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Changes in Tree Growth, Biomass and Vegetation Over a 13-Year Period in the Swedish Sub-Arctic

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Abstract This study was conducted in the Swedish sub-Arctic, near Abisko, in order to assess the direction and scale of possible vegetation changes in the alpine–birch forest ecotone. We have re-surveyed shrub, tree and vegetation data at 549 plots grouped into 61 clusters. The plots were originally surveyed in 1997 and re-surveyed in 2010. Our study is unique for the area as we have quantitatively estimated a 19% increase in tree biomass mainly within the existing birch forest. We also found significant increases in the cover of two vegetation types—"birch forest-heath with mosses" and "meadow with low herbs", while the cover of snowbed vegetation decreased significantly. The vegetation changes might be caused by climate, herbivory and past human impact but irrespective of the causes, the observed transition of the vegetation will have substantial effects on the mountain ecosystems.

Keywords Sub-Arctic · Vegetation change · Treeline · Biomass · Birch forest

INTRODUCTION

During the last 15 years, there has been an increasing focus on how climate change has and will affect the distribution and extent of ecosystems around the globe including alpine and Arctic areas (e.g., Callaghan et al. 2005). The impacts on ecosystem distribution and parameters such as plant growth and species richness are expected to be particularly substantial in Arctic and sub-Arctic areas, as the change and variation in climatic parameters such as temperature and precipitation may increase with distance from the equator (Callaghan et al. 2005; Kattsov et al. 2005; Anisimov et al. 2007). For example, there has been a mean annual temperature increase in the Arctic of about 2°C since the 1960s, exceeding the global warming trend by at least 1°C (McBean et al. 2005). Climate warming at Abisko in sub-Arctic Sweden has been slightly less pronounced, but has been sustained since 1913 and has accelerated during the last 20 years (Callaghan et al. 2010). It has been suggested that alpine plants may advance upslope or pole-ward, while they might be out-competed at their former localities and eventually displaced from local niches including mountaintops (Callaghan et al. 2005; Wilson and Nilsson 2009; Scherrer and Körner 2011). Models predict that the extent of mountain birch forest in Fennoscandia will increase with climate warming, substantially reducing the areal extent of alpine heaths (Moen et al. 2004). Indeed, field studies and remote sensing have revealed a recent increase in altitude of the treeline (e.g., Kullman 2002), and an extension and increased cover of mountain birch forest (Tømmervik et al. 2009; Rundqvist et al. 2011, this issue). Tømmervik et al. (2009) have—based on remote sensing data—estimated that tree biomass has doubled over a 43-year period, within an area of Finnmarksvidda, and Rundqvist et al. (2011) have observed an increased density and cover of mountain birch in the treeline over the last three decades, within an area near Abisko village.

Plants restricted to snowbeds are suggested to be particularly susceptible to decreased snow-fall and longer growing seasons (Callaghan et al. 2005; Björk and Molau 2007). However, it could also be suspected that heaths dominated by dwarf shrubs may be converted to heaths dominated by graminoids or larger shrubs, as experiments suggest that shrubs and graminoids may increase following warming (e.g., Walker et al. 2006). Indeed, comparison of old and new photographs has revealed an expansion of large shrubs throughout the Arctic (Sturm et al. 2001; Tape et al. 2006; Forbes et al. 2010).

A recent study in the Abisko area has, however, revealed a more complex pattern in treeline dynamics in that the treeline may be depressed at one location but increase in altitude at another nearby site that experienced the same climatic conditions (Van Boagert et al. 2011). Plant community composition and the distribution of mountain birch forest and alpine vegetation are, however, not solely determined by climate. Experiments and observations have revealed that herbivores may have a substantial impact on the distribution and abundance of plants in Arctic and sub-Arctic areas (Tenow et al. 2001; Cairns and Moen 2004; Olofsson et al. 2009; Van Bogaert et al. 2009, 2011; Babst et al. 2010). Human activities have also depressed the tree line in many areas of Scandinavia (Emanuelsson 1987; Karlsson et al. 2007).

In 1997, Dahlberg et al. (2004) conducted an extensive study in the Swedish sub-Arctic, near Abisko. They measured tree diameter on permanently marked sample plots, and estimated proportions of shrubs and vegetation cover based on the methodology of the Swedish National Forest Inventory. The rigorous sampling design used gives us a unique opportunity to resample these plots and quantitatively assess how vegetation has changed, in the tundra–birch forest ecotone between 1997 and 2010. Specifically, this study assess whether the cover of vegetation, shrub and tree cover, tree canopy cover, mean diameter of stems, number of trees, basal area and biomass have changed since 1997.

STUDY AREA

This study was conducted in two areas close to the Abisko village approximately 200 km north of the Arctic Circle, (68°20′ N, 18°50′ E; Fig. 1). One area was located on the southern side of Lake Torneträsk and the other on the

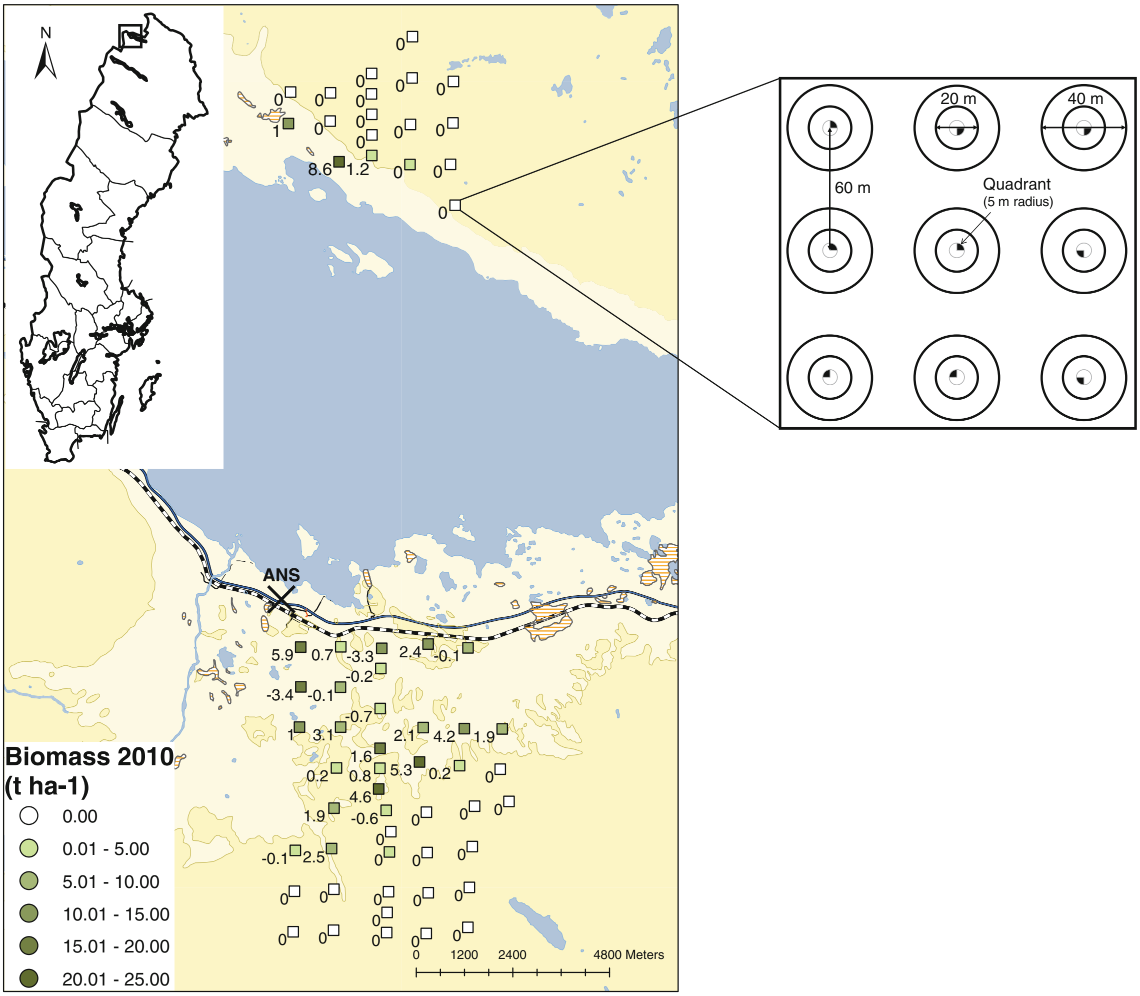


Fig. 1 Location of the study area. The large map shows the location of the area from which biomass of the 61 clusters (*squares*) were re-investigated in 2010. The location of the Abisko Scientific Research Station (ANS; *cross*) where the meteorological station is located is also included. The biomass estimate for a cluster in 2010 is denoted by *color*, see legend. Numbers close to each cluster represent the change in biomass between 1997 and 2010. Each cluster consisted of nine plots and each plot consisted of two concentric circular plots and one quadrant. © Lantmäteriet, ärende nr I 2010/0345

northern side. Climate change is accelerating at Abisko and the mean annual temperature recorded at the beginning of the 21st century was 0.7°C (Kohler et al. 2006) which is 2.5°C greater than in the beginning of the twentieth century (Callaghan et al. 2010). The mean annual precipitation, measured at Abisko Scientific Research Station (ANS), is ~310 mm for the period 1913–2000 (Kohler et al. 2006). The mean annual precipitation on the northern side of the lake could, however, be about twice as high as recorded at ANS (Sonesson and Hoogsteger 1983). The altitudinal limit of the treeline in the area varies between 650 and 700 m above sea level (Dahlberg et al. 2004; Van Bogaert et al. 2011).

MATERIALS AND METHODS

The 1997 survey established 88 clusters with 9 permanently marked circular plots within each cluster (Dahlberg et al. 2004; Fig. 1). We re-surveyed 61 of the original 88 clusters in the summer of 2010. The clusters were organized in a systematic grid. The distance between the clusters was 1 km except in the central grid-transect where the distance was 0.5 km between the clusters. Forty-three of the re-surveyed clusters were located on the southern side of the lake, and 18 on the northern side. The altitude ranged from 390 to 1350 m above sea level. The nine plots within each cluster formed a regularly spaced grid with 3 × 3 plots with 60 m distance, and each plot consisted of two concentric circular plots of different diameter and one quadrant (Fig. 1; Dahlberg et al. 2004). We "calibrated" between the years as one of the original observers (J. Bergstedt), who designed the original sampling procedures and also did a lot of the fieldwork in 1997, introduced the field-staff in 2010.

Measurements of Stem Diameters

All trees with a DBH (diameter at breast height) ≥30 mm were measured with a caliper in each 20 m diameter plot, in both 1997 and 2010. In addition, trees <30 mm DBH with at least 1.3 m height were measured within a quadrant with a radius of 5 m (Dahlberg et al. 2004). However, willows was only measured if DBH was ≥20 mm. A fork below breast height (1.3 m height) was considered as a branch if thinner than 20 mm and as a stem if thicker than 20 mm (Dahlberg et al. 2004).

Shrub and Tree Coverage

The cover, both separately for each species and total, of all shrubs and small trees <1.3 m height, were estimated in each 20 m diameter plot. Cover of each shrub and small tree were visually estimated in 10 equal percentage classes. A specific shrub or tree taxon needed to cover at least 3 m^2 to be noted. Similarly, the canopy cover of all trees, i.e., shrubs and trees ≥1.3 m height, was visually estimated in each 20 m diameter plot.

Vegetation Types

The cover of each vegetation type, in each 40 m diameter plot, was classified according to the Swedish vegetation map (Table 1; Liberkartor 1981; Rafstedt 1985). Proportional cover of each vegetation type was visually estimated in 10 equal percentage area classes. The occurrence of boulders and rocks was not considered in this estimation. A specific vegetation type needed to cover at least 3 m^2 to be noted.

Data Analysis

In order to avoid spatial auto-correlation, we calculated the average of all variables for the nine plots in each cluster, and used these variables in subsequent analyses. All 61 clusters were included in all analyses except in the vegetation-type analysis. One cluster was omitted from that analysis due to missing values in 1997. All statistical analyses were performed using the R statistical package (Ihaka and Gentleman 1996). The plots were permanently marked which made it possible to conduct paired *t*-tests.

Analysis of the Stem Diameter Measurements

Basal areas (i.e. the cross section areas of tree trunks, at breast height, expressed as square meters per hectares) were calculated for each tree species from stem diameters. The biomass of living trees (i.e. dry weight of living tree tissues) was calculated by using allometric relationships determined in the field and summarized in the following equation (Dahlberg et al. 2004):

$$\text{Tree biomass per plot} = \sum_{i=n}^{n} -5.4923 + 0.9803\text{TBA}_i$$

TBA_i is the cross sectional area of an individual tree trunk at breast height (mm^2), and n is the number of trees in a plot. Tree biomass per plot (kg; dry weight) was re-scaled to biomass per hectare.

We used paired *t*-tests to assess whether there were significant differences in mean diameter, number of trunks per ha, basal area and biomass between 1997 and 2010. Analyses were conducted for all tree species combined as well as for all focal tree species separately, i.e., mountain birch *Betula pubescens* ssp. *czerepanovii* willow *Salix* spp., alder *Alnus incana*, rowan *Sorbus aucuparia*, pine *Pinus sylvestris* and "other" tree species. We also conducted separate tests for large trees and small trees as well as for large and small trees combined. We used Spearman rank correlation tests to assess whether biomass in 1997 and 2010 and biomass change were correlated with altitude.

Table 1 The mean cover of each vegetation class in 1997 and 2010, respectively

Vegetation types[a]	Abbrevations	Year 1997		Year 2010		Paired *t*-test		
		Mean	SD	Mean	SD	*t*	df	*p*
Grass heath	H(g)	6.04	21.67	5.59	20.62	−0.30	59	0.77
Extremely dry heath	H(ex.dr)	3.57	11.72	4.49	13.03	0.98	59	0.33
Dry heath	H(dr)	35.01	30.23	38.79	32.99	1.98	59	0.052
Fresh heath	H(fr)	9.63	18.41	9.80	19.73	0.59	59	0.56
Meadow with low herbs	M(lh)	4.06	12.27	6.47	14.34	**2.08**	**59**	**0.042**
Meadow with tall herbs	M(th)	1.04	5.27	1.04	5.83	−0.47	59	0.64
Moderate snowbed	SB(mod)	13.86	26.24	7.38	18.55	**−4.43**	**59**	**<0.001**
Extreme snowbed	SB(ex)	0.37	2.87	0	0	−1.00	59	0.32
Bog and fen hummock vegetation	BoFe(hu)	1.41	5.44	1.19	4.80	−0.31	59	0.76
Dry fen	Fe(dr)	1.65	5.04	2.13	7.00	0.18	59	0.86
Sloping fen	Fe(sl)	0.67	2.66	0.67	2.66	–	59	–
Wet fen	Fe(we)	0.11	0.73	0.17	0.84	1.00	59	0.32
Mosaic mire between BoFe(hu) and Fe(dr)	M(mos)	0.17	1.29	0	0	−1.00	59	0.32
Willow-shrubs	W	4.33	9.89	4.11	9.63	−1.50	59	0.14
Birch forest, heath type with lichens	BFo(l)	1.06	4.03	0.96	4.06	−0.58	59	0.57
Birch forest, heath type with mosses	BFo(m)	8.69	21.21	10.63	22.89	3.09	59	**0.003**
Birch forest, meadow type with herbs	BFo(h)	0.65	2.45	0.65	2.51	−0.22	59	0.83
Birch forest, sparsely grown[b]	BFo(sp)	7.52	15.57	5.93	13.81	−1.96	59	0.055

The mean values are percentages. Paired *t*-tests were based on arcsin-transformed values from 60 clusters. One cluster was omitted from the analyses due to missing values in 1997

Bold figures denote significant changes in cover of vegetation classes between 1997 and 2010

[a] Vegetation types classified according to the Swedish vegetation map (Liberkartor 1981; Rafstedt 1985)

[b] Class 64, birch forest-sparsely grown has a canopy cover between 10 and 30%; it is in fact a mix of two birch forest types with low canopy cover, swampy birch forest and sparsely grown birches at drier soils

Shrub and Tree Coverage

The shrub cover (shrubs and trees <1.3 m in height) and tree canopy cover (cover of trees ≥ 1.3 m) were analyzed separately with the aid of paired *t*-tests. This was conducted for all shrub and tree species combined as well as for all focal shrub and tree species separately. The percentage classes were arcsin-transformed prior to analysis to meet the assumptions of normality.

Vegetation Types

We assessed whether the cover of different vegetation types had changed since 1997 until 2010 with the aid of paired *t*-tests on arcsin-transformed data.

RESULTS

Mean Diameter, Number of Trunks, Basal Area and Tree Biomass

We measured the trunk diameter for a total of 6054 mountain birches, 138 alders and 207 rowans in 2010. In 1997, 154 of 549 plots had trees (≥ 1.3 m height) compared to 163 plots in 2010. The number of small trunks (<30 mm DBH) made up about 70% of all trunks whereas large trees (≥ 30 mm DBH) made up 89% of the basal area and total biomass. The mean above ground tree biomass was 4176 (SD = 6475) kg ha^{-1} based on all 61 clusters in 2010 (Fig. 1; Table 2). The biomass was 8785 (SD = 6923) kg ha^{-1} in 2010 if we instead use the mean biomass based on clusters where at least one plot had trees higher than 1.3 m ($n = 29$).

The biomass values in 1997 and 2010, respectively, were both negatively correlated with altitude ($r = -0.845$, $p < 0.001$ and $r = -0.837$, $p < 0.001$, respectively; Figs. 1, 2). The change in tree biomass documented for 1997–2010 was positively correlated with tree biomass in 1997 ($r = 0.389$, $p = 0.002$) and negatively correlated with altitude ($r = -0.295$, $p = 0.021$).

There was a 19% overall increase in basal area and tree biomass (Table 2). The increase depended mainly on the large mountain birches (≥ 30 mm DBH), as their mean diameter and, number of trees per hectare increased significantly (Table 2). We also found that there was a decrease (Table 2) of small willow trees (20 to <30 mm

Table 2 Tree characteristics of the studied clusters in 1997 and 2010, for small trees (trees <30 mm at DBH and higher than 1.3 m), large trees (trees >30 mm at DBH) and all trees (all trees higher than 1.3 m)

	Small trees					Large trees					All trees					
	1997		2010			1997		2010			1997		2010			
	Mean	SD	Mean	SD	*p*	Mean	SD	Mean	SD	*p*	Mean[a]	SD	Mean[a]	SD	*t*[a]	*p*
Mountain birch																
Mean diam. (mm)	5.4	7.2	4.6	6.2	0.23	27.3	33.8	29.2	35.7	**0.005**	16.5	24.3	15.7	26.2	−0.45	0.66
No. of trunks (ha^{-1})	826.6	1695.5	804.3	1364.1	0.86	252.7	429.7	300.7	496.4	**0.008**	1079.2	1069.8	1105.0	1081.3	0.21	0.83
Basal area (m^2 ha^{-1})	0.15	0.33	0.13	0.22	0.39	0.79	1.26	0.99	1.54	**<0.001**	0.94	0.93	1.12	1.10	**2.98**	**0.004**
TDW (kg ha^{-1})	544	1216	461	808	0.39	2741	4384	3452	5330	**<0.001**	3285	5216	3914	5968	**2.92**	**0.005**
Willow																
Mean diam. (mm)	1.7	5.8	0.3	2.7	**0.038**	11.4	18.0	11.1	19.4	0.83	10.3	16.4	10.9	19.2	0.35	0.73
No. of trunks (ha^{-1})	13.8	49.7	0.9	7.2	**0.047**	9.0	22.5	7.9	26.7	0.55	22.7	23.0	8.9	9.0	**−2.20**	**0.032**
Basal area (m^2 ha^{-1})	<0.01	0.02	<0.01	<0.01	0.09	0.01	0.04	0.01	0.05	0.82	0.02	0.02	0.01	0.01	−0.91	0.37
TDW (kg ha^{-1})	15	64	1	9	0.09	49	142	51	173	0.83	64	174	52	173	−0.94	0.35
Alder																
Mean diam. (mm)	0.4	3.2	0.2	1.0	0.45	2.0	11.3	2.3	12.6	0.19	2.0	11.1	1.3	7.0	−1.43	0.16
No. of trunks (ha^{-1})	0.5	3.8	9.31	65.5	0.27	9.4	67.4	11.4	83.4	0.32	9.9	10.0	20.7	21.0	1.09	0.28
Basal area (m^2 ha^{-1})	<0.01	<0.01	<0.01	<0.01	0.30	0.04	0.32	0.06	0.45	0.30	0.04	0.04	0.06	0.06	1.03	0.30
TDW (kg ha^{-1})	0.9	6.8	1.7	13.2	0.30	148.7	1104	208.0	1553	0.30	150	1111	210	1566	1.03	0.30
Rowan																
Mean diam. (mm)	1.0	4.5	0	–	0.09	2.7	13.7	1.2	6.5	0.40	3.7	14.3	1.2	6.5	−1.41	0.16
No. of trunks (ha^{-1})	7.9	53.8	0	–	0.26	0.2	0.7	0.2	1.4	0.68	8.0	8.1	0.23	0.24	−1.16	0.25
Basal area (m^2 ha^{-1})	<0.01	0.01	0	–	0.22	<0.01	<0.01	<0.01	<0.01	0.62	<0.01	<0.01	<0.01	<0.01	−1.56	0.12
TDW (kg ha^{-1})	7	43	0	–	0.22	2	10	1	6	0.64	8	44	1	6	−1.54	0.13
Pine																
Mean diam. (mm)	0.4	2.88	0	–	0.32	0	–	0	–	–	0.4	2.8	0	0	−1.00	0.32
No. of trunks (ha^{-1})	0.5	3.8	0	–	0.32	0	–	0	–	–	0.5	0.5	0	0	−1.00	0.32
Basal area (m^2 ha^{-1})	<0.01	<0.01	0	–	0.32	0	–	0	–	–	<0.01	<0.01	0	0	−1.00	0.32
TDW (kg ha^{-1})	<1	5	0	–	0.32	0	–	0	–	–	<1	5	0	0	−1.00	0.32
Other Tree species																
Mean diam. (mm)	0.1	1.0	0	–	0.32	0	–	0	–	–	0.1	1.0	0	0	−1.00	0.32
No. of trunks (ha^{-1})	0.5	3.8	0	–	0.32	0	–	0	–	–	0.5	0.5	0	0	−1.00	0.32
Basal area (m^2 ha^{-1})	<0.01	<0.01	0	–	0.32	0	–	0	–	–	<0.01	<0.01	0	0	−1.00	0.32
TDW (kg ha^{-1})	<0.1	0.7	0	–	0.32	0	–	0	–	–	<0.1	0.7	0	0	−1.00	0.32

Table 2 continued

	Small trees					Large trees					All trees					
	1997		2010			1997		2010			1997		2010			
	Mean	SD	Mean	SD	p	Mean	SD	Mean	SD	p	Mean[a]	SD	Mean[a]	SD	t[a]	p
All Trees																
Mean diam. (mm)	5.9	7.4	4.7	6.2	**0.050**	26.6	32.2	29.0	33.8	**0.006**	14.8	20.5	15.7	22.6	0.66	0.51
No. of trunks (ha^{-1})	849.6	1702.9	814.5	1374.8	0.78	271.1	448.7	320.3	514.9	**0.009**	1120.8	1112.0	1134.8	1111.6	0.11	0.91
Basal area (m^2 ha^{-1})	0.15	0.34	0.13	0.22	0.29	0.84	1.35	1.07	1.69	**<0.001**	1.00	1.00	1.19	1.18	**2.84**	**0.006**
TDW (kg ha^{-1})	568	1235.9	464	812.4	0.29	2940	4701.5	3712	5862.6	**<0.001**	3507	5520	4176	6476	**2.78**	**0.007**

Paired t-tests were based on all 61 clusters, df = 60. Bold figures denote significant changes in tree variables between 1997 and 2010

[a] The mean diameter for all trees was weighted as small and large trees, respectively, were measured on different plot size

Number of trunks is the mean number of trunks based on all clusters

Basal area is the mean basal area based on all clusters

TDW is Total dry weight (kg ha^{-1}) and corresponds to mean tree biomass per hectare

DBH), as mean diameter and number of willow trunks and basal area of willow trees decreased significantly. None of the other tree species showed any statistically significant changes.

Shrub and Tree Cover Estimates

There was an overall significant increase, from 25.0 to 32.5%, in the total cover of shrubs (i.e., all shrubs and trees <1.3 m) between 1997 and 2010. There was also a significant cover increase of dwarf birch *Betula nana*, juniper *Juniperus communis* and willows *Salix* spp. (Table 3). The cover of mountain birch <1.3 m and other shrub species did not differ significantly between the years. The change in shrub cover between 1997 and 2010 was positively correlated with cover of shrubs in 1997 ($r = 0.417$, $p < 0.001$). There was also a significant overall increase of tree canopy cover (trees ≥1.3 m height; Table 4), although mountain birch was the only tree species with a statistically significant increase.

Vegetation Types

Analyses of vegetation classes revealed that the cover of two vegetation types, "Meadow with low herbs M(lh)" and "Birch forest of heath type with mosses BFo(m)", increased significantly, while the cover of the vegetation type "Moderate snowbed vegetation SB(mod)" decreased significantly (Fig. 3; Table 1). The cover of the vegetation type "Dry heath H(dr)" increased also, while the cover of the vegetation type "Sparsely grown birch forest BFo(sp)" decreased although neither of the changes were statistically significant.

DISCUSSION

Tree basal area and biomass increased by 19% between 1997 and 2010 with the main increase occurring in the established birch forest. There were significant transitions in the cover of vegetation types; the cover of "Meadow with low herbs M(lh)" and "Birch forest of heath type with mosses BFo(m)" increased significantly, while the cover of "Moderate snowbed vegetation SB(mod)" decreased significantly. Our study concurs with the results of other studies which suggest that there has been a general increase in cover and biomass of trees and shrubs in sub-Arctic and Arctic areas (e.g., Sturm et al. 2001; Tape et al. 2006; Danby and Hik 2007; Tømmervik et al. 2009; Forbes et al. 2010; Hallinger et al. 2010; Van Bogaert et al. 2011; Rundqvist et al. 2011, this issue).

Tree biomass increased on average 1.5% per year from 3.5 t ha^{-1} in 1997 to 4.2 t ha^{-1} in 2010. We have found no

Fig. 2 Mean biomass of trees in relation to altitude. *Black circles* denote clusters on the north side of the lake in 1997, and *red circles* denote clusters on the south-side of the lake in 1997. *Arrows* denote the change in biomass between 1997 and 2010

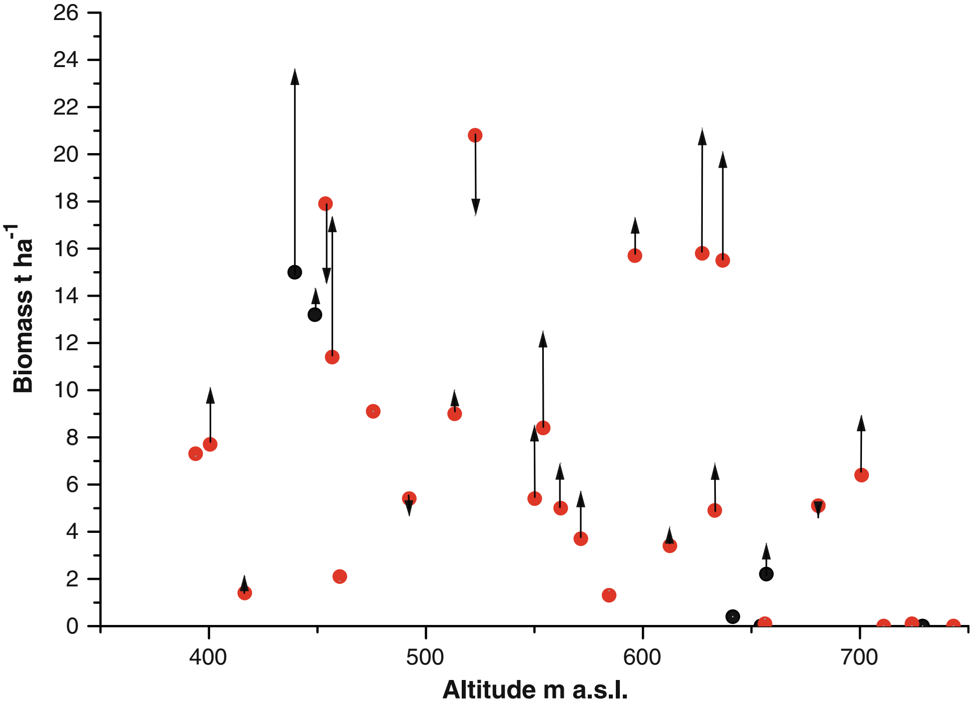


Table 3 The mean of percentages of cover, of shrubs, i.e. shrubs and trees <1.3 m height

Tree species	1997		2010		Paired *t*-test		
	Mean	SD	Mean	SD	*t*	df	*p*
Mountain birch	1.5	2.5	1.2	2.2	0.63	60	0.53
Willow	7.8	8.1	8.9	9.9	2.45	60	**0.017**
Dwarf birch	14.0	11.5	20.1	16.0	5.97	60	**<0.001**
Juniper	1.4	2.9	2.1	4.3	3.49	60	**<0.001**
Other shrub species	0.2	1.0	0.3	1.3	0.17	60	0.86
All species	25.0	17.0	32.5	22.7	6.13	60	**<0.001**

Paired *t*-tests were based on arcsin-transformed values from all 61 clusters. Bold figures denote significant changes in shrub and tree cover between 1997 and 2010

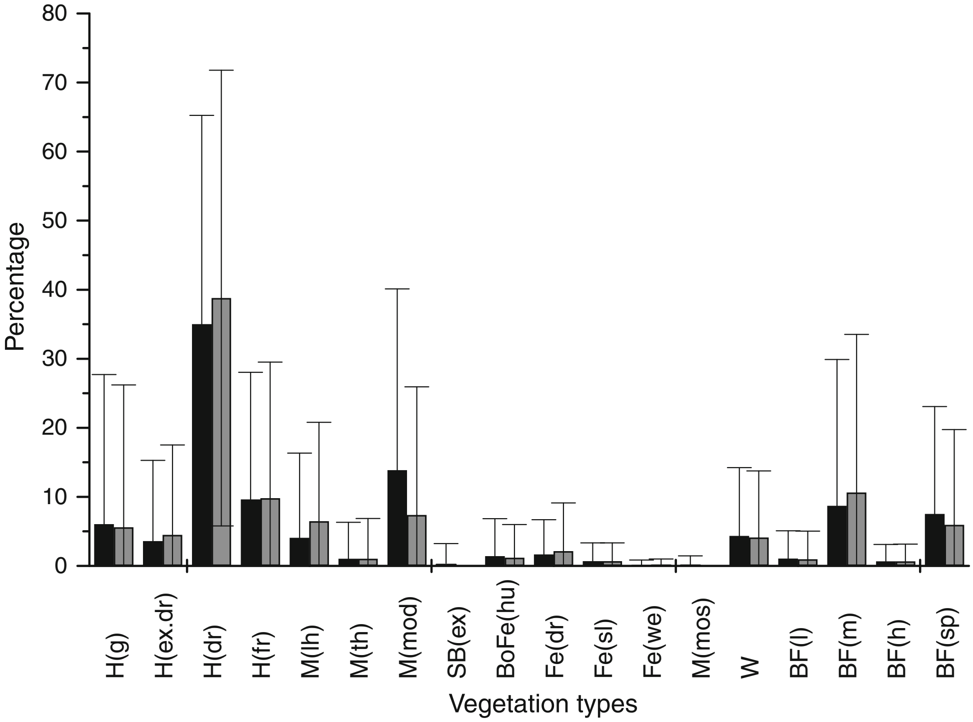
Table 4 The mean of percentage tree canopy cover for trees ≥1.3 m high

Tree species	1997		2010		Paired *t*-test		
	Mean	SD	Mean	SD	*t*	df	*p*
Mountain birch	6.9	11.6	12.6	19.0	**5.10**	**60**	**<0.001**
Willow	0.3	0.7	0.3	0.9	−1.18	60	0.24
Other tree species	0.2	1.3	0.4	3.3	−0.01	60	0.99
All species	7.5	12.0	13.4	20.1	**4.91**	**60**	**<0.001**

Paired *t*-tests were based on arcsin-transformed values from all 61 clusters. Bold figures denote significant changes in tree canopy cover between 1997 and 2010

other study that has estimated the tree biomass changes in the alpine–birch forest ecotone by re-surveying systematically sampled field plots. Karlsson et al. (2005) estimated—based on tree-ring series—the relative growth rate of above-ground biomass of individual trees to be 10, 5 and 2% per year in 25–30-, 50- and 100-year old trees, respectively. These results are, however, only representative for individual trees, and do not include turnover of trees in the forest. Though, it is apparent that individual mountain birch trees may have a relatively high growth potential despite the constraints of climatic conditions and browsing. Tømmervik et al. (2009)—using remote sensing techniques—estimated the annual increase in biomass to be ∼2.7% in Finnmarksvidda, northern Norway over a 43-year period. Birches may, however, expand slower in steeper than in flat areas, as they are limited by the lower temperature and shorter growing season upslope (Chapin 1983; Karlsson et al. 2005). Our study was located in an area that is steeper than Finnmarksvidda, and we could thus not expect a similar expansion rate as Tømmervik et al. (2009) observed. We observed only a minor expansion of the mountain birch forest, and the biomass increase was mainly due to the growth of birches higher than 1.3 m that where already present in 1997. We also noted that the very open birch forest type decreased while the denser birch forest of heath type increased, that together with increased canopy cover suggest a densification of the mountain forest near Abisko.

Fig. 3 Mean cover (mean percentage ± SD) of specific vegetation classes. *Black bars* denote 1997 and *grey bars* denote 2010 data, respectively. For abbreviations of the vegetations types and statistics describing vegetation change see Table 1



It has been suggested that increased nutrient availability associated with higher soil temperatures, and a longer growing season could underpin increased tree and shrub abundance and biomass in the Arctic (e.g., Chapin 1983; Weih and Karlsson 1997; Hartley et al. 1999; Tape et al. 2006). Kammer et al. (2007) on the other hand, suggest that the observed increase may merely be a delayed re-expansion of shrubs and trees following the "Little Ice-age" that ended in the early twentieth century (Grubb 2008; see discussion in Rundqvist et al. 2011, this issue).

The observed increase in shrub and tree cover and tree biomass may, however, be related to several factors other than climate, such as reduction in herbivory pressure (e.g., Olofsson et al. 2009) or changed land management (Emanuelsson 1987; Karlsson et al. 2007). It is well known that shrubs and trees increase in abundance and biomass with decreased herbivory (Cairns and Moen 2004; Olofsson et al. 2009; Van Boagaert et al. 2011). However, the browsing pressure has probably increased rather than decreased over the last 13 years as the population of the major herbivore, reindeer, has increased in the study area since 1995 (Van Boagaert et al. 2011). Similarly, our study area has a history of outbursts of geometrid moths (mainly autumnal moth, *Epirrita autumnata*; Tenow et al. 2001; Karlsson and Weih 2003). The latest in 2004 severely defoliated birches in our study area, both at the north and south side of the lake (Babst et al. 2010). Thus, the biomass of shrubs and trees could potentially have been even higher without reindeers or geometrid moths (Cairns and Moen 2004; Karlsson et al. 2005; Olofsson et al. 2009; Babst et al. 2010; Van Bogaert et al. 2011). Further, we cannot exclude the possibility that the observed increased biomass and cover of shrubs and trees was caused by past anthropogenic activities associated with railway construction. Gathering of fuelwood and cutting of trees during the construction led to an unnaturally low tree line and tree cover in the Abisko area (Emanuelsson 1987). Thus, the observed increased biomass and cover of shrubs and trees may be caused by a recovery of shrubs and trees since the railroad was finished in 1903 (Emanuelsson 1987; cf. Karlsson et al. 2007).

In addition to forest changes, we observed a particularly dramatic decrease of snowbed vegetation confirming the prediction that snowbed plant communities are particularly vulnerable to climate change (Björk and Molau 2007). The decrease of snowbed vegetation reflects a shift from a sparse vegetation cover to denser vegetation characterized by species found in the surrounding vegetation (Heegard 2002; Heegaard and Vandvik 2004; Björk and Molau 2007). It is suggested that snowbed plants are restricted by growing season length and the availability of phosphorus (Björk and Molau 2007). Earlier studies indicate, however, that the immediate response of snowbed species to changed snow-depth and growing season length is highly species-specific (Galen and Stanton 1995; Sandvik et al. 2004). An alternative explanation is that graminoids have increased due to decreased lemming grazing (Virtanen 2000; Hentton and Wallgren 2001).

Further, we also found that the cover of juniper increased in agreement with findings by Hallinger et al. (2010) in the same general location. Rundqvist et al. (2011) described, a more complex pattern in which juniper increased in plots with low cover of mountain birch while it decreased in a plot with much higher cover of mountain birch. Our study revealed a different pattern with a positive correlation between the cover of juniper and basal area and cover of mountain birch. This demonstrates the complexity of vegetation change over time and the importance of fine-scaled processes (e.g., Rundqvist et al. 2011).

An increased biomass of trees, and cover of shrubs and trees, will have substantial effects on Arctic and sub-Arctic ecosystems (Callaghan et al. 2005), and species composition and diversity of vascular plants and cryptogams may change (cf., warming experiments; Walker et al. 2006). In particular, boreal species may extend their altitudinal distribution (Sundqvist et al. 2008), while alpine plant species with lower ability to compete may prevail only if they may be able to migrate upward or northward (cf. Grabherr et al. 1994; Callaghan et al. 2005; Wilson and Nilsson 2009) or survive in small niches with favorable micro-climates (Scherrer and Körner 2011). Further, reindeer might be negatively affected as the availability of palatable, nutritionally rich plants that used to occur in snowbeds decrease (Edenius et al. 2003).

There are also implications for regulatory ecosystem services (Chapin et al. 2005). The mountain birch forest is a major sink for atmospheric CO_2 in the Torneträsk area (Christensen et al. 2007). Following an outbreak of the autumnal moth, such as that in 2004 (Babst et al. 2010), the defoliated forest becomes a source of CO_2 to the atmosphere (Heliasz et al. 2011). However, our study has shown that despite the 2004 defoliation, there has been a net increase in biomass—and carbon drawdown—of 19%.

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