



Autumn phenology of mountain birch at the sub-arctic treeline in comparison with silver birch in the cold and mild temperate zone

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Abstract

Key message Timing of autumn phenology of birch populations does not consistently follow the latitudinal gradient but varies according to the phenophase, the scale of measurements and the current year meteorological conditions.

Abstract Lack of knowledge on autumn phenology of deciduous trees still exists for high-latitude regions. We studied the leaf and wood growth autumn phenology of mountain birch in a sub-arctic climate (northern Sweden) and compared them with the same dynamics for silver birch in a temperate climate (southern Norway and Belgium). The first autumn phenophase for mountain birch was the decline of the remotely sensed Terrestrial Chlorophyll Index (TCI) at the end of July. This was followed by wood growth cessation, onset of chlorophyll degradation and of loss of canopy greenness, and the latter accompanied by onset of anthocyanin production and flavonoids degradation. The earlier timing of TCI decline than chlorophyll degradation was probably due to the different scales of measurements (ecosystem level *vs.* tree leaves, respectively). In 2020, the decline in canopy greenness started in the same period at the three studied sites, showing an unexpected early timing for Belgium, likely due to the very warm late summer conditions and drought stress or intraseasonal legacy effects. Accordingly, wood growth cessation also occurred unexpectedly earlier in Belgium than in Norway. The end of senescence was inversely related to latitude. Our study presents, for the first time, the autumn timeline of a deciduous species at the northern treeline, and indicates that the timing of autumn phenology of birch populations does not consistently follow the latitudinal gradient but varies according to the phenophase, the scale of measurements and the current year meteorological conditions.

Keywords *Betula pendula* · *Betula pubescens* · Deciduous trees · Leaf senescence · Terrestrial chlorophyll index · Wood phenology

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Abbreviations

Anth	Epidermal anthocyanin content
CCI	Chlorophyll content index
Chl	Epidermal chlorophyll content
CWG	Cessation of wood growth
CWG _B	Cessation of wood growth through breakpoint analysis
DBH	Diameter at breast height
DOY	Day of the year
ELCG	End of loss of canopy greenness
Flav	Epidermal flavonol content
OFS	Onset of foliar senescence
OLCG	Onset of loss of canopy greenness
SCL	Scene classification layer
SE	Standard error
TCI	Terrestrial chlorophyll index
WTC	% Of cells in the cell wall-thickening phase

Introduction

Autumn is a critical time in the annual life cycle of deciduous trees, characterised by the physiological processes of leaf senescence and growth cessation (Gallinat et al. 2015). With the onset of foliar senescence (OFS), leaf cells start to be degraded in an orderly manner, so that nutrients such as nitrogen, phosphorous and potassium are resorbed from the leaves before leaf abscission (Estiarte and Peñuelas 2015). One of the first types of macromolecules to be degraded is chlorophyll, whose sharp decline in leaves in late summer can be a good proxy for OFS (Mariën et al. 2019). The resorbed nutrients are stored for overwintering and used for new foliar growth in the next spring. During senescence, photoprotective pigments such as anthocyanins and flavonoids are produced. Together with the fast degradation of chlorophyll and the slower degradation of carotenoids, this contributes to the characteristic colour change in deciduous trees in autumn from green to yellow or red. The moment trees significantly start to lose the green colour can be defined as the onset of loss in canopy greenness (OLCG, *see* Dox et al. 2022a), while the timing when trees complete their leaf senescence, and 100% of the leaves are either discoloured or fallen, can be defined as the end of loss of canopy greenness (ELCG).

The later stages of autumn leaf senescence (*e.g.* ELCG) are dependent on autumn temperature (Fu et al. 2018; Zohner & Renner 2019; Zohner et al. 2023), but inconsistent correlations and findings point to a more complex environmental control on the timing of the earlier stages of autumn leaf senescence (*e.g.* OFS, OLCG) than expected if temperature was the only driving factor (Jiang et al. 2022). For example, it has been suggested that the competence to senescence (the physiological capacity to undergo senescence) is only reached after a certain photoperiodic threshold is met (Fracheboud et al. 2009). Despite the spatial variability (Jiang et al. 2022), the photoperiodic control has been found in synthesis studies to be distinctly stronger at high latitudes (Gill et al. 2015). Conversely, at high latitudes and at the northern treeline, the senescence rate can be accelerated by sharply decreasing autumn temperature, frost and precipitation (Fracheboud et al. 2009; Gill et al. 2015).

In the woody stems, at the end of summer, xylem production in the cambium halts (Dox et al. 2020). However, after the production of xylem cells has stopped, carbon allocation to wood continues until cell differentiation is completed and cessation of wood growth (CWG) is achieved (Rathgeber et al. 2016a, b). During this last phase of xylogenesis between the end of cell production and CWG, the process of wall-thickening (WTC) is completed (Dox et al. 2020). Analogously to leaf senescence,

the timing of CWG is affected by autumn conditions. Late summer temperature is particularly important for CWG timing, with warmer temperatures delaying it given that adequate water resources are available (Dox et al. 2022a). In fact, drought can lead to earlier cessation of wood growth (Delpierre et al. 2015; Dox et al. 2021), and so can the interaction between air temperature and cell water potential (Cabon et al. 2020).

At the single tree level, the optimal timing of autumn senescence is critical for maximising the photosynthetic uptake while avoiding the risk of exposure to early and sudden frost events, which can lead to premature leaf fall and loss of nutrients before the leaf senescence is completed (May and Killingbeck 1992; Estiarte & Peñuelas 2015). Moreover, the timing of wood growth cessation can affect frost hardening and influence the latewood vessel traits, which are also important for next year's water transport (Dox et al. 2021). At the ecosystem level, the length of the leafy season is strongly coupled to carbon, water and energy balances, which can affect the climate in different ways (*e.g.*, carbon sequestration, transpiration, and albedo). A longer wood growing season can be positively correlated with increased carbon sequestration and biomass accumulation in wood, creating a greater sink for atmospheric carbon (Piao et al. 2008; Lugo et al. 2012). Note that climate change is expected to affect seasons unequally, especially at high northern latitudes, with greater warming forecasted in autumn than in spring and summer (Bintanja and van der Linden 2013; Hannah et al. 2021). In the last two decades, research efforts have been devoted to leaf autumn dynamics in deciduous trees also at boreal and high latitudes (Delpierre et al. 2016; Mulder and Spellman 2019; Stridbeck et al. 2022; Silvestro et al. 2023). However, we lack comprehensive studies comparing leaf senescence and wood growth cessation dynamics in this climate zone or between this zone and more temperate climates.

Betula spp. are early successional trees with a wide distribution in the northern hemisphere, ranging from northern Scandinavia, Siberia and North America to central China and the northern tip of North Africa (Beck et al. 2016). The distributional range therefore covers a large gradient in photoperiod, diurnal and seasonal temperature and frost occurrence in spring and autumn. Trees of the genus *Betula* have a diffuse-porous wood anatomy, meaning that water vessels are more uniform, smaller, and therefore less prone to winter embolism caused by freeze–thaw cycles than ring-porous trees (Wang et al. 1992; Sperry et al. 1994). This enables new leaves to grow before new vessels have been produced in the spring. In Europe, silver birch (*B. pendula* Roth) is present in the temperate and mid-boreal zones, while mountain birch (*B. pubescens* ssp. *czerepanovii* (Orłowa) Hämet-Ahti) is present in the high boreal and sub-arctic zone (Beck et al.

2016). Genotypic variations in birch phenology are present both within populations (Possen et al. 2014) and between ecotypes (*e.g.*, Ovaska et al. 2005).

Our study had two objectives: **(1)** to determine the timing of onset of foliar senescence (OFS), loss of canopy greenness (OLCG and ELCG), and cessation of wood growth (CWG) in mountain birch in northern Sweden (sub-arctic climate, Dfc, according to the Köppen–Geiger climate classification, Peel et al. 2007), and **(2)** to compare the timing of the studied phenological phases (OFS, OLCG, ELCG, CWG) in mountain birch to the timing of the same phases in silver birch at lower latitudes in the temperate climate of southern Norway (cold-temperate climate: Dfb) and Belgium (temperate-oceanic climate: Cfb). These objectives were met by assessing **(i)** leaf senescence timing from ground-based measurements of leaf colour change and/or leaf pigment indices (*i.e.*, chlorophyll index, anthocyanin index, and flavonoid index) in the year 2020, **(ii)** cessation of wood growth through microscopic observation of xylem formation in wood microcores in the same year and by deriving **(iii)** information on autumn dynamics for 3 years (2018, 2019, and 2020) through remote-based data of Terrestrial Chlorophyll Index (TCI).

Methods

Study sites and tree selection

Mountain birch—Sweden

The Swedish research site is a natural sub-arctic mountain birch forest adjacent to the Abisko Scientific Research Station (68°21' N, 18°48' E, 406 m a.s.l.; Fig. 1). The region is characterised by discontinuous permafrost mires and mountain birch forest which forms the alpine treeline at approximately 700 m a.s.l. (*see* Campioli et al. 2009 for details about the area). Due to its latitude above the Arctic Circle, the area experiences polar day (the sun does not set below the horizon) from 25th May to 18th July and polar night (the sun does not rise above the horizon) from 6th December to 5th January. The mean annual temperature during the last normal period (1991–2020) was 0.3 °C, and the warmest and coldest mean monthly temperatures were 12.1 °C (July) and -10.1 °C (February), respectively (Swedish Meteorological Institute). Abisko belongs to the driest area of Sweden, with 347 mm mean annual precipitation between 1991 and 2020 (Swedish Meteorological Institute). During our study years (2018–2020), the annual average temperatures were -0.1,

Fig. 1 Map of central northern Europe with our experimental sites in Sweden (red), Norway (green), and Belgium (blue)



0.2, and 1.4 °C, respectively, and annual precipitation amounts were 287, 399, and 390 mm, respectively. Seasonal data of temperature, precipitation, and aridity (Aridity Index calculated with the equation of Budyko 1958) show rather normal conditions for 2020, with, however, a very dry June (Fig. 2).

We selected ten healthy-looking mature mountain birch trees ca. 30–40 years old with a mean diameter at breast height (DBH) of 9.4 ± 0.3 cm (\pm SE, standard error) and a height of ca 3–5 m (*visual estimations, no measurements available*). We sampled preferentially single stem trees but as the trees are often polycormic (multi-stemmed), two trees had more than one stem. The polycormic growth form in this area is thought to be caused by cyclic outbreaks of the autumn moth (*Epirrita autumnata* Bkh.) and the winter moth (*Operophtera brumata* L.) (Tenow, 1972). All our study trees had signs of leaf damage from the moth larvae.

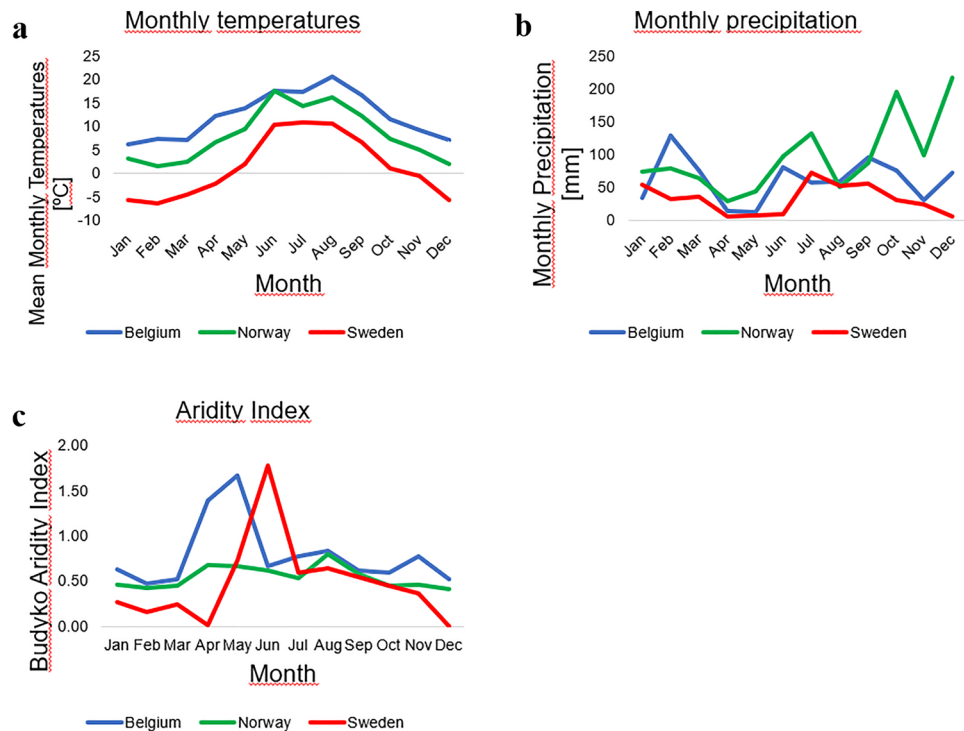
Silver birch—Norway and Belgium

The Norwegian research site was a natural stand of silver birch with presence of Norway spruce (*Picea abies* L.) located nearby the Hoxmark Experimental Farm in Ås, Norway (59°40' N, 10°42' E, 86 m a.s.l.; Fig. 1) and constitutes part of the northern distributional range of silver birch. The stand is characterised by moderate fertility and a steep slope facing North-East (Dox et al. 2022b). During

1991–2020, the mean annual temperature was 6.3 °C and the warmest and coldest mean monthly temperatures were 16.7 °C (July) and –2.8 °C (January), respectively (Norwegian Centre for Climate Service). During the same period, the mean annual precipitation was 892 mm. The annual average temperature and average rainfall at the nearest weather station were 6.9 °C and 795 mm in 2018, and 6.6 °C and 1133 mm in 2019. In 2020, the two parameters were 8.2 °C and 1171 mm, respectively, thus warmer and wetter than the average, without markedly dry periods (see also seasonal data in Fig. 2). For this study, we selected 11 dominant or co-dominant mature silver birch trees ca. 50 years of age with 28.7 ± 2.8 cm mean DBH and 25.0 ± 2.6 m mean height.

In Belgium, the study site was a natural birch stand in the Klein Schietveld (51°21' N, 4°37' E) forest which is part of the central distribution range of silver birch (Dox et al. 2020; Marchand et al. 2020). During 1991–2020, the average annual temperature was 10.7 °C, and the mean annual precipitation was 823 mm. The average annual temperature and rainfall were 11.8 °C and 724 mm in 2018, and 11.2 °C and 798 mm in 2019. The year 2020 was warmer and drier than average, with 12.7 °C and 746 mm precipitation, respectively. The spring of 2020 (April–May) was especially dry, while August was particularly warm (Fig. 2). We selected 17 dominant and co-dominant trees ca. 50 years old. The trees had 28 ± 12 cm mean DBH and 19.6 ± 1.4 m mean height.

Fig. 2 Mean monthly temperatures (a), precipitation (b), and Budyko Aridity Index (c) in 2020 at our sites in Sweden (red), Norway (green), and Belgium (blue)



Loss of canopy greenness

Crowns of the study trees were visually assessed for percentage of non-green leaves (α_t) and percentage of fallen leaves (β_t) approximately once per week from mid-summer (July) until almost all leaves had changed colour or dropped (September in Sweden, October in Norway, and November in Belgium). The loss of canopy greenness (x_t) was calculated according to (Vitasse et al. 2009)

$$x_t = \frac{\alpha_t * (100 - \beta_t)}{100} + \beta_t. \quad (1)$$

To compare this data with the gradual decrease in chlorophyll content (*see below*), we calculated canopy greenness as canopy greenness = 100 - x_t . (2)

End of loss of canopy greenness (ELCG) was calculated as the DOY at which canopy greenness reached 0.

Leaf pigment indexes

In Sweden, during the same period as the canopy greenness observations, the chlorophyll content index (CCI) of leaves was measured in situ with a CCM-200 + leaf absorption meter (ADC Bioscientific Ltd., 159 Hoddesdon, UK), which measures absorption at 653 nm and 931 nm. The leaves were chosen to comprise both young and old ones. Three leaves at the top and three at the bottom of each of five different branches (selected randomly) were measured. These leaves were accessible from the ground. As there was no significant difference between leaf location (*data not shown*), the data were pooled.

In addition, in Sweden, the adaxial side of leaves of the same branches was measured with a Dualex® optical leaf clip (ForceA, Orsy, France) to determine epidermal chlorophyll content (Chl) (based on a transmittance ratio of far-red (650 nm) and near-infrared (710 nm) light), epidermal anthocyanin content (Anth) [based on the absorption of green light (515 nm)], as well as epidermal flavonol content (Flav) [absorption of UV light (375 nm)].

Xylem formation

At each site, seasonal wood growth dynamics in late summer–autumn was monitored by microscopic observation of wood microcores collected every 1–2 weeks during July–October. On the first sampling, two equal cores were sampled with a Trephor wood corer at 1.5 m breast height on 4–5 of the 10–17 trees monitored for leaf phenology at each site. Each successive round of sampling was carried out in an upward spiral pattern (ca. 5 cm distance, both

horizontally and vertically, from the previous sample) to minimise wound reactions. Following the protocol described in Dox et al. (2020), the wood microcores were immediately placed in 1.5 ml Eppendorf tubes containing 1 ml of 70% ethanol and stored at room temperature until they were transported to the lab for further processing. The most recent xylem rings (approximately 2–4) were cut from the microcores and dehydrated in a series of rising ethanol concentrations. The segments were then infiltrated with a clearing agent (UltraClear, J.T. Baker, Avantor Performance Materials, Center Valley, USA) and paraffin (Paraplast plus, ROTH, Karlsruhe, Germany) and embedded in paraffin blocks. The blocks were sliced with a microtome (Leica Microsystems, Wetzlar, Germany) into 5–10 μm slices of cross-sections and the paraffin was removed with a clearing agent. The slices were then stained in an aqueous solution of safranin (Merck, Darmstadt, Germany) and Astra blue (Sigma-Aldrich, Steinheim, Germany) and mounted in Euparal (Waldeck, Münster, Germany) on microscope slides. The cross-sections were examined under a light microscope (Leica DM 4000 B/M, Wetzlar, Germany) to follow the seasonal wood formation. We measured the width of the layer of xylem cells still in the process of cell wall thickening (WTC) as a percentage of the total annual xylem ring width (Dox et al. 2020). The developing xylem cells were distinguished from fully formed xylem cells for having thinner cell walls and remaining content in the lumen.

Satellite data

Satellite-based phenological metrics were derived using the European Space Agency Sentinel-2 images available on the Google Earth Engine platform, which provides access to the full archive of processed Sentinel images covering our areas of interest. The top-of-canopy reflectance data from June to December of 2018, 2019, and 2020 were used in this study. From this dataset, we selected the 10-m resolution band 4 (665 nm) and the 20-m resolution bands 5 (705 nm) and 6 (741 nm). At each site, three different areas of about 2500 m² each were extracted. For each area, 25 and 9 pixels were extracted for the bands at a resolution of 10 m and 20 m, respectively. Pixels with low quality (*e.g.* clouds, snow) were filtered out using values of the quality band scene classification layer (SCL) provided in the Sentinel-2 (*i.e.*, 1 = saturated or defective; 2 = dark area pixels; 3 = cloud shadows; 6 = water; 7–10 = clouds and cirrus). To reduce the noise and data gaps in the time-series after data quality check, we followed (Descals et al. 2020). First, a moving average window with an average length of 10 days was applied. Second, a cubic interpolation to convert the 20 days composites to a daily time-series was applied. This analysis was performed adapting the method available on Google Earth Engine at https://github.com/adriadescals/LandSurfacePhenology_

[Sentinel2.git](#) to the extracted time-series for this study. From the processed data, we calculated the Terrestrial Chlorophyll Index (TCI), as

$$\text{TCI} = \frac{\text{Band6} - \text{Band5}}{\text{Band5} - \text{Band4}} \quad (3)$$

The TCI data showed good agreement with the colouration data of 2020 for the three sites (and for 2018 and 2019 for Belgium and Norway; Fig. S1). Moreover, the data were aggregated for the three years because of the similar pattern across years and the focus of the manuscript on the site differences rather than annual differences.

Data treatment and statistical analysis

All statistical analyses were performed using R (version 4.0.2, R Foundation for Statistical Computing, Vienna, Austria).

A breakpoint analysis was applied to the time-series of leaf variables (CCI, canopy greenness, Anth, Flav, TCI) to determine the day of year (DOY) on which these variables started to decrease abruptly due to leaf senescence. The dates corresponding to the breakpoints represent the key phenology events under study. For example, OFS was derived from the breakpoint analysis of the CCI time-series, whereas OLCG was derived from the breakpoint analysis of the canopy greenness time-series (Mariën et al. 2019; Dox et al. 2020). For this purpose, we applied the *segmented* R package (Muggeo 2008) which calculates piecewise linear regressions on the data set to determine the (break) point at which the two subsequent linear regression lines with the largest slope difference intersect. Breakpoints were calculated at single tree level and averaged at the stand level. To test for statistically significant differences ($p < 0.05$) between the same phenological event at different sites and different phenological events at the same site, a linear model was fitted with the timing of the phenological event (e.g., OFS) as the response variable. The model residuals were visually checked for compliance with the assumptions of normality, homogeneity of variance, and independence of observations. The p values were adjusted for multiple comparisons using the Holm's method. Autumn regression slopes for TCI vs. time data series were also calculated. For both breakpoint analysis and slope calculation, TCI data were averaged for each site across the three analysed years.

The cessation of wood growth (CWG) has been previously defined as the first date of a 3-week period when WTC is less than 0.5% (Dox et al. 2020). However, as this approach is rather conservative, we also determined cessation of wood growth from breakpoint analysis (CWG_B) of the time-series of WTC. Both CWG and CWG_B were statistically treated as the other response variables (e.g., OFS) as described above.

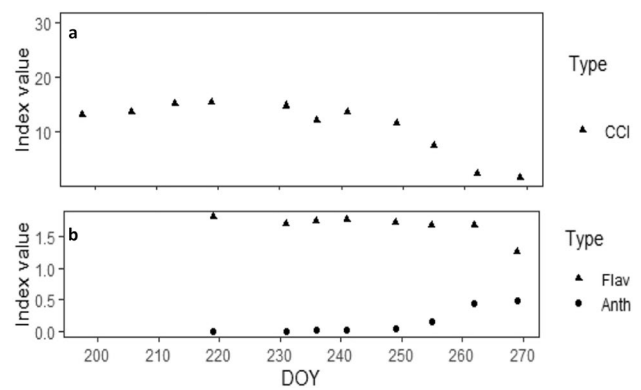


Fig. 3 Leaf pigment indexes measured in leaves of mountain birch in Sweden during autumn 2020. **a**: Chlorophyll content was measured with a CCM leaf absorption meter (CCI); **b**: Anthocyanin (Anth) and Flavonoid (Flav) indexes were measured with a Dualex Scientific + meter

Table 1 Breakpoints (mean \pm SE) and timing of CWG and ELCG for leaf and wood phenological events of birch at our three study sites in autumn 2020 (*B. pubescens* ssp. *czerepanovii* for Sweden, and *B. pendula* for Norway and Belgium)

Pheno-phase [DOY]	Sweden	Norway	Belgium
TCI	213 \pm 3	231 \pm 6	256 \pm 16
CWG _B	223 \pm 4	250 \pm 4	237 \pm 8
OFS	239 \pm 1 ($n=10$)	NA	NA
OLCG	251 \pm 1 ($n=10$)	249 \pm 3 ($n=11$)	251 \pm 3 ($n=17$)
CWG	NA	279	279
ELCG	270	310	340

TCI, decline of terrestrial chlorophyll index; CWG, cessation of wood growth; CWG_B, cessation of wood growth through breakpoint analysis; ELCG, end of loss of canopy greenness; OFS, onset of foliar senescence; OLCG, onset of loss of canopy greenness

Results

Foliar senescence from pigment indexes in mountain birch

The CCI of leaves of mountain birch in Sweden maintained rather stable values till late August (Fig. 3a). Since early September, chlorophyll declined steadily, with OFS recorded on DOY 239 (Table 1). A very similar chlorophyll pattern was found when using Dualex instead of CCM-200 + as chlorophyll meter (*data not shown*). The decline in chlorophyll was mirrored by an increase in anthocyanin production and a decrease in flavonoids (Fig. 3b). The breakpoints for anthocyanin and flavonoid content indicated almost the same date of abrupt

change, *i.e.*, DOY 250 ± 3 and 254 ± 3 , respectively ($p = 0.111$). They both occurred significantly later than OFS ($p < 0.001$).

Canopy greenness

Canopy greenness in mountain birch in Sweden started to decline at the beginning of September (OLCG on DOY 251 ± 1). At the same time ($p = 0.89$), canopy greenness started to decline also in Belgium (OLCG on DOY 251 ± 3) (Fig. 4). However, while, in Sweden, canopy greenness decreased steadily and reached zero already at the end of September, in Belgium, canopy greenness values stabilized (at around 25% of the maximum) from the end of September till late October, reaching zero only in mid-November (Fig. 4). The decline of canopy greenness in Norway also started concurrently to the Swedish site (OLCG on DOY 249 ± 3 , $p = 0.89$) but it progressed more slowly till mid-September. Only from late September, the canopy greenness decline in Norway proceeded with

similar rate as in Sweden. Thus canopy greenness decline in Norway was shifted forwards by approximately 2 weeks compared to the decline in Sweden (Fig. 4).

Autumn wood formation dynamics

The percentage of xylem cells in the wall-thickening phase (WTC) declined most rapidly in Sweden (Fig. 5). In Belgium, there was an unexpected drop in the percentage of WTC in the beginning of August (DOY 210) after which it rose again. The breakpoint in time-series of WTC, *i.e.*, CWG_B, was 10th August (DOY 223 ± 4) for Sweden, 24th August (DOY 237 ± 8) for Belgium and 6th September (DOY 250 ± 4) for Norway (Table 1). These differences were all significant one from the other ($p < 0.001$). Conversely, CWG occurred simultaneously on 5th October (DOY 279) in Norway and Belgium ($p = 0.41$) (Table 1), but it could not be calculated for trees in Sweden (*see Discussion*).

Fig. 4 Leaf senescence dynamics (decline in percentage of canopy greenness, CG) in *B. pubescens ssp. czerepanovii* (Sweden, red) and *B. pendula* (Norway, green and Belgium, blue) in 2020. The solid vertical lines indicate the breakpoint (OLCG, onset of loss of canopy greenness) at each site and the dashed vertical lines the standard error. For an explanation of the breakpoint analysis, see Methods

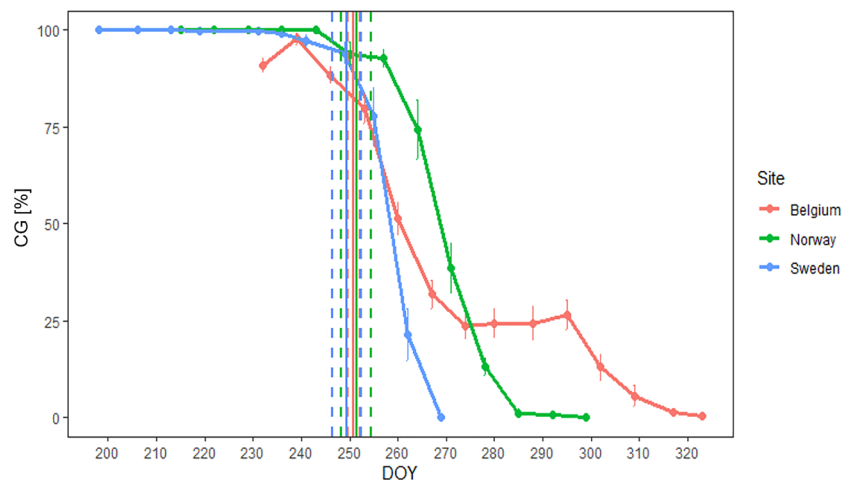
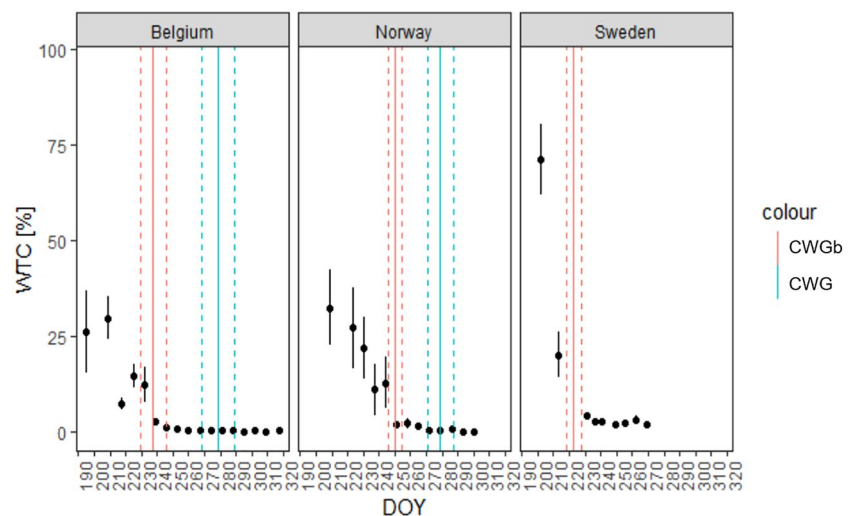


Fig. 5 Percentage of cells in wall-thickening phase (WTC) in relation to total annual ring width in birch trees from Belgium, Norway, and Sweden during autumn 2020. The mean breakpoint (CWG_B, red) and cessation of wood growth (CWG, point at which WTC < 0.05, blue) and standard errors are indicated for each site, when possible



Remote sensing index

As mentioned in Methods, for each site, the following description applies to the three years of data aggregated. The autumn decline in TCI started first in Sweden (TCI breakpoint: DOY 213 ± 3), then Norway (DOY 231 ± 6) and finally Belgium (DOY 256 ± 16) ($p < 0.0001$). The decline rates were nevertheless similar among latitudes: -0.024 , -0.019 , and -0.027 for Sweden, Norway, and Belgium, respectively. TCI first reached its minimum in Sweden in late September, followed by Norway and Belgium at half of November and beginning of December, respectively. The magnitude of the summer peak of TCI followed the latitudinal gradient of the sites with the highest values in Belgium (ca. 4.5) and the lowest in Sweden (ca. 3) (Fig. 6).

Summary timeline of leaf and wood phenology in mountain birch

The first autumn phenological event registered for mountain birch in Sweden was the decline in TCI at the end of July (DOY 213 ± 3). In August, significantly later ($p < 0.001$), an abrupt decline in wood growth took place, with cessation of wood growth (CWGb) on DOY 233 ± 4 . This event was followed shortly afterwards by the sharp decline in chlorophyll content (OFS), occurring on DOY 239 ± 1 ($p < 0.0001$). At the beginning of September, we observed a concurrent occurrence of OLCG (DOY 251 ± 1), of the sharp increase in anthocyanins (DOY 250 ± 3) and of the sharp decline in flavonoids (DOY 254 ± 3) ($p = 0.1\text{--}0.6$). The total loss of canopy greenness was reached by the end of September (ca. DOY = 270) (Fig. 7).

Discussion

Autumn leaf dynamics for mountain birch

This study is, to our knowledge, the first to describe in detail the autumn dynamics of both leaves and xylem for a key deciduous species of the sub-arctic treeline. The description of autumn senescence was robust and corroborated by the use of different proxies (*e.g.*, CCI, canopy greenness, and anthocyanins) and instruments (*e.g.*, CCM-200+ and Dualex for leaf pigments, TCI from remote sensing). The observed timings of OFS and anthocyanin increase are consistent with data from aspen in central Sweden, where chlorophyll decline occurred a few days before a rise in anthocyanin production (Keskitalo *et al.* 2005). Anthocyanins are produced in response to high light and low-temperature stress in autumn when the photosynthetic capacity decreases (Hoch *et al.* 2001). Anthocyanins are photoprotectants that preferentially absorb blue–green light. In fact, they prevent photooxidative damage to the leaf by reducing the imbalance between the light absorbed by chlorophyll and the utilisation of light energy in electron transport, which increases during senescence because of the dismantling of the photosynthetic apparatus (Steyn *et al.* 2002) and of the decreased absorption capacity of chlorophyll (Keskitalo *et al.* 2005). In the birch trees at our Swedish site, the sharp decrease in chlorophyll and increase in anthocyanins coincided with a drop in temperature (Fig. 7) while light levels were still high, confirming the correlation between low temperatures, high irradiation, and chlorophyll degradation (Hoch *et al.* 2001; Robakowski 2005). Flavonoids also tend to increase when chlorophyll starts to decline (Mattila *et al.* 2018), but in our case, their level was already at its peak in summer, before leaf senescence. This is probably a strategy adopted by birch at its northernmost distributional area to prevent oxidative stress caused by the high irradiation combined

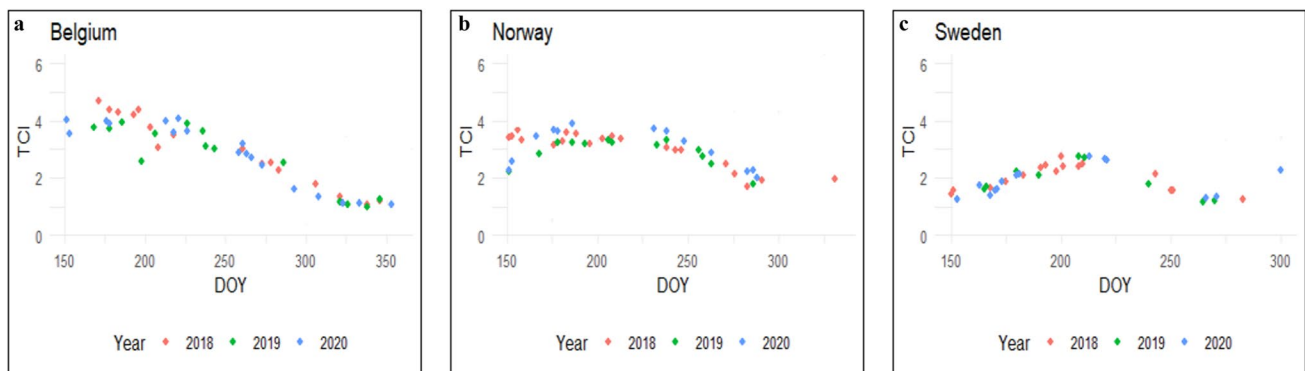


Fig. 6 Terrestrial chlorophyll index (TCI) from our study areas in Belgium (a), Norway (b), and Sweden (c) in 2018–2020. For a description of how the TCI was calculated, see Methods

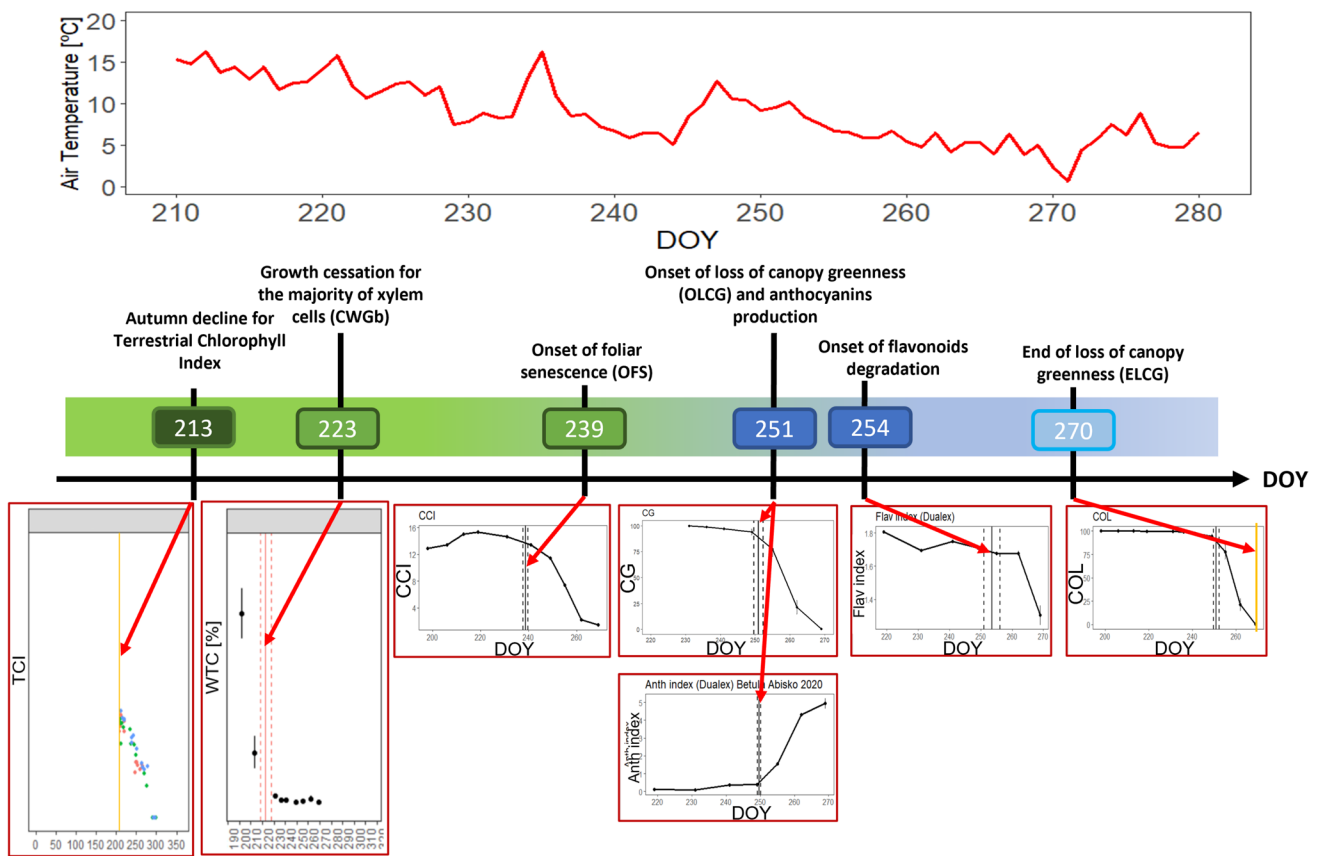


Fig. 7 Comparative timetable showing all the studied autumn phenophases (TCI breakpoint, CWGb, OFS, OLCG, Anth breakpoint, Flav breakpoint, ELCG) for *B. pubescens* in Sweden, with related graphs, and the daily temperature during the studied period. Anth, epider-

mal anthocyanin content; CWGb, cessation of wood growth through breakpoint analysis; ELCG, end of loss of canopy greenness; Flav, epidermal flavonol content; OFS, onset of foliar senescence; OLCG, onset of loss of canopy greenness; TCI, Terrestrial Chlorophyll Index

with low temperatures (*see above*), which at high latitudes can also occur during the peak vegetative period. The final degradation of flavonoids, long after chlorophyll degradation, suggests that these molecules represent a default system of defence for the plant, which is only dismantled prior to leaf abscission (Treutter 2005; Mattila et al. 2018).

Note that the results of our different measurements were very consistent. For example, the observed timing of anthocyanins production coincided also with the start of decrease in canopy greenness, which progressed very fast at the Swedish site (Fig. 4). The significant difference between OFS (239 ± 1) and OLCG (251 ± 1) can be easily explained. Foliar senescence starts with chlorophyll degradation (Matile 2000; Keskitalo et al. 2005), but leaf coloration usually appears later on, when the absence of a significant amount of chlorophyll makes visible other non-green pigments (*see above*).

The timing of canopy greenness decrease in Sweden matches the leaf yellowing found by Shutova et al. (2006) in mountain birch in Russian Lapland in 2003. Several studies found that the timing of leaf colouration in mountain birch

has not changed significantly in the northern boreal zone during the period 1964–2006, although latitudinal and altitudinal differences exist (Ovaska et al. 2005; Pudas et al. 2008; Shutova et al. 2006). This lack of variation over time despite the progressive rise in temperatures due to climate change (Piao et al. 2019) is probably associated with the high influence of photoperiod on autumn phenology at higher latitudes (Gill et al. 2015). Phenology of mountain birch is influenced by the autumn moth (*Epirrita autumnata*), as heavy damage in spring can lead to a delayed autumn senescence, possibly to make up for lost primary production (Hagen et al. 2003). The moth damage in spring 2020 caused moderate damage to the trees (*pers. observation*). However, autumn senescence did not occur later than usual in 2020 according to the multi-year remote-sensing comparison.

Autumn leaf dynamics for silver birch

The pattern of canopy greenness decline in Norway was expected, since it was similar to the one in Sweden but delayed and with slower progression of senescence due to

the more favourable climate in early September at lower latitudes (Fracheboud et al. 2009). The progression of leaf coloration in Belgium was initially similar to Sweden and Norway, which was not expected when considering the warmer climate and longer photoperiod in Belgium compared to the Scandinavian sites. Moreover, in Belgium, loss of canopy greenness halted in late September and maintained a constant value during the whole October 2020, which was also unexpected (Fig. 4). Dox et al. (2021), who studied the same birch site in Belgium between 2017 and 2019, did not observe this pattern, but similar dynamics occurred in October 2018, which was a year with a very severe drought. The year 2020 was characterised by a very warm August (without large rainfall) in Belgium, suggesting that heat and short-term drought stress could have triggered premature leaf coloration and that the observed OLCG was unrelated to the natural autumn senescence of the leaves, but it was rather due to leaf desiccation or accelerated leaf senescence (Breda et al. 2006; Marchin et al. 2015). Moreover, the exceptionally warm and dry spring of 2020 might have had a negative effect (e.g., high oxidative stress) on the leaf longevity, partially advancing leaf coloration in autumn (Juvany et al. 2013). This matches the general finding made by Zohner et al. (2023) that a warmer spring advances the onset of leaf senescence.

Wood phenology

The breakpoint analysis showed that wood growth ceased significantly earlier in Sweden (August 10th) than in Norway (September 6th), while in Belgium, this happened in the middle (August 24th). Interestingly, growth cessation occurred at both the Swedish and the Norwegian site when (weekly) mean air temperature was the same, i.e., 12.7 °C, which was higher than the daily mean threshold temperature of between 5 and 9 °C for active xylogenesis found in several conifer species at high altitudes and latitudes (Rossi et al. 2007; 2008). This possibly indicates different sensitivities of wood growth cessation to temperature between angiosperms and conifers at high-latitude sites. For Belgium, the average air temperature during the week around 24th of August was 18.8 °C. It is therefore likely that at the Belgian site, heat or short-term drought stress limited wood growth in 2020 (Dox et al 2021).

Schmitt et al. (2004) used the pinning technique to study tree-ring growth in *B. pendula* and *B. pubescens* along a latitudinal gradient in Finland. At a site at a similar latitude to our site in Sweden, he recorded the end of growth between the end of July and the beginning of August. Therefore, it is likely that CWGb is a good proxy of xylem maturation timing for the mountain birch in high latitudes. Other authors (Dox et al. 2020, 2022a) defined the end of wood growth when $WTC < 0.5\%$ (CWG). However, this threshold was

never reached in mountain birch at our site in Sweden. This was due to the fact that across the current tree ring (as well as in older growth rings), there appeared to be one layer of cells which did not complete the wall-thickening phase (*data not shown*) and, due to the narrow width of the growth rings in the high northern Swedish site, this single layer of cells made up to more than 0.5% of the whole growth ring. Moreover, the presence of marginal parenchyma at the growth ring boundary, which is typical of *Betula* spp., partly contributed to this value. Parenchyma cells could not be reliably distinguished from the developing fibres in the wood formation process. Thus, the 0.5% threshold seems therefore unsuitable for slowly growing trees with marginal (terminal) parenchyma at the growth ring boundary. The greater precision in estimating CWGb compared to CWG may support its use in phenological studies, regardless of the latitude of the species under analysis. Additionally, the timing of CWGb is closer than the timing of CWG to the cessation of cambial activity, which is also an important phenological event.

Ecosystem level data

Even though the Sentinel-2 data series for the study sites presented occasional gaps of multiple weeks, our basic exploration of interannual variability did not indicate major differences across years.

The TCI decline was advanced in comparison with the decline of the chlorophyll content index and of the canopy greenness (both monitored on the ground) (Fig. 7). This asynchrony can be partially explained by the methodological differences existing between remote sensing and ground measurements. TCI is a measurement at the ecosystem level, operationally different from the individual chlorophyll measurement in situ. The canopy of birch is very open, allowing significant understory. Therefore, subtle autumn dynamics of birch trees might be hidden to the eye of the satellite by the signals of understory or co-existing vegetation. Moreover, besides the obvious variation in scale (i.e., observation of few leaves vs. monitoring at the ecosystem level), differences between ground-based CCI and remote-sensing TCI might be related to the fact that the former is biased towards undamaged, healthy-looking leaves.

As for the end of loss of canopy greenness (ELCG, displaying a clear latitudinal gradient, Table 1), the inception of TCI decline was delayed between Sweden (the earliest), and Norway and Belgium (the latest). This showed that the temperate climate and longer photoperiod still are the most favourable conditions for longer vegetative periods, when the whole ecosystem senescence (thus of both overstory and understory) is considered. We note additionally that the gradient of the summer maximum of TCI, which decreased from Belgium to Sweden, can be well explained by the fact that plants living at higher latitudes and lower

temperatures tend to synthesize lower levels of chlorophyll (Li et al. 2018).

Conclusions

In autumn, mountain birch in Sweden displays a pattern in which the ecosystem level chlorophyll (TCI) declines first, followed by the cessation of wood growth, the onset of foliar senescence, and then by the onset of loss of canopy greenness, with the latter concurrent to the onset of anthocyanins production and flavonoids degradation. Differences in autumn phenology between sites were observed for TCI and for the cessation of both wood growth and leaf discoloration. A warmer climate and longer daylength were associated with delayed autumn phenology. However, for Belgium in 2020, start of senescence and cessation of wood growth were unexpectedly early than in Norway in the same year, likely because of heat and drought stress. We also conclude that, because of its higher precision, CWGb is a better proxy of xylem maturation timing than the more conservative cessation of wood growth (CWG) for slowly growing trees at high latitudes with marginal (terminal) parenchyma at the growth ring boundary and likely for other species and latitudes too.

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Author contributions All authors contributed to the study conception and design. Material preparation and data collection were performed by Friederike Gehrmann and Manuela Balzarolo. The first draft of the manuscript was written by Friederike Gehrmann. The following drafts were written and the following data elaborations were performed, until the final manuscript, by Paolo Zuccarini. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest All the authors declare they have no relevant financial or non-financial interests to disclose.

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