Soil temperatures at the birch treeline (Betula pubescens ssp. czerepanovii) - a 21-year record in the Swedish Scandes and a contribution to general treeline theory

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Abstract

This study addresses the issue of climate control of the elevational treeline, foremost the role of soil temperatures. During the period 1999 to 2020, soil temperatures were recorded over the year at a depth of 10 cm in a sparse stand (Betula pubescens ssp. czerepanovii) within the upper treeline ecotone of the Swedish Scandes. Over the years 2010 to 2020, the birch stand was repeatedly photographed. This endeavor, in combination with measurements of the tree heights provided an apprehension of individual responses to recent climate variability. This view was taken a step further by analyzing tree-ring patterns more than 100 years back in time. A main result was that the obtained growing season soil temperature of 7.1±0.7 degrees Celsius (°C) is well in accordance with earlier estimates of a global minimum threshold for tree growth at the treeline. Soil temperature was 2.7 °C lower than ambient air temperature. The tree-ring chronology displayed steadily increasing growth between 1880 and the late 1930s. It may be inferred that up to the latter date, the concerned birches were climatically suppressed specimens, entirely snow-covered during the winter. Thereafter, growth progression towards tree-size was initiated from the early 1940s and onwards, in response to climate warming. This process appears to be still in progress as temperatures remain fairly high.

Keywords: Treeline; Climate change; Soil temperature; Thermal threshold; Tree-ring chronology; Betula pubescens ssp. czerepanovii; Swedish Scandes

1. Introduction

By tradition, alpine treelines are considered to be controlled basically by heat deficiency and may in principle serve as sensitive indicators of past and recent climate-driven landscape ecological transformation at the interface between upper boreal forest and alpine tundra. (1, 2, 3, 4, 5, 6). This contention is based on several studies, which have evidenced different magnitudes of elevational and latitudinal landscape-scale treeline upshifts, broadly consistent with ambient regional air temperature rise over the past 100 years or so (7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17).

However, at smaller spatial scales, treeline positions and dynamics are modulated, to various degree, by complex interactions and feedbacks of local-scale factors, more or less decoupled from the regional climate, e.g. geomorphology, soil depth and wind as well as various disturbances, e.g. human and animal impacts (7, 18, 19). These constraints are spatially idiosyncratic, a circumstance which is even more influential at the upper limit of closed forest and its often diffuse character with relatively delayed responses to climate change (20, 21, 22, 23, 24, 25).

The detailed coupling between temperature and treeline performance is still imperfectly understood, which impairs projections of treeline shifts under scenarios of prescribed climate change. Since long there has been an aspiration among phytogeographers and plant ecologists to define a general principle behind the treeline phenomenon (e.g. 26). In that context, much effort and striving have been toa global or regional minimum thermal threshold temperature,
which sets the potential treeline position (e.g. 27, 28, 29, 30, 31, 32, 33, 34, 35). Most of these prior studies focused on ambient air temperature records during short sequences of years, often relying on extrapolation from far-distant meteorological stations and concerning differently defined treeline concepts. Scientific progress within this field has suffered from lack of local long-term climate assessments and records.

In recent years there has been increased attention in respect of treeline performance to the importance of local soil temperatures. Globally, retrieved soil temperature records have indicated a critical growing season limit for tree growth, defining the alpine treeline in general, ranging between 6.4 and 7.1 °C (36, 37, 38, 6, 39). Inhibition of tree growth on soils colder than the above-mentioned threshold interval may relate to insufficient soil nutrition (40, 41). However, this view of a global-scale common thermal threshold controlling the treeline position is questioned (42, 43, 5), stressing the ecological complexity of most treelines.

With this background, a single site study of soil temperature records over a 21-year period is here presented. During the past 11 of these years, the evolution of the birch tree cover at the same site is photographically surveyed from the same point.

The objective of the present study is (1) to obtain a growing season soil temperature at the birch tree line. This threshold is to be compared to above-mentioned temperature indices, of alleged global significance for tree growth at the alpine tree line, and (2) to correlate changes in various aspects of tree growth during the past 21 years with sampled soil temperature evolution.

1.1. Study area and site

The treeline ecotone in the concerned region of the Scandes is made up of distinct subalpine birch forest belt (Betula pubescens ssp. czerepanovii), which upslope grades into the alpine tundra and downslope into boreal coniferous forest, with Picea abies and Pinus sylvestris as alternating dominants (44, 45).

The study was carried out at the southeast-facing flank of Mt. Storsnasen in the southern Swedish Scandes (Fig. 1), 850 m a.s.l. (63° 12. 729’N, 12° 22. 959’E). This position is 45 m above the treeline prevailing by the early 20th century (12). Widely scattered solitary birch trees are currently growing somewhat higher upslope. Thus, this site represents the upper part of treeline ecotone. It comprises a south to north horizontally elongated cluster of birch trees at the transition between a local snow-accumulating lee slope and an exposed snow poor crest. This pattern and its ground-cover of dwarf-shrubs and some herbs is characteristic of the treeline ecotone in many parts of the Scandes.

Maximum snow depth, usually in mid-March, around the tree bases is about 1 m. As a rule, leafing takes place in mid-June at about the same time as soil temperature exceeds 0.0 °C. Most years, autumnal leaf shedding occurs in mid-September, which is by large earlier than soil freezing.

Initially (1999), seven distinct, multi-stemmed birch copses prevailed at this site. Four of these were tree-sized. Obviously, and to judge from autumnal discoloration patterns, they represent different genetic individuals. Tree-ring counts at the stem-root intersections shows that they were all present as low-growing shrubs well in advance to the onset of 20th century climate warming. There is nothing to suggest that this site and its tree cover have been affected by human impact in the past.

The climate has a weakly oceanic character. The nearest meteorological station (Storlien/Storvallen, 595 m a.s.l. displays mean temperatures (1961-1990) for January, July and the year; -7.6, 10.7 and 1.1 °C, respectively. During the summer, June, July, August (J, J, A) and winter, December, January, February (D, J, F) regional mean air temperatures (1901-2020) increased by 1.7 and 1.5 °C, respectively (45).
2. Methods

Since 1999, soil temperatures have been recorded twice a week. A resistance thermistor (TO-03R), manufactured by T. Johnsson Inc., was installed in the upper mineral soil at a depth of 10 cm, and annually calibrated. The receiver was located below the dense canopy of one of the surveyed birch copses, which precluded direct sun exposure during the summer (Fig. 2).

In the winter and well into the early summer, a deep snow pack around the stem bases filled the same purpose. This design mimics the one adopted by Körner & Paulsen (38). At this soil depth, short-term temperature variations are significantly damped (cf. 47, 48), as evidenced by daily readings over shorter periods (1-2 weeks in summer and winter 2005). Thus, this approach of intermittent readings is likely to provide a reasonably accurate view of seasonal soil temperatures and their recent trends, characteristic of a representative birch treeline site in the Swedish Scandes. The results provide a test of the local validity of a proposed global threshold value for a thermal treeline indicator in high
mountain regions worldwide (38, 6). Since one purpose of the tree-ring record was to address growth form change over time, rather than climate reconstruction, no standardization procedure was conducted.

Starting in 2010, this site with its sparse birch stand was repeatedly photographed during all seasons, which provides a rough measure of above-ground biomass change, to be compared with recorded soil temperature evolution.

Minimum ages were estimated by coring the thickest stem of each individual birch at the root/stem junction. Increment cores were analyzed in the laboratory following standard dendrochronological procedures (Stokes & Smiley 1968). All cores were visually cross-dated by use of a stereomicroscope with a magnification of x 20-50. Ring widths were measured with an accuracy of 0.01 mm.

3. Results

3.1. Temperature records

Mean annual values of soil temperature for the period mid-June to mid-September (1999-2020) are displayed in Fig. 3. For these years a value of 7.1±0.7 °C was obtained. A certain tendency of rising summer soil temperatures, although not significant, may be gleaned for the entire period after 1999, with particularly high values 2018-2020 (Fig. 3). Throughout, these soil temperatures, were consistently lower than the regional mean ambient air temperature of 11.3 °C (June-August), recorded at Storlien/Storvallen meteorological station (Fig. 4). Adjusted for vertical distance of 250 m between Storlien/Storvallen and the study site, the latter figure is reduced to 9.7 °C, based on a temperature lapse rate of 0.6 °C per 100 m elevation. This implies that the soil temperature is about 2.7 °C lower than ambient summer air temperature. The discrepancy is most pronounced during June, as a consequence of late-lying snow cover and persistent soil frost during the early part of this month. Pearson correlation between recorded soil temperature and regional air temperature (1901-2020) was weak (r= 0.39, p<0.01), although both parameters showed rising tendencies 1999 to 2020.

The soil temperatures usually peaked in mid-August, with record-breaking high values in 2020 (Fig. 3), when annual terminal shoots averaged about 30 cm, which is more than double the common value of 10-15 cm during the observation period.

![Figure 3](image-url)  
**Figure 3** Mean annual growth period soil temperature records, 1999-2020 at the study site

The mean winter soil temperatures (D, J, F) over the entire study period are depicted in Fig. 5. An exceptionally low outlier figure of -6.5 °C was recorded (2010), and omitted from analysis due to its anomalous character. Obviously the site was disturbed by repeated reindeer action during this winter, causing cold air penetration.

The mean soil temperature during the winter period was 0.54 ± 0.52 °C for the entire period 1999 - 2020. A weak tendency, although not statistically significant, for lower values towards the present was manifested (Fig. 5). No visible retrogressional physiognomic effects could be documented, relating to this slight winter cooling.
3.2. Photographic survey

During the period 2010-2020, repeat photos of the study site with its birch copses were captured from an east-facing aspect. This approach, in combination with measurements of individual maximum stem heights, enabled a rough estimate of biomass and leaf area change over this period of time. Repeat photography, winter and summer (Fig. 6 & 7), displays perceivable height increment and proliferation of ramets by four initially extant individuals. During the survey period another three new shrubby specimens, have emerged in the center of the formation. By 1999, the average maximum height of all tree-sized specimens was 2.3 ± 0.4 m, to be compared with 3.3 ± 0.3 m in 2020. During the study period, no seedlings and saplings have been observed on any side of the row of surveyed birch trees.

3.3. Tree ages and radial growth

The result of tree ring-counts of the four tree-sized birch trees is displayed in Fig. 6 B. They range between 142 and 176 years before 2010. Ring width measurements 1880-2020, as means of the four initially visible by 1999 are displayed in Fig. 8. The mean ring width over the period 1999 - 2020 was 0.56 ± 0.16 mm. Prior to that (1880 - 1940), annual growth was 0.38 ± 0.08 mm. For the period 1941-2020, average annual growth increased to 0.59 ± 0.9 mm. Thus, it appears that radial growth displayed a breakpoint substantially around 1940. Prior to that, growth increased steadily.
Thereafter it stabilized at a somewhat lower, but fairly high and fluctuating, level up to the present day (Fig. 8). The correlation coefficient (r) between ring width and regional summer air temperature was 0.71 (1901-2020).

Figure 6 A. Winter view of the surveyed treeline birches [Photo: 2010-02-03]. Figure 6 B. The same view 10 years later

It appears that the original birches have increased their height and density over the photographic survey period. Two new birches have emerged in the center of the formation.

Figure 7 A Summer view of the surveyed birches. Photo: 2010-07-29. Figure 7 B The same view 10 years later (Photo 2020-07-15).

Figure 8 Annual radial growth (1880-2020), expressed as means of four since 1999 surveyed birch trees
Closer inspection and tree-ring counts reveal that these existed as low-stature shrubs well in advance of the study period. Minimum ages of the 6 distinct clones are, from left to right, 152, 167, 104, 59, 142, 176 years, respectively. Soil temperatures were recorded beneath the canopy of the second birch copse from the left [Photo: 2020-03-07].

Increased canopy density over the photographic study period is evident and supported by individual measurements since 1999. One shrubby specimen, entirely snow covered in winter, appears in the lower slope. Delayed snow melt and phenological progression of the ground cover characterized the early summer of 2020 [Photo: 2020-07-15].

4. Discussion

The obtained growing season soil temperature of 7.1 ± 0.7 °C recorded during a 21-year period complies with analogous records worldwide (references above), consistent with the idea of a common lower thermal threshold (summer heat deficiency) for tree growth at the fringe of the alpine tundra (38, 6). Thus, at least with respect to Scandinavia, this threshold appears to be valid.

The controlling role of temperature conditions is further supported by the fact that emergence of tree growth at the study site coincided with 20th century climate warming (7, 12). Moreover, the visualized individual densification, height increment and radial growth pattern speak in favour of climate governing. Analogous physiognomic trends are reported from more northerly parts of the Scandes (49, 50, 51, 52).

Insignificant radial growth prior to about 1940 may relate to prevalence of low and shrubby growth forms with a limited leaf area. Presumably, these individuals were snow-covered and sheltered by a crest during this period (Fig.2). Relatively wide rings thereafter may relate to release of height-growth and gradual attainment of tree-sized stems with a productive foliage protruding above the snow cover. Prior studies showed that this type of old-age treeline birches reached tree-size (i.e. minimum 2 m) some decades after the temperature optimum in the late 1930s (7, 53).

The obtained individual ages of the concerned multi-stemmed birches are reasonably of minimum character. Similar specimens have displayed ages about 4800 years before the present (54). Thus, responses of Betula to shifting climates may be largely a question of phenotypical change of old-established individuals. However, a tendency of increasing sexual regeneration is evidenced for the past few decades (55).

![Figure 9](image9.jpg)

**Figure 9** Windward aspect of the study site, where a harsh local climate and associated wind-deflation of upper soil and plant cover preclude birch establishment and further upslope expansion [Photo: 2020-06-09].

Further territorial expansion of birch forest is currently precluded on the windward and upslope side by wind erosion and associated fine soil dissipation (Fig. 9). At the leeward side a deep and late-lying snow pack precludes expansion of tree growth into deeper parts of the local topography. This inertia contrasts with birch performance in similar settings at lower elevations in the birch forest. Hereabouts, infilling takes place in birch forest glades, where growth, prior to the climate amelioration during the past 100 years, had been precluded due to late-lying snow pack (56, 45). Presumably, it takes more warming than hitherto manifested to accomplish expansion into extreme snow accumulation sites close to the treeline. This may be true also for wind-exposed and snow-poor sites around and above the treeline.
For the above-mentioned reasons, the outcome of hypothetical future warming will be a patchily treed landscape surrounded by dominating treeless alpine tundra, much like the situation prevailing during the warmer-than-present early Holocene (46).

Obviously, birch tree growth is here constrained by these two local extreme habitat types (wind-swept crest and lee slope), as reflected by the lack of young birch recruits, which bears no relation to lack of viable seeds, as high germinability has been recorded in the treeline ecotone over the past 2-3 decades (56).

The present results provide no reason to invoke winter temperatures as primary controllers of deciduous mountain birch treeline growth and performance. In that respect, birch differs from evergreen conifers, *Pinus sylvestris* and *Picea abies*, which both are partly controlled at their treelines by annual variations in severity of winter desiccation of needles and shoots, mediated by sub-zero soil temperatures (57, 58, 59, 9, 20, 63, 64, 65). Injuries of this kind are rarely observed at the birch treeline (cf. Treter 1984). Not even the extreme low and anomalous soil temperatures during the winter of 2010 (-6.5 °C) made any visible imprint on the treeline birches during the subsequent summer.

5. Conclusion

- The average growing season soil temperature was found to be 7.1±0.7 °C at the treeline of *Betula pubescens* ssp. *czerepanovii*. This figure complies with earlier suggested values for a world-wide thermal indicator of the treeline position, and seem to be valid at least for Scandinavian treelines.
- In accordance with secular climate warming, the treeline birches have transformed from low-growing snow-covered shrubs, of assumed infinite age, to tree form and stature. This process took its start by the final phase of the Little Ice Age and has progressed to the present day.
- As tree-size developed, the ability to trap drifting snow, from higher positions upslope, increased. Reasonably, this boosted winter soil temperatures and provided sustained growing season soil moisture. In this way a positive, still ongoing, feedback loop was established.
- It appears that treeline growth is merely an affair of growing season thermal conditions. Winter temperatures seem to play a subordinate role in the case of deciduous *Betula*, in contrast to evergreen conifers, *Picea abies* and *Pinus sylvestris*.

Compliance with ethical standards

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References

[1] Tranquillini W. Physical Ecology of Alpine Treeline. Springer, Berlin. 1979.
[2] Kullman L. Tree-limits and montane forests in the Swedish Scandes: sensitive biomonitors of climate change and variability. Ambio. 1998; 27: 312-321.
[3] Smithson P, Addison K, Atkinson K. Fundamentals of the physical environment. Routledge, London. 2002.
[4] Gehrig-Fasel J, Guisan A, Zimmermann NE. Evaluating thermal treeline indicators based on air and soil temperature using an air-to-soil temperature transfer model. Ecological Modelling. 2008; 213: 345-355.
[5] Holtmeier FK. Mountain timberlines: ecology, patchiness and dynamics. Springer, Berlin. 2009.
[6] Körner C. Alpine treelines. Functional ecology of the global high elevation tree limits. Springer, Basel. 2012.
[7] Kullman L. Change and stability in the altitude of the birch tree-limit in the southern Swedish Scandes 1915-1975. Acta Phytogeographica Suecica. 1979; 65: 1-121.
[8] Kullman L. A review and analysis of factual change on the max rise of the Swedish Scandes treeline, in relation to climate change over the past 100 years. Journal of Ecology & Natural Resources. 2018; 2(6): 000150.
[9] Kullman L. A recent and distinct pine (*Pinus sylvestris* L.) reproduction upsurge at the treeline in the Swedish Scandes. International Journal of Research in Geography. 2018; 4(4): 39-52.
[10] Danby RK, Hik DK. Variability, contingency and rapid change in recent subarctic alpine treeline dynamics. Journal of Ecology. 2007; 95: 352-363.

[11] Harsch MA, Hulme, PE, McLclone MS, Duncan RP. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecology Letters. 2009; 12: 1040-1049.

[12] Kullman L, Öberg L. Post-Little Ice Age treeline rise and climate warming in the Swedish Scandes: a landscape ecological perspective. Journal of Ecology. 2009; 97: 415-429.

[13] Smith WK, Germino MJ, Johnson DM, Reinhardt K. The altitude of alpine treeline: a bellwether of climate change effects. Botanical Review. 2009; 75: 163-190.

[14] Elliott GP. Extrinsic regime shift drives abrupt changes in regeneration dynamics at upper treeline in the Rocky Mountains, USA. Ecology. 2012; 93: 1614-1625.

[15] Öberg L. Treeline dynamics in short and long perspectives – observational and historical evidence from the southern Swedish Scandes. PhD thesis. Mid Sweden University Doctoral Thesis 143. Sundsvall. 2013.

[16] Gaire NP, Koirala M, Bhuju DR, Borgaonkar HP. Treeline dynamics with climate change at the central Nepal Himalaya. Climate of the Past. 2014; 10: 1277-1290.

[17] Kullman L. Pine (Pinus sylvestris) treeline performance in the southern Swedish Scandes since the early 20th century. Acta Phytogeographica Suecica. 2017; 90: 1-46.

[18] Holtmeier FK, Broll G. Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. Global Ecology and Biogeography. 2005; 14: 395-410.

[19] Elliott GP, Köpflmueller KI. Multi-scale influences of slope aspect and spatial pattern on ecotonal dynamics at upper treeline in the Southern Rocky Mountains, U.S.A. Arctic, Antarctic, and Alpine Research. 2010; 42: 42-56.

[20] Rössler O, Bräuning A, Löfler J. Dynamics and driving forces of treeline fluctuation and regeneration in central Norway during the past decades. Erdkunde. 2008; 62: 117-128.

[21] Kullman L. One century of treeline change and stability - experiences from the Swedish Scandes. Landscape Online. 2010; 17: 1-31.

[22] Kullman L. Pine (Pinus sylvestris L.) penetration towards the head of the Handölan Valley: recent reversal of long-term retrogression trend - contrasting responses to climate change of tree- and forest limit. International Journal of Environmental and Agriculture Research. 2016; 2(5): 163-172.

[23] Hofgaard A, Tømmervik H, Rees G, Hansen F. Latitudinal forest advance in northernmost Norway since the early 20th century. Journal of Biogeography. 2013; 40: 938-949.

[24] Rannow S. Do shifting forest limits in south-west Norway keep up with climate change? Scandinavian Journal of Forest Research. 2013; 28: 574-580.

[25] Bandekar G, Odland A. Ecological characterization of northernmost birch forests and treeline ecotones in Norway. Phytocoenologia. 2017; 47: 111-124.

[26] Daubenmire R. Alpine timberlines in the Americas and their interpretation. Butler University Botanical Studies. 1956; 11: 119-136.

[27] Helland A. Traegraendser og sommervarmen. Tidsskrift for Skogbruk. 1912; 20: 131-146, 169-175, 303-313.

[28] Brochmann-Jerosch H. Baumgreze und Klimacharacter. Beiträge zur geobotanischen Landesaufnahme Schweiz. 1919; 6: 1-255.

[29] Enquist F. Trädgränsundersöknningar. Svenska Skogsbrädsföreningens Tidsskrift. 1933; 31: 145-191.

[30] Skre O. The regional distribution of vascular plants in Scandinavia with requirements for high summer temperatures. Norwegian Journal of Botany. 1979; 26: 295-318.

[31] Tuukkanen S. Climatic parameters and indices in plant geography. Acta Phytogeographica Suecica. 1980; 67: 1-110.

[32] Treter U. Die Baumgrezen Skandinaviens, Steiner, Wiesbaden. 1984.

[33] Dahl E. Zonation in Arctic and alpine tundra and fellfield ecobiomes. In: Polunin, N. (ed.): Ecosystem Theory and Application. Wiley & Sons, Chichester. 1986.
[34] Odland A. Differences in the vertical distribution pattern of Betula pubescens in Norway and its ecological significance. Palaeoclimate Research. 1986; 20: 43-59.

[35] Körner C. Are-assessment of high elevation treeline positions and their explanation. Oecologia. 1998; 115: 445-459.

[36] Mook R, Vorren KD. The temperature climate at the altitudinal vegetation limits in Skibotn, northern Norway. Palaeoclimate Research. 1996; 20: 61-74.

[37] Karlsson PS, Weih M. Soil temperatures near the distribution limit of mountain birch (Betula pubescens ssp. czerepanovii): Implications for seedling nitrogen economy and survival. Arctic, Antarctic, and Alpine Research. 2001; 33: 88-92.

[38] Körner C, Paulsen J. A world-wide study of high altitude treeline temperatures. Journal of Biogeography. 2004; 31: 713-732.

[39] Müller M, Schwab N, Schickhoff U, Böhner J, Scholten T. Soil temperatures and soil moisture patterns in a Himalayan alpine treeline ecotone. Arctic, Antarctic, and Alpine Research. 2016; 48: 501-521.

[40] Karlsson P, Nordell O. Effects of soil temperature on the nitrogen economy and growth of mountain birch seedlings near its presumed low temperature distribution limit. Écoscience. 1999; 3: 183-189.

[41] Weih M, Karlsson PS. The nitrogen economy of mountain birch seedlings: implications for winter survival. Journal of Ecology. 1999; 7: 211-219.

[42] Miehe G, Miehe S. Comparative high mountain research on the treeline ecotone under human impact. Erdkunde. 2000; 54: 34-50.

[43] Crawford RMM. Plants at the margin. Ecological limits and climate change. Cambridge University Press, Cambridge. 2008.

[44] Kullman L. Some aspects of the ecology of the Scandinavian subalpine birch forest belt. Wahlenbergia. 1981; 7: 99-112.

[45] Kullman L, Öberg L. Levande fjäll i ett föränderligt klimat. BoD, Stockholm. 2020.

[46] Kullman L, Öberg L. Shrinking glaciers and ice patches disclose megafossil trees and provide a vision of the Late-glacial and Early post-glacial subalpine/alpine landscape in the Swedish Scandes – review and perspective. Journal of Natural Sciences. 2020; 8(2): 1-15.

[47] Harris SA. Twenty years of data on climate-permafrost-active layer variations at the lower limit of alpine permafrost, Marmot Basin, Jasper National Park. Geografiska Annaler 83A. 2001; 1-14.

[48] Körner C. Climatic treelines: conventions, global patterns, causes. Erdkunde. 2007; 61: 316-324.

[49] Kullman L. Structural change in a subalpine birch woodland in Northern Sweden during the past century. Journal of Biogeography. 1991; 18: 53-62.

[50] Hedenås H, Olsson H, Jonasson C, Bergstedt J, Dahlberg U, Callaghan T. Changes in tree growth, biomass and vegetation over a 13-year period in the Swedish Sub-Arctic. Ambio. 2011; 40: 672-682.

[51] Rundqvist S, Hedenås H, Sandström A, Emanuelsson U, Eriksson H, Jonasson C, Callaghan TV. Tree and shrub expansion over the past 34 years at the tree-line near Abisko, Sweden. Ambio. 2011; 40: 683-692.

[52] Franke AK, Feilhauer H, Bräuning A, Rautio P, Brown M. Remotely sensed estimation of vegetation shifts in the polar and alpine treeline ecotone in Finnish Lapland during the last three decades. Forest Ecology and Management. 2019; 454: 117668.

[53] Devi N, Hagedorn F, Moiseev P, Shiyatov S, Mazepa V, Rigling A. Expanding forests and changing growth forms of Siberian larch at the Polar Urals treeline during the 20th century, Global Change Biology. 2008; 14: 1581-1591.

[54] Öberg L, Kullman L. Contrasting short-term performance of mountain birch (Betula pubescens ssp. czerepanovii) treeline along altitudinal continentality-maritimity gradient in the southern Swedish Scandes. Fennia. 2012; 190: 19-40.

[55] Kullman L, Öberg L. A one hundred-year study of the upper limit of tree growth (Terminus arboreus) in the Swedish Scandes – Updated and illustrated change in an historical perspective. International Journal of Research in Geography. 2018; 4(3): 10-35.
[56] Kullman L. Climate change and primary birch forest (*Betula pubescens* ssp. *czerepanovii*) succession in the treeline ecotone of the Swedish Scandes. International Journal of Research in Geography. 2016; 21(2): 36-47.

[57] Payette S. Contrasted dynamics of northern Labrador tree lines caused by climate change and migrational lag. Ecology. 2007; 88: 770-780.

[58] Kullman L. Treeline population monitoring of *Pinus sylvestris* in the Swedish Scandes, 1973-2005. Implications for treeline theory and climate change ecology. Journal of Ecology. 2007; 95: 41-52.

[59] Kullman L. Treeline (*Pinus sylvestris*) landscape evolution in the Swedish Scandes – a 40-year demographic effort viewed in a broader temporal context. Norwegian Journal of Geography. 2014; 68: 155-167.

[60] Kharuk VI, Ranson KJ, Im ST, Dvinskaya ML. Response of *Pinus sibirica* and *Larix sibirica* to climate change in southern Siberian alpine forest tundra ecotone. Scandinavian Journal of Forest Research. 2009; 24: 130-139.

[61] Mathisen IE, Hogaard A. Recent height and diameter 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. 2011; 4: 1-11.

[62] Hagedorn F, Shiyatov S, Mazepa VS, and 10 others. Treeline advances along the Ural mountain range – driven by improved winter conditions? Global Change Biology. 2014; 20: 1264-1277.