Oecologia
Montana 2017,
26, 19-33

Vegetation, soil- and air temperature studies within alpine treeline ecotones of southern Norway

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Abstract. The alpine treeline ecotone (ATE) is the transition zone between closed forest and the treeless alpine zone. The main objective of this study is to investigate air and soil temperatures within the ATE from seven different areas which have previously been described to be climatically limited. The study areas include a gradient in oceanity, wherein forest limits have been mapped to vary from below 800 m to higher than 1,100 m. In the ATE, soil temperatures were measured using data loggers at a depth of 10 cm in the top soil layer and gridded air temperatures (2 m above ground) were obtained from the Norwegian Meteorological Institute. The Kruskal-Wallis test showed statistically significant differences between the study areas, with higher summer temperature values in the oceanic influenced areas. Seven vegetation communities were categorized by TWINSPAN analysis and gradients in vegetation were explained using the soil- and air- temperature frost sum, growing season soil temperature and growing season length (calculated using soil temperature). The current ATE position could be explained by growing season length (air and soil temperature), temperature frost sum, and duration of the frozen soil period. The results suggest that temperatures may not be critical for current ATE altitudinal positions in oceanic areas.

Key words: Betula pubescens, growing season length, growing season temperature, heat sum, July temperature, vegetation communities

Introduction

Treelines are one of the most visible distribution limits in nature, appearing as a distinct line from a distance. However, when observed closely, there is usually a gradual transition from the uppermost limit of closed forests (forest limit) to the edge of scattered single/groups of trees (treeline) and to the treeless alpine zone (Ching-An *et al.* 2014; Körner and Paulsen 2004). This transition zone is often referred as the alpine treeline ecotone (ATE) (Kullman 2012; van der Maarel 1990).

ATE is spread over the world from the equator to high latitudes, at different elevations. The vast number of definitions proposed (Holtmeier 2003; le Roux 2009) indicate that such limits are in most cases spatially complex and represent a continuum of variation due to several environmental factors. Consequently, the vertical extension of ATE can be variable when different areas are compared (Broll *et al.* 2007; Heiskanen 2006; Holtmeier 2003). Slope angle and aspect have fundamental effects on the amount of radiation received and temperature conditions in ATE (Barry 1992). In general, south-facing slopes receive far more direct radiation than north-facing slopes (Barry 1992; Larcher and Wagner 2010). Thus, ATE is often forced at lower elevations on north facing slopes and it may therefore be assumed that the temperature conditions within the ATE on south and north-facing slopes should be equal despite occurring at different elevations.

It has previously been assumed that ATE has a bioclimatic characterization and can therefore be used as a reference for altitudinal positions of other spatial data. (Holtmeier 2003; Jobbágy and Jackson 2000; Nagy 2006; Paulsen and Körner 2014). The ATE has also been assumed to be sensitive to effects of climate change (Cairns *et al.* 2007; Körner 2012; Paulsen *et al.* 2000). Several studies have been performed to find general causal relationships for the treeline ecotone altitudinal limits on local and global scales (Aas and Faarlund 2000; Holtmeier 2003; Körner and Paulsen 2004; Müller *et al.* 2016). Factors including air temperature, soil temperature, mountain elevation, snow layer duration, edaphic factors, wind, latitude, slope, aspect, precipitation and degree of continentality have all been used to explain controlling effects on ATE (Elliott and Cowell 2015; Fang *et al.* 2014; Fang *et al.* 2012; Grace 1989; Kjällgren and Kullman 1998; Körner and Paulsen 2004; Müller *et al.* 2016; Paulsen and Körner 2014; Wöll 2008; Zhao *et al.* 2015; Zhao *et al.* 2014). Equally important is the influence of grazing, insect infestation and land-use in regulating the distribution of trees at high elevations (Cairns *et al.* 2007; Cairns and Moen 2004; Hecht *et al.* 2007; Tenow *et al.* 2007).

Among all, air and soil temperatures have been assumed to be the most important abiotic factors determining ATE altitude both in Scandinavia and globally (Holtmeier 2003; Körner and Paulsen 2004;

Moen *et al.* 2008; Müller *et al.* 2016). The slowing of tree growth that occurs with an increase in altitude has mostly been explained in terms of length of the growing season, growing season temperature and snow layer duration (Heikkinen 2005; Karlsson and Weih 2001; Körner and Paulsen 2004; Müller *et al.* 2016; Paulsen *et al.* 2000; Wieser and Tausz 2007). The growing season is considered to be the time of the year when environmental conditions are favorable for plant growth. Changes in growing season lengths have a profound influence on species composition and ecological functioning beyond forest limits (Pudas *et al.* 2008).

South-central Norway houses one of the tallest mountain ranges in Scandinavia i.e. the Jotunheimen mountain range (2,469 m a.s.l.) and has forest limits ranging above 1,200 m a.s.l. (Dahl 1998; Heikkinen 2005; Odland 2015). These highest forest limits then decrease in all directions. Aas and Faarlund (2000) and Moen (1999) have proposed a map consisting of the highest forest limit elevations in Norway. Treelines or forest limits that we observe and measure in nature should, however be defined as empiric limits because we cannot define them as climatic until temperature measurements have been performed.

Given the importance of temperature in treeline research, this study focuses on air and soil temperature conditions within the ATE in south Norway and its relation to other ATEs. Since variation in topographical features over short distances on the Norwegian landmass have led to subsequent climatic variations, an attempt is made to explain the current ATE position using temperature variables. This study quantifies vegetation communities in ATE and attempts to find a correlation with measured temperature data. The pattern of treelines in Norway as mapped on the iso-line map (Moen 1999) describe the treelines as climatically limited, thus suggesting similar temperature conditions in these ATEs (Körner and Paulsen 2004). The main aim is to investigate whether or not the studied ATEs are climatically limited as one could assume that there should be no significant differences between the areas

Material and Methods

Study areas

This study was conducted between 59.3° N - 60.1° N in south central Norway. We selected seven areas in Norway as shown in Fig. 1 and Table 1, representing both oceanic and continental areas (vegetation sections according to Moen (1999)). The bedrock in these areas was mainly composed of gneiss, granite and quartzite; which are hard and acidic. The soils are either podzols or leptosols (Jones *et al.* 2005). To truly understand the environmental factors responsible for ATE position, treelines obviously influenced by human activities were omitted from the study. Hence, ATE which were disturbed by logging, insect infestation, mechanical disturbance (e.g. avalanche tracks), fires or land-use were omitted. All forest areas in southern Norway are, however, grazed by reindeers and other herbivores.

Data collection

Sampling plots were selected between the forest limit (tree height ≥ 3 m) and uppermost occurrences of scattered single/groups of trees (tree height ≥ 2 m) i.e. treeline, both on north and south-facing slopes (Fig. 2). Altogether 98 plots of 2 x 2 m dimension were established in homogenous vegetation within ATE. Birch (*Betula pubescens* (ssp. *czerepanovii* (N.I.Orlova) Hämet-Ahti)) is the dominant tree species at high elevation forest limits in Norway (Heikkinen 2005; Moen *et al.* 2008). In every area, we selected at least five plots on south and north facing aspects. A few data loggers were lost and as temperature data could not be recovered, these plots were omitted from study.

In homogeneous stands, vegetation plots were randomly selected. All vascular plants and cryptogams were identified, and their abundances esti-

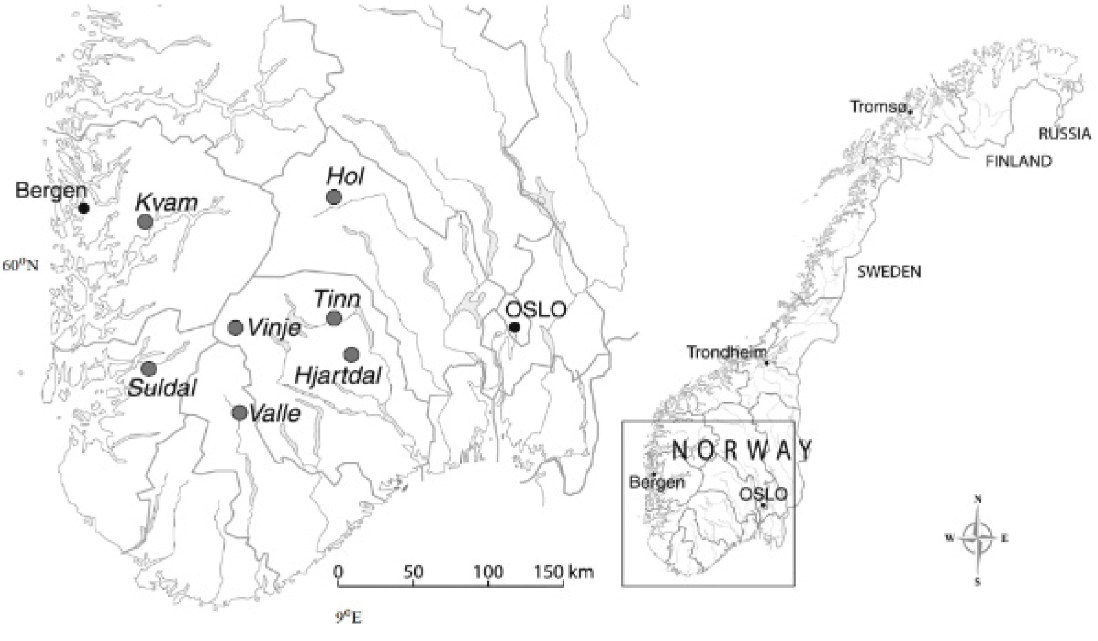

Fig. 1. Sampling areas in Southern Norway 1. Kvam, 2. Suldal, 3. Vinje, 4. Hol, 5. Tinn, 6. Hjartdal, and 7. Valle.

Area	Site description	Alt	DC	Slope	Number of plots		Diff N/S	Diff T/F	Lat	Long	P	Section**	FL
					N	S							
Suldal	Near Sandsa lake	765 ± 52	42	12 ± 11	4	4	94	36	59.4 N	6.4 E	2,299	O3	
Kvam *	Close to the Hardangerfjord	736 ± 53	47	22 ± 13	16	25	32	50	60.4 N	6.1 E	2,832	O2/O3	700-800 (Aas and Faarlund 2000)
Hjartdal	On Lifjell mountain	1,054 ± 31	162	12 ± 7	5	4	16	76	59.6 N	8.8 E	1,020	O1	1,060 (Økland and Bendiksen 1985)
Valle	Near lake Store Bjørnevatn	1,083 ± 30	96	22 ± 8	6	5	42	50	59.3 N	7.5 E	1,170	O1	1,000 -1,100 (Aas and Faarlund 2000)
Vinje	Includes two sub-areas in Vågsli and Rauland	1,065 ± 58	112	18 ± 11	5	8	68	44	59.8 N	7.6 E	1,067	OC	1,070-1,100 (Aas and Faarlund 2000; Odland and Munkejord 2008)
Hol	Near Ustevatn lake	1,097 ± 35	136	9 ± 2	4	4	51	52	60.5 N	7.9 E	747	OC	1,085 (Aas and Faarlund 2000)
Tinn	On eastern part of Hardangervidda mountain plateau.	1,124 ± 34	159	14 ± 5	4	4	55	41	60.1 N	8.5 E	795	OC	1,110 (Aas and Faarlund 2000)

*The 41 sites in the Kvam municipality represent nine different sub-areas, but due to similarities in the climatic conditions these were grouped together. **O3 = highly oceanic section, O2 = markedly oceanic section, O1 = slightly oceanic section and OC = indifferent section.

Table 1. Average characteristics of the study areas. Alt = Average altitude of the ATE in m a.s.l. ± standard deviation, DC= Distance to coastline (Km), Slope (measured in degrees) ± standard deviation, N = north facing, and S = south facing aspect, Diff N/S = average difference between the ATE on north and south facing slopes (m), Diff T/F=difference between the treeline and forest limit (m), Lat = Latitude, Long = Longitude, P = annual precipitation for normal period 1961-1990 (mm), Section = vegetation section according to Moen (1999) , FL = Forest limits (m a.s.l.) reported from previous studies.

mated as percentage cover. Distance to coastline (from the west coast of Norway) is defined as the nearest distance between sample plot and the coastline and is obtained using Arc GIS 10.4 software. GPS position, aspect, and altitude of plot have been collected using a Garmin GPS device. Slope was measured in degrees. Average precipitation for the normal period was obtained from the nearest meteorological station.

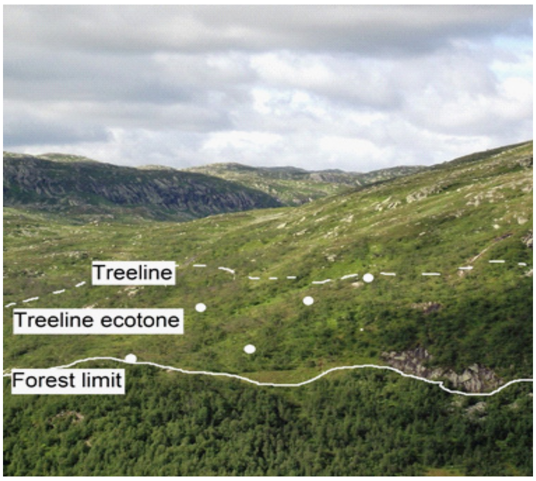

Fig. 2. Sampling plots within ATE located on the south facing aspect in Valle (59.3° N, 7.5° E). Five randomly sampled plots (2x2 m) at varying altitudes are represented in white circles.

In each plot, soil temperature was measured using data loggers, placed at a depth of 10 cm in the top soil layer. The TRIX 8 temperature data logger (LogTag recorders limited, Auckland, New Zealand) with < 0.1° C resolution for temperature ranges of -40° C to +40° C was used to measure soil temperatures. Temperature was measured twice daily at 1:00 and 13:00, and a daily average was estimated. Continuous soil temperatures were recorded from 2012 to 2013. Gridded, interpolated air temperature data was obtained from Norwegian Meteorological stations (2 m above ground), and this data was also obtained for 1:00 and 13:00 hours during 2012 to 2013.

From the daily temperature averages several temperature variables were estimated for each plot as defined in Table 2. The variables such as start of growing season (SGS) and date of snow melt (Snmelt) were calculated using day of the year (DOY) (where 1.01.2013 was taken as day 1 and 31.12.2012 as last day) to form a continuous dataset.

Statistical methods

Correlation analysis was conducted to measure the strength of association between measured temperature variables (air and soil), distance to coastline and altitude. Due to high association of predictor variables in our study, multiple regression analysis cannot be used directly to predict dependence of predictor the variable on the response variable (Abdul-Wahab *et al.* 2005; Mc-

Abbr.	Definition
Avg	Average annual temperature (° C).
Max	Maximum annual temperature (° C).
GSST	Growing season soil temperature (GSST) is defined as average soil temperature during the growing season (° C).
GSAT	Growing season air temperature (GSAT) is defined as average air temperature during the growing season (° C).
SGS	Start of growing season (SGS) given as day of the year (DOY) when temperature (air and soil) rose to 5° C for 5 consecutive days.
GSL	Growing season length (GSL) is measured as the number of days between SGS and the DOY when temperature (air and soil) dropped below 5° C.
Avg (Jul)	Average July temperature (° C).
STHS/ATHS	Soil temperature heat sum (STHS) and air temperature heat sum (ATHS) is the sum of all daily average soil and air temperatures (≥ 5° C) respectively, measured throughout the study period (Degree days (dd)).
STFS/ATFS	Soil temperature frost sum (STFS) and air temperature frost sum (ATFS) is the sum of all daily average soil and air temperatures (≤ 0° C) respectively, measured throughout the study period. (Degree days (dd)).
SF	Soil Frozen period (SF) is the number of days when soil temperature was ≤ 0° C (Days).
Snmelt	Snowmelt (Snmelt) is DOY when soil temperature exceeded 1° C.
ThD	Thaw days (ThD) is measured as number of days between snowmelt (Smelt) and start of growing season (SGS).
SWI	Summer warmth index (SWI) is the sum of mean monthly temperatures greater than > 0° C (Walker 2005; Young 1971)

Table 2. Overview of soil and air temperature variables, with abbreviations and measurement units used in the context of this study. In each plot, the following variables were estimated. (The variables Avg, Max, Avg (Jul) and GSL were calculated for air and soil temperatures and will be followed by suffix (A) and (S) respectively).

Adams *et al.* 2000). Therefore, we chose principle component analysis (PCA) to reduce errors due to multi-collinearity in further data analysis, and separated the associations to form independent principle components (Abdul-Wahab *et al.* 2005). For PCA, all the data was Log_{10} (x+5) transformed and standardized. Air and soil temperature frost sum values have been used as positive values for all analysis. A PCA was conducted using only the temperature variables; output generated from PCA were then used for two separate analysis. First, PC scores from PCA analysis were used as independent variables and ATE altitude as a dependent variable in stepwise multiple regression (also called as principle component regression (PCR)). This analysis helped in eliminating the non-significant independent/predictor variables and retaining the most important ones.

Secondly, PC loadings obtained from PCA analysis were rotated using varimax rotation. PCA analysis explains the same amount of variation before and after the varimax rotation. However, varimax rotation helps with better results interpretation as each variable tends to have high loadings on one (or few) factors (Hervé 2003). Based on the highest loading value we can select a variable on each PC to obtain information on the most important variable.

In the third step, we obtained the subset of independent or predictor variables by selecting the PCs with the highest standardized coefficient (from results of step 1), and variables associated with corresponding PCs (from results of step 2) and used these as independent variables for model fitting. The model fitting is conducted by using the above derived subset of variables as a predictor and ATE altitude as a response variable in multiple regression analysis. Finally, the multiple regression analysis generates a regression equation which could be used in prediction of ATE position. The individual contribution of each variable is calculated using standardized coefficient values, assuming all the variables together explain 100% of variation (Zhao *et al.* 2015).

The Kruskal-Wallis non-parametric multi comparison test was used to find out if differences existed in temperature conditions between the seven study areas.

Division of vegetation into communities (clusters), was achieved by using the TWINSPAN program (ter Braak and Šmilauer 2012). For the analysis, 6 cut levels were used (0, 5, 10, 20, 40 and 60) and species with less than 2 occurrences were excluded from the analysis. The relative species occurrence and abundance (SOA) values were calculated based on the formula given in Odland *et al.* (1990). A canonical correspondence analysis (CCA) with interactive forward selection (holm correction) was applied to find out which temperature variables best explained the floristic gradients. The Detrended correspondence analysis (DCA) was used to estimate the floristic turnover or compositional change along the main gradient as assessed by standard deviation (SD) units detrending by segments. The significant explanatory variables derived from CCA were included as supplementary variables. Species abundance data measured as percent cover was square-root transformed and temperature variables were Log_{10} (x+5) transformed for gradient analysis. Down-weighting of rare species was done in the CCA and DCA analysis. Bryophytes and lichens were identified to only genera level while *Betula pubescens* were selected as supplementary variables in the CCA and DCA analyses. The statistical analyses were conducted using Minitab-17 (2010), R-software (2014), WinTWIN and Canoco5 (ter Braak and Šmilauer 2012).

Results

Topography and temperature conditions at ATE

As can been seen from Fig. 3a), ATE altitude increases with increasing distance from the coastline (r = 0.886, p = 0.000). For all study areas combined, average forest limits were located at 949 m a.s.l and treelines at 977 m a.s.l. Slope inclination was steepest on south facing aspects (19° ± 13), followed by north facing aspects (16° ± 9). The altitudinal limit of ATE varied between from 603 m a.s.l in the westernmost oceanic areas to 1,177 m a.s.l. in the inland areas. Fig. 3b) shows that treelines were situated at higher altitudes on south facing aspects; average differences between north and south facing aspects are given in Table 1. The highest differences in elevation were observed in Suldal (94 m) and the lowest in Valle (16 m), and the average difference was 51 m ± 26 for all study areas. In analysis performed on combined effects of slope inclination and aspect on ATE position, no specific trends were found. The average vertical extent i.e. the difference between treeline and forest limit altitude of the ATE was 50 m ±12 (Table 1).

The average annual air temperature (1.1° C ± 2.1) was lower than the soil temperature (3.0° C ± 0.7) across all sampling areas. In all study areas, average annual air temperature recorded on south fac-

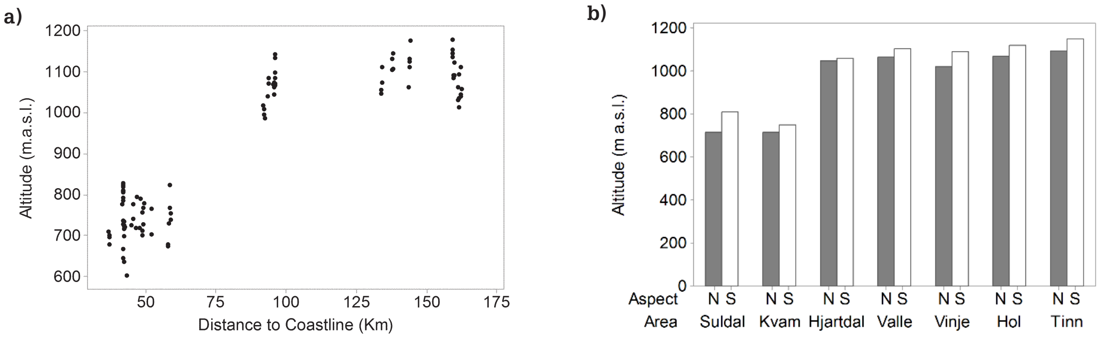

Fig. 3. a) Positions of the study plots in relation to altitude and distance to coastline. b) Bar graph showing altitudinal differences between plots on north (N) and south (S) aspects within and between the study areas.

Variables	Suldal	Kvam	Hjartdal	Valle	Vinje	Hol	Tinn
Avg (S)	2.6 (0.5)	3.5 (0.4)	3.0 (0.5)	2.8 (0.5)	2.7 (0.4)	1.7(0.3)	2.6(0.2)
Max (S)	14.5 (0.8)	14.3 (1.2)	12.3 (1.6)	11.5 (0.8)	12.6 (1.7)	11.9 (1.8)	11.6(0.7)
GSST	6.3 (0.5)	8.6 (0.6)	7.3 (0.6)	8.3 (0.5)	7.5 (0.5)	5.6 (0.5)	6.5 (0.2)
GSL (S)	133 (12)	123 (8)	124 (6)	111 (15)	108 (8)	106 (8)	115 (5)
Avg (Jul) (S)	11.4 (0.5)	10.8 (0.7)	10.1 (1.1)	9.2 (1)	9.6 (1)	9.2 (1.0)	9.3 (0.3)
STHS	805 (110)	1143 (127)	858 (135)	888 (159)	841 (123)	530 (72)	701 (39)
STFS	-141 (133)	-45 (59)	-21 (30)	-50 (78)	-42 (72)	-137 (54)	-10 (26)
SF	178 (12)	183 (11)	183 (50)	206 (15)	206 (16)	211 (14)	197 (18)
SnMelt	135 (6)	139 (4)	137 (4)	144 (3)	141 (5)	140 (2)	143 (4)
ThD (S)	9 (7)	7 (6)	9 (3)	16 (13)	14 (7)	22 (7)	13 (5)
SGS	144 (7)	147 (6)	146 (2)	159 (13)	154 (7)	162 (7)	156 (5)
SWI (S)	39.6 (3.3)	45.4 (3.9)	40.7 (5.4)	35.0 (4.6)	35.8 (4.1)	31.3 (2.5)	37.2(2.0)
Avg (A)	1.8 (0.6)	3.0 (1.1)	0.4 (0.4)	-0.4 (0.1)	-1.1 (0.3)	-2.2 (0.6)	-0.3 (0.2)
Max (A)	16.6 (0.6)	17.5 (1.2)	16.5 (0.6)	15.7 (0.1)	15.8 (0.7)	15.2 (0.3)	15.4(0.3)
GSAT	8.6 (0.5)	9.3 (0.9)	9.4 (0.5)	9.0 (0.1)	8.7 (0.5)	8.9 (0.4)	8.2 (0.3)
GSL (A)	127 (10)	140 (20)	128 (2)	114 (1)	109 (5)	113 (4)	109 (4)
Avg (Jul) (A)	11.4 (0.7)	12.3 (1.3)	12.6 (0.6)	11.6 (0.1)	11.3 (0.6)	11.5 (0.4)	10.8 (0.3)
ATHS	1212 (136)	1421 (274)	1301 (80)	1082 (21)	1025 (83)	1061 (65)	972 (52)
ATFS	-763 (66)	-544 (140)	-1260 (44)	-1371 (0)	-1565 (53)	-2009 (139)	-1227 (31)
SWI (A)	44.0 (4.4)	51.1 (9.1)	43.9 (2.9)	37.6 (0.6)	36.1 (2.4)	36.8 (2.2)	34.0 (1.5)

Table 3. Average air and soil temperature variables from the ATE in the study areas. Common air and soil temperature variables have been represented by suffix (A) and (S) respectively (e.g. Avg = average annual temperature (° C), Max = maximum temperature (° C), GSL = growing season length (days), SWI = summer warmth index, Avg (Jul) = average July temperature (° C)). The other variables such GSST= growing season soil temperature (° C), STHS = soil temperature heat sum (dd), Snmelt = snow melt day (DOY), ThD= Thaw period (days), SGS = start of growing season (DOY), SF= soil frozen days (days), GSAT= growing season air temperature (° C), ATFS= air temperature frost sum (dd) and ATHS = air temperature heat sum (dd). Standard deviations are given in brackets.

ing aspects (1.4° C) was higher than on north facing aspects (0.7° C). Likewise, average annual soil temperatures recorded on south facing aspects (3.2° C) was higher than on north facing aspects (2.7° C). The growing season lengths for all study areas calculated using air and soil temperatures were 118 days (± 10), and this decreases as we move inland. Growing season soil and air temperatures ranged from 4.5 to 10.1° C (with an average of 7.7° C) and 7.9 to 11.1° C (with an average of 9.0° C) respectively. There was a weak correlation between the growing season air and soil temperatures ($r = 0.277$, $p = 0.006$). Average July temperatures were 11.8° C ±1.1 and 10.2 ° C ±1.1 for air and soil temperatures respectively. The soil heat sums reach as low as 530 dd in Hol, (the lowest heat sum value recorded among all areas). The heat sum values calculated based on air temperatures had an average of 1153 dd for all areas. The summer warmth index was approximately 40 for both air and soil temperatures. The snowmelt event occurred on DOY 140 ± 5 at all sites irrespective of the large environmental differences along major gradients, and the onset of growing season was on DOY 151 ± 9. The time period between snowmelt and start of growing season (called thaw days) increases as we move inland, i.e. increased with decreasing oceanity with an average of 11 ± 8 days for all study areas. The soil remained frozen for 192 ± 23 days. Average soil frost sums were -55 ± 78 dd; contrastingly, frost sums due to air temperature go very low reaching a value of -1,031 ± 502 dd indicating air temperatures are below 0° C for most of the winter.

With Kruskal-Wallis tests we established significant differences in air and soil temperature variables when tested individually among all seven study areas. Tests revealed that (results given in Supplement 1) maximum soil temperature, average July soil temperature, start of growing season, soil frozen period, average annual air temperature, growing season length, air temperature frost sum and summer warmth index varied strongly between the oceanic (O3 and O2 sections) and the inland areas (O1 and OC sections). Differences were evident between Kvam and the remaining six areas for variables such as average annual soil temperature, thaw days, soil temperature heat sum and summer warmth index (calculated based on soil temperatures). The remaining variables varied randomly among the study areas without displaying any specific trends between oceanic and inland areas.

Relationships between ATE position and temperature variables

The results of correlation analysis (results given in Supplement 2) indicate strong association between air and soil temperature variables. Direct use of multiple regression methods would give rise to errors in results, thus conducted PCA analysis first, using all temperature variables, and the output of analysis was obtained in two forms i.e. PCA loadings and PCA scores. The eigenvalues / explained variation for axis 1 and 2 were 0.53 / 53.1 and 0.17 / 70.5 respectively (Fig. 4). Variables such as SF,

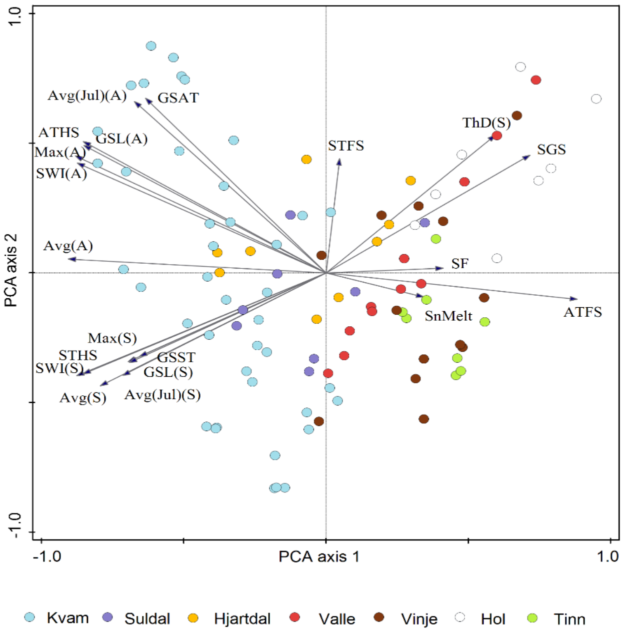

Fig. 4. PCA biplot of sample plots and temperature variables. The temperature variables are explained in Table 2.

Term	Constant	PC1	PC3	PC4	PC6	PC7	PC10
Regression coefficient	0	-0.234	0.078	0.136	-0.620	-0.174	0.105
P-value	0.000	0.000	0.006	0.000	0.000	0.003	0.049

Table 4. Results of Principle component regression analysis.

Variables	Coef	SECoef	DF	p-value	CR	95% CI	r^2_{Adj}
Constant	0.000		5				0.98
GSL (S)	1.703	0.591	1	0.005	35.1	(0.529, 2.878)	
GSL (A)	1.393	0.555	1	0.014	28.7	(0.290, 2.495)	
SF	0.954	0.351	1	0.008	19.7	(0.257,1.651)	
STFS	0.440	0.109	1	0.000	9.1	(0.223, 0.657)	
ATFS	-0.363	0.023	1	0.000	7.5	(-0.410, -0.317)	

Table 5. Results of stepwise multiple regression analysis. The model includes 98 sample plots from seven ATE areas in southern Norway. Coef = coefficient, SE Coef = Standard error of coefficient, DF = Degrees of freedom, CR = contribution rate (%) and CI = confidence interval.

ATFS, SnMelt and SGS were positively correlated with axis 1 (Fig 4). Study areas such as Kvam, Suldal and Hjartdal with oceanic influence having warm temperature conditions were positioned in the left part of the diagram.

PCA scores thus obtained were used in a stepwise multiple regression as independent variables and ATE altitude as dependent variables to find significant variables responsible for position of ATE; this is called Principle Component Regression (PCR). The results of PCR are given in Table 4, and the regression model had an $r^2_{Adj} = 0.86$. Significant results are obtained at ($p < 0.05$) for PC1, PC3, PC4, PC6 and PC7.

We conducted varimax rotation of PCA loadings (obtained from PCA analysis) to obtain the variables associated with these PCs. Varimax rotation maximizes the loadings of a single variable on each PC and ensurs zero association of that variable with subsequent PCs; thusallowing identification of the variables that contribute ito explaining the majority of the variation on that particular PC. From the results given in Supplement 3, it is clear that the first three PCs explained 80% of total variation. The first PC is loaded heavily on air temperature frost sum i.e. ATFS and average annual air temperature (Avg (A)) which together contributed 53 % of total variation. The second PC explained 18% of total variation and is heavily loaded with summer warmth index (SWI (S)). Lastly, PC 3 was heavily loaded with GSL(A) and contributed around 9% of the total variation. The variation explained by successive PCs decreases and has been mentioned in detail in Supplement 3.

In the subsequent step, we compared the output from stepwise multiple regression (Table 4) and varimax rotation of PCA loadings (Supplement 3) to isolate variables explaining the ATE position. We have selected PCs (with $p < 0.05$ from Table 4) and associated variables with high loadings on those respective PCs (Supplement 3). For instance, ATFS on PC 1, GSL(A) on PC 3, Thaw days (ThD) on PC 4, GSL(S) on PC 4, STFS on PC 6 and SF on PC 7. Finally, these selected variables were used for model fitting as independent variables (used original data) and ATE altitude as dependent variables. From the results it was clear that ATE position could be explained by GSL (S), GSL (A), SF, STFS, ATFS by 35.1%, 28.7%, 19.7%, 9.1% and 7.5% respectively (Table 5). The multiple regression analysis also yielded an equation for prediction of ATE position with respect to these selected temperature variables.

$$\text{ATE position} = 0.0000 + 1.703 * \text{GSL(S)} + 1.393 * \text{GSL(A)} + 0.954 * \text{SF} + 0.440 * \text{STFS} - 0.363 * \text{ATFS}$$

This regression model had an r^2_{Adj} value of 0.98, with the coefficients of regression being highly significant at $p < 0.05$ and normal distribution of residuals. For model validation we analyzed residuals; the residual are distributed around zero and are normally distributed (Supplement 4). There were nine outliers in the data, with data points from Kvam, Suldal and Valle area. This was because of the high temperatures recorded at these areas.

Vegetation communities and its relationship with temperature

Vegetation composition of the 98 studied plots were mostly dominated by common oligotrophic and mesotrophic boreal species. The most common species were *Vaccinium myrtillus* (98.0%), *Avenella flexuosa* (94.9%), *Vaccinium vitis-idaea* (74.5%), *Trientalis europaea* (68.4%), *Empetrum nigrum* (68.4%), *Vaccinium uliginosum* (66.3%), *Pleurozium schreberi* (60.2%) and *Cornus suecica* (51.0%). Several alpine species were frequently recorded, especially *Athyrium distentifolium*, *Eriophorum scheuchzeri, Carex brunnescens, C. bigelowii, Arctous alpinus, Salix lanata, S. glauca, S. lapponum, S. herbacea, Alchemilla alpina, Gentiana purpurea, Potentilla crantzii, Saussurea alpina, Vahlodea atropurpurea, Betula nana, Poa alpina, and Phyllodoce caerulea*. In the oceanic areas, some coastal plants were recorded, such as *Galium saxatile, Polygala serpyllifolia, Blechnum spicant*, and *Plagiothecium undulatum*.

TWINSPAN analysis was used to classify the plot vegetation, and seven communities were separated (Table 6). Seven clusters (vegetation types) were selected: *Avenella flexuosa -Vaccinium myrtillus - Juniperus communis* (AVJ), *Sphagnum* spp. - *Vaccinium myrtillus - Avenella flexuosa* (SVA), *Vaccinium myrtillus - Avenella flexuosa - Empetrum nigrum* (VAE), *Avenella flexuosa - Betula nana - Empetrum nigrum* (ABE), *Vaccinium uliginosum - Empetrum nigrum - Betula nana* (VEB), *Empetrum nigrum - Vaccinium uliginosum - Avenella flexuosa* (EVA) and *Avenella flexuosa - Betula nana - Vaccinium myrtillus* (ABV).

The results of CCA analysis with interactive forward selection showed explanatory variables accounting for 18.1% of total variation. The eigenvalues/explained fitted variation on axis 1, 2, 3 were 0.213/44.4 0.082/61.50 and 0.063/74.53 respective-

Vegetation type	**AVJ**	**SVA**	**VAE**	**ABE**	**VEB**	**EVA**	**ABV**
No. of plots	15	9	41	15	7	5	6
Maianthemum bifolium	21		7	1		3	3
Anemone nemorosa	13						
Galium saxatile	6		1				
Phegopteris connectilis	19	4	2				
Polygala serpyllifolia	2						
Blechnum spicant	8		9				
Calluna vulgaris	31		31			17	
Athyrium distentifolium	6	9	3				
Hylocomium splendens	28	15	31				
Eriophorum scheuchzeri		13	2				
Lycopodium annotinum	3	28	14	2			
Cornus suecica	11	35	33	11	14	3	
Nardus stricta	6	11	5			13	
Pleurozium schreberi	36	7	43	12	1	3	8
Sphagnum spp.	2	**78**	17		5	41	
Trieentalis europaea	19	19	15	17		13	11
Vaccinium myrtillus	**52**	**57**	**61**	41	29	37	**47**
Vaccinium vitis-idaea	31	11	35	38	33	3	3
Rubus chamaemorus	2	31	5		12	21	3
Gymnocarpium dryopteris	31	13	4	8			11
Juniperus communis	**41**	11	11	21	2	27	11
Avenella flexuosa	**53**	**52**	**51**	**61**	33	**43**	**72**
Vaccinium uliginosum	11	19	33	21	**62**	**43**	33
Empetrum nigrum	9	15	**47**	**51**	**62**	**47**	22
Arctous alpinus			2		12		
Carex bigelowii		2	4		2	11	3
Geranium sylvaticum	9					3	14
Solidago virgaurea	11	6	2	3		13	17
Alchemilla alpine	3					3	6
Salix glauca	8	9	1	2		27	36
Gentiana purpurea		2	1	2		11	8
Potentilla cranzii						11	3
Saussurea alpine	1			1			11
Salix herbacea					5	11	
Salix lapponum	3	2	1		7	13	33
Betula nana		4	4	**58**	**43**	3	**61**
Poa alpine				1	12		6
Phyllodoce caerulea			2	3	7	3	3

Table 6. Shortened table of TWINSPAN classification of ground vegetation communities in ATE. The values given in the table are relative species occurrence and abundance (SOA) values (Odland *et al.* 1990). Only the most common species are included in the table. The following seven vegetation types have been obtained: *Avenella flexuosa - Vaccinium myrtillus - Juniperus communis* (AVJ), *Sphagnum* spp. -*Vaccinium myrtillus - Avenella flexuosa* (SVA), *Vaccinium myrtillus - Avenella flexuosa - Empetrum nigrum* (VAE), *Avenella flexuosa - Betula nana - Empetrum nigrum* (ABE), *Vaccinium uliginosum - Empetrum nigrum - Betula nana* (VEB), *Empetrum nigrum - Vaccinium uliginosum - Avenella flexuosa* (EVA) and *Avenella flexuosa - Betula nana - Vaccinium myrtillus* (ABV). No of plots = Number of plots in each vegetation type.

ly. Percentage contribution by STHS was (20.5%), ATFS (7.2%), GSST (6.5%), closely followed by GSL (5.3%), and the remaining variables with < 5% contribution are presented in Supplement 5.

Lastly, we integrated these separated vegetation communities from TWINSPAN and environmental variables selected from CCA analysis into a DCA diagram (Fig. 2). The environmental variables are

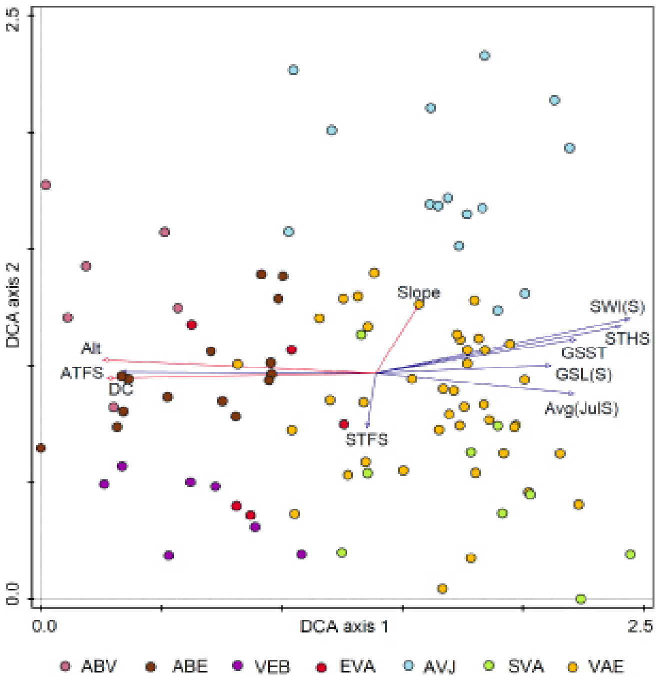

Fig. 5. DCA biplot illustrating vegetation communities classified using TWINSPAN and temperature variables chosen using CCA. 1. *Avenella flexuosa - Betula nana - Vaccinium myrtillus* (ABV), 2. *Avenella flexuosa - Betula nana - Empetrum nigrum* (ABE), 3. *Vaccinium uliginosum - Empetrum nigrum - Betula nana* (VEB), 4. *Empetrum nigrum - Vaccinium uliginosum - Avenella flexuosa* (EVA), 5. *Avenella flexuosa -Vaccinium myrtillus - Juniperus communis* (AVJ), 6. *Sphagnum spp. - Vaccinium myrtillus - Avenella flexuosa* (SVA) and 7. *Vaccinium myrtillus - Avenella flexuosa - Empetrum nigrum* (VAE). The temperature and topography variables are introduced as supplementary variables in DCA analysis. The temperature variables are explained in Table 2. Alt = altitude (m a.s.l.), DC= distance to coastline (km) and slope (degree).

used as supplementary variables in the DCA analysis (relative differences between the studied plots are shown in Fig 5).

The eigenvalues/gradient length on DCA axis 1, 2, 3 were 0.293/2.44, 0.221/2.33 and 0.166/2.45 respectively. The floristic gradients are relatively equal on DCA axis 1 and 2. On DCA axis 1, the gradient in vegetation communities from left to right changes from *Avenella flexuosa - Betula nana - Vaccinium myrtillus* (ABV) to *Vaccinium myrtillus - Avenella flexuosa - Empetrum nigrum* (VAE), *Avenella flexuosa - Vaccinium myrtillus - Juniperus communis* (AVJ) and *Sphagnum - Vaccinium myrtillus - Avenella flexuosa* (SVA). Vegetation communities rich in *Betula nana* growing in well drained and nutrient poor conditions were placed towards left; whereas, *Empetrum nigrum, Juniperus communis* and *Vaccinium myrtillus* dominated communities associated with oceanic conditions were located towards right on DCA axis 1. On DCA axis 2, the vegetation on the lower part of the axis was dominated by *Vaccinum uliginosum* and *Sphagnum* spp. while *Avenella flexuosa* and *Juniperus communis* were most dominant in the upper part. The floristic gradient on PCA axis 2 represents a gradient from wet soil condition to dry, exposed ridges or heath communities.

Discussion

Floristic variation

The study plots selected from the ATE within seven study areas show relatively small variation in floristic composition (ca. 2.5. SD units as measured by DCA), but there was a gradient from continental to oceanic areas, and from dry to moist soil conditions. The limited variation is partly because most of the sample plots have a large number of species in common, which is characteristic for oligotrophic forest communities. The vegetation types show variations in soil moisture (high moisture in SVA, EVA and low moisture in VEB). Typically, alpine species were common close to the treeline, previously described as subalpine forest communities in Nordhagen (1943).

TWINSPAN separated seven vegetation communities along two main DCA axes (Fig 5). Firstly a gradient from continental to oceanic climate in which gradual changes from ABV dominated to VAE, AVJ and SVA dominated communities were observed. This gradual change can be characterized by higher temperature and precipitation conditions. The second gradient showed a gradual change from dry, exposed ridges to moist meadows. The majority of variation was explained by growing season temperatures, although variables such as ATFS and STFS were also significant in explaining the current vegetation communities.

Alpine treeline ecotone (ATE)

In this study, ATE was defined differently than in Körner (2012), wherein the upper limit of the treeline ecotone has been drawn at the tree species limit. The reason behind this alternative method of defining ATE is that in Scandinavia, birch saplings are frequently found 300 - 500 m higher than the treeline (Dalen and Hofgaard 2005; Kilander 1955; Kullman 2001; Kullman 2010) and we have not found the species to be a useful criteria for determining the treeline, as the tree seedlings found above treeline do not develop into trees (Körner and Paulsen 2004). According to Aas and Faarlund (2000), forest and treelines are theoretical lines, drawn through the uppermost forest projections and isolated single/groups of trees respectively. The studied ATE in the oceanic areas (Kvam and Suldal) lie 300 - 400 m lower than in the inland area (Table 1). Similar patterns have also been found in earlier studies (Aas and Faarlund 2000; Moen 1999; Odland 1996). Average differences in elevation between forest limit and treelines at all study sites were less than 50 m (Table 1). According to Körner (2007), a variation of 50 m in elevation represents generally a 0.3° K difference in air temperature which is acceptable in ecological studies. In the current study, average difference between forest limits in north and south facing slopes were generally less than 50 m (Table 1) which correlates with most previous studies (Kjällgren and Kullman 1998; Nordhagen 1943).

Daubenmire (1954) suggested that where alpine timberlines were concerned, he would use the mid-point of the area between the timberline and the tree limit, even though some studies use the highest point of occurrence of trees or continuous forests. Due to this, comparisons between different study areas were difficult, and it has been suggested that an average of several local measurements between the uppermost trees and uppermost forest stands (within the ATE) should be used. Comparisons between distribution limits from different geographic areas should be based on average data as local measurements are often strongly modified by topographic or edaphic factors (Bekker *et al.* 2001; Broll *et al.* 2007; Fries 1913; Heiskanen 2006; Malanson *et al.* 2001).

Role of temperature on ATE position and comparison with other studies

Treelines are associated with a minimum July temperature of 10° C (e.g. Grace (1989) and Körner (1998)). In this study, average ATE July temperatures were mostly higher than 10° C in all areas. Present study agrees with previously stated knowledge regarding treeline temperatures being higher in oceanic areas than in inland areas. This is probably a result of both an oceanic climate and relatively low mountains in coastal areas (e.g. Fang *et al.* 2012; Holtmeier 2003; Odland 1996; Zhao *et al.* 2014).

The World-wide treeline study (Körner and Paulsen 2004) found that climatic treelines were associated with a seasonal mean ground temperature of 6.7° C ± 0.8, ranging from 5.5 to 7.5° C. This discrepancy between our study and Körner and Paulsen (2004) was probably due to the growing season being estimated from a lower soil temperature threshold of 3.2° C, measured at 10 cm soil depth. Körner and Paulsen (2004) established that the ground temperatures in climatic treeline sites do not increase beyond 15° C, and this presumption appears to be applicable to the current study wherein the warmest oceanic areas (Kvam and Suldal) experienced maximum soil temperatures below 15° C. High average daily temperatures caused early thawing of frozen soil resulting in lower thaw days, speedy attainment of the threshold temperature (5° C) and longer GSL in highly oceanic areas. The growing season lengths (calculated by air and soil temperatures) estimated in this study varied between 106 to 115 days in the continental areas, and from 123 to 140 days in oceanic areas. Globally, the variation in growing season length has mostly been found to range from 100 to 150 days measured for alpine treelines (Holtmeier 2003; Körner and Paulsen 2004; Odland 2011).

The soil temperature during growing season in our study is lower than birch forest limits in Iceland (8 - 11° C) and in Mount Njulla, Sweden (11.1° C) (Davis *et al.* 1991; Hecht *et al.* 2007). Our results are similar to forest limit studies in North Sweden where a growing season temperature of 6.6° C was recorded (Karlsson and Weih 2001). Average growing season temperature and temperature during the warmest month (July) found in the current study are lower than the northernmost birch forests of Norway (Bandekar and Odland 2017).

In general, the ATEs in the oceanic areas were associated with higher air and soil temperature heat sums, longer growing season, and higher temperatures (Table 3, Fig. 4). This indicated that the ATE have not reached their potential temperature limit. This may partly be an effect of relative low mountain height, influence from the ocean, or both; indicating that ATE may not be climatically limited in oceanic areas i.e. Kvam and Suldal.

The study shows that there were significant differences between the ATE, particularly between the oceanic and continental areas. Results of multiple regression analysis suggest that on a regional scale ATE are controlled by a subset of variables i.e. GSL (S), GSL (A), SF, STFS and ATFS provide the best explanation for the current ATE position. The majority of variation (35.1%) is explained by the GSL(S) which decreases with increasing distance to the coastline because of increasing mountain heights inland. Similar results are found in Kjällgren and Kullman (1998) where the inverse relationship between forest limits and treelines is found with increasing distance to sea.

Although this study has been conducted on regional scale, we have gathered spatially explicit regional scale data on topography and temperature variables. Unlike global scale studies on ATE, regional studies are conducted on finer scales with a specific focus on microclimate and topography (Müller *et al.* 2016). Care should be taken when generalizing the results and methods used in this study as this particular dataset cannot be considered fully representative of the entire region and the method may not be applicable to other regions of the World. However, the study can be used for expanding and deepening current knowledge of the ATE of southern Norway, as regional studies are relevant in understanding the underlying complex influence of each variable on ATE. It is clear that additional long term data sets on environmental variables will be required to stimulate further research and to have a complete understanding of this ATE phenomenon.

Conclusions

Main conclusions from the study are

- The air and soil temperature conditions are warmer in oceanic areas than in inland areas. The results suggests that temperatures may not be critical for current ATE altitudinal positions in oceanic areas.
- Average growing season temperatures were lower in studied ATEs when compared with other ATE studies.
- Seven vegetation communities were classified and could be explained with STHS, ATFS, GSST and GSL.
- Kruskal-Wallis test results showed significant differences between the temperature conditions in the studied ATEs.
- Position of the ATE could be explained with temperature variables such as GSL (S), GSL (A), SF, STFS and ATFS.

Acknowledgements

We are grateful to Inger Hanssen-Bauer (The Norwegian Meteorological Institute) for the gridded air temperature data

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Received 4 September 2017; accepted 20 December 2017.

Supplement 1. Main results of Kruskal-Wallis multi comparison test. Common air and soil temperature variables have been represented by suffix (A) and (S) respectively. For instance Avg =average annual temperature (˚ C), Max= maximum temperature (˚ C), GSL= growing season length (days), SWI =summer warmth index, Avg (Jul) =average July temperature (˚ C). The other variables such GSST= growing season soil temperature (˚ C), STHS= soil temperature heat sum (degree days), Snmelt= snow melt day (DOY), ThD= Thaw days (days), SGS= start of growing season (DOY), SF= soil frozen days (days), GSAT= growing season air temperature (˚ C), ATFS= air temperature frost sum (degree days), ATHS= air temperature heat sum (degree days).

Temperature variables	Observed difference	Critical difference	P value	Chi -square
Avg (S)	23.5	37.8	<0.001	58.5
Max (S)	24.9	37.8	<0.001	47.7
ThD (S)	19.9	37.8	<0.001	32.2
STFS	24.9	37.8	<0.001	26.8
GSL (S)	28.0	37.8	<0.001	44.7
GSST	29.9	37.8	<0.001	71.5
SWI (S)	24.6	37.8	<0.001	62.9
STHS	25.5	37.8	<0.001	72.4
Avg (Jul) (S)	27.1	37.8	<0.001	49.9
SnMelt	21.2	37.8	0.001	22.4
SGS	26.1	37.8	<0.001	40.9
SF	22.2	37.8	<0.001	35.5
Max (A)	27.1	37.8	<0.001	60.5
Avg (A)	30.7	37.8	<0.001	85.5
GSL (A)	27.9	37.8	<0.001	64.7
GSAT	22.1	37.8	<0.001	26.1
ATFS	30.4	37.8	<0.001	87.4
ATHS	27.9	37.8	<0.001	58.4
SWI (A)	28.6	37.8	<0.001	69.0
Avg (Jul) (A)	23.6	37.8	<0.001	31.7

Supplement 2. Results of correlation analysis. Common air and soil temperature variables have been represented by suffix (A) and (S) respectively. For instance Avg =average annual temperature (˚ C), Max= maximum temperature (˚ C), GSL= growing season length (days), SWI =summer warmth index, Avg (Jul) =average July temperature (˚ C). The other variables such GSST= growing season soil temperature (˚ C), STHS= soil temperature heat sum (degree days), Snmelt= snow melt day (DOY), ThD= Thaw days (days), SGS= start of growing season (DOY), SF= soil frozen days (days), GSAT= growing season air temperature (˚ C), ATFS= air temperature frost sum (degree days), ATHS= air temperature heat sum (degree days).

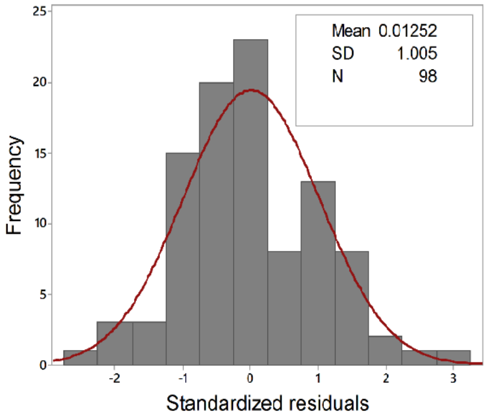
	Avg(S)	Max(S)	ThD(S)	STFS	GSL(S)	GSST	SWI(S)	STHS	Avg(Jul) (S)	SnMelt	SGS	SF	Max(A)	AVG(A)	GSL(A)	GSAT	ATFS	ATHS	SWI(A)	Ave-rage (July)	Alt	DC
Max (S)	0.562**																					
ThD (S)	-0.665**	-0.509**																				
STFS	-0.522**	0.172	0.287*																			
GSL (S)	0.566**	0.539**	-0.6**	-0.05																		
GSST	0.795**	0.558**	-0.469**	-0.23	0.275*																	
SWI (S)	0.908**	0.711**	-0.66**	-0.29**	0.754**	0.667**																
STHS	0.909**	0.688**	-0.667**	-0.22	0.621**	0.894**	0.892**															
Avg (Jul) (S)	0.589**	0.902**	-0.548**	0.037	0.67**	0.524**	0.745**	0.693**														
SnMelt	-0.071	-0.338*	-0.12	-0.387**	-0.435**	0.02	-0.34*	-0.192	-0.34*													
SGS	-0.645**	-0.615**	0.787**	0.092	-0.832**	-0.413**	-0.792**	-0.722**	-0.699**	0.444**												
SF	-0.396**	-0.193	0.069	0.188	-0.389**	-0.1	-0.48**	-0.268*	-0.21	0.415**	0.291*											
Max (A)	0.541**	0.438**	-0.32*	0.074	0.395**	0.462**	0.591**	0.595**	0.419**	-0.300	-0.415	-0.3**										
AVG(A)	0.7**	0.567**	-0.497**	-0.04	0.569**	0.58**	0.746**	0.749**	0.576**	-0.200	-0.545**	-0.4**	0.83**									
GSL (A)	0.457**	0.405**	-0.29*	0.152	0.428**	0.364**	0.546**	0.511**	0.406**	-0.300	-0.386**	-0.3**	0.95**	0.812**								
GSAT	0.264*	0.178	-0.05	0.137	0.184	0.28	0.287*	0.316*	0.177	-0.200	-0.162	-0.2**	0.84**	0.518**	0.85**							
ATFS	-0.644**	-0.579**	0.456**	-0.06	-0.524**	-0.544**	-0.72**	-0.711**	-0.56**	0.210	0.486**	0.3**	-0.82**	-0.95**	-0.8**	-0.5**						
ATHS	0.466**	0.394**	-0.28*	0.135	0.413**	0.383**	0.544**	0.519**	0.397**	-0.300	-0.385**	-0.3**	0.96**	0.792**	0.99**	0.89**	-0.8**					
SWI(A)	0.502**	0.454**	-0.32*	0.146	0.442**	0.416**	0.587**	0.565**	0.447**	-0.300	-0.412**	-0.3**	0.96**	0.837**	0.99**	0.84**	-0.86**	0.992**				
Avg (Jul) (A)	0.293*	0.179	-0.11	0.114	0.246	0.25	0.334*	0.326*	0.197	-0.200	-0.221	-0.3**	0.87**	0.557**	0.89**	0.97**	-0.53**	0.927**	0.879**			
Alt	-0.538**	-0.599**	0.442**	-0.16	-0.514**	-0.437**	-0.658**	-0.634**	-0.569**	0.250	0.485**	0.3**	-0.66**	-0.83**	-0.7**	-0.28	0.907**	-0.638**	-0.721**	-0.33*		
DC	-0.528**	-0.61**	0.48**	-0.13	-0.42**	-0.49**	-0.578**	-0.633**	-0.536**	0.140	0.442**	0.2**	-0.55**	-0.74**	-0.5**	-0.16	0.8**	-0.486**	-0.581**	-0.17	0.9**	
Slope	0.262*	0.064	-0.04	-0.06	0.061	0.33**	0.181	0.297*	0.014	0.000	-0.076	0.1	0.11	0.21	0.1	0.05	-0.24	0.084	0.105	0.024	-0.1	-0.14

** P<0.001 and *p<0.01

Supplement 3. Loadings of 22 variables on principle components rotated using varimax rotation method for 98 sample plots. Common air and soil temperature variables have been represented by suffix (A) and (S) respectively. For instance Avg =average annual temperature (° C), Max= maximum temperature (° C), GSL= growing season length (days), SWI =summer warmth index, Avg (Jul) =average July temperature (° C). The other variables such GSST= growing season soil temperature (° C), STHS= soil temperature heat sum (degree days), Snmelt= snow melt day (DOY), ThD= Thaw days (days), SGS= start of growing season (DOY), SF= soil frozen days (days), GSAT= growing season air temperature (° C), ATFS= air temperature frost sum (degree days), ATHS= air temperature heat sum (degree days).

Variable	**PC1**	PC2	**PC3**	**PC4**	PC5	**PC6**	**PC7**	PC8	PC9	PC10
Avg (S)	0.03	0.48	0.04	0.03	0.03	0.18	0.02	-0.01	-0.05	0.20
Max (S)	-0.01	0.34	0.03	0.20	0.04	-0.26	0.01	0.00	0.61	-0.06
ThD (S)	-0.02	-0.05	-0.03	-0.09	-0.25	0.05	-0.01	0.77	0.02	0.03
STFS	0.03	-0.15	0.05	-0.05	-0.03	**-0.90**	0.01	-0.01	-0.02	0.09
GSL (S)	0.00	0.07	-0.01	**-0.93**	0.03	-0.04	0.01	-0.01	0.02	0.01
GSST	-0.04	-0.04	-0.09	0.10	0.05	-0.02	-0.01	0.07	0.03	0.79
SWI (S)	0.04	0.63	0.08	-0.09	-0.07	0.00	0.01	0.01	0.02	0.00
STHS	0.04	0.15	-0.02	-0.08	-0.03	-0.04	-0.01	-0.07	-0.03	0.51
Avg (Jul) (S)	0.00	-0.20	-0.03	-0.14	-0.02	0.16	-0.01	0.00	0.78	0.03
SnMelt	0.00	-0.06	0.00	-0.05	0.91	0.04	0.00	-0.01	0.01	0.02
SGS	0.05	0.05	0.02	0.10	0.30	-0.05	0.02	0.61	-0.02	-0.05
SF	0.01	-0.03	0.03	0.00	0.00	0.01	**-0.99**	0.00	0.00	0.02
Max (A)	0.06	-0.05	0.36	0.15	-0.06	0.06	0.03	-0.07	0.01	0.05
AVG (A)	0.56	-0.34	0.18	-0.03	-0.07	0.20	0.08	-0.05	0.07	0.17
GSL (A)	0.07	0.07	**0.41**	-0.04	0.02	-0.03	-0.05	0.03	-0.02	-0.08
GSAT	-0.44	-0.16	0.36	-0.04	0.01	0.05	0.05	0.05	0.04	0.16
ATFS	**-0.57**	-0.08	-0.25	0.02	-0.04	0.06	0.02	-0.07	0.03	-0.01
ATHS	-0.03	0.03	0.40	-0.02	0.01	-0.01	0.00	0.00	0.00	-0.02
SWI (A)	0.07	0.06	0.38	0.00	0.03	-0.05	0.00	0.01	0.01	-0.03
Avg(Jul) (A)	-0.38	-0.07	0.40	-0.04	-0.01	0.07	0.01	0.00	-0.01	0.04
Eigenvalue	10.62	3.47	1.85	1.28	0.86	0.61	0.44	0.31	0.22	0.10
Proportion	0.53	0.17	0.09	0.06	0.04	0.03	0.02	0.02	0.01	0.01
Cumulative	0.53	0.71	0.80	0.86	0.90	0.94	0.96	0.97	0.98	0.99

Supplement 4. Histogram of standardized residuals obtained from stepwise multiple regression.



Supplement 5. Results of CCA analysis. STHS = Soil temperature heat sum (dd), ATFS = air temperature frost sum (dd), GSST = growing season soil temperature (° C), GSL(S) = growing season length estimated using soil temperature (days), Avg(Jul)(S) = Average July soil temperature (° C), STFS = Soil temperature frost sum (dd) and SWI(S) = summer warmth index estimated from soil temperatures.

Variable	**Explains %**	**Contri-bution %**	**pseudo-F**	**P-value**
STHS	7.0	20.5	7.2	0.001
ATFS	2.5	7.2	2.6	0.001
GSST	2.2	6.5	2.4	0.002
GSL (S)	1.8	5.3	2.0	0.003
Avg (Jul) (S)	1.6	4.7	1.8	0.002
STFS	1.6	4.6	1.7	0.008
SWI (S)	1.5	4.3	1.6	0.016