

**Local variation in mountain birch spring phenology
along an altitudinal gradient in northern coastal
Fennoscandia**



Maja Sjöskog

Master's thesis in Biology (BIO-3910)
Northern Populations and Ecosystems

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Table of contents

1. Abstract	1
2. Introduction	3
3. Material and methods	5
3.1. Study species	5
3.2. Study area and study design	6
3.3. Data sampling, processing and analysis	7
3.3.1. Budburst measurements	7
3.3.2. Thermal sum modelling	8
3.3.3. Remote sensing data	9
3.3.4. Ground and satellite imagery	9
3.3.5. Image processing	11
3.3.6. Interpolation and validation of NDVI values	12
4. Results	12
4.1. Climatic conditions	12
4.2. Budburst and thermal sum models	13
4.3. Satellite analyses and field measurement comparison	16
5. Discussion	19
5.1. Budburst and thermal sum models	19
5.2. Satellite analyses and field measurement comparison	21
5.3. Conclusions	22
6. Acknowledgements	23
7. References	24
8. Appendix	28

1. Abstract

Phenology studies are an important and a well-used tool for observing environmental changes, but there is a lack of spring phenology studies covering small-scale altitudinal gradients of mountain birch in the sub-arctic coastal regions. Previous studies from other boreal and arctic-alpine regions have shown that temperature is a key factor influencing spring phenology, however the coastal northern Fennoscandia is a region characterized by exceptionally high precipitation of snow, which gives reason to investigate the influence of snow cover on birch budburst in this area. Furthermore, during recent years, satellite data observations (remote sensing) have opened up unique opportunities for consistent long-term phenological monitoring of large areas. Ground phenology studies are today increasingly replaced by satellite data studies, but only too rarely is the latter approach properly validated. In order to provide a better basis for studies of local variation in spring phenology of birch in coastal altitudinal gradients, this study aimed at exploring how well (1) thermal sum models could predict budburst in individual birch trees with the inclusion of local conditions such as snow depth, soil temperature and altitude as predictors, and (2) NDVI values from high-resolution satellite images reflect leaf phenology in birch. The result for (1) showed that a simple thermal time model with spring air temperatures provided the best explanation for budburst, and that other local environmental factors such as snow depth, soil temperature and altitude did not improve the predictions. The results for (2) showed that the correspondence between NDVI values and leaf phenology was generally high, but there were still some variation between in situ measurements and the satellite-derived NDVI, probably reflecting the limited capacity of satellite imagery to capture the phenology of merely one species.

Key words: thermal sum model; degree days; *Betula* spp.; mountain birch; phenology; altitudinal gradient; NDVI; budburst

2. Introduction

The latitudinal gradient creates naturally diverse habitats in Fennoscandia, with high latitude plants being adapted to long photoperiods and low temperatures during short growing seasons, whereas low latitude plants perform best at higher temperatures during shorter photoperiods and longer growing seasons (Körner, 2003, Ovaska *et al.*, 2005, Wielgolaski and Inouye, 2003). But there is one factor that is replicated across all latitudes and expose organisms to important climatic gradients over very short distances, i.e. the altitudinal gradient. Small-scale altitudinal gradients thus present another challenge when seeking to understand plants response to environmental factors. Plant phenology, i.e. the study of the timing of seasonal biological activity driven by environmental factors, has long been used as a basic indication of yearly climatic fluctuation (Menzel and Fabian, 1999). Leafing, flowering, fruiting, and senescence are events that directly respond to climatic and environmental changes, and are therefore important when studying locally varying environmental conditions (Lechowicz, 1995, Sparks *et al.*, 2009). In boreal trees the bud phenology consists of two major events due to the environmental seasonality; in the autumn a dormancy stage is entered when growth is prevented even under favourable conditions, while in the spring the dormancy stage is finished and the ontogenetic development can be started as the growth conditions improves (Perry, 1971, Heide, 1993). In the northernmost forest zone in Fennoscandia the mountain birch (*Betula pubescens* ssp. *czerepanovii*) forms the natural upper climatic treeline, as it grows at lower summer temperatures than spruce and pine (Hämet-Ahti, 1963). In the coastal parts of northern Fennoscandia, naturally large-scale fragmented mountain birch forests are created due to the exposed coastline, together with areas of mountains and tundra. Ecosystems in these sub-arctic areas are commonly characterized by highly synchronized relationships in the food chain (van Asch and Visser, 2007). Mountain birch and higher trophic levels may suffer large consequences of only small effects of climate change, making studies of plant phenology particularly important to improve our understanding of possible ecological responses to climatic changes.

A common approach to gain knowledge on phenology is by developing models based on ground data on the timing of budburst and evaluating the importance of environmental variables such as temperature and soil characteristics. Several studies that model budburst have shown that in arctic-alpine and boreal regions, the temperature is a more important factor for phenological changes than factors such as precipitation and soil conditions (e.g. Karlsson

et al., 2003, Wielgolaski, 2001a, Richardson *et al.*, 2006, Pop *et al.*, 2000). But various local environments host birch trees that differ in their response to temperature, which makes general models poorly fitted to all locations (Ovaska *et al.*, 2005). The coastal regions of northern Fennoscandia are characterized by mild and unstable winters due to the temperate sea, which gives exceptionally high precipitation of snow. In addition, the temperature and consequently also the type of precipitation vary along the altitudinal gradients. Studies have shown that birch provenances from coastal and high altitudes require higher thermal sums (degree-days) for budburst than more continental or low altitude provenances within the same latitude (Ovaska *et al.*, 2005). However, northern trees must additionally adapt to shorter growing seasons by an increase of their photosynthetic rate (Ovaska *et al.*, 2005). This presents a survival/capacity trade-off for coastal high-altitude trees at high latitudes, between the risk of frost damage at early budburst (survival adaptation), and the timing of the beginning of the growing season for maximizing growth (capacity adaptation) (Kallio *et al.*, 1983, Leinonen and Hänninen, 2002). Currently there is a lack of phenology models that accounts for small-scale altitudinal variation of temperature and precipitation (Ovaska *et al.*, 2005). Thus, although the air temperature seems to be a key factor influencing budburst, local snow conditions and soil temperatures along a topographical gradient may be other factors possible influencing the timing of birch budburst in this area.

Nonetheless, field measurements are often spatially limited, rather costly, and may result in unintentional observational human bias. In later years, phenological satellite data studies (remote sensing) that observe vegetation reflectance patterns have become more common. Remote sensing includes methods of measuring the characteristics of the environment, like quantifying plant biomass, and is based on a technique where imaging sensors captures and stores reflected radiation from the ground (Lillesand, 1990). When sun energy hits a surface, the properties of the light reflected is decided by the amount and the composition of the solar irradiance (Lillesand, 1990). To avoid misinterpretation of a simple light reflection measure, the use of two or more spectral bands is common, creating a vegetation index (VI) that enhances the vegetation signal while disturbances like solar irradiance variation and soil effects are minimized (Jackson and Huete, 1991). The Normalized Difference Vegetation Index (NDVI) is a vegetation index frequently used for studying phenology from remote sensing data. Vegetated areas have relatively high reflectance in the near infrared light whereas the reflectance in the visible (red) light is very small (Lillesand *et al.*, 2004). With NDVI it is therefore possible to measure the amount of chlorophyll in the leaves and

determine the variability of the vegetation activity, by measuring the visible red and near-infrared red light that is reflected from the surface (Jackson and Huete, 1991, Mesev, 2008). However, there are still difficulties in applying remote sensing studies to environmental measurements, due to cloud cover data loss or calibration mismatches (Schwartz *et al.*, 2002). In addition, local small-scale altitudinal gradients present a challenge when predicting the consequences of climate change on food webs (Hagen *et al.*, 2008). Only too rarely are satellite image analyses properly validated by integrating them with field measurements of phenology (but see e.g. Karlsen *et al.*, 2007, Ahl *et al.*, 2006, Fisher *et al.*, 2006, and Richardson *et al.*, 2006).

In order to provide a better basis for studies of local variation in spring phenology of birch in coastal altitudinal gradients, this study have two goals: (1) to assess how well thermal sum models can predict budburst in individual birch trees with the inclusion of local environmental variables such as snow depth, soil temperature and altitude as predictors, and (2) assess how well NDVI values from high-resolution satellite images reflect leaf phenology in birch measured on the ground.

3. Material and methods

3.1. Study species

In northern Fennoscandia, forests of mountain birch (*Betula pubescens* ssp. *czerepanovii*) are the dominant forest ecosystem, instead of conifers, as is the case in most other regions of the northern boreal zone (Aas and Faarlund, 2001). The mountain birch is a deciduous, monoecious tree that is most common in the higher latitudes of Fennoscandia, Iceland, and the eastern Kola Peninsula (Väre, 2001). It grows in areas with short growing seasons, but as a compensation maximally utilizes the long day lengths (Kallio *et al.*, 1983). The mountain birch is a result of introgressive hybridization between the dwarf birch (*B. nana*) and the downy birch (*B. pubescens*), and consequently it has a highly variable morphology (Väre, 2001, Elkington, 1968, Vaarama and Valanne, 1973). In addition, it may be mechanically suppressed due to wind, soil and snow conditions, causing variable growth forms depending on the microclimatic conditions where it grows (Kallio *et al.*, 1983, Ovaska *et al.*, 2005). The average tree height is two to three meters, and the low summer temperatures together with

strong winds is believed to be the reason behind a reduced length at increasing altitudes, while better moisture and nutrition conditions at lower altitudes allow the tree to get taller (Wielgolaski, 2001b, Vaarama and Valanne, 1973).

3.2. Study area and study design

The study area was situated on a southward facing mountain slope at Kvaløya island (69°42'N 18°47'E), located in Troms County in northern Norway. The climate is coastal, with monthly mean air temperatures ranging from -4.4 °C to 11.8 °C for January and July, respectively, and average precipitation is 1031mm/year. Mountain birch forest extends to the tree line at approx. 240 m.a.s.l. The study plot covered four parallel transects at 50, 100, 170 and 240 m.a.s.l., with 10-12 stations at each altitude (n=44) (Fig. 1). The forest is dense at the lowest altitude (50 m) and thinner with tall trees at the two middle altitudes (100 and 170 m), with small trees in combination with more open areas at the highest altitude (240 m). Other common tree species are rowan (*Sorbus aucuparia*), spruce (*Picea* spp.) and willow (*Salix* spp.). The stations were distanced 200 m from each other, each represented by a birch tree (hereafter referred to as the station tree). The geographical coordinates were registered for each station tree, which were used when framing the stations on the satellite images. The trees used for the development of a thermal sum budburst model were situated 30 m from the station trees in either a westerly or easterly direction along the same altitude (n=44).

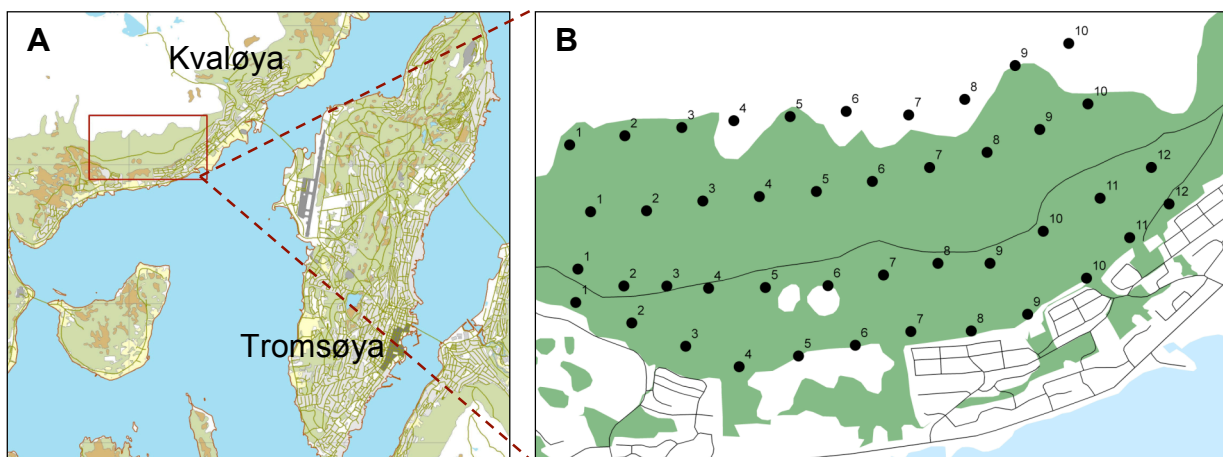


Fig. 1. Map showing (A) a cut-out of Tromsø municipality, with the study area at Kvaløya Island framed in red, and (B) the study plot covering four parallel transects with 10-12 stations at each altitude of 50, 100, 170 and 240 m.a.s.l. Each station, represented by a birch tree (the station trees) is marked with a black dot.

3.3. Data sampling, processing and analysis

3.3.1. Budburst measurements

In 2009 and 2010 each study tree were equipped with two Ibutton® ThermoChron temperature loggers (Maxim Integrated Products, 2011), allowing temperature recording with four hours interval, giving six recordings per day. One of the two temperature loggers were attached to the trunk at 1.5 m height (recording what is hereafter referred to as air temperature), and one were buried 15 cm down into the soil about one meter north from the tree (recording what is hereafter referred to as soil temperature). The temperature loggers were placed out in the autumn before snowfall, in this way allowing them to collect temperature data during the period of interest; from the start of the year until they were collected in mid-July. The trees were visited twice a week during the spring and summer of 2009 and 2010, from two-three weeks prior to the estimated beginning of snowmelt until all trees on all altitudes had leaves fully developed. This amounted to a time period of eight weeks for each of the two years (April 24 – June 15 and April 22 – June 14 for 2009 and 2010, respectively). During each visit and until snow was entirely gone, the snow depth was measured with 5 cm accuracy at 5 random places 1.5 meters from the study tree, and the mean of these 5 measurement was used in the analysis. The bud development of the study tree was rated twice a week on a 1 - 4 scale,



Fig. 2. Example of buds and leaves corresponding to the different stages in Table 1.

Table 1. Criteria for bud scoring in the field, budburst represents stage 2. See also Fig. 2.

Stage	Criteria
1	Unexpanded buds, may be swollen
2	Bud tips visible, not expanded from each other
3	'Mouse ears', petiole not yet visible
4	Petiole visible, full summer condition

1 representing winter state with unexpanded buds, and 4 representing full summer state with leaves fully expanded (see Table 1 and Fig. 2 for detailed explanation and examples of all stages). Budburst was defined as when the majority of the buds of a tree had reached stage 2 (Table 1).

3.3.2. Thermal sum modelling

A simple thermal sum model was used, where the number of degree-days (DD, i.e. the temperature sum) needed for budburst to occur was calculated. The cumulative air temperature at budburst, cTa , in the basic thermal time model is a function of temperature T and expressed as:

$$cTa = \sum_{D=1}^B T_D - T_{crit} \quad \text{for } T_D \geq T_{crit} \quad \text{else } T_D - T_{crit} = 0 \quad (\text{Eq. 1})$$

where T_{crit} is the temperature threshold, $D=1$ corresponds to 1st of January and B the day of year (DOY, Jan 1st=1) of budburst.

The 6 temperature measurements per day from the two temperature loggers were averaged. Cumulative temperatures for air temperature and soil temperature were calculated with 7 values of T_{crit} in the range of 0 – 6 °C. The cTa for the different critical values of the individual trees in the two years were then subjected to linear modelling with the aim to see to what extent the inclusion of local environmental predictors reduced the variance in cTa . The following environmental predictors were included: *maximum snow depth* (over the entire measurement period), *mean snow depth* (at the day of budburst), *cumulative soil temperature*, and *altitude* (as a categorical variable). Altitude was included to account for possible climatic effects not captured by temperature and snow measurements, as well as for the possibility that birches at different altitudes have adapted different phenologies. The effect of inclusion of the different variables (i.e. the reduction of the residual error) was evaluated by means of R^2_{adj} . The predictive powers of thermal sum models with different T_{crit} for both air and soil temperatures were compared using the square root of the mean square error (RMSE: Karlsson *et al.* 2003). The assumption of approximate linearity was confirmed by plotting the residuals of the best models. All statistical analysis was performed with the statistical package R, version 2.10.1 (R Development Core Team, 2009).

3.3.3. Remote sensing data

In the satellite image analyses, 8 m multispectral resolution images were used from the satellite Formosat-2. The images were delivered by Metria Lantmäteriet (the Swedish mapping, cadastral and land registration authority) in Kiruna, Sweden. Formosat-2 is a high-resolution satellite that was launched in 2004 by the National Space Organization (NSPO) of the Republic of China (Taiwan). It has an orbital cycle that is completed within a day, with a remote sensing instrument having a two meter panchromatic resolution (0.45-0.90 μm), and an eight meter multispectral resolution that includes four bands (blue: 0.45-0.52 μm , green: 0.52-0.60 μm , red: 0.63-0.69 μm , and near-infrared: 0.76-0.90 μm) (Satellite Imaging Corporation, 2010). An overview of the images and their technical details can be seen in Table A1 (in appendix). Topographical data from a 10 m resolution digital elevation model (DEM) was used in the processing of the images, covering the municipality of Tromsø.

3.3.4. Ground and satellite imagery

Once a week during eight (May 20 – July 8 2008) and nine (May 11 – July 6 2009) weeks, digital photographs were taken in the four different cardinal directions from the station tree, photos that were later given a phenology score according to the ‘greenness’. The photos were randomized and the scoring was done on a 0–4 scale by sixteen (in 2008) and nine (in 2009) different people. All observers scoring the images were asked to focus on the overall greenness of the images, according to examples given as explained in Table 2 and Fig. 3. This approach has previously shown to capture the spatio-temporal variation in phenology well (Richardson *et al.*, 2006, Fisher *et al.*, 2006). The observer-based phenology score showed a strong correlation with field measured leaf length (Fig. 4).

In addition to the digital image scoring, high-resolution satellite images from the Formosat-2 satellite were collected approx. once a week in 2008 and 2009 from the period of snowmelt until leaves were in full summer condition. For 2008 eight scenes of the time period of interest were available, while for 2009 the number was seven. Cloud cover limited the number of images originally collected, and snow cover and some haze further limited the images appropriate for NDVI analyzing, leaving five images in 2008 and four images in 2009 (Table A1 in appendix).

Table 2. Scoring criteria for digital image scoring. See also Fig. 3.

Score	Criteria
0	No change from winter conditions, no expanded buds or leaves visible
1	Swollen green buds or leaf tips visible
2	Very small leaves visible, leaves obscure <50% of sky/background
3	Leaves 50-70% of full length, leaves obscure >50% of sky/background
4	Canopy in full summer condition, leaves fully expanded, little sky/background visible through crowns

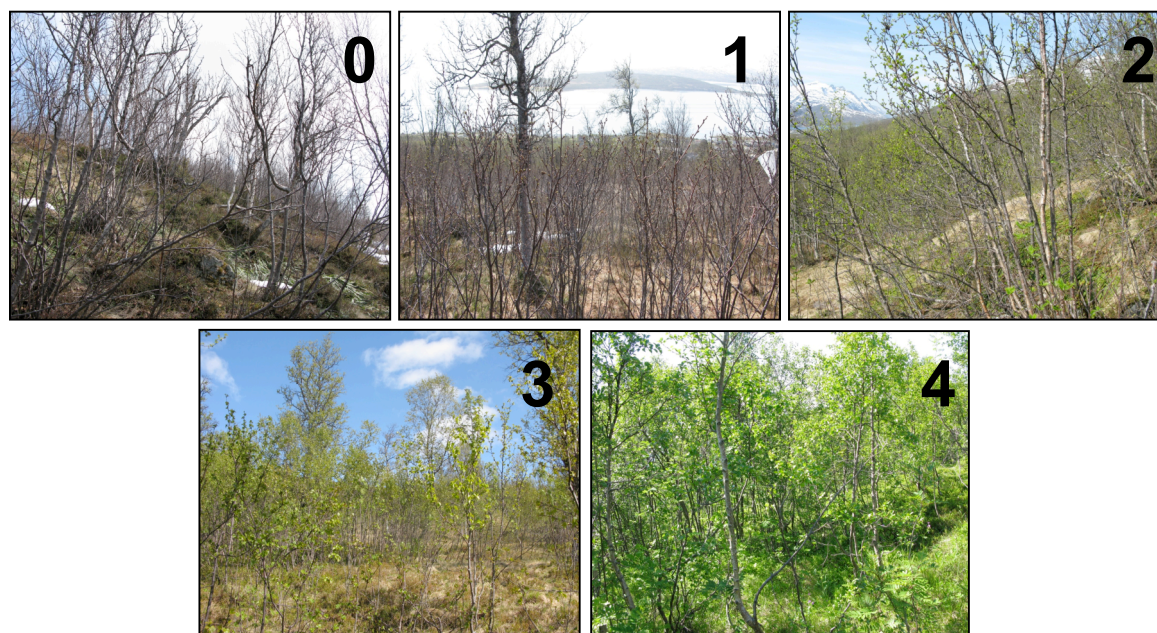


Fig. 3. Photos of image scoring 0 to 4 given as an example to people rating the images. Detailed explanations of scoring criteria for each stage is given in Table 2.

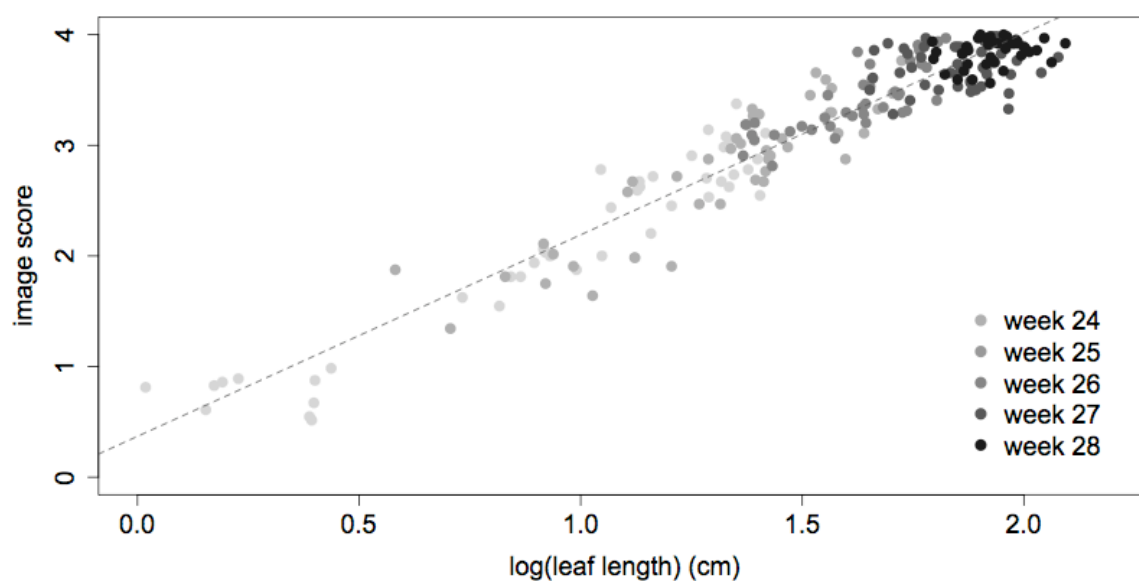


Fig. 4. The relationship between image score and log(leaf length) in 2008 ($R^2=0.92$). Weeks are separated by different shades of grey.

3.3.5. Image processing

A mean of the digital image scoring made by the observers were calculated, giving each station one unique image score value per date. For the satellite images, orthorectification was done in order to geometrically correct the images to make them an accurate representation of the ground coordinates on the Earth's surface. A digital elevation model (DEM) was required in the process to eliminate terrain displacements (Westin, 1990, Schowengerdt, 2007). The process of orthorectification uses ground control points and a priori data by relating each raw image pixel to the desired coordinate system, simultaneously adjusting for satellite sensor position and attitude variations, the shape and rotation of the Earth, and other factors (Westin, 1990, Schowengerdt, 2007, ENVI, 1999, Lillesand *et al.*, 2004). After the orthorectification, the images had to be reprojected from UTM zone 33 to the correct UTM zone 34 North. The Formosat-2 satellite is delivered as 8-bytes digital count data, covering image output values between 0-255. A calibration from digital counts to radiance of the channels used in the vegetation index calculations were done prior to the NDVI was calculated, using the calibration coefficients presented in Table A1 (in appendix). Normalized Difference Vegetation Index is defined as:

$$\text{NDVI} = (\text{NIR} - \text{RED}) / (\text{NIR} + \text{RED}) \quad (\text{Eq. 2})$$

where NIR is the near infrared light reflectance and RED is the red light reflectance. As Formosat-2 has its red spectral channel in band three (Ch3) and near-infrared spectral channel in band four (Ch4), NDVI was calculated as:

$$\text{NDVI} = (\text{Ch4} - \text{Ch3}) / (\text{Ch4} + \text{Ch3}) \quad (\text{Eq. 3})$$

The stations were thereafter framed by using map vector data (polygons), creating squares the size of 3 x 3 pixels with the resolution of 8 m around each station, representing a ground measurement of 24 m x 24 m. All negative NDVI values were set to zero, assuming these values were caused by snow. The mean NDVI values of the squares were calculated, giving a mean NDVI value of each station for each date. The satellite image processing was done in ArcGIS 9.2 and ENVI 4.4.

3.3.6. Interpolation and validation of NDVI values

The dates of the NDVI images did not correspond to the dates of field measurements. To interpolate NDVI values for field dates, curves were fitted to the original NDVI data with logistic regression formula, given as:

$$p = \frac{\exp^{a+bx}}{1 + \exp^{a+bx}} \quad (\text{Eq. 4})$$

where a and b are fitted parameters and x is the DOY of field measurements. Initially, separate curves were fitted for each of the 44 stations to reveal any systematic variation in the parameter values a and b between altitudes. Altitude specific curves were fitted in the cases where systematic deviations in a and b were apparent. Interpolated NDVI values for each station and date (of field measurements) were obtained by multiplying the output p from the logistic regression with the maximum NDVI for the present station for 2008 and 2009 respectively. The interpolated NDVI values were validated against the image scoring for each of the two years 2008 and 2009 by means of plotting and linear models.

4. Results

4.1. Climatic conditions

Climatic variations between the two years 2009 and 2010 are presented in Fig. 5 and Table A2 (in appendix). In conclusion, 2009 was a warmer year than 2010 with a higher snow depth maximum and earlier snowmelt, but 2010 had a sudden rise of temperatures around DOY 137 that led to a fast snowmelt and a fast green up.

Climatic data from the Norwegian Meteorological Institute for the three years 2008, 2009 and 2010 in Tromsø at 100 m.a.s.l. for May 1 show that 2009 had the highest cumulative air temperatures and that 2010 had less precipitation during May compared to the two other years (Table A3 in appendix), while the onset of staying snow cover in 2010 was much later than the preceding two years, in that way allowing ground frost to penetrate deeper into the ground before an isolating snow cover stabilized soil temperatures (Fig. A1 in appendix).

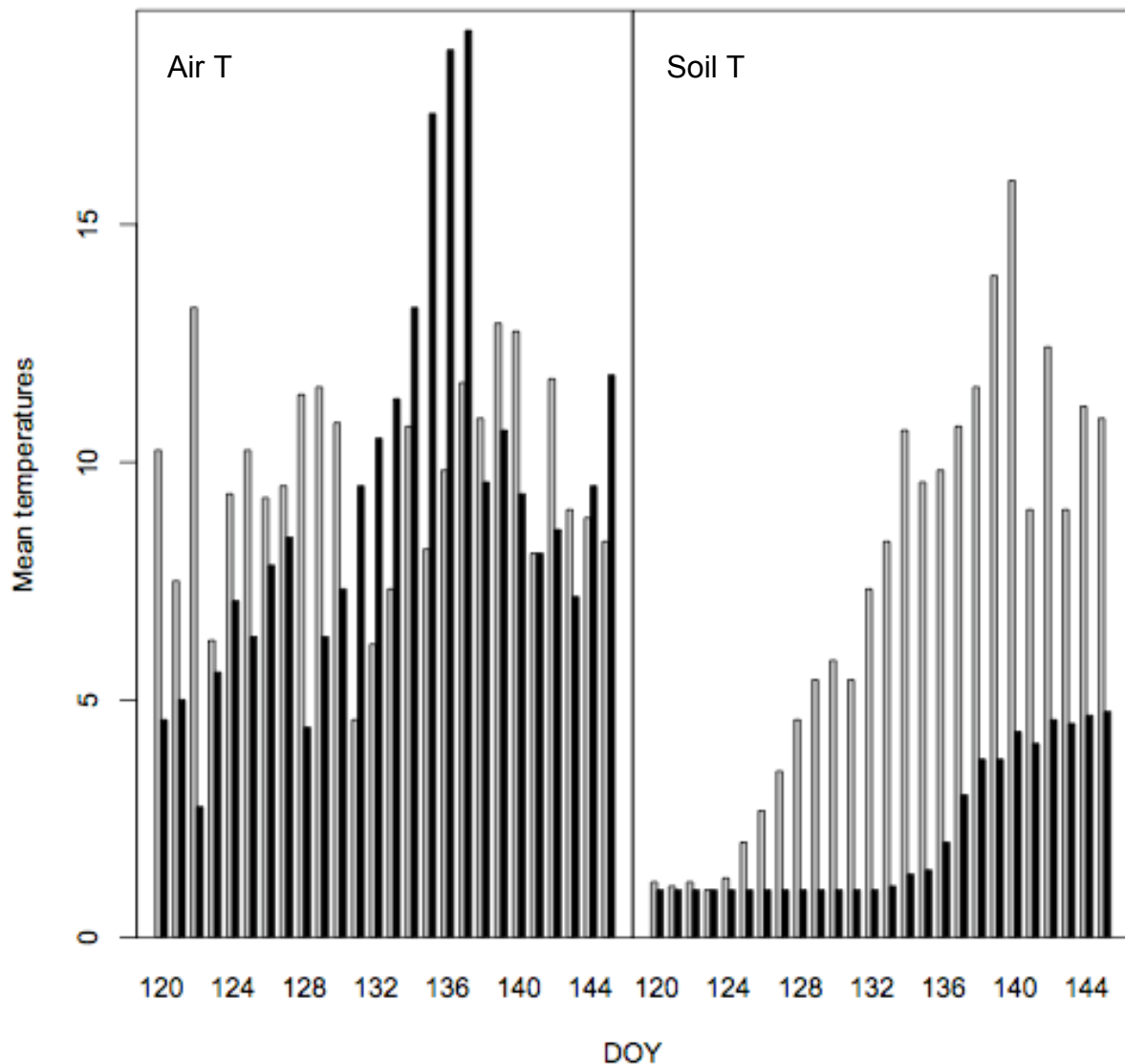


Fig. 5. The mean air and soil temperatures across all sampling stations per day from DOY 120 (April 30) to DOY 145 (May 25) for 2009 (grey) and 2010 (black).

4.2. Budburst and thermal sum models

Budburst took place at mean DOY= 134.2 ± 4.5 (SD) in 2009 and at mean DOY= 136.4 ± 1.3 (SD) in 2010. While the large variation in DOY for budburst showed a clear altitudinal pattern with later budburst at higher altitudes in 2009, the much less variable timing of budburst in 2010 was more constant among the altitudes (Fig. 6). The appropriate base temperatures for air and soil was according to RMSE $T_{crit} = 6$ for cumulative air temperature and $T_{crit} = 3$ for cumulative soil temperature (RMSE = 9.7 DD). The mean thermal sum for this model was 37.7 DD, and budburst for all trees was assumed to occur when this thermal sum was reached. Plotting the cumulative air temperature against DOY of budburst revealed

that this was not the case, as later budburst appeared to require higher thermal sums (Fig. 7). The effects of the local environmental predictor variables (i.e. maximum or mean snow depth, soil temperature and altitude) were very small and statistically insignificant (Table 3) and their overall contribution amounted to only $R^2_{adj} = 0.06$. In terms of RMSE the model with inclusion of the predictors showed only a marginal improvement compared to a constant model ($\Delta RMSE = 0.3DD$). The RMSE values for $T_{crit} 0 - 6$ (both cumulative air and soil temperatures) were in the range of $27.7 - 9.4 DD$, and RMSE was declining with higher T_{crit} values. Plotting the residuals of best model residuals on the sampling grid for the two years (not shown) revealed no systematic temporal or spatial patterns.

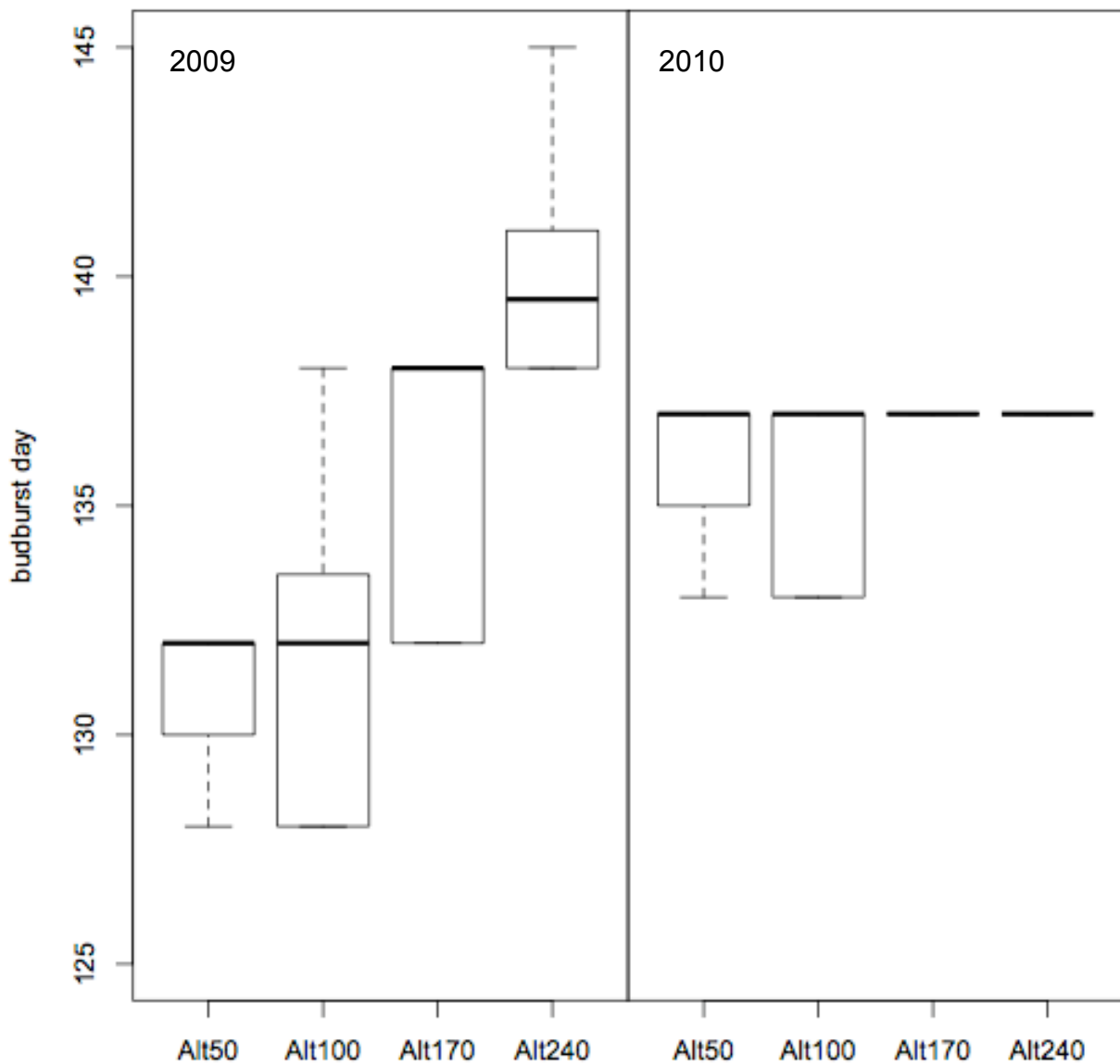


Fig. 6. Box plots of the distribution of timing of budburst (days since 1st January) for individual trees across different altitudes for the two years 2009 and 2010.

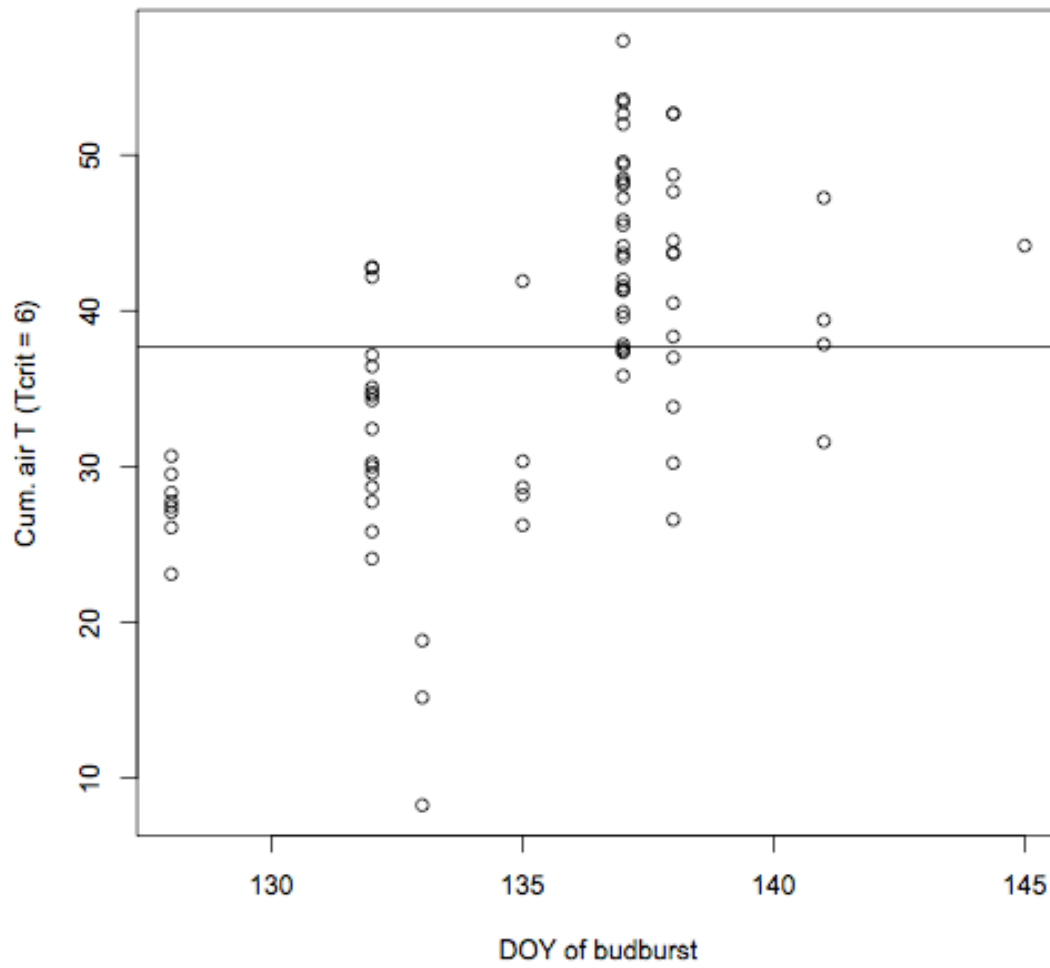


Fig. 7. Cumulative air temperatures at budburst for T_{crit} 6. The horizontal line is the mean cumulative temperature at budburst, 37.7 DD.

Table 3. Coefficients from the linear model with lowest RMSE (9.4 DD) for the thermal sum (cTa , $T_{crit}=6$) at budburst with 95% confidence intervals in brackets and the p-value of each coefficient.

Parameter	Thermal sum	P-value
Intercept (Altitude 50)	30.2 [± 8.8]	<0.001
Cum. soil T, $T_{crit}=3$	0.2 [± 0.4]	0.3
Maximum snow depth	0.14 [± 0.1]	0.2
Altitude 100	-0.7 [± 6.0]	0.8
Altitude 170	5.1 [± 6.8]	0.1
Altitude 240	-1.4 [± 7.4]	0.7

4.3. Satellite analyses and field measurement comparison

Inspecting the parameter values (not shown) from the logistic fitting of scaled NDVI values against DOY per altitude showed that separate logistic curves were needed for 50 m and 100 – 240 m combined in 2008, and for 50 – 100 m and 170 – 240 m combined in 2009. The parameter values are presented in Table 4 and the fitted curves are presented in Fig. 8. Note that the curve fitted for 240 m in 2009 was based on only three stations as these were the only ones thoroughly snow free.

The correspondence between image score and interpolated NDVI was good when considering the relationship within each week the image scoring was conducted (Fig. 9). Linear models with separate slopes and intercepts per week yielded $R^2=0.72$ ($p<0.001$) for 2008 and $R^2=0.82$ ($p<0.001$) for 2009. The regression lines per week indicated that both years had the same trend of a declining slope as the weeks advance along the season. This was due to a greater variation of image scoring during the start of the season compared to the NDVI values that had the same low values with little variation, while late in the season when the trees approach full summer condition (towards image score 4 and high NDVI values), the trees at all stations showed decreasing variation of image scoring whereas there were still some variation in NDVI. The first week in 2008 was an outlier compared to the later weeks for this year, while all weeks in 2009 appeared in a more homogenous cluster.

Table 4. Parameter values of the logistic models (Eq. 4) for the groupings of altitudes called for by investigating box plotted parameter values. The logistic curves based on the parameter values are shown in Fig. 8.

Year	Altitudes	Median of coefficient a	Median of coefficient b
2008	50	-59.8	0.36
2008	100, 170, 240	-67.5	0.41
2009	50, 100	-15.4	0.10
2009	170, 240	-17.9	0.11

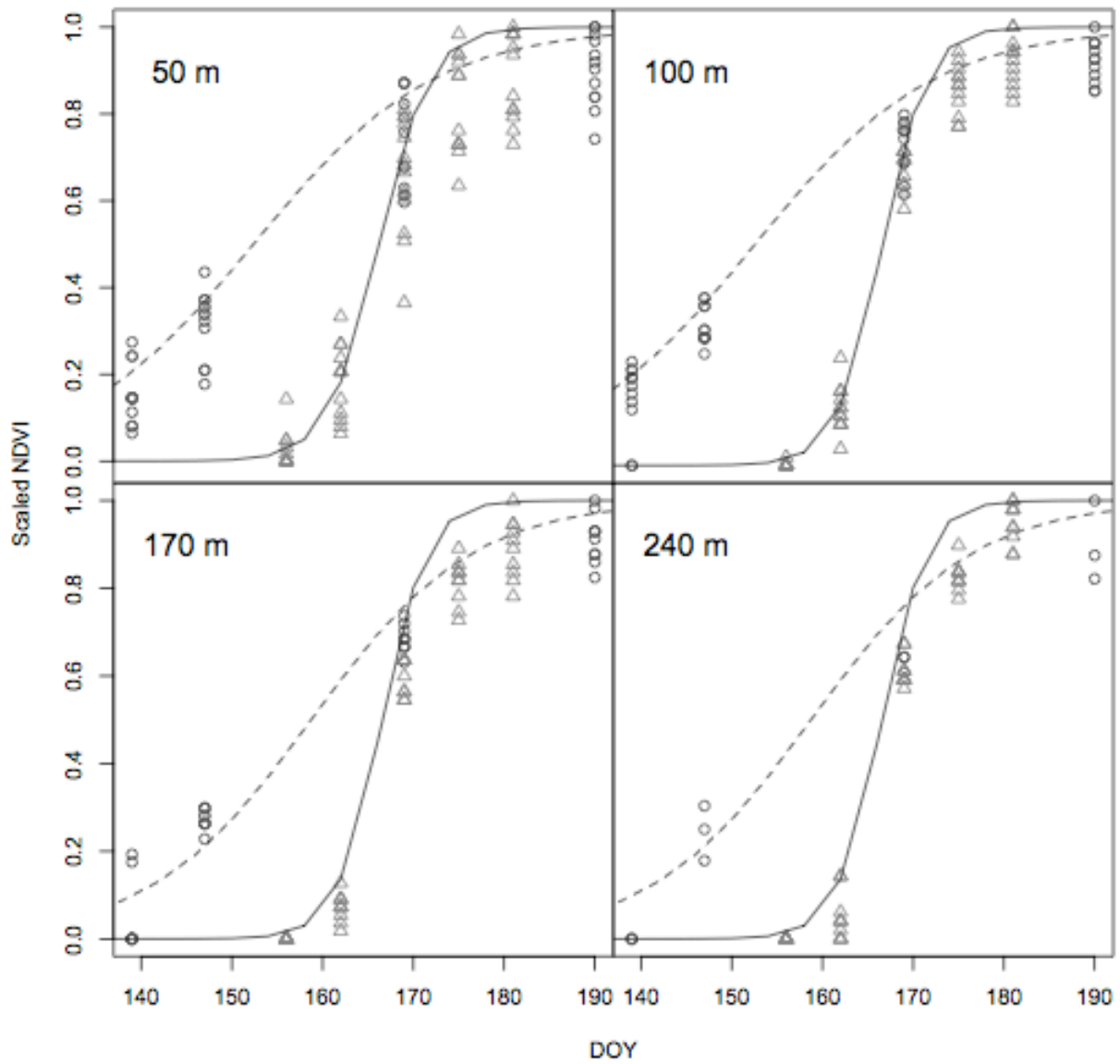


Fig. 8. Fitted curves of scaled NDVI per day for 2008 (Δ , solid line) and 2009 (O, dashed line) for each altitude, varied on a station-specific data. Parameter values for the logistic regression curves are given in Table 4.

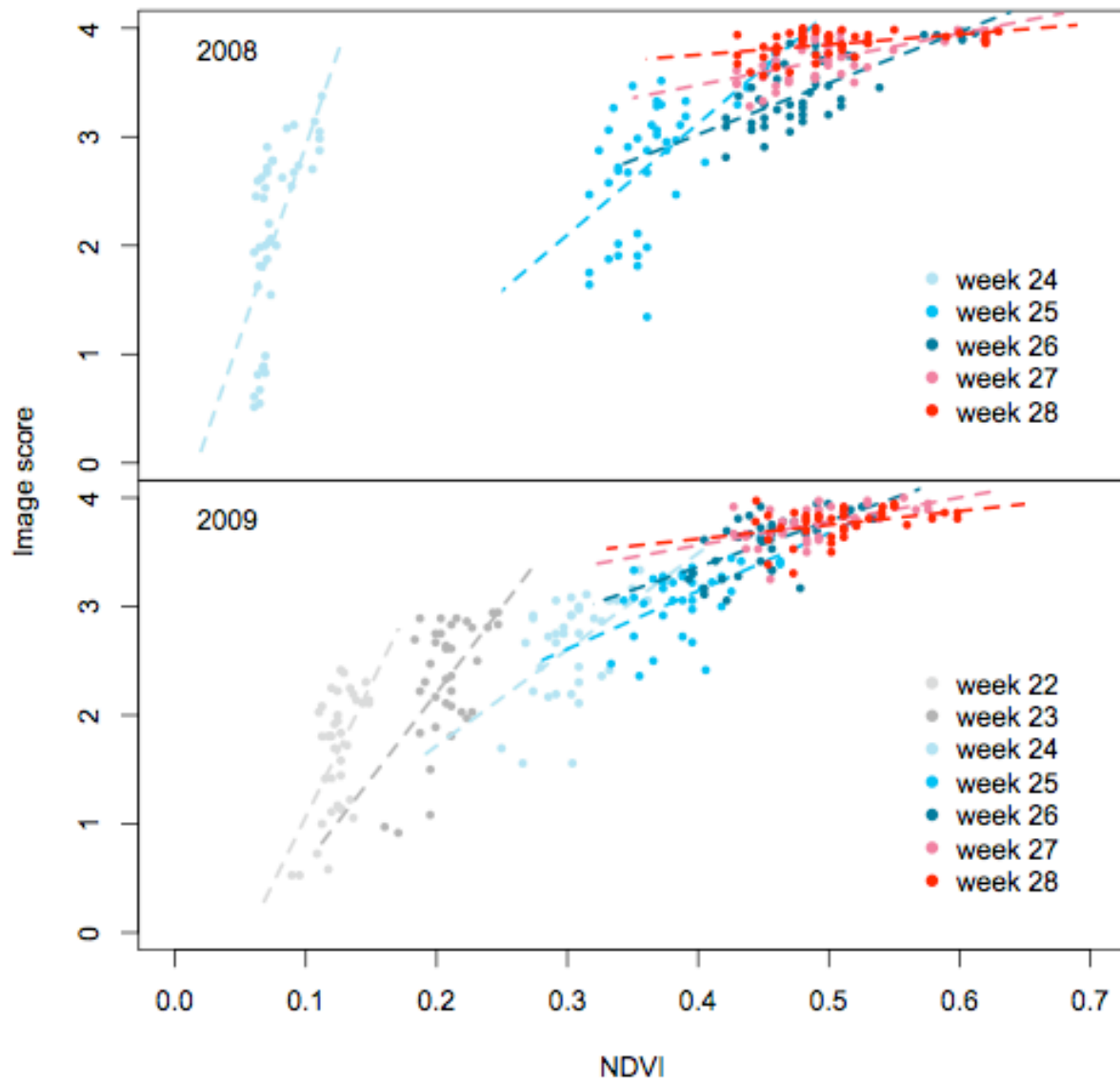


Fig. 9. Correspondence between mean image score (from 0 to 4) and mean NDVI at all stations for 2008 and 2009. Each week covers all altitudes, and every week is presented with its own regression line.

5. Discussion

5.1. Budburst and thermal sum models

Previous studies has shown that northern and high-altitude birch trees require higher air temperature sums for budburst to occur than southern and low-altitude trees, suggesting a higher degree of *B. nana* genes in the former provenances (Sulkinoja and Valanne, 1987, Ovaska *et al.*, 2005). In this study, the thermal sum needed for budburst appeared to be similar along the altitudinal gradient, as the constant thermal sum model had a fairly low RMSE of 9.7 DD. The inclusion of altitude as predictor variable in the thermal sum model did not explain any significant amount of variation and there was not even any consistent trend over the altitudinal gradient (i.e. the altitude coefficients in Table 3). Moreover, soil temperature and snow depth (mean or maximum), gave a poor improvement to the constant model as none of the predictors could significantly lower the RMSE. The fact that no altitudinal differences in thermal time requirements to budburst could be established, may reflect that the same genotype (*B. pubescens* ssp. *czerepanovii*) is present over the whole gradient. However, there were still clearly visible deviations from the mean thermal sum of 37.7 DD, were trees scored for budburst later in the season had acquired higher thermal sums (Fig. 7). This indicates that measurement errors or other environmental variables not accounted for were responsible for the residual variation in the air temperature sums at budburst.

The ontogenetic development of buds takes place long before budburst, and the precise processes underlying bud development of boreal trees are still unknown (Linkosalo *et al.*, 2008). Observations on budburst dates are therefore simply an indirect measure of the preceding ontogenetic development, and there is an ongoing discussion in the literature about potential factors influencing the timing of budburst. Possible confounding variables not measured, and which might be assumed to explain some of the variation left for discussion in this study, could be local soil conditions (e.g. soil humidity, soil grain size or soil nutrients) or the age of the individual trees (Sulkinoja and Valanne, 1987, Wielgolaski, 2001a). Yet in all the mentioned cases, it would be expected that the same trees would show the same tendency of early or late budburst in both years. This was the case in a study by Karlsson *et al.* (2003), who accordingly applied a ‘memory’ function by including the budburst of preceding year, and in that way successfully decreasing the variation (i.e. lowering the RMSE). However, this

appeared not to be the case in this study, as plotting the model residuals for each of the 44 trees revealed no systematic patterns across the two years.

There are a number of environmental sources of variation that potentially can have contributed to the rather small unsystematic residual variation in thermal sums at budburst. For instance, the level of herbivory by geometrid moth in one year could effect the timing of budburst in the subsequent year, and could cause mismatched birch and moth phenology (van Asch and Visser, 2007). Karlsson *et al.* (2003) tested this in case of the autumnal moth *Epirrita autumnata* but found no effects. There had not been any recent moth outbreaks in the present study area that should affect the budburst pattern. The two years of study had notable differences in air temperature, timing of the onset of snow cover as well as duration of snow cover, and thus soil temperature (Table A2, Fig. A1), and it is possible that certain genotypes, vegetative phenophases or individual trees of certain ages have different (unknown) reaction norms to such factors that may cause unexplained variation. Furthermore, the phenology of high-altitude trees is for some species strongly tied to snowmelt (Wielgolaski, 2001a, Ovaska *et al.*, 2005, Inouye and Wielgolaski, 2003), however the contrasting years in terms of snowmelt in this study did not cause any systematic difference in thermal sums at budburst between the two years. Birch budbreak has also shown to be positively correlated with precipitation as well as air humidity (Wielgolaski, 2001a). 2010 had indeed later budbreak and less precipitation during May compared to 2009 (Fig. 6, Table A3), but the thermal sums at budburst were still the same between the two years. Modelling spring phenology can also be done by including the dormancy phase, involving the number of accumulated days below a threshold temperature that is needed before dormancy is released (Hänninen and Kramer, 2007). While these models might be assumed to give a more accurate picture of the underlying ontogenetic development preceding budburst, have simple thermal time models shown to be a satisfying and sometimes even better approach, as the forcing temperature generally seems to play a prominent role compared to chilling temperatures (Chuine, 2000, Karlsson *et al.*, 2003, Pop *et al.*, 2000). Note however that a warmed climate might increase the significance of chilling temperatures in future budburst modelling (Bennie *et al.*, 2010).

The existence of error and biases related to the scoring of time of budburst cannot be excluded. There may have been imprecision and biases in personal judgement of budburst. However, the most likely source of error is associated with the temporal resolution of measurements. The bud measurements took place with approx. three days interval, and a

thermal sum of 9.7 DD could very well accumulate only during one day. For instance such errors could easily give rise to the observed relationship between the thermal sum at budburst and DOY shown in Fig. 7. This demonstrates the importance of frequent bud observations, especially during sudden warm periods as the one seen around DOY of mean budburst in 2010. Nevertheless, the results of this study still indicates that a simple thermal time model without modifying local variables gives a reasonable good reflection of mountain birch budburst in coastal northern Fennoscandia, in agreement with studies from other boreal regions.

5.2. Satellite analyses and field measurement comparison

The NDVI values at each station showed a greater within altitude variation at lower altitudes for both years, while the higher altitudes have a more synchronized spring phenology (Fig. 8). At the highest altitude in 2009, only three stations were throughout snow free, making interpretations difficult. However, the curve for 240 m show the same trend as the other curves in 2009, with a faster green up during the start of the season compared to 2008. The first week in year 2008 has a slow start, while in 2009 the development of buds and leaves happens without delay (Fig. 9). The fast development of the leaves in 2009 in the beginning of the season may be due to the warmer spring in 2009 compared to 2008 that reflects on the rate of spring phenology (Table A3).

The correspondence between NDVI and image scoring had less unexplained variation for 2009 compared to 2008 ($R^2=0.82$ for 2009 and $R^2=0.72$ for 2008), although the NDVI for both years can be considered to reflect the image scores well. There are interesting variations within the two approaches (Fig. 9). Mountain birches are the dominant tree species in the study area, but the surrounding ground layer also influences the spectral signal and thus the NDVI. Hence, the low NDVI values in the beginning of the season may be due to that the surrounding ground layer does not have the exact same rate of phenology as the birch trees, the latter in this case having a faster development rate at some places (i.e. higher image score) than the understory plants. The trend is still there later in the season, however inverted, when all trees according to the image scoring are fully developed (i.e. image score ~ 4) yet there are still variations in the NDVI values. So despite the overall high correspondence, suggest this that cautions must be taken when using satellite-derived NDVI for studying detailed spring phenology where not all species have the same reaction norms.

5.3. Conclusions

The results from this study indicated that the timing of budburst for mountain birch along an altitudinal gradient in coastal northern Fennoscandia is controlled by simple air temperature sums, and that the inclusion of other local environmental variables such as snow depth and soil temperature do not improve a thermal sum model for this region. Neither were there any indications that birch at high altitudes have adapted phenological strategies that differ from those at lower altitudes in the gradient. This lowers the possibility of mismatching phenologies of birch and their herbivores across such altitudinal gradients (Mjaaseth *et al.*, 2005). However, this study has also shown that measuring budburst in situ with high precision across environmental gradients can be difficult especially when budburst take place rapidly in periods of high temperatures. Furthermore, the satellite analysis and field measurement comparison showed that there is a good correspondence between high-resolution satellite image analysis of phenology and ground phenology measurements, possibly opening up opportunities for using phenological remote sensing studies where in situ observations may fall short. However, the correspondence between NDVI (which cannot focus on merely one species) and phenology studies in the field (that in this case only focus on one species) may show some variation, especially in sparsely located or mixed species stands.

6. Acknowledgements

Many people have contributed making this project come true. I want to thank my supervisors Jane U. Jepsen and Rolf A. Ims for giving me the opportunity to undertake this study. Their guidance, encouragement and sharing of knowledge have been invaluable. I am very grateful to the people in the ClimMoth-project who have helped with the data collection; Lauri Kapari, Saga Svavarsdóttir, Tino Schott and Ole Petter Vindstad, I thank them for their friendship and assistance in rainy, windy, sunny and mosquito-filled days. Thanks also to all the above-mentioned people for help and suggestions with the thesis, especially to Jane who have given me lots of her time providing invaluable help throughout the project. It has been an honour for me to have the opportunity to spend time at Norut AS while I was working with the satellite images, and for this I am deeply grateful to Stein Rune Karlsen, Kjell Arild Høgda and Bernt Johansen, without their great hospitality and fundamental supervising this thesis would not have been successful. I wish to express a special thanks to Bernt who did the orthorectification of the images. Many thanks also to Stian Solbø at Norut who looked through and gave suggestions to calibration methods. The data for year 2008 was collected by Ingrid Aalstad, I acknowledge her for kindly letting me use her data. The scoring of the digital images was partly done by students in the course BIO-8102 and partly by the ClimMoth-project; I am very grateful for their help. At last, thanks to all my friends and family, and a special thanks to Stian who never lost faith in me, giving me full support during these two years.

This study was funded by the Research Council of Norway through the project ClimMoth, 'Climate warming and insect outbreaks in sub-arctic birch forest' (NFR prosjektnr. 184885/S30).

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8. Appendix

Table A1. The technical details of the satellite images used for the development of NDVI images. To check for any discrepancy between the images, the time, the sun azimuth, and the sun elevation of the images is presented. The calibration factors for band three (red) and band four (near-infrared) are the calibration values used to calibrate the images.

	Date	Time	Sun azimuth	Sun elevation	Calibration factor Band 3 (red)	Calibration factor Band 4 (nir)
2008	4/Jun	10:25:38	174.50°	42.61°	0.5315	0.8163
	10/Jun	10:25:23	174.06°	43.22°	0.5315	16.326
	17/Jun	10:25:04	173.50°	43.62°	21.259	16.326
	23/Jun	10:24:53	173.03°	43.71°	21.259	16.326
	29/Jun	10:24:40	172.59°	43.55°	21.259	16.326
2009	19/May	10:06:35	169.35°	39.44°	0.1805	0.6125
	27/May	10:06:08	168.90°	41.03°	0.5105	17.322
	18/Jun	10:04:58	167.15°	43.33°	14.441	12.250
	9/Jul	10:03:55	165.61°	42.53°	0.2552	0.4330

Table A2. Climatic variation between altitudes and the years 2009 and 2010. The standard error is given in brackets. Mean DOY of snowmelt was calculated from the averaged day per altitude of when one of the five snow measurement was first measured as zero, i.e. the snow had begun to disappear.

Parameter	Year	50 m	100 m	170 m	240 m
Mean cumulative air temp (°C) (May 1)	2009	122.2 [±12.4]	109.2 [±12.0]	97.3 [±6.8]	76.7 [±5.6]
	2010	119.8 [±14.6]	105.6 [±15.3]	97.4 [±9.6]	73.4 [±4.7]
Mean cumulative soil temp (°C) (May 1)	2009	80.4 [±60.1]	93.1 [±59.2]	58.5 [±40.7]	29.3 [±37.8]
	2010	12.3 [±26.9]	15.3 [±23.1]	10.2 [±21.9]	5.5 [±17.5]
Max snow depth (cm) (of whole season)	2009	76.0 [±23.0]	80.7 [±16.8]	98.2 [±14.5]	105.4 [±27.5]
	2010	57.5 [±17.0]	59.0 [±25.2]	77.0 [±12.8]	77.0 [±21.7]
Mean snow depth (cm) (at mean DOY of budburst)	2009	3.1 [±5.6]	8.4 [±15.0]	2.4 [±5.6]	1.5 [±3.2]
	2010	1.6 [±5.4]	1.7 [±2.5]	7.8 [±8.0]	9.8 [±9.3]
Mean DOY of snowmelt	2009	126.8 [±5.0]	129.3 [±3.8]	132.0 [±3.1]	132.8 [±5.1]
	2010	129.1 [±5.3]	128.8 [±9.5]	137.2 [±2.0]	137.6 [±1.3]

Table A3. Cumulative air temperatures in the present study area for 2008, 2009 and 2010. (Norwegian Meteorological Institute.)

	2008	2009	2010
Cumulative air temp 100 m.a.s.l. ($T_{crit}=0$)	61.8	82.3	70.8
Precipitation in May (mm)	100-200	100-200	<100

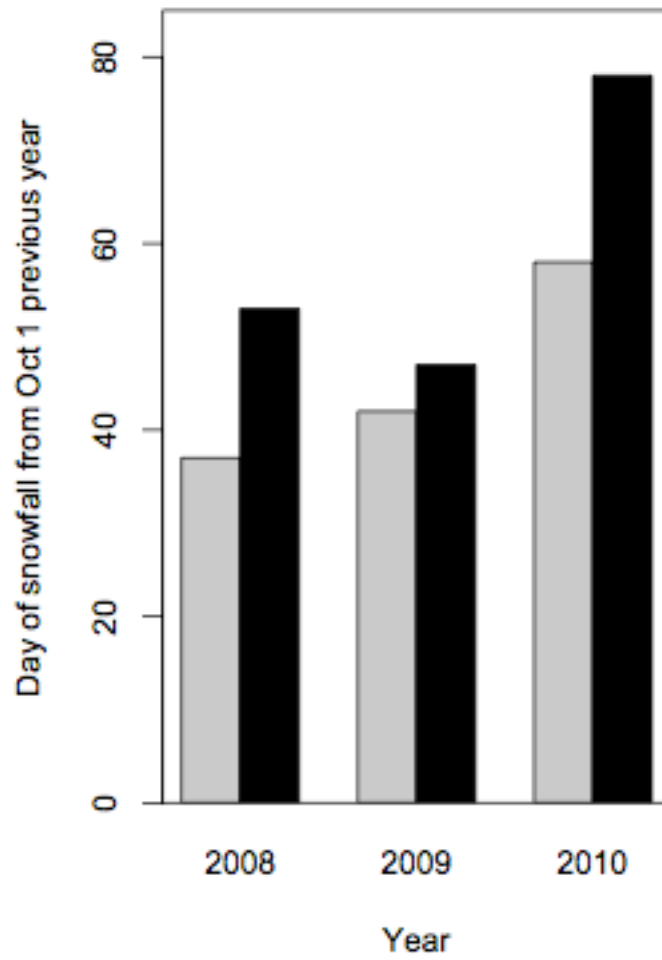


Fig. A1. The onset of staying snow cover in Tromsø (100 m.a.s.l.), above 0 cm (grey) and 10 cm (black) expressed in days after Oct 1st for the three years 2008-2010. (Norwegian Meteorological Institute.)