oijen, M. & Wallin, G. 2007. The likely impact of elevated [CO<sub>2</sub>], nitrogen deposition, increased temperature and management on carbon sequestration in temperate and boreal forest ecosystems: a literature review. *New Phytologist* 173: 463–480.
- IPCC 2007. Climate Change 2007. *Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. pp. 104. Cambridge University Press, Geneva, CH.
- Kaplan, J.O. & New, M. 2006. Arctic climate change with a 2 °C global warming: timing, climate patterns and vegetation change. *Climatic Change* 79: 213–241.
- Kapralov, D.S., Shiyatov, S.G., Moiseev, P.A. & Fomin, V.V. 2006. Changes in the composition, structure, and altitudinal distribution of low forests at the upper limit of their growth in the Northern Ural Mountains. *Russian Journal of Ecology* 37: 367–372.
- Kononov, Y.M., Friedrich, M. & Boettger, T. 2009. Regional summer temperature reconstruction in the Khibiny low Mountains (Kola Peninsula, NW Russia) by means of tree-

- ring width during the last four centuries. *Arctic, Antarctic, and Alpine Research* 41: 460–468.
- Kullman, L. & 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.
- Lavoie, C. & Payette, S. 1992. Black spruce growth forms as a record of a changing winter environment at treeline, Quebec, Canada. *Arctic and Alpine Research* 24: 40–49.
- Lid, J. & Lid, D.T. 2005. *Norsk flora*. Det Norske Samlaget, Oslo, Norway.
- Lloyd, A.H. & Fastie, C.L. 2003. Recent changes in treeline forest distribution and structure in interior Alaska. *Ecoscience* 10: 176–185.
- Mathisen, I.E. & Hofgaard, A. 2011. Recent height and diameter growth variation in Scots pine (*Pinus sylvestris* L.) along the Arctic margin: the importance of growing season versus non-growing season climate factors. *Plant Ecology and Diversity* 4: 1–11.
- McManus, K.M., Morton, D.C., Masek, J.G., Wang, D.D., Sexton, J.O., Nagol, J.R., Ropars, P. & Boudreau, S. 2012. Satellite-based evidence for shrub and graminoid tundra expansion in northern Quebec from 1986 to 2010. *Global Change Biology* 18: 2313–2323.
- Moen, A. 1999. *National Atlas of Norway: Vegetation*. Norwegian Mapping Authority, Hønefoss, NO.
- Moen, J., Cairns, D.M. & Lafon, C.W. 2008. Factors structuring the treeline ecotone in Fennoscandia. *Plant Ecology and Diversity* 1: 77–87.
- Montesano, P.M., Nelson, R., Sun, G., Margolis, H., Kerber, A. & Ranson, K.J. 2009. MODIS tree cover validation for the circumpolar taiga–tundra transition zone. *Remote Sensing of Environment* 113: 2130–2141.
- Myagkova, A.S. 1988. Estestvenniye i antropogenniye izmeneniya Khibin za golocen [Natural and anthropogenic changes in Khibiny mountains during the Holocene]. Candidate of Sciences in Geography PhD Thesis, Lomonosov Moscow State University, Moscow, RU.
- Næsset, E. & Nelson, R. 2007. Using airborne laser scanning to monitor tree migration in the boreal–alpine transition zone. *Remote Sensing of Environment* 110: 357–369.
- Næsset, E., Gobakken, T., Holmgren, J., Hyyppä, H., Hyyppä, J., Maltamo, M., Nilsson, M., Olsson, H., Persson, A. & Söderman, U. 2004. Laser scanning of forest resources: the Nordic experience. *Scandinavian Journal of Forest Research* 19: 482–499.
- Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P.E., Oksanen, T. & Suominen, O. 2009. Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology* 15: 2681–2693.
- Payette, S. 2007. Contrasted dynamics of northern Labrador tree lines caused by climate change and migrational lag. *Ecology* 88: 770–780.
- Payette, S., Fortin, M.J. & Gamache, I. 2001. The subarctic forest–tundra: the structure of a biome in a changing climate. *BioScience* 51: 709–718.
- Rees, W.G. 2007. Characterisation of Arctic treelines by LiDAR and multispectral imagery. *The Polar Record* 43: 345–352.
- Rice, W.R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223–225.
- Shiyatov, S.G., Terent'ev, M.M., Fomin, V.V. & Zimmermann, N.E. 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.
- Stow, D.A., Hope, A., McGuire, D., Verbyla, D., Gamon, J., Huemmrich, F., Houston, S., Racine, C., Sturm, M., Tape, K., Hinzman, L., Yoshikawa, K., Tweedie, C., Noyle, B., Silapaswan, C., Douglas, D., Griffith, B., Jia, G., Epstein, H., Walker, D., Daeschner, S., Petersen, A., Zhou, L.M. & Myrneni, R. 2004. Remote sensing of vegetation and land-cover change in Arctic Tundra Ecosystems. *Remote Sensing of Environment* 89: 281–308.
- Sturm, M., McFadden, J.P., Liston, G.E., Chapin, F.S., Racine, C.H. & Holmgren, J. 2001. Snow–shrub interactions in Arctic tundra: a hypothesis with climatic implications. *Journal of Climate* 14: 336–344.
- Sveinbjörnsson, J., Hofgaard, A. & Lloyd, A. 2002. Natural causes of the tundra–taiga boundary. *Ambio Special Report* 12: 23–29.
- Van Bogaert, R., Haneca, K., Hoogesteger, J., Jonasson, C., De Dapper, M. & Callaghan, T.V. 2011. A century of tree line changes in sub-Arctic Sweden shows local and regional variability and only a minor influence of 20th century climate warming. *Journal of Biogeography* 38: 907–921.
- Villalba, R. & Veblen, T.T. 1998. Influences of large-scale climatic variability on episodic tree mortality in northern Patagonia. *Ecology* 79: 2624–2640.
- Vlasenko, P.V. 1988. *Nauchno-prikladnoy spravochnik po klimatu SSSR [Science and applied guide to the climate of USSR]* Series 3: Multi-year data. Gidrometeoizdat, Leningrad, RU.

### Supporting Information

Additional supporting information may be found in the online version of this article:

**Appendix S1.** Construction of DEMS used in the analyses, including airborne and satellite images from the birch site illustrating the tree selection methods of the images.

**Appendix S2.** Correlation between numbers of established birch and pine individuals per hectare and monthly, seasonal and annual mean temperatures and total precipitation for the period 1960–2004.



# Paper III

Is not included due to copyright





## Paper IV

Is not included due to copyright



**Doctoral theses in Biology**  
**Norwegian University of Science and Technology**  
**Department of Biology**

<b>Year</b>	<b>Name</b>	<b>Degree</b>	<b>Title</b>
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr. philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of <i>Pisum sativum</i> and <i>Arabidopsis thaliana</i>
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympatric species of newts ( <i>Triturus</i> , <i>Amphibia</i> ) in Norway, with special emphasis on their ecological niche segregation
1984	Eivinn Røskaft	Dr. philos Zoology	Sociobiological studies of the rook <i>Corvus frugilegus</i>
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinizing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exposed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies ( <i>Trichoptera</i> ) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders <i>Oweniimorpha</i> and <i>Terebellomorpha</i> , with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song

			repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit <i>Parus montanus</i>
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coast-inland transect at Nord-Møre, Central Norway
1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of <i>Nicotiana sanderae</i> and <i>Chrysanthemum morifolium</i>
1987	Bjørn Åge Tømmerås	Dr. scient. Zoolog	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggerget	Dr. philos Zoology	Reproduction in Atlantic Salmon ( <i>Salmo salar</i> ): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels ( <i>Mytilus edulis</i> )
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon ( <i>Salmo salar</i> L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose <i>Alces alces</i>
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose <i>Alces alces</i> , and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two workplaces with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmon ( <i>Salmo salar</i> ) and brown trout ( <i>Salmo trutta</i> ): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie <i>Pica pica</i>
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx ( <i>Lynx lynx</i> ) in Norway
1991	Jan Henning L'Abêe	Dr.	Reproductive biology in freshwater fish, brown trout

	Lund	philos Zoology	<i>Salmo trutta</i> and roach <i>Rutilus rutilus</i> in particular
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera <i>Coregonus</i> and <i>Salvelinus</i> : Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos	Aspects of migration and spawning in salmonids
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy ( <i>Phleum pratense</i> L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins <i>Fratercula arctica</i>
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O <sup>6</sup> -methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, <i>Salmo salar</i> L.: Basal and stressor-induced variations in plasma levels and some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter <i>Lutra lutra</i> .
1993	Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe ( <i>Gallinago media</i> ): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient	Nutritional effects of algae in first-feeding of marine

		Botany	fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant <i>Phalacrocorax carbo carbo</i>
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry ( <i>Rubus idaeus</i> L.)
1994	Inga Elise Bruteig	Dr. scient Bothany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, <i>Vulpes vulpes</i>
1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cuckoo
1994	Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss <i>Dicranum majus</i> Sm. as influenced by nitrogen supply
1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995	Hanne Christensen	Dr. scient Zoology	Determinants of Otter <i>Lutra lutra</i> distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink <i>Mustela vison</i>
1995	Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel <i>Thalassoica antarctica</i> ; the effect of parental body size and condition
1995	Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995	Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of <i>Mysis relicta</i> and constraints on Cladoceran and Char populations
1995	Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the <i>Schistidium apocarpum</i> complex in Norway and Sweden
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; impact fish-bacterial interactions on growth and survival of larvae
1996	Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjörg Einarsdóttir	Dr. scient Zoology	Production of Atlantic salmon ( <i>Salmo salar</i> ) and Arctic charr ( <i>Salvelinus alpinus</i> ): A study of some physiological and immunological responses to rearing routines
1996	Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996	Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of <i>Mytilus edulis</i> and the effects of organic xenobiotics



1996	Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal <i>Halichoerus grypus</i> and Harbour seal <i>Phoca vitulina</i> in the Barents sea region
1997	Gunvor Øie	Dr. scient Bothany	Eevaluation of rotifer <i>Brachionus plicatilis</i> quality in early first feeding of turbot <i>Scophthalmus maximus</i> L. larvae
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997	Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming
1997	Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture
1997	Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997	Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors
1997	Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper <i>Cinclus cinclus</i> in southern Norway
1997	Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil ( <i>Hylobius abietis</i> ), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997	Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in <i>Acinetobacter calcoaceticus</i>
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos Zoology	Population responces of Arctic charr ( <i>Salvelinus alpinus</i> (L.)) and brown trout ( <i>Salmo trutta</i> L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon ( <i>Salmo salar</i> )
1997	Jan Østnes	Dr. scient Zoology	Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998	Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose ( <i>Alces alces</i> ) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic

			plasticity
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls <i>Strix aluco</i> : An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway
1999	Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker <i>Dendrocopos leucotos</i>
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod ( <i>Gadus morhua</i> L.) and Halibut ( <i>Hippoglossus hippoglossus</i> L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting ( <i>Micromisistius poutassou</i> ), haddock ( <i>Melanogrammus aeglefinus</i> ) and cod ( <i>Gradus morhua</i> ) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes <i>Dicranum majus</i> , <i>Hylocomium splendens</i> , <i>Plagiochila asplenigides</i> , <i>Ptilium crista-castrensis</i> and <i>Rhytidiadelphus lokuus</i>
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon ( <i>Salmo salar</i> ) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from <i>Brassica napus</i> hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat ( <i>Luscinia s. svecica</i> )
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon ( <i>Salmo salar</i> L.) and Brown trout ( <i>Salmo trutta</i> L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host spesificity as parameter in estimates of arthropod species richness
1999	Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient	Microbial ecology in early stages of marine fish:

		Botany	Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient	The Cuckoo ( <i>Cuculus canorus</i> ) and its host: adaptations and counteradaptations in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient	Sexual segregation in the African elephant ( <i>Loxodonta africana</i> )
2000	Odd A. Gulseth	Dr. philos	Seawater tolerance, migratory behaviour and growth of Charr, ( <i>Salvelinus alpinus</i> ), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient	Biochemical impacts of Cd, Cu and Zn on brown trout ( <i>Salmo trutta</i> ) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient	Production and nutritional adaptation of the brine shrimp <i>Artemia</i> sp. as live food organism for larvae of marine cold water fish species
2001	Olga Hilmo	Dr. scient	Lichen response to environmental changes in the managed boreal forest systems
2001	Ingebrigt Uglem	Dr. scient	Male dimorphism and reproductive biology in corkwing wrasse ( <i>Symphodus melops</i> L.)
2001	Bård Gunnar Stokke	Dr. scient	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer ( <i>Rangifer tarandus platyrhynchus</i> )
2002	Mariann Sandsund	Dr. scient	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient	The function of scent marking in beaver ( <i>Castor fiber</i> )
2002	Janne Østvang	Dr. scient	The Role and Regulation of Phospholipase A <sub>2</sub> in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr. philos	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in <i>Arabidopsis thaliana</i> and the Ral GTPase from <i>Drosophila melanogaster</i>
2002	Henrik Jensen	Dr. scient	Causes and consequences of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient	Behavioural effects of environmental pollution in threespine stickleback <i>Gasterosteus aculeatus</i> L.
2003	Dagmar Hagen	Dr. scient	Assisted recovery of disturbed arctic and alpine

		Biology	vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo ( <i>Syncerus caffer</i> ) in Chobe National Park, Botswana
2003	Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species ( <i>Helicoverpa armigera</i> , <i>Helicoverpa assulta</i> and <i>Heliothis virescens</i> )
2003	Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, <i>Pogonatum dentatum</i>
2003	David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Arctic environments
2003	Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon ( <i>Salmo Salar</i> L.) parr and smolt
2004	Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in <i>Arabidopsis thaliana</i>
2004	Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species ( <i>Heliothis virescens</i> , <i>Helicoverpa armigera</i> and <i>Helicoverpa assulta</i> )
2004	Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry ( <i>Fragaria x ananassa</i> ): characterisation and induction of the gene following fruit infection by <i>Botrytis cinerea</i>
2004	Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr.scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	ph.d	Functional characterisation of olfactory receptor

2005	Erlend Kristiansen	Biology Dr.scient	neurone types in heliothine moths Studies on antifreeze proteins
2005	Eugen G. Sørmo	Biology Dr.scient	Organochlorine pollutants in grey seal ( <i>Halichoerus grypus</i> ) pups and their impact on plasma thyrid hormone and vitamin A concentrations
2005	Christian Westad	Dr.scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	ph.d Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	ph.d Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	ph.d Biology	Investigation of the biological activities and chemical constituents of selected <i>Echinops</i> spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	ph.d Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	ph.d Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr.scient Biology	The European whitefish <i>Coregonus lavaretus</i> (L.) species complex: historical contingency and adaptive radiation
2006	Kari Mette Murvoll	ph.d Biology	Levels and effects of persistent organic pollutants (POPs) in seabirds Retinoids and $\alpha$ -tocopherol – potential biomarkers of POPs in birds?
2006	Ivar Herfindal	Dr.scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	ph.d Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on <i>Calanus finmarchicus</i>
2006	Jan Ove Gjershaug	Dr.philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr.scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	ph.d Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	ph.d Biology	Metal-mediated oxidative stress responses in brown trout ( <i>Salmo trutta</i> ) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	ph.d Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	ph.d Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006	Anna Maria Billing	ph.d Biology	Reproductive decisions in the sex role reversed pipefish <i>Syngnathus typhle</i> : when and how to invest in reproduction
2006	Henrik Pärn	ph.d Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	ph.d Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	ph.d Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	ph.d Biology	Metal binding proteins and antifreeze proteins in the beetle <i>Tenebrio molitor</i> - a study on possible competition for the semi-

2007	Kasper Hancke	ph.d Biology	essential amino acid cysteine Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	ph.d Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	ph.d Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth <i>Heliothis virescens</i>
2007	Stig Ulland	ph.d Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, ( <i>Mamestra brassicae</i> L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	ph.d Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	ph.d Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	ph.d Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	ph.d Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007	Shombe Ntaraluka Hassan	ph.d Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	ph.d Biology	Functional development and response to dietary treatment in larval Atlantic cod ( <i>Gadus morhua</i> L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	ph.d Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	ph.d Biology	The Svalbard reindeer ( <i>Rangifer tarandus platyrhynchus</i> ) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	ph.d Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	ph.d Biology	The ecology and behaviour of the Masai Ostrich ( <i>Struthio camelus massaicus</i> ) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	ph.d Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, ( <i>Taeniopygia guttata</i> )
2008	Sølvi Wehn	ph.d Biology	Biodiversity dynamics in semi-natural mountain landscapes. - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	ph.d Biology	"The Role of Androgens on previtellogenic oocyte growth in Atlantic cod ( <i>Gadus morhua</i> ): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations"
2008	Katarina Mariann Jørgensen	Dr.Scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation

2008	Tommy Jørstad	ph.d Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	ph.d Biology	<i>Arabidopsis thaliana</i> Responses to Aphid Infestation
2008	Jussi Evertsen	ph.d Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	ph.d Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	ph.d Biology	Somatic embryogenesis in <i>Cyclamen persicum</i> . Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	ph.d Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	ph.d Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	ph.d Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	ph.d Biology	Neurons forming the network involved in gustatory coding and learning in the moth <i>Heliothis virescens</i> : Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	ph.d Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	ph.d Biology	Coevolutionary interactions between common cuckoos <i>Cuculus canorus</i> and <i>Fringilla</i> finches
2009	Zsolt Volent	ph.d Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	ph.d Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	ph.d Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions ( <i>Panthera leo</i> ) in Tanzania
2010	Huy Quang Nguyen	ph.d Biology	Egg characteristics and development of larval digestive function of cobia ( <i>Rachycentron canadum</i> ) in response to dietary treatments -Focus on formulated diets
2010	Eli Kvingedal	ph.d Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	ph.d Biology	Molecular studies of genetic structuring and demography in <i>Arabidopsis</i> from Northern Europe
2010	Iddi Mihijai Mfunda	ph.d Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. The Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	ph.d Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	ph.d Biology	Population Ecology of <i>Eriophorum latifolium</i> , a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	ph.d Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brønne Arbo	ph.d	Nutritional lifestyle changes – effects of dietary



		Medical technology	carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	ph.d Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	ph.d Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	ph.d Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	ph.d Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby ( <i>Gobiusculus flavescens</i> )
2011	Ann-Iren Kittang	ph.d Biology	<i>Arabidopsis thaliana</i> L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS:- The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	ph.d Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	ph.d Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in <i>Arabidopsis thaliana</i>
2011	Grethe Robertsen	ph.d Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	ph.d Biology	Life-history trait dynamics in experimental populations of guppy ( <i>Poecilia reticulata</i> ): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	ph.d Biology	Regulation in Atlantic salmon ( <i>Salmo salar</i> ): The interaction between habitat and density
2011	Torunn Beate Hancke	ph.d Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology
2011	Sajeda Begum	ph.d Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadala	ph.d Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	ph.d Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	ph.d Biology	Conflict over the conservation of the Asian elephant ( <i>Elephas maximus</i> ) in Bangladesh
2011	Gro Dehli Villanger	ph.d Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	ph.d Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	ph.d Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	ph.d Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	ph.d Biology	Evolutionary consequences of seed banks and seed dispersal in <i>Arabidopsis</i>
2012	Jakob Hønborg Hansen	ph.d Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance



2012	Elin Noreen	ph.d Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	ph.d Biology	Theoretical and empirical approaches to studying foraging decisions: the past and future of behavioural ecology
2012	Aleksander Handá	ph.d Biology	Cultivation of mussels ( <i>Mytilus edulis</i> ): Feed requirements, storage and integration with salmon ( <i>Salmo salar</i> ) farming
2012	Morten Kraabøl	ph.d Biology	Reproductive and migratory challenges inflicted on migrant brown trout ( <i>Salmo trutta</i> L) in a heavily modified river
2012	Jisca Huisman	ph.d Biology	Gene flow and natural selection in Atlantic salmon
2012	Maria Bergvik	ph.d Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in <i>Calanus finmarchicus</i>
2012	Bjarte Bye Løfaldli	ph.d Biology	Functional and morphological characterization of central olfactory neurons in the model insect <i>Heliothis virescens</i> .
2012	Karen Marie Hammer	ph.d Biology.	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	ph.d Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. Philos.	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	ph.d Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	ph.d Biology	The ecological significance of space use and movement patterns of moose in a variable environment
2012	Erlend Kjeldsberg Hovland	ph.d Biology	Bio-optics and Ecology in <i>Emiliana huxleyi</i> Blooms: Field and Remote Sensing Studies in Norwegian Waters
2012	Lise Cats Myhre	ph.d Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	ph.d Biology	Demographic, environmental and evolutionary aspects of sexual selection
2012	Bin Liu	ph.d Biology	Molecular genetic investigation of cell separation and cell death regulation in <i>Arabidopsis thaliana</i>
2013	Jørgen Rosvold	ph.d Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	ph.d Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	ph.d Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	ph.d Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon ( <i>Salmo salar</i> ) farming