

20th century tree-line advance and vegetation changes along an altitudinal transect in the Putorana Mountains, northern Siberia

ALEXANDER V. KIRDYANOV, FRANK HAGEDORN, ANASTASIA A. KNORRE, ELENA V. FEDOTOVA, EUGENE A. VAGANOV, MUHTAR M. NAURZBAEV, PAVEL A. MOISEEV AND ANDREAS RIGLING

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Ongoing climatic changes potentially affect tree-line ecosystems, but in many regions the observed changes are superimposed by human activities. We assessed how the forest-tundra ecotone has changed during the last century in the Putorana Mountains, northern Siberia, an extremely remote and untouched area in Eurasia. A space-for-time approach was used to determine the spatio-temporal dynamics of forest structure and biomass along an altitudinal transect. From the closed larch forest to the upper tree line, the mean age of *Larix gmelinii* (Rupr.) decreased considerably from 220 to 50 years ago. At the current upper species line, there is a strong and successful germination of larch, with 1500 saplings per hectare, indicating an ongoing filling-in, a densification of a formerly open forest and an upslope shift of the tree-line position (approximately 30 to 50 m in altitude during the last century). The forest expansion coincided with large increases in winter precipitation during the 20th century. In contrast, tree growth rates were significantly positively related to summer temperatures, neither of which increased markedly. The total aboveground biomass decreased from approximately 40 t ha⁻¹ in the closed larch forest to 5 t ha⁻¹ at the tree line. Our study demonstrates that ongoing climatic changes lead to an upslope expansion of forests in the remote Putorana Mountains, which alters the stand structure and productivity of the forest-tundra ecotone. These vegetation changes are very probably of minor importance for aboveground carbon sequestration, but soil carbon data are needed to estimate the impact of the forest expansion on the total ecosystem carbon storage.

Alexander V. Kiralyanov (e-mail: kiralyanov@ksc.krasn.ru), Anastasia A. Knorre, Elena V. Fedotova and Muhtar M. Naurzbaev, V. N. Sukachev Institute of Forest SB RAS, Akademgorodok, Krasnoyarsk, 660036, Russia; Frank Hagedorn and Andreas Rigling, Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland; Eugene A. Vaganov, Siberian Federal University, pr. Svobodny 79, Krasnoyarsk, 660041, Russia; Pavel A. Moiseev, Institute of Plant and Animal Ecology UrB RAS, 8 Marta str. 202, Ekaterinburg, 620144, Russia; received 5th July 2010, accepted 21st March 2011.

The average surface temperature around the world has risen by about 0.56 to 0.92 °C over the past 100 years, and by 0.13 ± 0.03 °C per decade over the last 50 years (IPCC 2007). It is likely that in the Northern Hemisphere the last few decades have been warmer than the past 1300 years (e.g. Briffa *et al.* 2001; Mann *et al.* 2008). The climatic warming has affected the phenology of plants (e.g. Myneni *et al.* 1997; Keyser *et al.* 2000), the range and distribution of species (e.g. Grabherr *et al.* 1994; Dobbertin *et al.* 2005) and the composition and dynamics of communities (e.g. Bugmann & Pfister 2000; Walther *et al.* 2002). In the extratropical land areas, and especially arctic and alpine regions, the estimated temperature anomalies for the past 100 years were twice as large as those averaged for the Northern Hemisphere (Kelly *et al.* 1982; IPCC 2007). Temperature-limited ecosystems in sub-arctic and arctic regions are thought to be particularly sensitive to this warming (Körner 1999; Becker & Bugmann 2001).

The upper tree line is one the most striking vegetation boundaries (Holtmeier 2003). Worldwide, the elevation position of the tree line is at 5 to 8 °C (6–7 °C in the boreal zone) of ground temperature during the vegetation period (Körner & Paulsen 2004), very probably as a result of growth limitation by low temperatures (Körner 1999). Most ecosystems at the mid and northern European tree line are strongly disturbed by human

land use, and thus climate-change-driven rises in tree-line positions cannot be separated from land abandonment (Gehrig-Fasel *et al.* 2007). In contrast, the anthropogenic influence in high-latitude and high-elevation regions in Asia is minimal. Case studies in the Urals (Shiyatov 2003; Devi *et al.* 2008) and East Taymir Mountains (Kharuk *et al.* 2006) but also in sub-polar Siberia (Esper & Schweingruber 2004) indicate rising tree lines and species-line positions, as well as increasing tree densities and productivities of the forest-tundra ecotone – the transition between forest and tundra – during the 20th century. Thus, trees are expanding into former tundra (Shiyatov *et al.* 2005; Kharuk *et al.* 2006). Similar changes have also been detected for other arctic and alpine forest-tundra ecotone areas (e.g. Payette & Fillion 1985; Kullman 1986, 2002; Hessel & Baker 1997). A meta-analysis of a global data set, including 166 sites for which tree-line dynamics had been recorded since AD1900, showed tree-line advances at 52% of sites, and only 1% reporting tree-line recession (Harsch *et al.* 2009).

The widespread northward and upward shift of trees and shrubs caused by global warming decreases the albedo of forest-tundra land surfaces and profoundly affects the heat transfer between surface and atmosphere, inducing a positive feedback of vegetation changes on atmospheric heating over Arctic landmasses

(Chapin *et al.* 2000, 2005). This might result in an even more accelerated warming and possibly in further advances of forests into tundra (Chapin *et al.* 2000). In contrast to these positive feedbacks, an upward- and northward-shifting forest-tundra ecotone could also induce negative feedbacks by increasing ecosystem productivity and net carbon storage across large areas. Remote sensing data show that net primary production did significantly increase at northern high latitudes during the 1980s and 1990s, but started to decrease after 2000 (Myneni *et al.* 1997; Bunn *et al.* 2007). Direct, time-consuming field measurements of vegetation biomass are necessary to validate these data. This is especially important for the remote regions of Russia and Canada, which are still largely unstudied. Hence inventory data from these areas are very poor (Houghton 2005). We have only limited knowledge on the distribution of biomass between the various components of forest ecosystems (trees, shrubs, ground cover) as well as between biomass components (stem, twigs, leaves, roots), making it difficult to quantify current trends in the carbon sequestration and productivity of boreal ecosystems (Lapenis *et al.* 2005; Knorre *et al.* 2006; Prokushkin *et al.* 2006).

In the extremely remote and one of the least-populated areas in Eurasia, the Putorana Mountains in northern Siberia, we studied the spatio-temporal dynamics of forest stand structure and aboveground plant biomass in a space-for-time approach along an altitudinal gradient. These results were combined with an analysis of tree-age structures. The aims of our study were (i) to assess how the forest-tundra ecotone has changed during the last century; (ii) to quantify how

larch is regenerating, and thus to estimate if forests and tree lines are currently advancing or not; and (iii) to determine changes of aboveground biomass in trees, shrubs and ground vegetation in space and time to assess how tree-line shifts possibly affect carbon sequestration in vegetation.

Material and methods

Study area and sampling design

The study was conducted in the northwestern region of the Putorana Mountains (70°30'N, 92°50'–93°00'E) (Fig. 1). The Putorana Mountains are located in the northwestern part of the Central Siberian Plateau, which is characterized by a sub-arctic continental climate. According to the Climatic Research Unit data set (CRU TS 2.1, 0.5°×0.5° resolution, 1901–2002; Mitchell & Jones 2005) the mean annual air temperature at the nearest grid point to our site (70°15'N, 92°45'E) is –14.5°C. Annual precipitation is 428 mm, with 40% of it falling in the vegetation period (June–August). The only tree species in this region is larch (*Larix gmelinii* Rupr.), with the uppermost tree individuals growing at an elevation of about 400–450 m a.s.l. Gmelin larch is one of the most adapted species for the permafrost zone in Siberia, which has poor soils and a cold continental climate. It grows best on fertile drained soils with a deep active layer, but also on soils with a variety of conditions (Abaimov 2010). On the slopes and in the northern part of the Putorana Mountains, other tree species cannot compete with Gmelin larch (Abaimov *et al.* 1997). To the south of our study area, however, *Picea obovata* Ledeb grows on well-drained sites

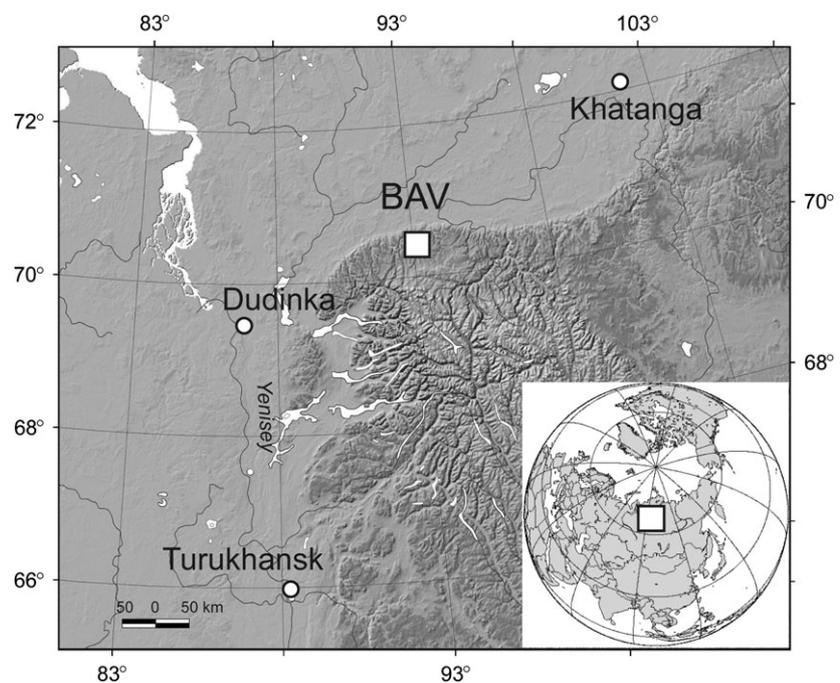


Fig. 1. Location of the study area BAV (rectangle) and meteorological stations (circles) in northern Siberia.

in river valleys, and *Betula alba* L. occurs at much lower elevations.

A 1100-m-long transect covering 220 m in elevation was established on the southwestern slope of the river valley of Bolshoi Avam in July–August 2003. It reached across the main vegetation belts, from the closed larch forest at 170 m to the alpine tundra at 390 m a.s.l. (Fig. 2A). With the exception of three rock outcrops, each 1–3 m in height, the topography along the slope is relatively homogenous: the whole transect has a mean slope of 12–15°, with 6–7° in the lower part of the transect.

The transect (Fig. 2A) is considered to be typical for characterizing altitudinal vegetation changes in the region (according to data from the joint expedition campaigns of the Swiss Federal Research Institute WSL and V. N. Sukachev Institute of Forest SB RAS teams in the 1990s and 2001, organized by Professor F. H. Schweingruber). The vegetation in this remote study area has not been influenced by fire or by any other strong external disturbances during the last millennium, as we did not observe fire scars in any of the tree disks, and Sidorova *et al.* (2007) documented that the subfossil wood lying on the ground was up to 1118 years old. The location of the transect was chosen to represent the continuous change of vegetation from the forest to the tundra occurring over a wider area of the forest-tundra ecotone (across at least several kilometres). In the Putorana Mountains, the continuous change along the forest-tundra ecotone is typical for south-facing slopes, whereas on the north-exposed slopes, tree stand structure is more heterogeneous, with tree islands separated by tundra.

The most productive larch stands grow at the bottom of the valley. Forest cover is up to 50%. These ‘closed forests’ are characterized by single-tree growth, well-developed shrubs (*Betula nana* L., *Duschekia fruticosa*

(Rupr.) Pouzar and *Salix* sp.) and thick moss layers. Dwarf shrubs (*Vaccinium uliginosum* L., *Empetrum nigrum* L.) are omnipresent. At approximately 270 m a.s.l., the first trees growing in multi-stemmed clusters can be observed. Because of these clusters with up to 10 tree stems per individual, the forest becomes more open, although the density of trees (number of individual stems per hectare) increases. At 300 m a.s.l., the distance between single trees and clusters reaches 10–20 m. The herb layer is characterized by *Dryas octopetala* L. and mosses. At the tree line (360 m a.s.l.), the upper border of the open forests, larch grows mainly in clusters. These multi-stemmed trees developed from formerly creeping growth forms (krumholz), where horizontal shoots started to grow upright under more favourable conditions (Devi *et al.* 2008). The herb layer is characterized by the dwarf shrub *Vaccinium uliginosum* L. and by some graminiae (*Calamagrostis* sp., *Carex ensifolia* V. Krecz.). At the upper species line at about 390 m a.s.l., scattered, mostly creeping larch (krumholz) is replaced by alpine dryad-stony tundra. Although the upper part of the altitudinal transect is dominated by larches with multi-stemmed growth forms (clusters and creeping), single-stem tree regeneration developing from seeds is frequent.

Most of the slope contains few stones, except for the upper part (Fig. 3), where 50% of the surface on the slope is covered by stones and blocks (up to 2 m, mostly in ‘stone rivers’ or ‘kurum’). Soils developed by *in situ* weathering of the Putorana trap basalt. They are of homogeneously loamy texture, show hydrotropic properties, and are classified as Haplic Cryosols according to the IUSS Working Group WRB (2006).

Sample plots were established at four altitudinal levels along the transect primary: at 170 m a.s.l. (CF: closed forest at river valley), 320 m a.s.l. (OF: open

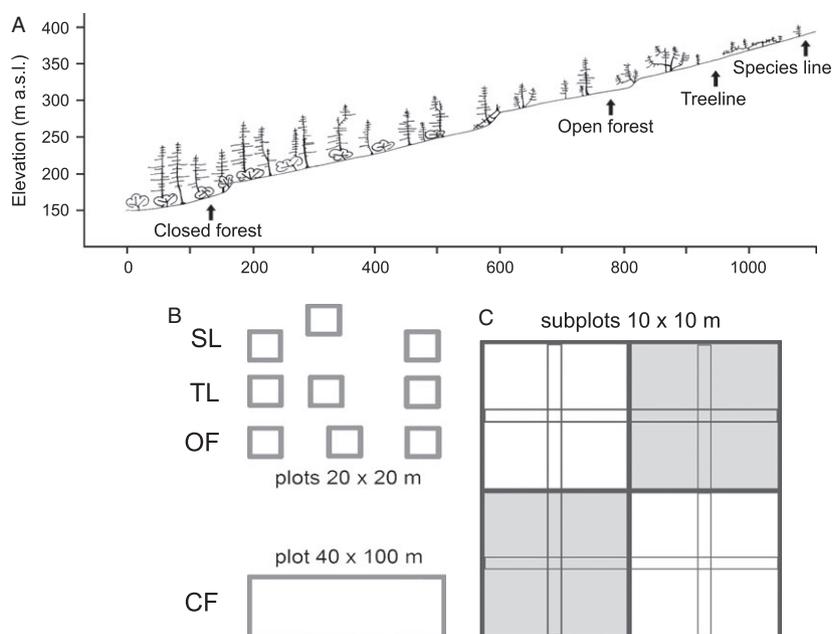


Fig. 2. A. Altitudinal transect in the Putorana Mountains, northern Siberia. B. Sampling design. Plan of the sampling plot distribution along the transect. Distance between the subplots is 10, 20 or 30 m. C. Single plot 20×20 m² divided into subplots. White subplots, 10×10 m², are for sampling (larch age structure, ground-cover biomass estimation, soil profiles); grey subplots, 10×10 m², are for monitoring. Along the lines in the middle of subplots, detailed surveys of ground-cover estimations were carried out.

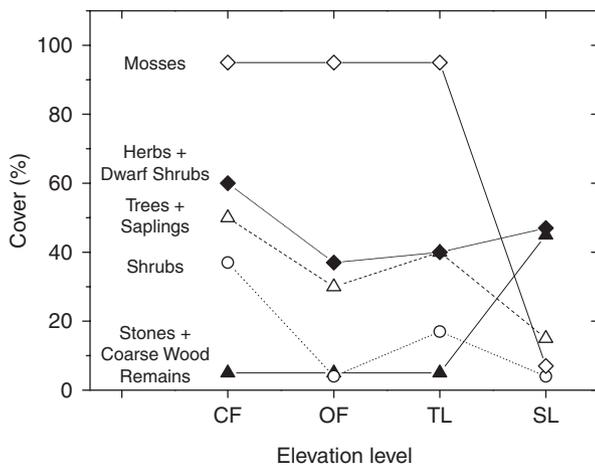


Fig. 3. Crown projection of stand and vegetation cover; percentage of area covered by stones. CF = closed forest; OF = open forest; TL = tree line; SL = species line.

forest), 360 m a.s.l. (TL: tree line of open forest, multi-stemmed trees) and 390 m a.s.l. (SL: species line, creeping and multi-stemmed trees) (Fig. 2A). The plot sizes were defined to include approximately 200 trees in order to represent forest stand structure adequately (State Standard 56-69-83 1983). At each of the three upper altitudinal levels, three plots of $20 \times 20 \text{ m}^2$ were established, with 10 to 20 m between plots (Fig. 2B, Table 1). Each of the plots was divided into four sub-plots, $10 \times 10 \text{ m}^2$ each (Fig. 2C). The larger plots were used for characterizing the forest stand structure. In two of the sub-plots, intensive destructive sampling for above-ground biomass measurements and cutting of larch individuals for age-structure definition took place, while the other two sub-plots were reserved for monitoring purposes. To compare the data of the species (SL) and tree (TL) lines and open forest (OF) with those of the most productive and closed forest (CF) with a spatially homogeneous stand structure, one large plot of $100 \times 40 \text{ m}^2$ was established at the lowest altitudinal level.

Inventory and age structure of larch

For the characterization of the current stand structure, all trees (including single stems in tree clusters) and

saplings were mapped with a tachymeter in each of the large plots. Larches taller than 1.5 m were regarded as trees, those from 0.2 to 1.5 m as saplings, and those smaller than 0.2 m as seedlings. Basic morphometric parameters of trees and saplings, such as their growth form, tree height, stem diameter and crown length, were recorded. Seedlings were counted, and their growth form as well as general information about location was registered.

To estimate past and present changes of the forest-tundra ecotone, we assessed the age structure of larch at each of the four altitudinal levels. In total, we analysed the ages of 206 trees and saplings (Table 1) by cutting and boring living and dead larch individuals and counting tree rings at 0.0 and 0.25 m height from the ground. For the living trees, for which cores were taken at 0.25 m only, tree age was estimated according to the difference in the number of tree rings at 0.0 and 0.25 m obtained for the cut trees ($n = 95$). Tree-ring width was measured with an accuracy of 0.01 mm by means of the semi-automatic system LINTAB-3.0 (Rinntech, Germany) and cross-dated to define the calendar year of each tree-ring formation. Wood cores collected at 1.3 m from trees in closed forest (15 trees, 15 cores) and at the tree line (19 trees, 34 cores) were also used to build the tree-ring width (TRW) chronologies, according to standard techniques in dendrochronology (Fritts 1976). Individual TRW series were standardized to remove age-related trend by dividing the measured value by the estimated TRW from a fitted curve (Cook & Kairiukstis 1990). For fitting, a modified negative exponential curve, or, if it failed, a linear regression line of negative slope or horizontal line through the mean, was applied. Elevation-level chronologies were calculated by averaging the detrended dimensionless individual chronologies from each elevation. In order to identify the influence of climate on radial growth, we correlated the chronologies with monthly temperature and precipitation data from the nearest meteorological stations, namely Dudinka (69.40°N , 86.17°E), Khatanga (71.98°N , 102.47°E) and Turukhansk (65.78°N , 87.93°E). Because the climatic signals contained in the chronologies from different elevation levels are similar, the chronologies were averaged to build a site chronology.

Table 1. Number of plots described and samples measured at each altitudinal level along the transect. The asterisk indicates the number of trees measured for tree-line and species-line altitudinal levels.

Altitudinal level	Number of plots	Number of individuals for stand description			Number of individuals/plots for aboveground biomass measurements			
		Trees and saplings	Seedlings	Age structure	Trees	Shrubs	Herbs and dwarf shrubs	Mosses and lichens
Species line	3 plots, $20 \times 20 \text{ m}^2$	288	45	61	7*	5	20	17
Treeline	3 plots, $20 \times 20 \text{ m}^2$	331	3	59		11	21	24
Open forest	3 plots, $20 \times 20 \text{ m}^2$	191	16	56	6	9	21	22
Closed forest	1 plot, $40 \times 100 \text{ m}^2$	213	53	30	5	5	10	10

Table 2. Characteristics of larch stands and regeneration along the transect. The asterisks indicate data obtained only for trees – data on saplings ($H < 1.5$ m) and seedlings ($H < 0.2$ m) are not included. CF = closed forest at river valley at 170 m a.s.l.; OF = open forest at 320 m a.s.l.; TL = tree line of open forest, multi-stemmed trees at 360 m a.s.l.; SL = species line, creeping and multi-stemmed trees at 390 m a.s.l.; DBH = diameter at breast height; H = height.

Sample plot	Average DBH of trees* (cm)	Average H of trees* (m)	Age of trees at 0.0 m* (years)		Average density of living/dead ($n \text{ ha}^{-1}$)		
			Mean	Max	Trees	Saplings	Seedlings
SL	2.5	2.6	50	106	867/0	1483/67	375
TL	5.6	4.1	130	260	1975/133	417/242	25
OF	10.4	7.4	210	331	975/450	17/150	142
CF	12.5	9.0	220	490	736/57	167/no data	133

Aboveground biomass measurements

The aboveground biomass of the various life forms (trees, shrubs and ground vegetation) was measured at each sample plot (Table 1). The biomass of larch stands was estimated from the inventory data and the aboveground biomass measurements of 18 model trees (five for CF, six for OF, and seven for TL and SL): the trees were first cut, and the various fractions such as stems, branches, needles and cones were then measured and weighed, and subsamples were taken to the laboratory and dried at 110 °C until a constant weight was reached. A similar procedure of oven-drying was applied to all the field samples. The aboveground biomass of each plot was estimated by first fitting allometric functions to the measured fractions of tree components. These functions were then used to quantify tree biomass. The total aboveground biomass per area was finally calculated with the mapped tree densities, heights and diameters. The biomass of seedlings was not measured.

The aboveground biomass of shrubs was estimated using two techniques. For small shrubs (e.g. *Betula nana*), we cut branches and leaves within frames of 0.25 m² square plots (50 × 50 cm²). The vegetation of three to ten frames was cut at each altitudinal level, and weighed after drying the samples in the laboratory. The measured biomass was extrapolated to a larger area by measuring the area covered by each species, taking into account if they grow under or out of tree crowns. For bigger plants (e.g. *Duschekia fruticosa*), the biomass was extrapolated using 'model' branches, whereby we first counted the number of branches and then sampled morphometrically typical model branches. The branches were transported to the laboratory, oven-dried and weighed.

The aboveground biomass of the ground cover, namely dwarf-shrubs, herbs, mosses and lichens, was estimated by cutting individuals in 78 micro-plots (25 × 20 cm²). Moss biomass was divided into living biomass and necromass. Only living biomass was used for the analysis.

Results

Stand parameters

As expected, the average height of trees (H) and their diameter at breast height (DBH) decreased with in-

creasing elevation (Table 2). However, there was only a slight decrease, of less than 20%, for these two morphometric parameters from the stands in the river valley at 170 m a.s.l. to the open forest 150 m higher. A much stronger reduction in tree size occurred between the stands of the upper part of the forested slope and towards the species line (Table 2). The stand density of living trees increased from the closed forest upslope. At the upper border of the open forest at 360 m a.s.l., the stand density was highest, with 1975 trees per hectare (Table 2). However, most of the trees here were small and grew in clusters, and hence the crown cover of larch stand was lower than in closed forest (Fig. 3). At the species line, the density of trees was less than 900 individuals per hectare.

The forested area (covered by tree crowns) and vegetation cover (Fig. 3) indicated more favourable growing conditions for vegetation at the lowest altitudinal level in the river valley. The tree crown cover decreased significantly to the species line, in accordance with the declining tree DBH and height. The cover of the moss-lichen layer decreased on the upper slope; this was, however, related mainly to the increase of stony and vegetation-free areas.

Aboveground biomass

The total aboveground biomass of all the vegetation components decreased from 38.2 t ha⁻¹ in the closed forest at 170 m a.s.l. to 4.7 t ha⁻¹ at the species line at 390 m a.s.l., and thus they decreased by a factor of eight. These changes were mostly due to the significant decrease in tree biomass (one-way ANOVA; $P < 0.05$; Fig. 4A). The relative contribution of trees to ecosystem aboveground biomass was 86% in the closed forest, 79% in the open forest, 68% at the tree line with in-group growing larches, but only 18% at the species line. These changes in stand biomass for the three lower altitudinal levels were attributed mostly to decreases of tree DBH and H, but not to stand density (Table 2). The main part of the aboveground tree biomass was stored in the stems. At lower elevations (up to 320 m a.s.l.), stem biomass accounted for 75–80% of the total aboveground tree biomass, while at the upper part of

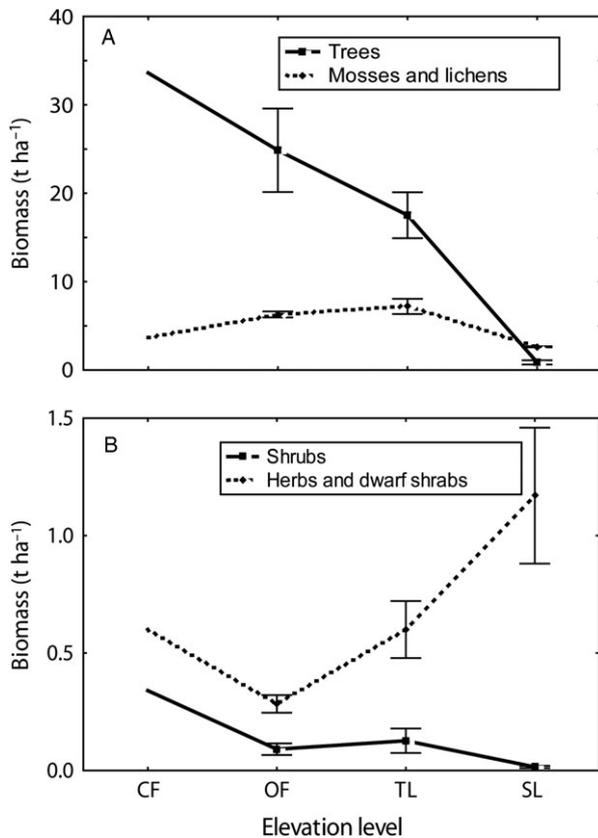


Fig. 4. Distribution of aboveground biomass in various vegetation components of the forest-tundra ecosystem along the altitudinal transect, absolutely dry weight, $t\ ha^{-1}$. A. Trees and mosses and lichens. B. Shrubs and herb-dwarf shrubs. Lines connect average values obtained for three plots $20 \times 20\ m^2$; whiskers indicate the standard error interval among data for each $20 \times 20\ m^2$ plot. The highest coefficients of variation (CV) were found for the aboveground biomass of shrubs (0.71), while those for trees and herb-dwarf shrubs varied from 0.23 to 0.48 among plots. The total aboveground biomass of mosses and lichens was the least variable, with CVs between 0.04 and 0.21. A one-way ANOVA indicated significant ($P < 0.05$) differences between mean biomass accumulated in different types of vegetation at each elevation level, and in the mean biomass of trees and also mosses and lichens from different elevations. CF = closed forest; OF = open forest; TL = tree line; SL = species line. Note the different scales for the y-axis in graphs A and B.

the forested slope (360–390 m a.s.l.) its portion decreased slightly to 66%.

The aboveground biomass of shrubs was very irregularly distributed along the transect (Fig. 4B) and related mainly to the area covered (Fig. 3). The most productive site, the closed larch stand in the river valley, had the highest shrub aboveground biomass and cover. Although shrubs covered up to 40% of the total area, their biomass made up less than 10% of the total aboveground biomass at all elevations.

The contribution of ground vegetation to total aboveground biomass increased from 11% in the river valley to 77% at the species line ($P < 0.05$). At all elevations, mosses and lichens stored more aboveground biomass than shrubs, dwarf shrubs and herbs; at the highest site, they accumulated $2.6\ t\ ha^{-1}$ (56% of the

total aboveground biomass), being the most important aboveground biomass component. The aboveground biomass of herbs and dwarf shrubs was greatest at the species line ($1.2\ t\ ha^{-1}$), while mosses and lichens had the greatest biomass at the tree line at 360 m a.s.l. ($7.2\ t\ ha^{-1}$) (Fig. 4).

Stand age and larch recruitment

The tree age structure changed considerably along the altitudinal gradient (Fig. 5). The mean tree ages were slightly higher than 200 years both in the closed forest and in the open forest (Table 2, Fig. 5). Further up, the mean tree age decreased gradually to 130 years at the tree line at 360 m a.s.l. and to 50 years at the species line. The decrease in age with increasing elevation was also observed for the maximum ages of trees. The oldest trees found at each elevation started to grow in 1510, 1640, 1740 and the 1890s at the four altitudinal levels from the river valley to the species line, respectively.

The total number of living saplings and seedlings decreased from $300\ n\ ha^{-1}$ in the river valley stand to $160\ n\ ha^{-1}$ in the open forest (320 m a.s.l.) and then increased to $440\ n\ ha^{-1}$ at the tree line (360 m a.s.l.), and finally to $1860\ n\ ha^{-1}$ at the species line. At the species line with the most intensive larch regeneration, the average age of saplings was 22 years (Fig. 5; note: Table 2 shows only the average tree age). Here, larch establishment started mostly in the 1940s, with a strong increase in the 1980s. For younger seedlings emerging after 1989, the density but not the age was assessed (see Material and Methods). At the species line, only two of the 50 trees and saplings sampled were as old as 104 and 106 years. Tree height and age were significantly correlated ($r = 0.82$), which allowed us to extrapolate tree age structure to larger areas by mapping tree heights. The results showed that at the species line more than 90% of larches were younger than 100 years.

Climatic changes and their relation to forest dynamics

Climate data from the nearest meteorological stations, Dudinka, Khatanga and Turukhansk, indicate that during the last century winter precipitation increased significantly (Fig. 6A), whereas winter temperatures show different trends at these stations (Fig. 6C). An approximately 100-mm increase in winter precipitation was observed at Dudinka, 290 km to the southwest, from 1907 to 1983 ($P < 0.0001$) and at Turukhansk, 550 km to the southwest, during the 20th century ($P < 0.0001$). At Khatanga, 390 km to the northeast, measured winter precipitation increased from 80 mm in 1930 to 125 mm in 2000 ($P < 0.05$). The data indicate increases in winter precipitation of between 5 and 12 mm per decade at these three climate stations.

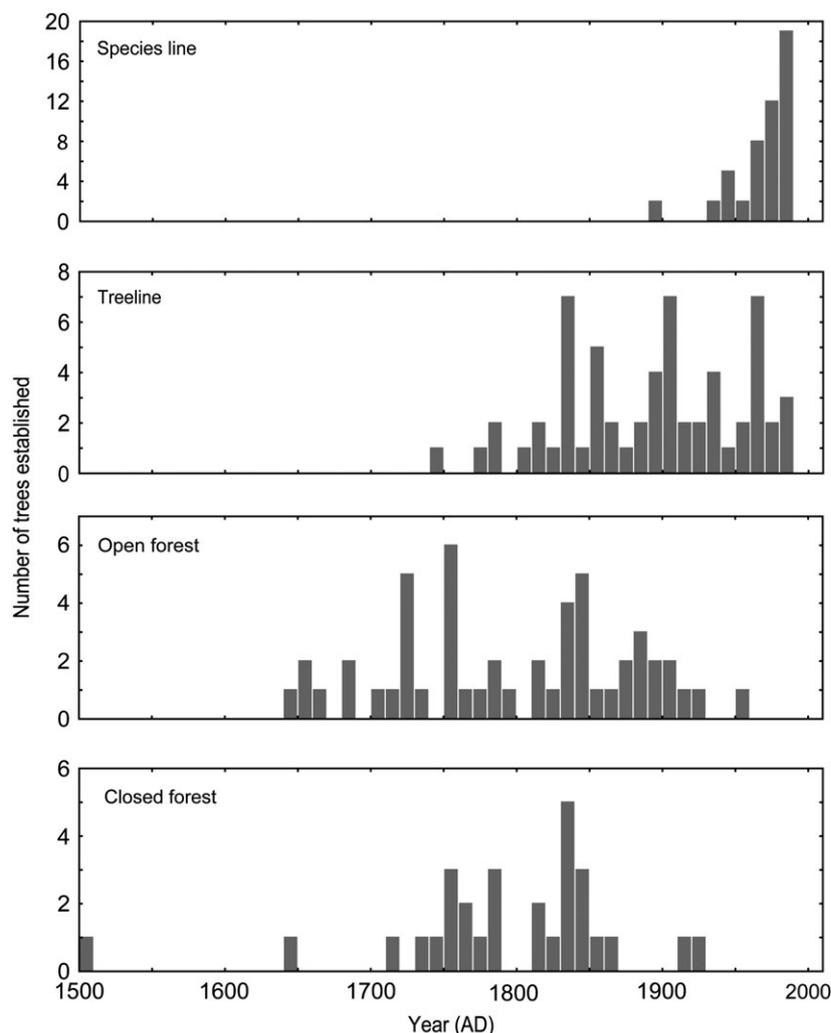


Fig. 5. Age structure of larch trees and saplings at various elevation levels.

Changes in summer precipitation and temperatures were negligible (Fig. 6B, D).

Larch recruitment and winter precipitation increased simultaneously during the last century, but the correlation was not significant. In contrast, tree-radial growth was significantly related to June, July and June–July temperatures ($r = 0.30, 0.46$ and $0.48, P < 0.05$). However, neither summer temperature (Fig. 6) nor tree-ring width increased significantly during the 20th century.

Discussion

Tree-line advances

Our analysis of tree age structure and larch establishment indicates that in the extremely remote and untouched Putorana Mountains, the forest-tundra ecotone is currently shifting upwards, as: (i) both the mean and the maximum age of trees strongly decreased from the closed forest at the river valley to the upper tree line; and (ii) there was highly successful germina-

tion of larch at its current upper growth limit at the end of the 20th century. The significantly younger tree ages at the species line than in the closed forest and the finding that more than 90% of the trees are younger than 100 years (Fig. 5) indicate that the forest has advanced into tundra during the last decades. This age structure is in agreement with that of expanding tree lines in coastal Labrador (Payette 2007), but it contrasts with tree ages of non-upward-shifting tree lines in the Alps, interior Labrador, and northwestern Canada, where trees at the species line are more than 200 year old and have ages similar to trees at lower elevations (Szeicz & MacDonald 1995; Carrer & Urbinati 2004; Payette 2007). At and above the tree line in the Putorana, we observed neither long-living krummholz nor subfossil wood. This is in contrast to what is observed in other areas of northern Siberia with a similar continental climate, where decaying wood can be preserved for centuries (Esper & Schweingruber 2004; Mazepa 2005). The high densities of young living saplings (Table 2; Fig. 5) at the species line show that larch has been germinating successfully during the last decades, and

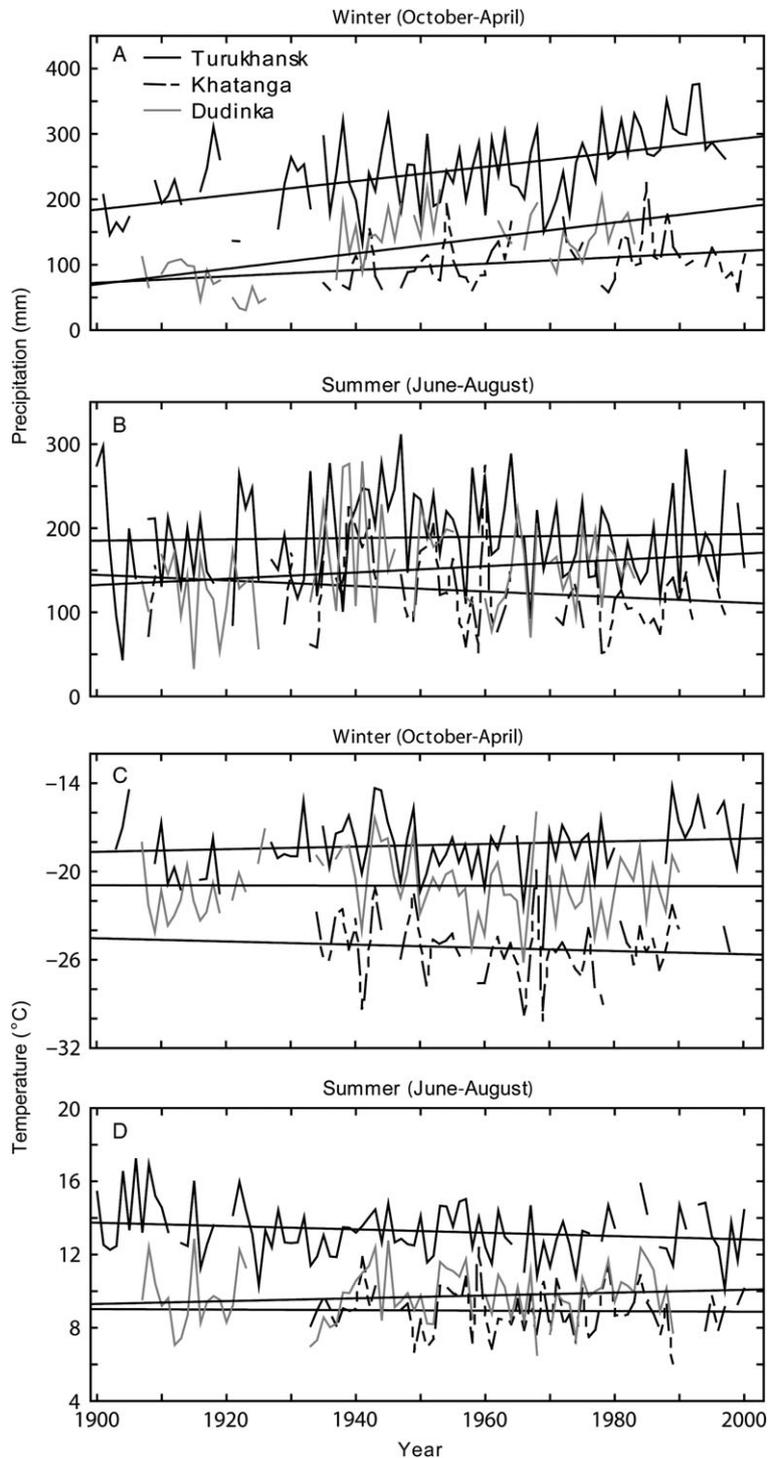


Fig. 6. Climate data from the nearest meteorological stations, Dudinka, Khatanga and Turukhansk. Straight lines indicate the linear trend in the record.

thus that the forest is still expanding. The age structure at the tree and species line, with some 100-year-old tree individuals but a high density of younger trees, also gives an indication of the dynamics of the forest during the last decades: apparently, the advance of the upper growth limit of larch is linked to the increase of the population density, leading to a significant filling-in between established single trees. This indicates that the

expansion of the forest is more pronounced than the upward shift of the uppermost tree individuals, which is in agreement with observations in the forest-tundra ecotones of the Polar Urals, Alaska, Rocky Mountains and eastern Taymir (e.g. Bekker 2005; Lloyd 2005; Shiyatov *et al.* 2005; Kharuk *et al.* 2006).

If we assume that the upward expansion of the forest-tundra ecotone is reflected in the decreasing mean tree

age with increasing elevation, the rate of the upward shift of the forest can be estimated to be between 30 and 50 m in altitude during the last century. The estimate from our single transect agrees closely with the advances of the forest-tundra ecotone in the Polar Urals (Shiyatov *et al.* 2005; Devi *et al.* 2008), where a large-scale mapping, an age structure analysis and historic photographs show that the forest-tundra ecotones shifted upslope by 20 to 50 m from the 1910s until 2000. In the southern Ural Mountains, the forest has advanced by 60 to 80 m in altitude, but the uppermost growth limit of trees has hardly changed (Moiseev *et al.* 2004). Kullman & Kjällgren (2006) observed a maximum rise in the elevation of a tree line formed by Scots pine (*Pinus sylvestris* L.), of 150–190 m, during the 20th century in the Caledonian mountain range in Sweden. Kullman & Öberg (2009) demonstrated that *Betula pubescens* ssp. *czerepanovii*, *Picea abies* and *Pinus sylvestris* experienced a regional-scale tree-line rise in the southern Swedish Scandes by 70–90 m on average, with a common maximum of about 200 m since around 1915. Our data at the altitudinal tree line in the Putorana Mountains are also in accordance with the observations of Esper & Schweingruber (2004) at the northern tree line in Siberia from their analysis of a multi-species network of forest-tundra ecotone sites. They reported an upward shift at the Gmelin larch altitudinal tree line in the region of our study and an ongoing establishment of new forests at tree-line sites in Siberia. Moreover, from satellite data from Middle Siberia (in the Ary-Mas forest, the world's northernmost forest island located approximately 500 km northeast of our study area), Kharuk *et al.* (2006) inferred a northward horizontal migration of Gmelin larch into the tundra at a rate of between 30 and 100 m per decade from the 1970s until 2000.

Drivers for tree-line changes

According to Körner & Paulsen (2004), temperature is the key climatic factor in defining the tree-line position of the world's mountains. Hence, the most evident explanation for the observed tree-line advances is the climatic warming during the last century (Payette 2007). In agreement with other dendrochronological studies in northern Asia (e.g. Vaganov *et al.* 1999; Kirilyanov *et al.* 2003; Esper *et al.* 2010), our tree-ring data clearly show that higher summer temperatures have a stimulating effect on radial growth. However, neither temperature records in the region nor tree-ring widths at the study site show significant increases during the 20th century. Climatic warming occurred only in winter. In contrast to the non-significant increases in summer temperatures, climate records reveal significant increases in winter precipitation that coincided with the increase in larch recruitment. At the upper elevations, larch seedlings established mainly under

wind-protected micro-conditions close to bigger trees, suggesting that snow cover plays a key role in the protection of young trees from frost and wind damage (Holtmeier 2003; Moiseev *et al.* 2004; Koshkina *et al.* 2008). Increases in snowfall can induce a positive feedback, with more snow allowing trees to grow more successfully, and bigger trees promoting the accumulation of additional snow (Bekker 2005). Furthermore, increased winter precipitation may provide additional water supply for trees during the vegetation period. A recent field study by Devi *et al.* (2008) in the Polar Urals indicated that it was mainly the large increase in snowfall that led to substantial changes in the forest-tundra ecotone: multi-stem larch trees that were growing for several centuries in a creeping form started to grow upright when winter precipitation doubled at the beginning of the 20th century. We therefore suggest that, while tree growth is controlled mainly by summer temperature, with negligible changes during the last century, the forest expansion in the Putorana Mountains might be driven mainly by significant increases in snowfall.

Recent model assessments on tree species redistribution in Siberia (Tchebakova *et al.* 2006) under the HadCM3GGal scenario (4–6 °C summer temperature increase and annual precipitation changes between –4 and +25% over the studied territory) (Gordon *et al.* 2000) suggest that the potential growing area of *Larix* spp. will shift by as much as 700 km to the north and several hundred metres upslope until the end of the 21st century. There is also empirical evidence for significant tree-line shifts during the Holocene: under warmer conditions during the period 10 000–3500 a BP, the northern tree line in Russia (formed mostly by larch) was probably located up to 200 km north of its modern position and even reached the current Arctic coastline between 9000 and 7000 a BP (MacDonald *et al.* 2008). The density of larch tree cover north of the current tree line had its maximum between 8000 and 4000 a BP (MacDonald *et al.* 2000). In the surrounding area, in the east of Taymir, Naurzbaev (2005) concluded, based on 44 radiocarbon-dated megafossils of larch, that maximum northward extensions of Gmelin larch up to 73°38'N occurred around 8000 and 6000 a BP. The northern tree line in Taymir, as well as over most of Russia, retreated to its present position between 4000 and 3000 a BP (MacDonald *et al.* 2000; Naurzbaev 2005). In the Polar Urals, a large number of tree remains of Siberian larch can be found up to 60–80 m above the currently upward-shifting tree line (Mazepa 2005). The oldest remains date back to 1300 years, with the maximal abundance occurring during the Medieval Warm Period. These reconstructions indicate that the tree line migrates considerably under a changing climate. However, the rate of tree migration in response to climate changes will be delayed because seed production, seed dispersal and tree survival at the timberline depend on multiple factors during the first decades of a

tree's life (Körner 1999; Bugmann & Pfister 2000). Our study in an extremely remote area has shown that it has taken more than 100 years from the first larch establishment to convert a previously unforested area to a sparse forest (distance between trees 10–20 m). Similar estimates for spruce in Alaska (Chapin & Starfield 1997; Lloyd 2005) suggest a time-span of more than 150 years for an open forest at the tree line to develop from the first tree seedling. Thus, although trees have apparently been advancing into tundra in both Eurasia and some regions of Alaska during recent decades, the areas of these shifts of tree line are relatively small compared with areas with documented increases in tree density in previously sparsely forested areas (Lloyd 2005; Shiyatov *et al.* 2005; Kharuk *et al.* 2006). Data from Alaska compiled by Lloyd (2005) and from Labrador (Payette 2007) show that tree-line advances are extremely heterogeneous. This suggests that tree-line shifts are dependent on local drivers, because climate has warmed similarly across large regions. Very likely, permafrost depth plays a key role for the rate of tree-line shift by limiting the establishment of new trees (Lloyd & Fastie 2002). For instance, Suarez *et al.* (1999) did not detect tree-line advances on Alaskan arctic tundra soils with shallow 0.5-m-deep active layers. Permafrost depth at our site in the Putorana Mountains was approximately 0.5 m, which may explain why tree-line advances and forest expansions rates over 30 to 50 m were much slower than in the permafrost-free southern Ural Mountains (Moiseev *et al.* 2004), but comparable to tree-line shifts in the Polar Urals (Shiyatov *et al.* 2005). In our study, the active soil layer at the three lower altitudinal levels was even shallower than that at the species line and was associated with higher larch crown projection and ground vegetation cover (Fig. 3). Unfavourable conditions for larch seedlings owing to competition with ground vegetation (especially mosses; Fig. 3) could explain the lower larch regeneration at these elevations. Another factor affecting larch establishment and growth at the species line is the poor soil development, which limits the substrate available for germination. At the highest altitudinal level, up to 50% of the surface was covered by stones, and this percentage further increased in the tundra. Moreover, soils were poorly developed and shallow, which probably restricts further larch advances to higher elevations.

Impact of tree-line advances

The lagged response of the forest-tundra ecotone has implications for the feedbacks between vegetation and climate. Forest expansion into former tundra has a high potential to accelerate warming by increasing the amount of absorbed radiation, but it may also counteract it by sequestering additional atmospheric CO₂ (Chapin *et al.* 2000). The slow rates of change in the forest-tundra ecotone observed in our study, however,

support the estimates of Chapin *et al.* (2005) for Alaska, with the current climatic-driven advances in snow-melt being more significant than the slow expansion of forests. Moreover, larch trees, being defoliated in winter, absorb less radiation than spruces and pines. In the long run, forest expansions into formerly treeless tundra will certainly increase carbon storage in the above-ground biomass in northern Siberia. Our results allow some rough estimates on carbon sequestration in biomass through the upslope shift of the forest-tundra ecotone by assuming (i) that the increasing mean age of forest stands from the tundra to the closed forest reflects the forest expansion rate, (ii) that tree roots store 35% of the biomass (27% for larch at the Swiss alpine tree line; Bernoulli & Körner (1999); 36% contribution of roots for larch in the Polar Urals; Devi *et al.* (2008)), which is similar to our field estimates made for eight trees with excavated and weighed roots (39% for the wet weights), and (iii) that roots of shrubs and dwarf-shrubs contain three times as much carbon as their aboveground biomass (Polar Urals: Andreyashkina & Peshkova 2005). Under these assumptions, the mean carbon sequestration rate in tree biomass would range between 2 and 10 g C m⁻² a⁻¹. Trees make the major contribution to the increase in biomass carbon, while the biomass of shrubs and dwarf-shrubs is much smaller than that of trees (Fig. 4).

The estimated amount of carbon sequestration is rather small – much smaller than in the managed but much faster-growing forests of the temperate zones. For instance, Janssens *et al.* (2003) estimated that the mean carbon uptake by Europe's forest amounts to 50 g C m⁻² a⁻¹, although the greatest fraction of net forest growth is removed through harvest. At first glance, these results conflict with the striking increase in biomass from the tree-free tundra to the forest (Fig. 4). However, the rates of change from the establishment of seedlings to a dense forest are slow, and thus the net carbon uptake by the vegetation is small. Moreover, the negligible increase in the ring widths of already established trees during the 20th century indicates small carbon sequestration rates in the older stands of the forest-tundra ecotone.

The forest expansion might have additional impacts on soil carbon storage, either directly through an increased litter input or indirectly through an altered microclimate (Chapin *et al.* 2005; Sturm *et al.* 2005). Comparative studies in northwest Alaska between forests and tundra suggest that aboveground carbon gains through advancing tree lines can be more than offset by belowground carbon losses (Wilmking *et al.* 2006). In contrast, negligible changes in soil carbon storage were observed across forest-tundra ecotones in the Ural Mountains (Kammer *et al.* 2009). Here, because of the lack of soil carbon data, we can only speculate on the potential impacts of a forest expansion on soil carbon and thus on total ecosystem carbon storage. We think,

however, that the current upward expansion of forest is only a minor carbon sink, because the rates of carbon stock changes in biomass that also drive potential changes in soil carbon are rather small.

Conclusions

Our age structure analysis of trees and saplings along an altitudinal gradient across the forest-tundra ecotone indicates that the tree line of the remote Putorana Mountains, Siberia, has shifted upwards considerably and that the forests have become much denser during the 20th century. While the tree growth of established trees was controlled mainly by summer temperatures, with negligible changes during the last century, it seems likely that the forest expansion in the Putorana Mountain was driven mainly by the 25 to 70% increase in winter precipitation, which improved protection through snow. There is a strong and successful germination of larch at the current upper species line, which signifies an ongoing filling-in, a densification of formerly open forest, but also an upslope shift of the tree-line position. Tree and sapling ages suggest that the forest expanded by approximately 30 to 50 m in altitude during the last century. Total aboveground biomass increased substantially with decreasing elevation. The assumption that the decrease of tree ages with elevation reflects the rate of change suggests, however, that biomass accumulated slowly, and thus carbon sequestration rates in biomass have been very low, namely 2 to 10 g C m⁻² a⁻¹. In summary, our study demonstrates that the ongoing climatic changes are altering the structure and productivity of forest-tundra ecotones in the remote Putorana Mountains.

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