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Severe drought can delay autumn senescence of silver birch in the current year but advance it in the next year

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Abstract

Historically, the autumn dynamics of deciduous forest trees have not been investigated in detail. However, autumn phenological events, like onset of loss of canopy greenness (OLCG), onset of foliar senescence (OFS) and cessation of wood growth (CWG), have an important impact on tree radial growth and the entire ecosystem's seasonal dynamics. Here, we monitored the leaf and wood phenological events of silver birch (*Betula pendula*) at four different sites in Ås, southeastern Norway: (a) a natural mature stand, (b) a plantation on former agricultural ground, (c) young natural trees, and (d) young trees in pots under different fertilization levels. The study took place over four consecutive years (from 2017 to 2020), with a particular focus on 2018, a year in which there was a severe summer drought, and the next year, 2019, which featured more normal conditions. First, we provided a description of birch phenology within its mid-north distributional. Second, we showed that drought advanced CWG by about 5 to 6 weeks and it delayed OLCG and OFS up to 30 days. Third, we observed an unexpected advance in OLCG in 2019 compared to 2018 (30 days) and 2020 (14 days). OFS presented similar dynamics as OLCG, whereas CWG was advanced only in 2018. These findings might indicate lag-effects of severe drought on the next year autumn leaf phenology but not on wood growth. On the other hand, the comparison between the natural stand and the plantation showed that, under drought conditions, wood growth is more sensitive to site fertility than autumn leaf phenology. In summary, our study elucidated the autumn dynamics of an important deciduous forest species in the northern temperate zone and showed unexpected impacts of a severely dry and warm summer on the current and next year leaf phenology.

Keywords: Betula pendula, silver birch, cessation of wood growth, autumn leaf phenology

Introduction

Phenology is the study of lifecycle events in plants and animals (Lui *et al.*, 2016, Chen *et al.*, 2018). Changes of phenological events, due to global change, can have a considerable impact on deciduous forest ecosystems (Forrest & Miller-Rushing, 2010). In spring, the buds of deciduous trees break, unfolding their leaves. Furthermore, the cambium reactivates and starts to make new xylem and phloem cells. In the xylem, the produced cells first enlarge and then undergo a maturation process (deposition of a secondary cell wall and lignification of the cell walls). When the xylem cells reach maturation, the wood growth ceases (cessation of wood growth: CWG) and, with the exception of parenchyma cells, the cells undergo programmed cell death (Plomion *et al.*, 2001). At the end of the growing season, deciduous trees start the process of foliar senescence (onset of foliar senescence: OFS), which allows trees to reabsorb nutrients before leaf shedding (Estiarte & Peñuelas, 2015). OFS is defined as coinciding with the start of chlorophyll degradation in autumn (Mariën *et al.*, 2019). OFS should not be confused with onset of loss of canopy greenness (OLCG), which is the moment in autumn when the tree starts to change canopy color (and lose leaves) rapidly (Mariën *et al.*, 2021). OLCG and OFS can be concurrent (Mariën *et al.*, 2019, Dox *et al.*, 2020) but OLCG can also occur significant earlier, e.g. in case of drought (Mariën *et al.*, 2021). To better understand tree growth dynamics under future climate change, it is important to further study wood and leaf phenology and their relationship with the climate. Most phenological studies on deciduous forest ecosystems have focused on spring phenology (Gallinat *et al.*, 2015). Even though spring phenological events are important for the beginning of the growing season, autumn phenology is also very important for ecosystem functioning. The timing of wood growth cessation and onset of foliar senescence is of fundamental importance to, among other things, the development and survival of the tree, ecosystem nutrient cycling, trophic relationships, the seasonal exchange of matter and energy between the biosphere and the atmosphere and can affect the feedbacks of forests to global change (Peñuelas *et al.*, 2009; Richardson *et al.*, 2010; Richardson *et al.*, 2013; Gallinat *et al.*, 2015). However, autumn events are difficult to assess (Gallinat *et al.*, 2015) as, for instance, it is much harder to pinpoint the timing of OFS compared to the clear bud-burst timing in spring. Furthermore, whereas cell production and enlargement can partly be studied through the changes in stem diameter, observation of cell maturation requires microscopic anatomical analyses (Deslauriers *et al.*, 2017). Therefore, our main focus here will be on the understudied autumn phenology of deciduous forest trees.

Multiple internal (e.g. genes regulations, hormones) and environmental (e.g. temperature, day length) factors have been shown to play a specific role in controlling autumn phenology for different species, sites and regions (Estiarte & Peñuelas, 2015; Lim & Nam, 2005; Fracheboud *et al.*, 2009). However, we still do not know the primary driver or triggering mechanism of OFS, OLCG and CWG and the timing relationships between them. Here, we want to study the timeline and relationships between OFS, OLCG and CWG in a very dry year (2018) and more normal years (2017, 2019 and 2020) for the silver birch (*Betula pendula* Roth.), a model species, at the northern edge of the temperate zone, i.e. Southern Scandinavia. This zone experienced a very severe drought in 2018 (Thompson *et al.*, 2020). Moreover, drought frequency and intensity is expected to increase in such climate zones (IPCC, 2018) where tree genotypes might be less adapted to drought stress (Hamanishi & Campbell, 2011).

Specifically, we tested three hypotheses. The first hypothesis is that OFS, OLCG and CWG are all advanced by severe drought in the Northern temperate zone. With respect to OFS, advancements due to drought are supported by physiological studies (Munné-Bosch & Alegre, 2004; Jan *et al.*, 2019). A recent study on birch showed no significant changes of OFS due to drought (Mariën *et al.*, 2021), but it pertained to a sandy site in the central part of the European zone (Belgium), where birch populations might be more adapted to drought. A similar reasoning applies to CWG. In more southern locations, the response of CWG of deciduous tree species to drought was found to depend on species (Dox *et al.*, 2021) or regions (see the different timing of CWG between beech sites reported in del Castillo *et al.*, 2016 and Dox *et al.*, 2020 for Spain). Cases in which CWG was advanced in a dry year were also reported in Liang *et al.* (2016) and Swidrak *et al.* (2014). However, northern genotypes might be more sensitive to drought. With respect to OLCG, our expectations regarding drought-related advancement are solid as this is reported for southern birch populations (Mariën *et al.*, 2021), in manipulative experiments on seedlings (Wendler & Millard, 1996) and – independent of the autumn senescence dynamics – severe drought is regularly associated with leaf yellowing and fall due to severe heat damage or as protective mechanism of the trees to avoid hydraulic failure (Breda *et al.*, 2006). Advancement of OLCG in response to the 2018 drought has been reported (Brun *et al.*, 2020, Buras *et al.*, 2020). The second hypothesis is that the severe drought would have a legacy effect on the next year wood growth but not on leaf phenology. Therefore, for the year following a year with a severe summer drought, we expect that CWG would be advanced but no effect would be visible on leaf senescence dynamics. In fact, lag-effects of drought have been shown on the ring width of the following years, being more narrow than expected (Kannenberg *et al.*, 2019), and lag-effects on wood growth phenology have been shown after mast years (Hacket-Pain *et al.*, 2015). Moreover, it is well known that drought reduces the canopy cover of subsequent year(s) (Campioli *et al.*, 2012), but not much has been reported on inter-annual drought effects on autumn phenology (but see Le Dantec *et al.*, 2000; Kannenberg *et al.*, 2019; Massonnet *et al.*, 2021). The third hypothesis postulates that drought responses are less pronounced at more fertile sites, where fertility assures a larger growth rate. This reasoning is based on an overall higher tree fitness under optimal compared to suboptimal growth conditions.

We tested these hypotheses for different populations, trees and experimental settings of silver birch at the same location, in Ås, southeastern Norway. In particular, we investigated five groups of individuals: (i) a mature natural stand growing under suboptimal conditions (moderate site fertility); (ii) a mature experimental plantation on previous agricultural land under optimal growth conditions (high site fertility); (iii) young trees growing in natural soil; (iv) young trees grown in pots under suboptimal conditions (low fertilization) and (v) young trees grown in pots under optimal conditions (high fertilization). The study was performed over a four-year period (2017-2020), but with a greater focus on the exceptionally severe dry and warm 2018 and the next more normal 2019. We had two objectives. First, describe the (understudied) leaf and wood phenology of birch. For example, a previous study showed that the wood growing season of birch in northern Scandinavia is only two months long (Schmitt *et al.*, 2004) but no information is available for Southern Scandinavia, which lies at the border of the temperate and boreal zones. Second, test the aforementioned hypotheses.

Materials and Methods

Species

Birches (Betulaceae) are common deciduous tree species in temperate and boreal ecosystems. Birch species are economically important and in Northern Europe they are even the main source of hardwood (Hynynen *et al.*, 2010). They are light-demanding pioneers, with a low demand for soil resources and an abundant production of seeds that are easily dispersed by the wind. In the boreal zone, birch can even co-dominate in late-successional vegetation.

Birch species have a sympodial height growth, with a straight and rather slender stem (Hynynen *et al.*, 2010). They have a non-deterministic leaf growth, meaning that their leaves can be formed throughout the growing season. If the conditions for growth are very favorable, the annual ring width increment can be as much as 3 to 4 mm (Hynynen *et al.*, 2010). Birches can reach a height up to 25 m at 30 years (Eriksson *et al.*, 1997), although height differences can be very pronounced as a result of genetics and soil fertility (Eriksson *et al.*, 1997; Skrøppa & Solvin, 2019). Skrøppa and Kohmann (2018) showed also that silver birch trees from the same provenance can show a considerable diversity in height growth. According to Wang and Tigerstedt (1993), genetic variation in silver birch is mainly visible by means of the monitoring of phenological events such as bud-burst.

Mature trees

Birch individuals were studied from two populations located at Hoxmark Experimental Farm, Ås, Norway (latitude 59° 40’ N, longitude 10°42’ E, altitude 86 m a.s.l.; Figure 1): an experimental plantation and a natural stand. Whereas the former was selected to sample trees with an optimal and higher growth rate, the natural stand was selected to study wild-type individuals in suboptimal conditions with a lower growth rate. At the natural stand, the phenological monitoring occurred throughout the growing season of 2018 and 2019 to establish a phenological timeline for leaf and wood phenology of the silver birch in the northern temperate zone. Additionally, the autumn phenology was monitored for the years 2017 and 2020. At the plantation, the autumn phenology was monitored in 2018, 2019 and 2020.

Experimental plantation. In the spring of 1976, nine trees originating from the same property at Søndre Land, Oppland County, Norway (latitude 60° 33′ N, longitude 10° 16’ E, altitude 300 m a.s.l.), were used as genetic material for the plantation. These trees (parent trees) were all randomly selected, standing more than 50 m apart from each other and growing next to agricultural land (for more details on pollination and seedling development, see Skrøppa & Solvin 2019). The seedlings were planted in August of 1977 on former cultivated soil at Hoxmark Experimental Farm, following a randomized blocks design with squared plots (composed of four trees per plot) for different families, 12 replicates and an overall spacing of 1 m. Six of the replicates were thinned after the sixth growing season when the mean height was 2.8 m. At the stage of thinning, the tallest tree without visible damage was left in each four-tree plot, changing the mean spacing to 2 m. The trees in the other six replicates were cut. A second thinning, ignoring family relationships and based on growth and quality considerations, was made in the remaining six replicates after 19 growing seasons (1995) when the mean tree height was 14.1 m, reducing the number of trees to a spacing equivalent from 2500 to 1350 trees per hectare. Of the 4080 trees planted at the establishment of the trial, 504 remained after the first and 285 after the second thinning (Skrøppa & Solvin, 2019). From this population, we randomly selected 12 trees (with a mean height of 19.9 ± 0.6 m and a mean diameter at breast height (DBH) of 18.5 ± 0.8 cm; Table 1). The trees were randomly located within the plantation and not on its borders to exclude place and edge effects. These trees were monitored for leaf and wood phenology in late summer and autumn.

Natural stand. Dominant and codominant healthy individuals of silver birch were selected in a natural mixed stand of moderate fertility with mainly silver birch and Norway spruce (*Picea abies* L.), close to the plantation, about 115 m apart (Figure 1). Compared to the plantation, the natural stand had a less favorable exposition (NE vs SW) and a significantly steeper slope (18 vs 8.5 degrees; Table 1). Moreover, the birch trees there experienced more competition for light due to the presence of the Norway spruce. Groups of individuals ranging in number from 3 to 8 were selected for observations of leaf and wood phenology. Leaf phenology of the same eight individuals was monitored between spring 2018 and autumn 2020. For wood phenology, the same four trees were measured for the whole growing seasons of 2018 and 2019. As a third year of sampling might have damaged the trees, an additional four individuals were selected in 2019, sampled in summer-autumn of 2019 and again in summer-autumn of 2020. Leaf and wood phenology measurements in 2017 were limited to three trees (two of which were further studied in the other years) but are added here for completeness (see the detailed tree sampling scheme in Supplementary Table 1). The mean DBH was 28.7 ± 2.8 cm and the height was 25.0 ± 2.6 m (Table 1).

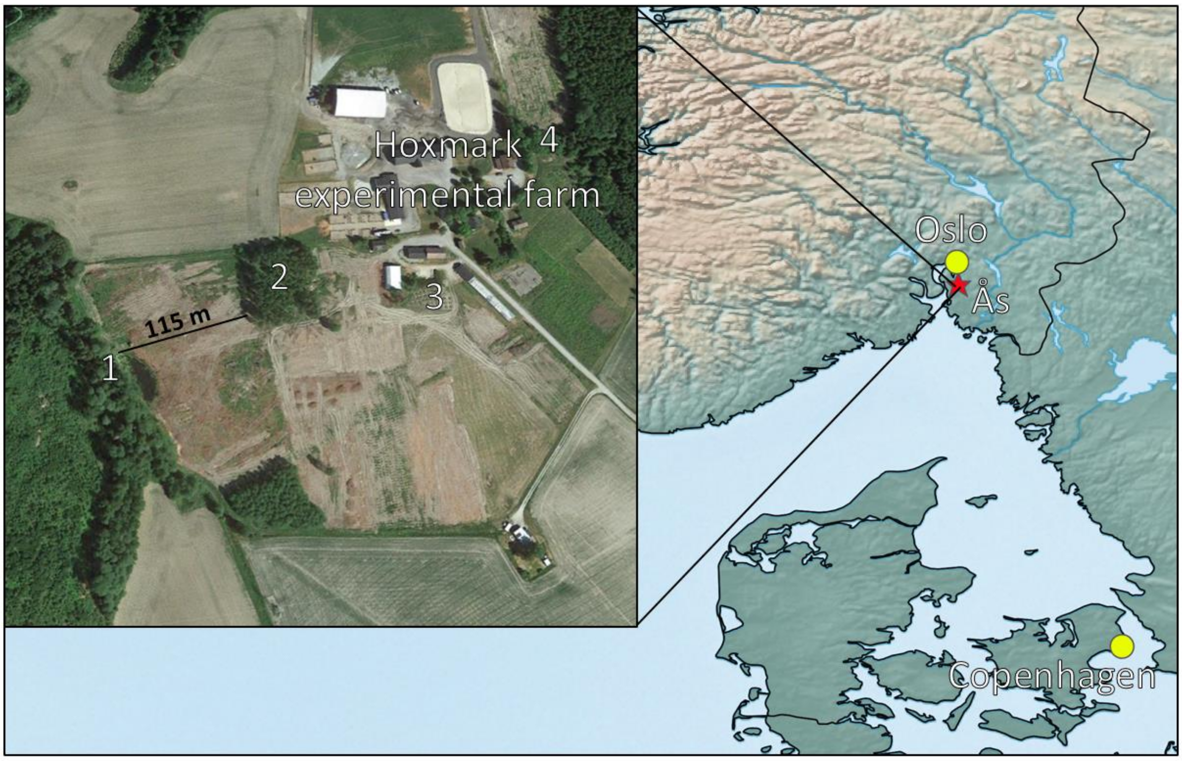


Figure 1: Location of Hoxmark Experimental Farm, showing (1) the mature natural stand; (2) the plantation; (3) young trees in pots; and (4) natural young trees.

Natural young trees

Three young birch trees (height: 7.6 ± 1.1 m; DBH: 4.8 ± 1.1 cm; likely ca. 8-10 years old) were additionally selected for complementary measurements of leaf phenology (see below). In fact, in contrast to the mature trees, the leaves of these individuals were reachable from the ground and could be measured in more detail. These trees were located 210 meters from the experimental plantation and 370 meters from the natural stand (Figure 1).

Young trees in pots

Young individuals in pots were grown next to the experimental plantation (Figure 1). The saplings were obtained from a private nursery growing local plants and were planted in April 2017 into 35 l pots, filled with a nutrient-poor substrate made of 90% fine sand and 10% peat. The pots were organized in square plots (approximately 1.5 × 1.5 m), each of which contained 16 pots (four rows of four pots). The spaces in between the pots were filled with soil to provide thermal isolation. The trees were part of a larger experiment (comprising different species and treatments). For this study, we considered 12 trees under high fertilizer treatment (per year 140 mg NPK, plus micro-elements) and 12 under low fertilizer treatment (per year 20-40 mg NPK, plus micro-elements) distributed in multiple plots. However, some trees died in the first year and in the summer of 2018 and our data analysis eventually comprised 9 and 11 replicates, respectively. The trees were irrigated regularly during dry periods, with a uniform amount of water for each individual. Because irrigation was applied only in this experimental setting, we will not compare the timing of autumn dynamics of the potted young trees with similar data from other settings. Instead, we will use this experimental setting to primarily investigate inter-annual dynamics for different fertilization levels.

Table 1: Information on stand location, tree characteristics (mean ± 1SE) and overview of the measurements done. OLCG: Onset of loss of canopy greenness; OFS: Onset of foliar senescence; CWG: Cessation of wood growth; DBH: diameter at breast height

Stand	Height (m)	DBH (cm)	Tree-ring width 2018 (µm)	Tree-ring width 2019 (µm)	Soil	Exposition and slope (°)	age	Measurements		
								OLCG	OFS	CWG
Plantation	19.9 ± 0.6	18.5 ± 0.8	469 ± 40	1451 ± 89	Former agricultural land, well drained, highly fertile	South-west 8.5	44	2018-2020 (n = 12)	NA	2018-2019 (n = 12)
Natural stand	25.0 ± 2.6	28.7 ± 2.8	565 ± 56	460 ± 135	Soil with a thick humus top layer over a layer with a large amount of clay, well-drained on the slope but with poorer drainage on the slope base; moderate fertility	North-east 18	65(a)	2017-2020 (n = 3-8)	NA	2017-2020 (n = 3-8)

Natural young trees	7.6 ± 1.1	4.8 ± 1.1	NA	NA	Soil with a thick humus top layer over a layer with a large amount of clay, well-drained	North-west 3.8	8-10(a)	2018-2019 (n=3)	2018-2019 (n=3)	NA
Potted young trees	ca. 1.5	ca. 2	NA	NA	90% sand and 10% peat, different level fertilizer	No slope	4	2018-2019 (n=9-11)	2018-2019 (n=9-11)	NA

(a) Indirectly derived from yield-tables

W*eather*

The year 2017 was a rather warm year, with a mean annual temperature of 6.7°C, compared to a long-term average of 5.9°C (1980-2010) (Table 2). The winter months (Jan-Mar, Nov-Dec) were warmer than the long-term mean (up to 1.2°C, Table 2) but summer values were well within the normal range. The amount of precipitation that fell in 2017 was 975 mm, compared to a long term-average of 855 mm. Only July was drier than usual with approximately only 50% of the long-term precipitation in this month (Table 2). In 2018, the weather in Ås was dry and exceptionally warm, particularly between May and August. The mean temperature in 2018 was 7.5 °C, which is 1.6°C higher than the long term average (Table 2). On May 8, the first summer day (max temperature > 20 °C) was registered. In total, 86 summer days and 44 high summer days (max temperature > 25 °C) were recorded in 2018 in Ås, mainly in the months May, June and July (meteo report NMBU 2018). May, in particular, was extraordinarily warm, with a mean temperature of 15.5 °C, which is the highest mean temperature ever measured in May in Ås and 4.6 °C higher than the normal May temperature (meteo report NMBU 2018; Table 2). Not only were the months May – August very warm, they were also very dry, with only 168 mm precipitation, of which 58.4 mm fell on one day, the 17th of June (Figure 2b). This is very low compared to the long-term average of 308 mm for May – August (Table 2). The year 2019 was also warm (mean temperature 6.8 °C), but wet (1036 mm). The early spring (March and April) was warmer in 2019 compared to 2018 (Table 2; Figure 2). However, late spring and summer (May – August) were in 2019 substantially cooler than in 2018 (Table 2). The mean temperature in 2020 was very high (8.2°C). This was due to the warmer winter months (Jan-Mar, Nov-Dec), which were up to 4.5°C warmer than the long-term mean, though June was also warmer than the long-term mean (2.9°C) (Table 2). The year 2020 was also an exceptionally wet year with a total precipitation of 1139 mm, but drier periods were recorded in April-May and August-September (Table 2). As the extreme 2018 and the subsequent 2019 were of particular interest, additional information were reported for these two years: (i) 5-days mean of air temperature (Figure 2a), (ii) monthly precipitation (Figure 2b) and, as index of soil water content (Figure 2c), (iii) the relative soil moisture. Furthermore, as and index for the atmospheric aridity, 5-days mean of the vapor pressure deficit is shown (Figure 2d). The relative soil moisture is based on simulations (done with the HBV-H19 hydrological model; Bergström, 1976; Huang *et al.*, 2019) of the water contained in the unsaturated zone, i.e. down to the respective groundwater level. The temporal resolution is daily and the spatial resolution is 1 km^2, centered in Hoxmark Experimental Station. The HBV-simulated value (in mm) is rescaled by the highest value obtained in the period 1981-2010 for each particular calendar day separately. This implies that for the years 1981-2010, all the values are bound to be <= 1; outside that period, values > 1 may occur (and indicate an extreme wetness at least at a 30 years return period). The vapor pressure deficit (VPD) is calculated using the formulas of Buck (1981; Eq. 1-3; Figure 2d):

$$e_0 = 613.75 \times \exp\left(\frac{17.502 \times T}{240.97+T}\right) \qquad \text{Eq. 1}$$

$$e = \frac{RH}{100} \times e_0 \qquad \text{Eq. 2}$$

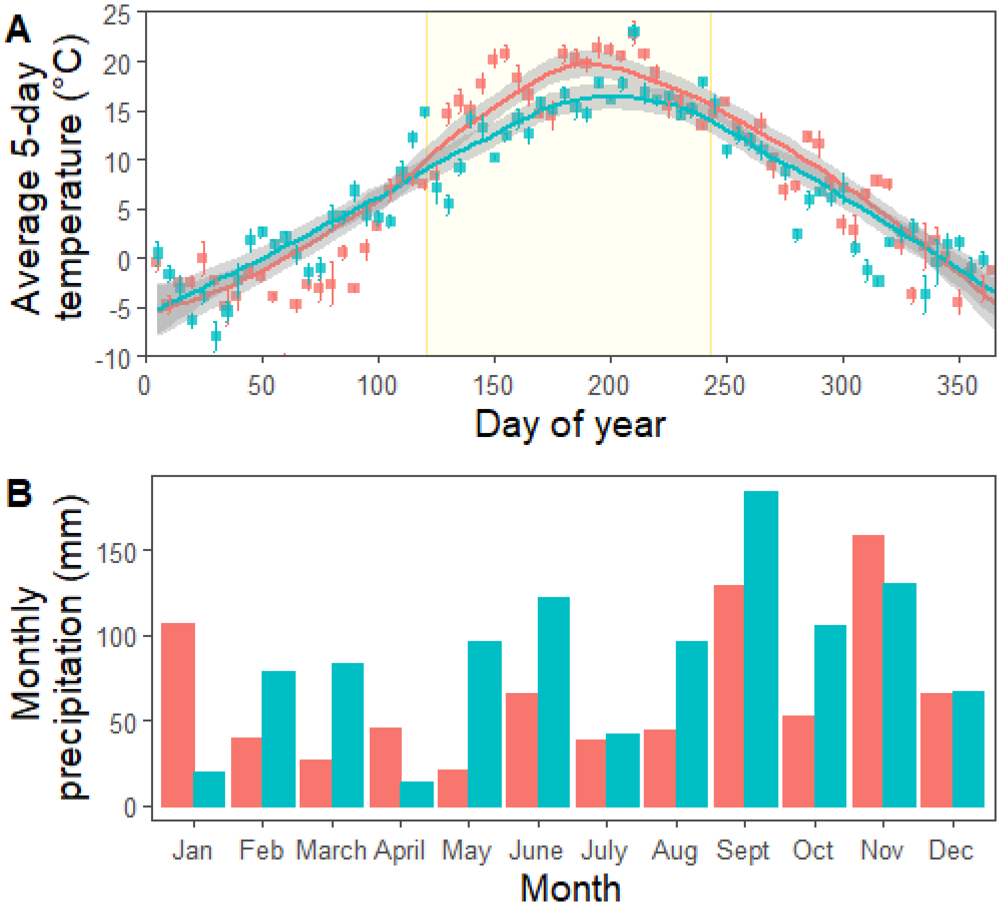
$$VPD = e_0 - e \qquad \text{Eq. 3}$$

with e_0 as the saturation vapor pressure (in Pa), T as the air temperature (in °C), e as the actual vapor pressure deficit (in Pa), RH the relative humidity (in %) and VPD the vapor pressure deficit (in Pa).

Table 2: Monthly temperature (°C) and precipitation (mm) for 2017, 2018, 2019 and 2020 and the long-term average (1981-2010) in Ås, southeastern Norway. Data from meteo report NMBU 2018 and from the NMBU weather station.

Temperature													
	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Mean
2017	-1.4	-1.9	2.1	4.6	11.1	14.5	16.1	14.6	11.6	6.7	1.3	-2.0	6.7
2018	-2	-4.4	-2.9	5.7	15.5	17.4	21.1	16	12.5	7.4	3.5	-1.2	7.5
2019	-3.9	0.2	2.1	7.9	9.9	14.6	17.2	16.3	11.3	5.2	0.2	0.2	6.8
2020	3.2	1.7	2.6	6.6	9.5	17.6	14.4	16.2	12.3	7.5	5.1	2.0	8.2
Long-term	-3.4	-3.1	0.1	4.9	10.7	14.3	16.5	15.4	11	6	1.2	-2.9	5.9

Precipitation													
	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
2017	61	63	43	44	67	95	41	133	122	139	101	66	975
2018	107	40	26	45	21	66	38	43	129	53	159	66	794
2019	19	78	83	13	96	122	42	96	184	105	130	67	1036
2020	74	79	64	29	45	98	133	51	75	165	95	230	1139
Long-term	60	44	53	48	56	72	84	96	83	105	94	62	855


A
Average 5-day temperature (°C)
25
20
15
10
5
0
-5
-10
0
50
100
150
200
250
300
350
Day of year
B
Monthly precipitation (mm)
150
100
50
0
Jan
Feb
March
April
May
June
July
Aug
Sept
Oct
Nov
Dec
Month

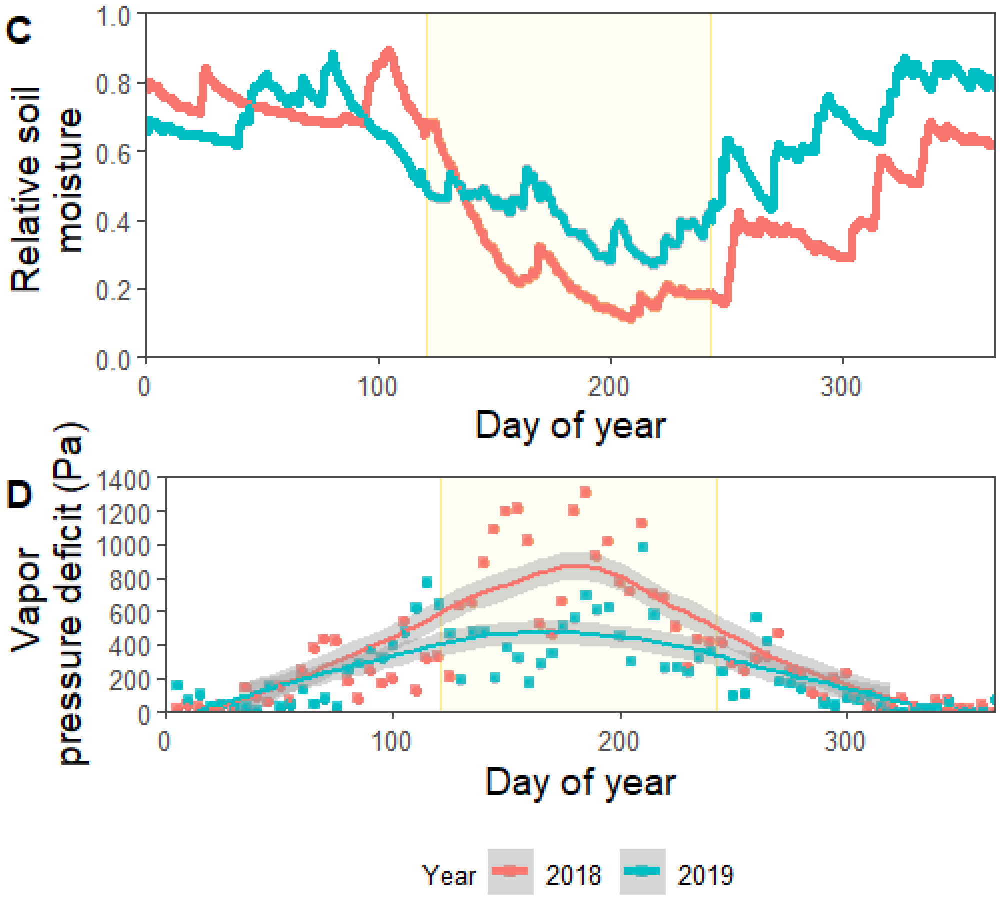


Figure 2: (a) The squares indicate the mean five-day temperature (°C), with bars indicating ± 1SE, for Ås, Norway, in 2018 (red) and 2019 (blue). The continuous lines (interpolation) and the grey band around the lines (uncertainty) are the output of the smooth function of R package ggplot2. (b) Monthly precipitation for Ås, Norway, in 2018 (red) and 2019 (blue). (c) Relative soil moisture (the seasonal soil water content compared to the maximum soil water content observed in the period 1981-2010) for 2018 (red) and 2019 (blue) at the Hoxmark area. (d) The squares indicate the mean five-day vapor pressure deficit (Pa), for Ås, Norway, in 2018 (red) and 2019 (blue). The continuous lines (interpolation) and the grey band around the lines (uncertainty) are the output of the smooth function of R package ggplot2. For panel (a), (c) and (d) the light yellow band shows the period May, June, July and August, which was severely warm and dry in 2018. Data in panel (a) and (b) originate from the weather station at Hoxmark and, when gaps were present, from the NMBU weather station (at 3.7 km), corrected with regression equations for Hoxmark. Data in panel (c) are from the Norwegian Water and Energy Directorate (see text). To calculate the vapor pressure deficit (see text) in panel (d), air temperature originated from the weather station at Hoxmark, whereas the relative humidity was from the NMBU weather station (at 3.7 km).

Bud-burst

Bud-burst was followed weekly at the natural stand in 2018 and 2019 from mid-April to mid-May. Each week, five random buds of the upper third of the crown and five random buds of the lower third of the crown (to account for possible variability in bud-burst timing within the crown) were assigned a score according to a five-stage scale: 0: Dormant bud; 1: Swelling bud; 2: Bud-burst; 3: Emerging leaves, and 4: One leaf at least is completely detached from the bud. For more details and bud-burst calculations, see Marchand *et al.* (2020).

Onset of loss of canopy greenness (OLCG) and onset of foliar senescence (OFS)

OLCG and OFS were derived from seasonal measurements of loss of canopy greenness and chlorophyll content index (CCI), respectively. The loss of canopy greenness was measured for both mature and young trees, whereas CCI only for young trees (the canopy of mature trees was not accessible). The loss of canopy greenness (x_t, %) was estimated visually by a combined rating of the percentage of leaves that had changed color (α_t) and the percentage of leaves that had fallen (β_t), as described by Vitasse *et al.* (2009):

$$x_t = \frac{\alpha_t \times (100-\beta_t)}{100} + \beta_t \qquad \text{Eq. 4}$$

Observations were recorded weekly from early August to late October when all trees had reached an x_t of ca. 100%. In the same period, chlorophyll content index (CCI) was measured once a week for three leaves per tree using a CCM-200+ leaf absorption meter (ADC Bioscientific Ltd., 159 Hoddesdon, UK). The leaves were in the upper third of the crown for young potted trees and in lower third of the crown for the natural young trees for reason of accessibility. However, none of the latter leaves were over-shaded and could be considered sun leaves like those of the potted trees. The CCI can be considered a proxy of chlorophyll content. For more details on CCI and its measurement, see Mariën *et al.* (2019) and Dox *et al.* (2020).

For both mature and young trees, OLCG was determined at single tree level as the date on which the seasonal loss of canopy greenness increased significantly by performing a breakpoint analysis using the R package 'segmented' (Muggeo, 2008). Before OLCG, some leaf coloration and abscission is possible and mainly related to stress damage, premature senescence associated with stress, leaf mortality due to drought avoidance, mortality of older leaves etc. (Mariën *et al.*, 2021). In this study, loss of canopy greenness was negligible before mid-August and on average about 11% at OLCG for adult (see below). The package 'segmented' (i) builds linear regressions for dependent variables that can be fitted by two or more straight lines with different slopes linked at a breakpoint and (ii) calculates these breakpoints (Mariën *et al.*, 2019, Dox *et al.,* 2020.). Similarly, OFS was calculated for the young trees from a breakpoint analysis of a seasonal series of CCI for each individual tree. In 2017, measurements of loss of canopy greenness and CCI started only in mid-September and OLCG and OFS of young trees could not be determined for this year. For the natural stand, an estimate of OLCG was obtained by taking the mid-August value of 2017 as the average of the same value for the other years. This approximation is sound, as in mid-August the loss of canopy greenness is minimal at the natural stand (< 5%) and without differences across years (see below).

To gain additional information about the results provided by the breakpoint analysis, we compared OLCG obtained with the breakpoint approach and OLCG obtained by applying different thresholds of canopy greenness, i.e. 10%, 20%, 30%, 40% and 50% (Mariën *et al.*, 2019). This was done for both the natural stand and the plantation, for all years available.

Xylem formation

The stem micro-cores were collected at breast height with a Trephor tool (Rossi *et al.*, 2006). An upward spiral pattern of sampling was followed throughout the season to minimize wound reactions (Gričar *et al.*, 2017). The samples were stored in 1.5-ml Eppendorf micro-tubes containing a 70:30 EtOH:H_2O solution for conservation. The micro-cores were cut in the lab to maintain only the most recently created xylem rings (at least two), the cambium and the inner phloem. These segments were then dehydrated in a series of rising ethanol concentration, 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 paraffin blocks were cut into 5-10 µm cross-sections with a microtome (Leica Microsystems, Wetzlar, Germany). Next, the paraffin was removed with a clearing agent (UltraClear) and ethanol. The sections were then stained in an aqueous solution of safranin (Merck, Darmstadt, Germany) and Astra blue (Sigma–Aldrich, Steinheim, Germany). The slices were supported by mounting in Euparal (Waldeck, Munster, Germany) (Gričar *et al.*, 2017). The slides were then examined under a light microscope (Leica DM 4000 B/M, Wetzlar, Germany) and a Leica LAS image-analysis system using both transmission and polarized light to do observations of xylogenesis. For each year, and for both mature stands, the micro-cores were taken weekly in August, September and October. In 2018 and 2019, at the natural stand, micro-cores were also taken in April, May, June and July. However, in 2018, the micro-cores were taken in this period less frequently (every 2-3 weeks) than for the same period in 2019 (every 1-2 weeks). As such, the annual xylogenesis dataset for 2019 was more complete and it will be shown here in more details. We determined the following critical points: 1: Onset of cambial activity (increase in the number of cambial cells; onset production of new xylem and phloem cells); 2: Appearance of initial earlywood vessels (enlargement of the first vessels of the current year-ring); 3: Fully differentiated initial early wood vessels (early wood vessels and the neighboring fibers are fully lignified and sap can run through them); 4: End of cambial activity (decrease in the number of cambial cells; no new expanding xylem and phloem cells); 5: End of xylem growth, defined as the point when the cells of latewood are lignified and thus have completed cell wall thickening (Gričar *et al.*, 2017). This stage is recognizable by a completely red cell wall through the safranin/Astra blue staining, whereas cells that have not completed wall thickening are colored blue (i.e. non-lignified) on the inside of the cell wall and red (i.e. lignified) on the outside. In late summer and autumn, we estimated the weekly percentage of xylem cells still in the wall thickening phase (wall thickening cells: WTC) as the ratio between the width of the layer of WTC and the width of the current year ring. The width of the layer of the WTC can also be used directly as an index of growth (Dox *et al.*, 2020), but we preferred to use the percentage of the WTC, because of its value relative to annual growth. We defined the end of wood growth (CWG) as the start of (at least) a 3-week period with the percentage of WTC < 0.50%. Therefore, the date of CWG per tree was set as the first sampling date with WTC < 0.50% of a series of at least three consecutive sampling dates with WTC < 0.50% (Dox *et al.*, 2020 for details). A basic sensitivity analysis for this procedure was done here by determining CWG also when applying a 0.25% and 1% threshold of WTC. Specific information about sample collection (start date, end date, sampling frequency and the number of trees sampled) can be found in Table 3.

Table 3: Information on the monitoring of xylem formation for the different years and settings of birch in southeastern Norway.

Site	**Year**	**Starting date**	**End date**	**Sampling frequency**	**Number of trees**
Natural stand	2017	28/08/2017	19/10/2017	weekly	3
Natural stand	2018	18/04/2018	11/10/2018	Every 2-3 weeks till 28/06; weekly from 07/08	4
Natural stand	2019	23/04/2019	28/10/2019	Weekly (in June-July occasionally each 2 weeks)	4 in spring/ 8 in autumn
Natural stand	2020	27/07/2020	26/10/2020	weekly	4
Plantation	2018	07/08/2018	11/10/2018	weekly	12
Plantation	2019	14/08/2019	22/10/2019	weekly	12

Statistical analysis

Stand data were the average of individual tree data (n = 3-8 for the natural stand and n = 12 for the plantation). The normality of residuals and homogeneity of variances were tested with a Shapiro-Wilk test and a Score Test for Non-Constant Error Variance (ncvTest) or LeveneTest (‘car’ package), respectively. The significance level was set at $p < 0.05$. For all statistical analyses and graphs, we used Rstudio version 3.2.2 (R Core Team 2016).

Cessation of wood growth and onset of loss of canopy greenness. To test for significant difference in CWG or OLCG between the plantation and the natural stand, an ANOVA – corrected for non-homogeneity of variances (White-corrected ANOVA) when necessary – was performed for each year separately. For both stands, a repeated measures ANOVA was used to test for the significant difference over the years. When different methods to determine OLCG and CWG were compared (see above), similar statistical analyses to the ones just described were used. For the young trees, significant difference between OLCG and OFS estimates for each year was also tested with a standard ANOVA. In contrast, significant difference in OLCG or OFS between years was tested with a repeated measurements ANOVA.

Comparison cessation of wood growth and onset of loss of canopy greenness. To test for significant difference between CWG and OLCG dates per stand and year, a repeated measurements ANOVA – corrected for non-homogeneity of variances (White-corrected ANOVA) when necessary – was performed.

Tree-ring width. Comparison between tree-ring width of the same stand over years was done with a repeated measurements ANOVA or Wilcoxon test for the natural stand (because it did not pass the normality test). Comparison between stands for the same year was done with a standard ANOVA.

Results

Seasonal phenological description of natural birch stand

First, a detailed seasonal phenological description of wild birch is reported for the more typical 2019, for both leaf and wood growth dynamics. Second, the timing difference between the key phenological events between 2018 and 2019 is reported. Third, the differences between OLCG and CWG in the year 2017, 2018, 2019 and 2020 are reported.

Phenology in 2019. Mean bud-burst of our natural birch stand at the study site occurred on the 24th of April (DOY 114 ± 0.4, mean ± SE). The wood growth (cambial reactivation) started at the beginning of May (DOY 125 ± 1.5; significant difference with bud-burst: $p = 0.01$; Figure 3 & Figure 4b). Initial early wood vessels (IEWV) started to form by the end of May (Figure 3 & Figure 4b) and were functional by the end of June (Figure 3 & Figure 4c). Cambial activity ceased in late July/early August (Figure 3 & Figure 4d). CWG took place at the beginning of September (DOY 248 ± 2.3; Figure 3 & Figure 4e), whereas OLCG took place on the 25th of August (DOY 237 ± 1.3; significant difference in date with CWG: $p = 0.001$).

Figure 3: Timeline of leaf (red) and wood (yellow) phenology for a natural birch stand in southeastern Norway for 2019. BB: Bud-burst; OLCG: Onset of loss of canopy greenness; CA: Cambium activity; IEWV: Initial early wood vessels; CWG: Cessation of wood growth. The horizontal lines above the timeline indicate the length of the leaf (red) and wood (yellow) growing season.

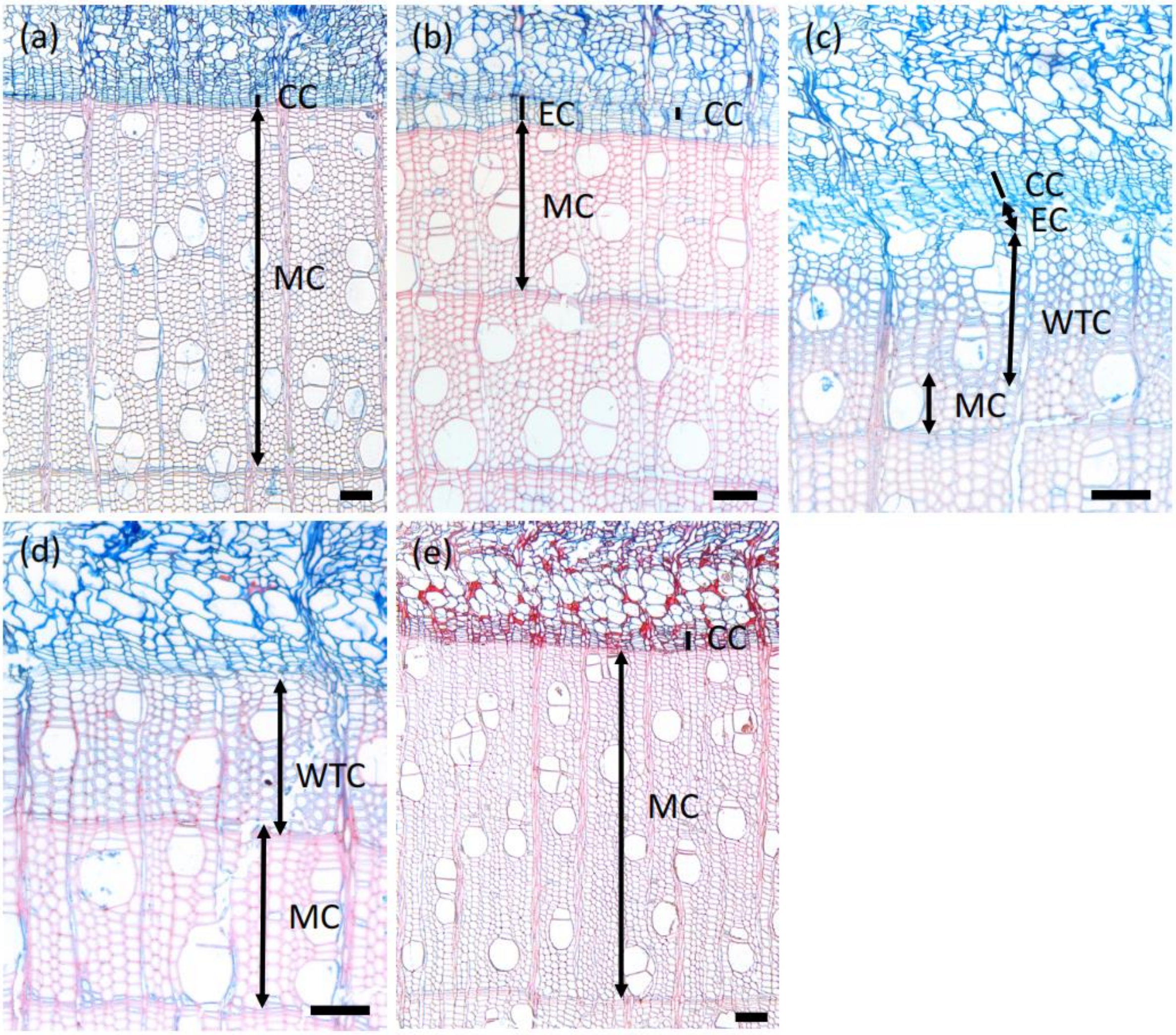


Figure 4: Intra-annual xylem formation in birch. (a) In the second half of April (18th April) cambium (CC) was still unproductive. Cells in the previous year growth ring were fully mature (MT). (b) At the end of May (27th May), the number of cells in cambium (CC) increased, indicating the onset of cell production. Furthermore, cells in the phase of enlargement (EC) including initial earlywood vessels were also present. (c) In the middle of June (13th June) cells

in the initial part of xylem growth ring were fully mature (MC) with potentially operative vessels. The predominant part of the xylem ring is in the wall thickening phase (WTC). (d) At the end of July, cambium ceased productivity, but the last formed cells were still in the phase of secondary wall formation. (e) In the second half of August growth rings were completely formed. Scale bars = 100 µm.

Phenological comparison of 2018 and 2019. Bud-burst at the natural stand occurred in 2018 at the beginning of May (DOY 123 ± 0.5). This was 9 days later than in 2019 (see above; significant difference at $p \leq 0.001$). Cambial reactivation occurred by the end of April in 2018 (DOY 116 ± 5.4), with no significant difference between 2018 and 2019 ($p = 0.29$). As reported above, in 2019, bud-burst occurred about two weeks before cambial reactivation, with a significant difference. In 2018, bud-burst took place after cambial reactivation, but the difference was not significant ($p = 0.29$). In 2018, CWG took place at the end of July (DOY 206 ± 10.1), about 43 days earlier than in 2019 (significant difference $p = 0.04$, Figure 5). Note that growth cessation occurred very rapidly in 2018, with trees still in cambial activity on DOY 193 and with full cessation on DOY 206 (Figure 5). However, OLCG occurred in late September in 2018 (DOY 267 ± 2.1, Supplementary Table 2) a month later compared to 2019 ($p < 0.001$). In 2019, there was a significant difference between CWG and OLCG (see above). In 2018, OLCG was about two weeks later than CWG ($p = 0.006$). The leafy season thus started later in 2018 than in 2019, but it also ended a month later. The leafy season had a length of 144 and 124 days in 2018 and 2019, respectively. The wood growing season started around the same time in both years, but ended much later in 2019. The wood growing season was 90 and 125 days in 2018 and 2019, respectively. The tree-ring width was 565 ± 56 µm and 460 ± 135 µm in 2018 and 2019, respectively ($p < 0.001$).

Autumn phenological comparison of 2017, 2018, 2019 and 2020. The seasonal pattern of loss of canopy greenness differed between years. In 2017, 2018 and 2020, the loss of canopy greenness increased slowly from mid-August (<5%) till mid-late September (ca. 20%). Afterwards, it sharply increased > 90% in two weeks. In 2019, however, the loss of canopy greenness presented a different pattern with a marked and constant increase from early September (ca. 10%) till late October (100%) (Figure 5). During the 2017-2020 period, the earliest OLCG occurred on DOY 237 in 2019, which was significantly different to all years except 2017 ($p = 0.11$; Figure 6). In 2017, OLCG was on DOY 248, significantly different only to 2018. OLCG occurred on DOY 251 in 2020 (significant difference with

2018 and 2019) and, latest in the study period, on DOY 267 in 2018 (significant difference with all years; Figure 6).

The seasonal trend of the percentage of WTC, from which CWG was derived, was similar across years, except for 2018 when (as mentioned above) both the end of cambial activity and CWG occurred within < 2 weeks. The earliest CWG during the 2017-2020 period took place on DOY 206 in 2018 (significant difference with all other years with $0.01 < p < 0.05$). The latest CWG was observed in 2020 (Table 4) at DOY 276 (significant difference with only 2018, see above). No significant difference was observed in CWG between 2017, 2019 and 2020 ($p > 0.13$). For each year, CWG and OLCG were significantly different (Figure 6).

Table 4: Mean date of cessation of wood growth (CWG), with standard error (SE), its minimal and maximal spread among replicate trees per year and site (n indicates number of replicates).

Stand	**Year**	**Mean CWG**	**SE CWG**	**Min CWG**	**Max CWG**	**n**
Natural	2017	262	2.3	260	267	3
Natural	2018	206	10.1	177	220	4
Natural	2019	248	2.3	240	255	8
Natural	2020	276	10.5	251	293	4
Natural	Mean 2017-2020	248	15.1	206	276	4
Plantation	2018	236	4.0	225	275	12
Plantation	2019	257	3.1	240	269	12

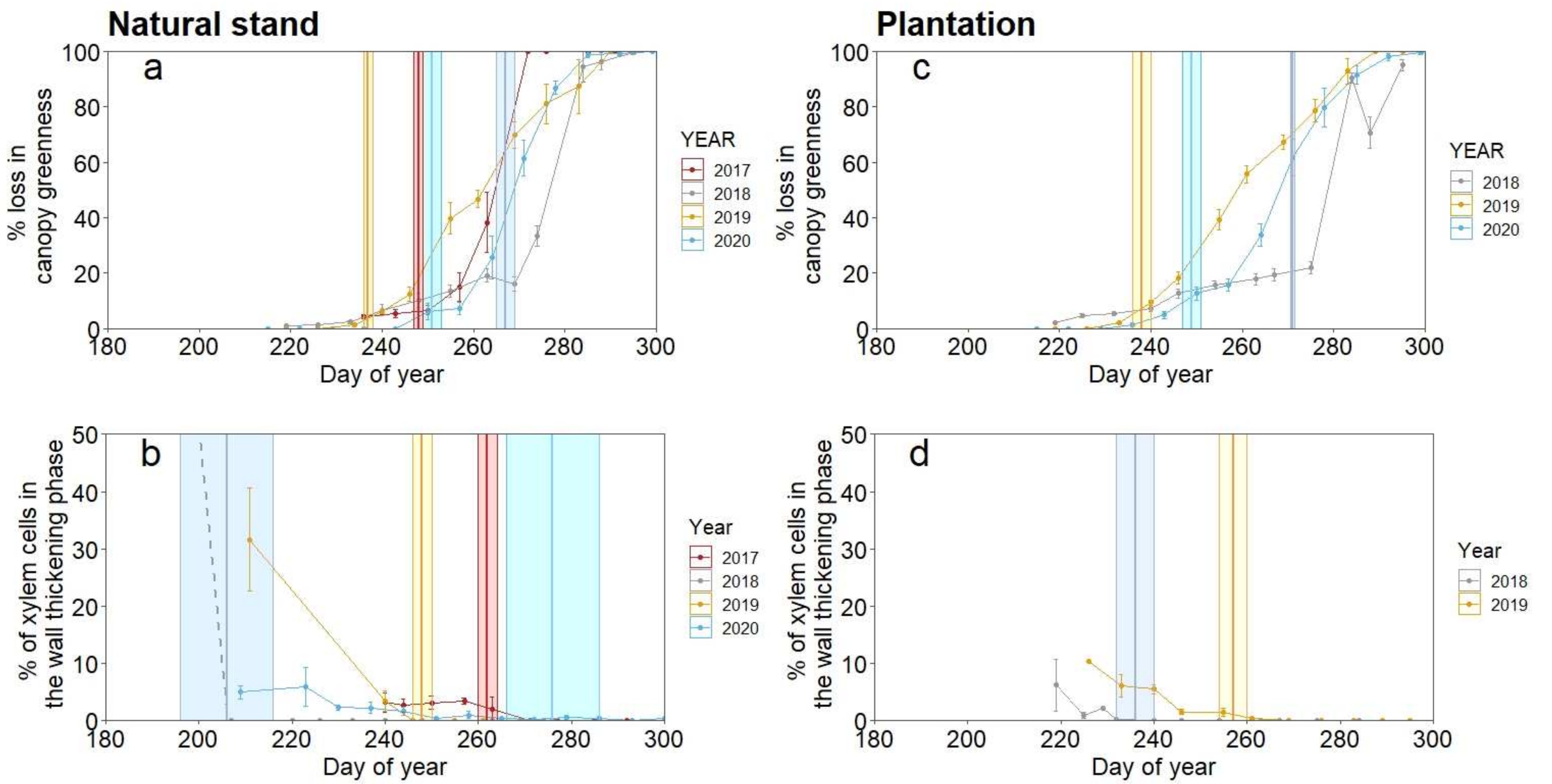


Figure 5: Seasonal trends of loss of canopy greenness for the natural stand (a; mean values as points, with ± 1 SE as bars) and the plantation (c; mean values as points, with ± 1 SE as bars) and percentage of xylem cells in the wall thickening phase for the natural stand (b; mean values as points, with ± 1 SE as bars) and the plantation (d; mean values as points, with ± 1 SE as bars). The vertical lines in (a) and (c) represent mean OLCG dates (with bands indicating ± 1 SE). The vertical lines in (b) and (d) represent mean CWG dates (with bands indicating ± 1

SE). Data are presented for 2017 (red), 2018 (grey), 2019 (yellow) and 2020 (blue) For the natural stand in 2018 (b), the sampling event before CWG was still characterized by cambial activity. The dotted line represents the change from cambial activity to CWG.

Comparison of autumn phenology in natural stand and plantation

Onset of loss of canopy greenness. The seasonal pattern of loss of canopy greenness was very similar between stands (Figure 5). No significant difference was found between the OLCG of the natural stand and the plantation in 2018, 2019 and 2020 ($p = 0.12, 0.75$ and 0.49, respectively). However, as for the natural stand, also at the plantation, there was a clear difference in OLCG between years. OLCG occurred at the end of September in 2018 and a month earlier in 2019 ($p < 0.001$). In 2020, OLCG occurred in between – in early September – in both other years (significantly difference with other years at $p < 0.03$).

Cessation of wood growth. The seasonal trend of the percentage of WTC was similar between sites. In 2018, CWG occurred at the natural stand at the end of July, whereas the trees at the plantation ceased growth only at the end of August ($p = 0.004$). A similar difference between stands ($p = 0.001$) was observed also in 2019, as CWG occurred at the beginning of September at the natural stand and in mid-September at the plantation (Figure 7 & Table 4).

Inter-tree and inter-annual variability. Data from the natural stand (Table 4) show that the inter-annual variability of CWG resulted in a standard error (SE) of 15.1 and a min-max range of DOY 206-276. These estimates are larger than the maximal inter-tree variability recorded for any single years (i.e. SE of 10.5 and min-max range of 43 days; Table 4). Data for the plantation is also reported in Table 4 but the dataset is too limited for further analysis. Inter-tree variability in dates of CWG (and other xylogenesis events) was larger than the inter-tree variability in dates of OLCG (and leaf phenology). For more info, see Supplementary Table 2.

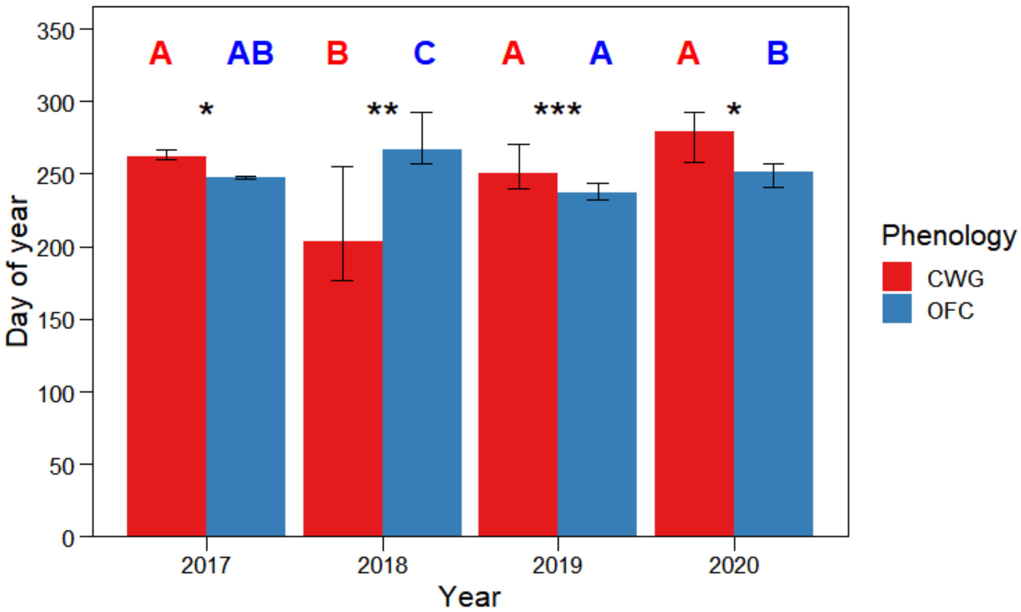


Figure 6: Mean day of year of cessation of wood growth (CWG, red) and onset of loss of canopy greenness (OLCG, blue), with error bars showing the inter-tree variability, in the 2017-2020 period for a natural birch stand in southeastern Norway. For each phenological event, the same letters indicate no significant difference between years, whereas different letters indicate a significant difference between years (at $p < 0.05$). Asterisks indicate a significant difference between CWG and OLCG for each year (* for $p < 0.05$, ** for $p < 0.01$ and *** for $p < 0.001$).

Tree-ring width at natural stand and plantation

The mean tree-ring width in 2018 was very similar between the natural stand and the plantation ($p = 0.62$). This was not the case in 2019, when the tree-ring width at the plantation was 3.2 times larger than the tree-ring width at the natural stand ($p = 0.004$). As at the natural stand, the tree-ring width at the plantation was also significantly different over the two years ($p < 0.001$). However, compared to 2018, tree-ring width in 2019 increased at the planation whereas it decreased at the natural stand (Table 1).

Loss of canopy greenness and foliar senescence in young trees

Natural young trees. The recorded patterns of loss of canopy greenness for the mature trees were also similar to the patterns observed in young natural trees, with OLCG significantly later in 2018 (Figure 8a). For the young natural trees, the CCI seasonal pattern matched the pattern of the loss of canopy greenness. In 2018, the CCI started to decline significantly at the time the loss of canopy greenness started to increase significantly, resulting in similar dates of OFS and OLCG when derived from both series (Figure 8a, Figure 9 & Table 5; $p = 0.067$). In 2019, CCI started to decline much earlier than in 2018, but less rapidly and at a more constant rate, paralleling the consistent decrease in loss of canopy greenness (Figure 8a & Figure 8b). Also for 2019, OFS and OLCG estimates were not different ($p = 0.91$; Figure 7 & Table 5). For 2017, data of OLCG and OFS could not be estimated (see Methods). However, for the weeks available, CCI and especially loss of canopy greenness showed similar patterns to those in 2019 (Figure 8a & Figure 8b).

Young potted trees. Young potted trees also showed the same pattern of loss of canopy greenness like the mature trees and the young natural trees, although they showed a less steep late-season increase in 2018 (Figure 8c). Furthermore, as for the mature and young natural trees, in 2018, they presented a significantly later OLCG than in 2019 (Figure 7). In fact, there was a significant difference between years in OLCG for both the low ($p = 0.001$) and high ($p = 0.002$) fertilization treatment. On the other hand, highly fertilized trees showed slightly but consistently larger values of loss of canopy greenness than lowly fertilized trees (Figure 8c). CCI values were lower in the low fertilization treatment (Figure 7d). CCI values were also lower in 2019 compared to 2018. OFS was significantly different between years for the high fertilization treatment ($p = 0.01$) but not for the low fertilization treatment ($p = 0.21$). In 2018, there was no difference between OLCG and OFS. However, in 2019, there was a difference between OLCG and OFS for the low fertilization treatment ($p = 0.002$). This may have been due to the low chlorophyll content (inferred from CCI values), which might have affected coloration change before OFS had taken place.

Table 5: Onset of foliar senescence (OFS) and onset of loss of canopy greenness (OLCG) for the natural young trees and the young potted trees under high (H) and low (L) fertilization treatment for the years 2018 and 2019. The p-value is given for the difference between date of OFS and OLCG per treatment and year.

Year	Group	OFS	OLCG	p-value
2018	natural trees	267 ± 2	271 ± 3	0.067
2019	natural trees	236 ± 3	236 ± 6	0.91
2018	potted trees H	257 ± 3	252 ± 4	0.071
2019	potted trees H	249 ± 5	233 ± 2	0.21
2018	potted trees L	257 ± 2	253 ± 3	0.84
2019	potted trees L	252 ± 3	233 ± 1	0.002

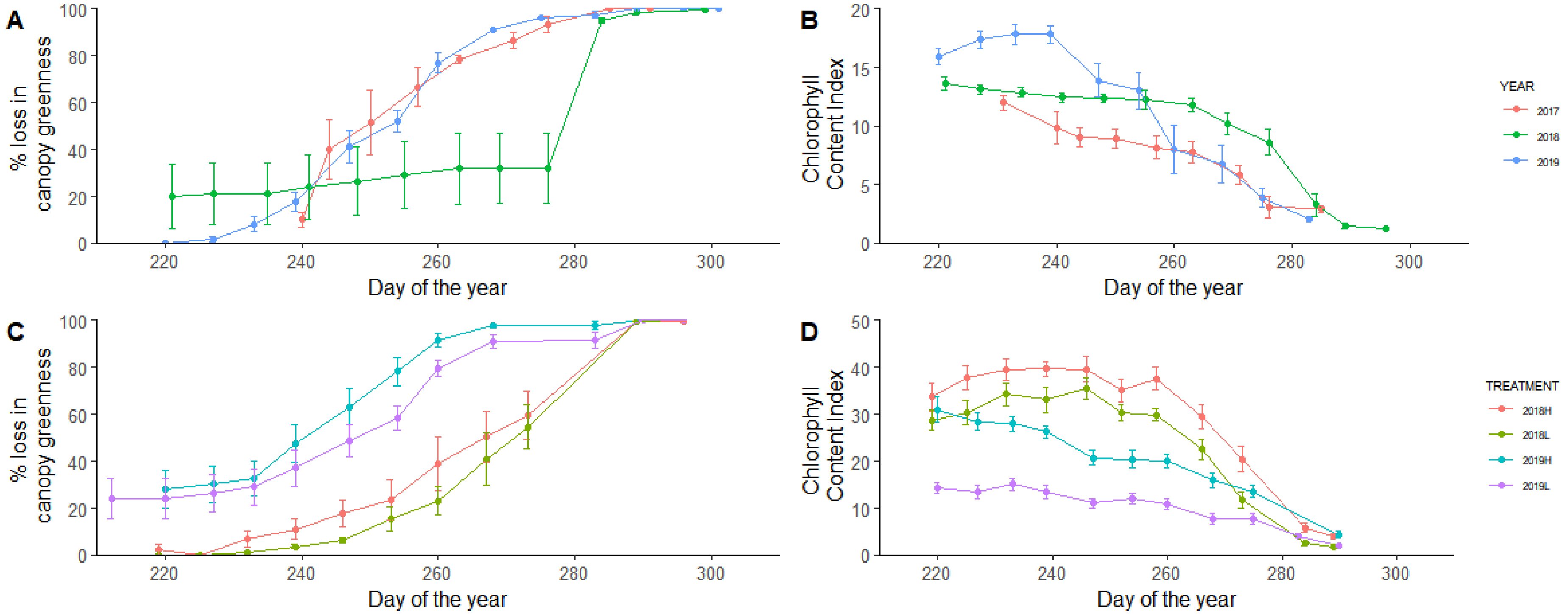


Figure 8: Seasonal pattern of loss of canopy greenness (top; a & c) and chlorophyll content index (down, b & d) (mean values, as points, with ± 1 SE as bars) for the natural young birch trees (left) and the potted young birch trees (right) under high (H) and low (L) fertilization treatment in Ås, Norway, in 2017, 2018 and 2019.

Methodological comparisons

For OLCG, the results of the comparison between breakpoint analysis and thresholds of canopy greenness (i.e. 10%, 20%, 30%, 40% and 50%) are reported in Supplementary Figure 1 & Supplementary Figure 2, for the natural stand and the plantation, respectively. Contrary to the results obtained with the breakpoint analysis, the use of the lowest threshold (10%) of canopy greenness did not result in differences in OLCG between years. However, the application of higher thresholds showed more consistency between methods. In fact, OLCG trends and dates very similar to the ones obtained with the breakpoint analysis were found by applying the 40% or 50% threshold for the natural stand (Supplementary Figure 1) and the 20%, 30%, 40% or 50% threshold for the plantation (Supplementary Figure 2). Moreover, even at the natural stand, and in agreement with the breakpoint analysis, the difference between OLCG in 2018 and 2019 was already significant at the 20% threshold.

Concerning the choice of the most suitable threshold of xylem cells in the wall-thickening phase to determine CWG, the comparison of the standard threshold of 0.5% to a lower and higher threshold (0.25% and 1%) resulted in small (up to 4 days for the natural stand and 7 days for the plantation) and not significant differences in CWG (Supplementary Figure 3).

Discussion

First, we will begin by discussing the phenology of birch during the year 2018, which featured a severe summer drought, and during 2019, a more normal year. This will then be followed by a discussion of the different hypotheses and our conclusions. These tasks are made easier by the presentation of two summarizing displays: Figure 7, which summarizes the overall findings according to the experimental settings and years, and Table 6, which provides an overview of the validity of the hypotheses after testing.

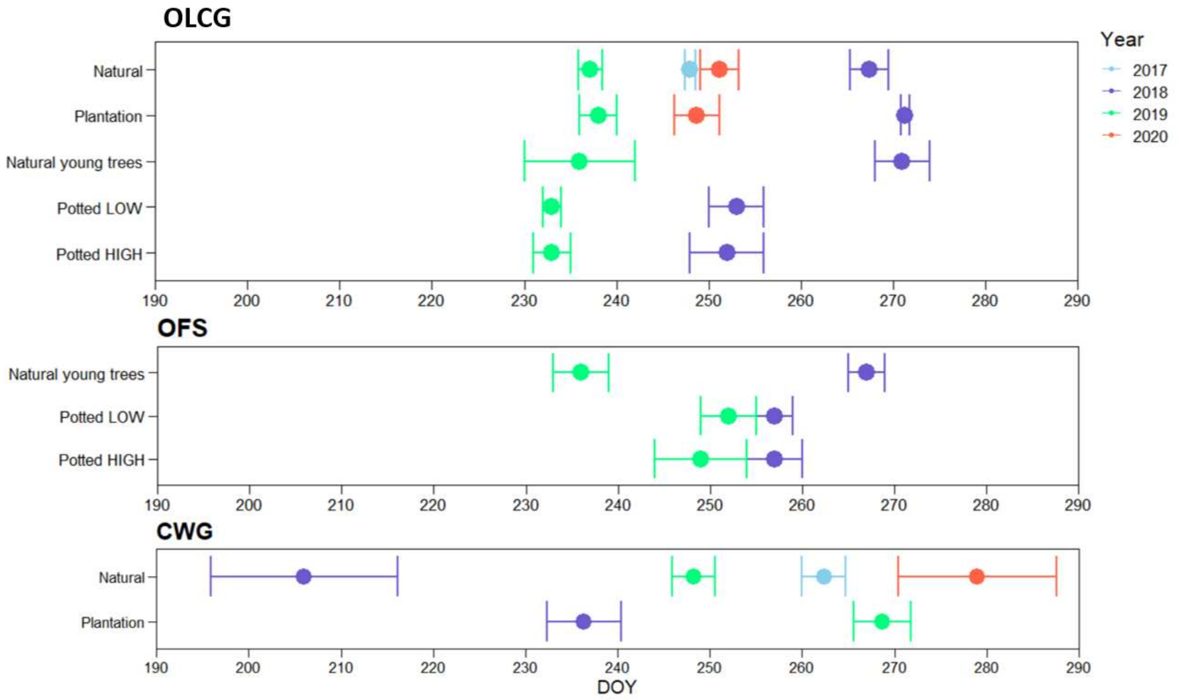


Figure 7: Summarizing figure of the data of autumn phenology obtained for different experimental settings on birch in Ås, southeastern Norway, for different years but especially for the dry 2018 and the wet 2019. OLCG: onset of loss of canopy greenness; OFS: onset of foliar senescence; CWG: cessation of wood growth, measured in the following settings: natural mature stand on moderately fertile soil (natural stand), mature plantation on fertile soil (plantation); natural young trees; young potted trees under low fertilization treatment (potted low) and young potted trees under high fertilization treatment (potted high).

Birch phenology

The earlier bud-burst in 2019 than 2018 is likely related to the warmer spring in 2019 (Basler & Körner, 2014; Polgar & Primack, 2013; Fu *et al.*, 2012; Fu *et al.*, 2013). Cambium reactivation took place after (in 2019) or concurrently (in 2018) to bud-burst. This is not unexpected. In fact, due to its diffuse-porous character, likely not all conduits are fully embolized in birch in winter and it is therefore not necessary for birch to produce new conduits before leaf expansion in spring (Barbaroux & Bréda, 2002). In another study conducted on birch in Belgium (Marchand *et al.*, 2021), cambium reactivation took place in 2018 at the end of March, about 19 days before bud-burst (occurring on DOY 101). Cambial reactivation can take place before bud-burst as trees can use carbohydrate reserves from the previous year to fuel the new wood growth (Barbaroux & Bréda, 2002). In 2018, cambial reactivation in birch took place in Belgium a month earlier than in Norway. However, the timing difference between cambium reactivation and appearance of IEWV (about a month) and between appearance of IEWV and first operative IEWV (also about a month) were similar between studies. In Norway, our birch trees had an earlier end of cambial activity and cessation of wood growth compared to birch populations and other diffuse porous species in Belgium, Slovenia and Northern Spain (Dox *et al.*, 2020; Marion *et al.*, 2007).

Table 6: Overview of the validity of the different hypotheses, experimental settings used to test the hypotheses and key remarks about the hypotheses testing in this study on the autumn phenology of birch in the northern temperate zone. OFS: Onset of foliar senescence; OLCG: onset of loss of canopy greenness; CWG: cessation of wood growth. The year 2018 was characterized by a severe drought, whereas the years 2017, 2019 and 2020 presented more normal meteorological conditions in summer.

Hypotheses	**Experimental setting**	**Is the hypothesis valid?**	**Key remark**
OFS, OLCG and CWG are advanced by a severe summer drought			
CWG	Natural stand (2017, 2018, 2019, 2020)	yes	NA
	Plantation (2018-2019)	yes	NA
OLCG	Natural stand (2017, 2018, 2019, 2020)	no	OLCG delayed by severe drought when compared to other years
	Plantation (2018, 2019, 2020)	no	OLCG delayed by severe drought when compared to other years
	Natural young trees (2018-2019)	no	OLCG in 2018 later than OLCG in 2019
	Potted young trees (2018-2019)	no	OLCG in 2018 later than OLCG in 2019
OFS	Natural young trees (2018-2019)	no	OFS in 2018 later than OFS in 2019
	Potted young trees (2018-2019)	no	OFS in 2018 later than or concurrent to OFS in 2019
A severe summer drought has a legacy effect on the next year wood growth but not on leaf phenology			

Legacy effect CWG	Natural stand (2017, 2018, 2019, 2020)	no	CWG in 2019 no different than CWG in 2017 and 2020
No legacy effect leaf phenology	Natural stand (2017, 2018, 2019, 2020)	no	OLCG in 2019 is advanced compared to OLCG in 2018 and 2020 but not to OLCG in 2017
	Natural young trees (2018-2019)	no	OLCG and OFS in 2018 later than OLCG and OFS in 2019
	Potted young trees (2018-2019)	no	OLCG and OFS in 2018 later than or concurrent to OLCG and OFS in 2019
Drought responses are less pronounced on more fertile sites			
CWG	Natural stand vs plantation (2018)	yes	Earlier CWG at the natural stand
OFS	Low fertilized vs. high fertilized potted young trees (2018)	no	No difference between treatments
OLCG	Natural stand vs plantation (2018)	no	No significant difference between natural stand and plantation
	Low fertilized vs. high fertilized potted young trees (2018)	no	No difference between treatments

Hypothesis 1: onset of foliar senescence, onset of loss of canopy greenness and cessation of wood growth are advanced by a severe summer drought

Cessation of wood growth. Both the natural stand and the plantation had an earlier CWG in 2018. This is very likely the result of the dry summer months, as has been observed in other xylogenesis studies (Arend & Fromm, 2007; Eilmann *et al.*, 2011; Giagli *et al.*, 2016). However, to the best of our knowledge, our study is the first to report a drought-induced advancement of CWG for birch and indicates, in agreement with our hypothesis, that the severe 2018 conditions significantly (5-6 weeks) advanced the end of the wood growing season. In another study on autumn phenology (Dox *et al.*, 2020), birch populations were followed over a latitudinal range spanning Northern (Norway), central (Belgium) and Southern (Spain) temperate Europe during the autumn of 2017. CWG was found to be relatively constant along this gradient. This is likely an indication that severe drought has a larger impact than general climate on CWG of birch in the temperate zone.

Onset of loss of canopy greenness and onset of foliar senescence. Very surprisingly, contrary to our hypothesis, OLCG was not advanced by drought, but delayed. This contrasts with the literature on autumn canopy coloration (Mariën *et al.*, 2021; Marchin *et al.*, 2010; Massonnet *et al.*, 2021) and general physiological responses of trees (e.g. leaf mortality) to drought (Breda *et al.*, 2006). One possibility is that leaf mortality occurred earlier than the start of our observations (drought started in late May but the canopy greenness monitoring only started in early August), which would then be based on younger leaves. In other words, the delayed pattern of OLCG in 2018 might be due to the non-deterministic growth pattern and the later senescence of younger leaves in birch (Koike 1990) and the early start of the summer drought. The alternative is that trees subjected to drought stress (the stress was evident as showed by the exceptional earlier CWG) would have triggered a delayed senescence to enhance carbon assimilation. There are some studies in the literature that report delayed OLCG in case of drought (Leuzinger *et al.*, 2005, Xie *et al.*, 2015) or carbon shortage (Zani *et al.*, 2020). For instance, according to Xie *et al.* (2015), a severe summer drought followed by rains in autumn would cause a delayed leaf senescence. Perhaps temperate trees could delay autumn senescence in a dry year to sustain fine roots, whose turnover can increase under drought due to enhanced mortality (Olmo *et al.*, 2014). In the gradient study reported above (Dox *et al.*, 2020), OLCG in 2017 occurred in late September in Spain and Norway and in mid-October in Belgium, with a significant difference of 20 days. Again, this difference is smaller than the one observed here between 2018 and 2019 (up to 42 days) at the same site. Thus, like CWG, OLCG in silver birch is likely more sensitive to drought than to long-term climate. Stress factors, both biotic (pests) and abiotic (insolation, drought, etc.), can result in earlier coloration and fall of the leaves. However, the method used to determine OLCG and OFS (the breakpoint analysis) partially accounts for earlier (moderate) leaf coloration and fall that are not related to the autumn senescence process (see below).

Data on OFS on the natural young trees confirm that the OLCG pattern observed is truly linked to autumn senescence dynamics, represented by the chlorophyll degradation. Therefore, in contrast to other studies (Fracheboud *et al.*, 2009; Mariën *et al.*, 2021), we note that OFS can vary between years, and that photoperiod alone could not be the trigger for OFS, at least not in birch populations of the northern temperate zone.

Hypothesis 2: A severe drought will have an effect on the wood growth but not on the leaf phenology in the next year

Contrary to our expectations, there was no evidence of a lag-effect of drought on the CWG of the next year. In fact, CWG was not different between 2017, 2019 and 2020. It is, however, important to note two points. First, we were not able to sample the same trees in the four-year period (only for 2018-2019, and for 2019-2020), so inter-tree variability might have affected the results (Sass-Klaassen *et al.*, 2011). Second, the results are puzzling given the finding that, at the natural stand, the tree-ring width was larger during 2018 than 2019. There are four possible explanations for this: (1) the early cambium reactivation in 2018 (though not significant; Supplementary Table 2), (2) a deficit in carbohydrates of reserves in 2018 negatively effecting wood growth in 2019 (Breda *et al.*, 2006; Dietze *et al.*, 2014), (3) fast wood production during the spring of 2018 or (4) the presence of tension wood in 2018 overestimating the tree-ring width in that year (Groover, 2016; Abedini, 2015).

In 2019 we observed an earlier OLCG than 2018 for all the trees considered (i.e. natural stand, plantation, natural young trees, young potted trees) and a more gradual loss of canopy greenness (especially for trees in natural soil). In 2019, OLCG was also significantly earlier than in 2020 but not 2017 ($p = 0.11$). In 2019, OFS was also advanced, except for the low fertilization level. Nonetheless, these datasets cannot proof unequivocally that the earlier senescence in 2019 was due to the severe drought of the previous year. In fact, on the one hand, advanced senescence in 2019 might have been promoted by the advanced bud-burst in that year and, on the other hand, the environmental conditions in 2019 might have contributed to advance the senescence. However, previous studies indicate only moderate advances in senescence in response to advances in bud-burst (0.4 till 1.1 day advanced senescence per 1 day advanced bud-burst; Fu *et al.*, 2014; Keenen & Richardson, 2015) and that the more wet and humid conditions of 2019 should have delayed rather than advanced the senescence timing (e.g. see for birch Rosenvald *et al.*, 2020 and Pliūra *et al.*, 2018, and for deciduous trees of high latitude Gill *et al.*, 2015). Therefore, our results show an unexpected autumn dynamics in 2019. As the conditions in 2018 were exceptionally dry, the data suggest a possible legacy-effect of severe drought on leaf phenology of the next year.

Lag-effects after a drought have been shown on different organs of the tree (Huang *et al.*, 2018), but we are not aware of any studies showing carry-over effects of drought on leaf autumn dynamics of the next year. It is possible that the increased fine root mortality expected in case of severe drought (Brunner *et al.*, 2015; Mainiero & Kazda, 2006; Olesinski *et al.*, 2011) and the lower mineralization rate due to dryness (Birch, 1958) might have reduced the nutrient reserves of the trees in 2019, stimulating an earlier senescence to have a complete remobilization of the leaf nutrients before leaf shedding (Estiarte & Peñuelas, 2015). Longer-term datasets and future dedicated manipulative experiments in more controlled conditions will allow to elucidate the mechanisms behind our observations.

Hypothesis 3: drought responses are less pronounced at more fertile sites

It is interesting to observe that OLCG was very similar between the plantation and the natural stand in the years with data available (2018, 2019 and 2020), while CWG was significantly different between stands, with an earlier CWG at the natural stand in both 2018 and 2019. Also note that at the plantation the 2019 tree-ring growth was threefold larger than in 2018, even though OLCG was 4 weeks earlier. CWG and wood growth thus seem to be more affected by the water availability and site fertility than leaf autumn dynamics (Dox *et al.*, 2021). The low impact of nutrient availability on the drought sensitivity of the leaf senescence dynamics was confirmed by the fertilization experiment that, in 2018, showed no difference in the timing of OLCG and OFS between treatments.

Methodological notes and challenges

Determination of onset of loss of canopy greenness. As expected, and in contrast to the breakpoint approach, the application of a low threshold of canopy greenness (e.g. 10%) to determine OLCG did not result in differences between years. This is very likely due to the fact that the effects of the accumulated seasonal stress damage and earlier loss of canopy greenness were not separated from the effects of the onset of autumn senescence. However, the application of higher thresholds (20% and larger) largely confirmed the results of the breakpoint analysis, our preferred method for determining OLCG (and OFS). In fact, the main advantage of the breakpoint approach is being able to determine the timing of a "sharp change" in canopy greenness (or relative chlorophyll content index; Mariën *et al.*, 2019). This reduces the confounding effects of early, modest coloration and leaf fall on the timing of the autumn senescence (Marchin *et al.*, 2010; Mariën *et al.*, 2019).

Threshold in xylem cells in the wall-thickening phase to determine cessation of wood growth. The differences in CWG obtained when applying different thresholds in WTC (i.e. 0.25, 0.5 and 1%) were not significant. Therefore, the validity of the standard threshold of 0.5% (Dox *et al.*, 2020; Dox *et al.*, 2021) was confirmed. In fact, smaller thresholds (<0.5%) might enhance the impact of outliers, noises (e.g. caused by heterogeneous growth patterns of the sampled tree stem) and the very marginal role played by sporadic cells still active in late autumn. On the other hand, larger thresholds (>0.5%) might be less suitable as, occasionally, periods with low growth can happen (e.g. because of drought or extreme bad weather) but growth is resumed later on (Dox *et al.*, 2020; Dox *et al.*, 2021).

Inter-tree variability. Inter-tree variability in wood phenology can be significant (Sass-Klassen *et al.*, 2011; Marchand *et al.*, 2021) and it can affect the population average. It is always preferable to study a large amount of trees, but due to the very time consuming workflow of the wood phenology measurements (e.g. sample treatment, slide preparation, microscopic observation), a larger sample size was not possible in this study. The natural stand was characterized by a small statistical sample size (n=3-8). While this is a weakness, such a small sample size is not uncommon in xylogenesis studies (Begum *et al.*, 2010; Cruz-García *et al.*, 2019; Stangler *et al.*, 2021; Larysch *et al.*, 2021). Moreover, the size of the statistical sample was taken into account in the statistical analysis. On the other stand, the plantation could be sampled more extensively (n=12). It is relevant to note that, though timing of wood phenology events is different, the inter-annual patterns of wood phenology recorded at the natural stand and plantation for 2018-2019 are very similar.

Fertilization experiment on young trees. As stated in methodology, in our fertilization experiment with the young potted trees, some trees died in the first year, probably because the roots were too damaged during transplantation from the nursery to the experimental site and a few others were unable to withstand the hot summer of 2018, despite regular irrigation. The death of trees likely more sensitive to drought might result in a slight bias towards individuals that were better adapted to drought and therefore have a small effect on the phenological results.

Conclusions

This study elucidated the leaf and wood phenology dynamics of birch on the northern edge of the temperate zone in a year characterized by a very severe dry and warm late spring-summer (2018), the next, more normal, year (2019) and two additional years (2017 and 2020). As expected, wood formation dynamics were affected by the severe weather in 2018, with an advanced cessation of wood growth (CWG). However, we also found unexpected leaf senescence dynamics in 2018 and especially in 2019, which were delayed and advanced, respectively. These findings were consistent across the different populations and experimental settings considered. While there are some other reports of delayed leaf coloration in case of drought, we believe we are the first to show a potential legacy effect of drought on the leaf autumn dynamics of the next year in a deciduous tree species.

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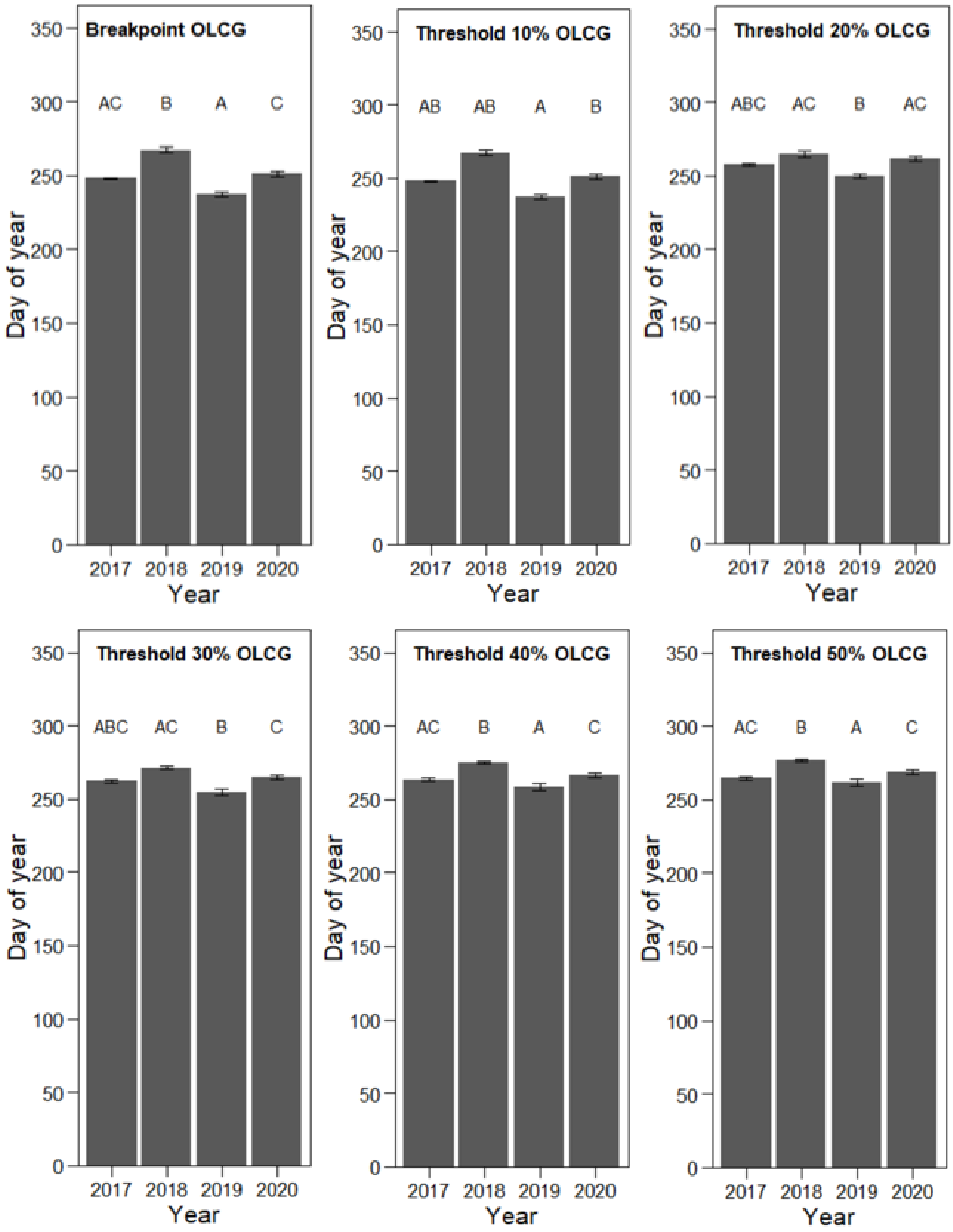
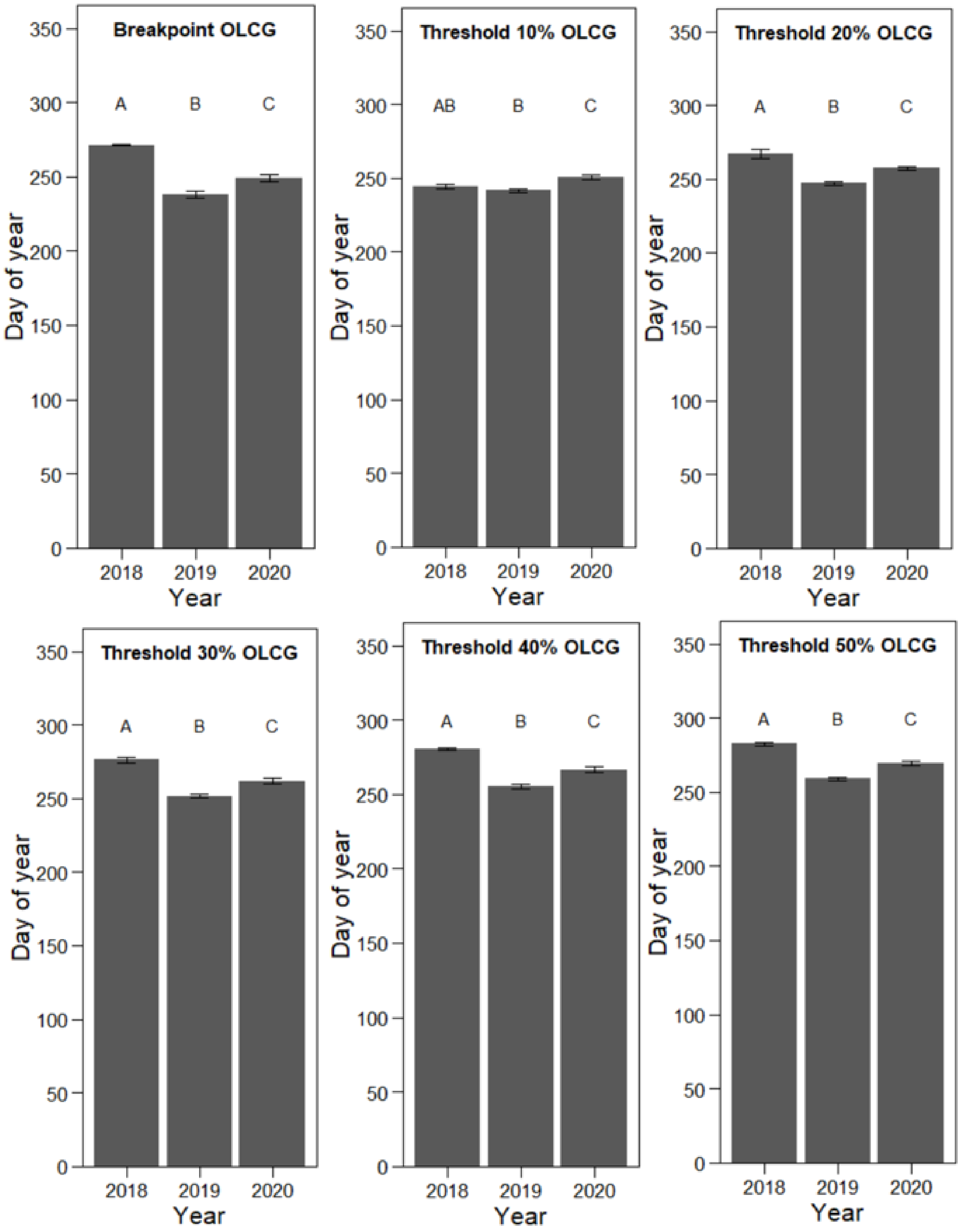
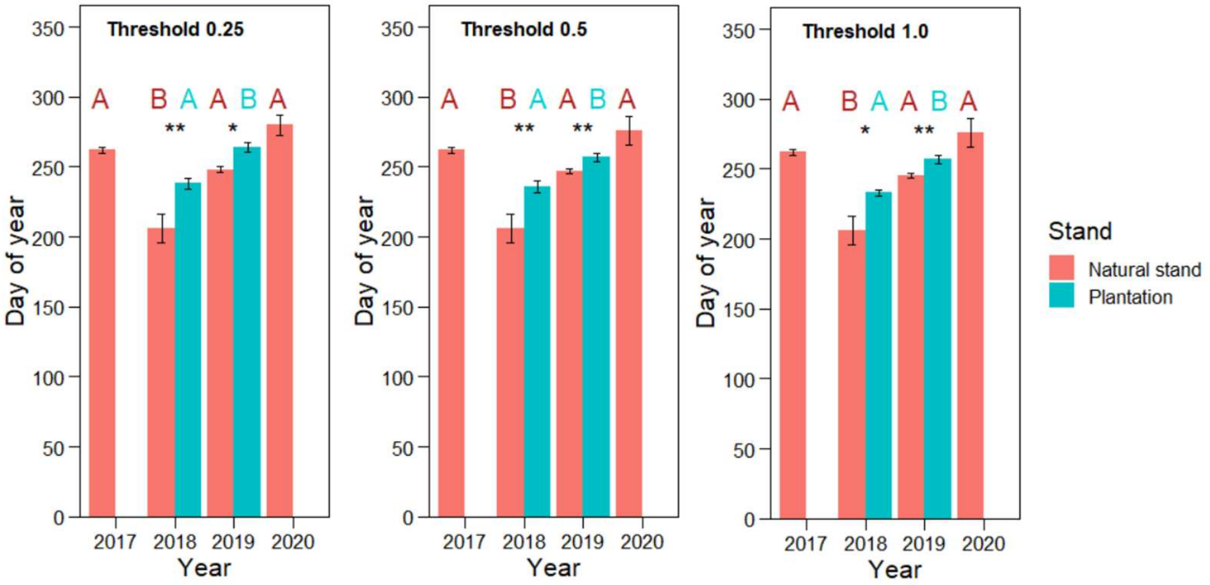
Supplements



Suppl. Figure 1: Day of year of onset of loss of canopy greenness (OLCG, mean ± 1 SE) based on different methods: breakpoint analysis and different thresholds in loss of canopy greenness (i.e.10, 20, 30, 40 and 50%) for a natural stand of birch in Ås, southeastern Norway, for the years 2017-2020. Same letters indicate no significant difference between years, whereas different letters indicate a significant difference between years (at $p < 0.05$).



Suppl. Figure 2: Day of year of onset of loss of canopy greenness (OLCG, mean ± 1 SE) based on different methods: breakpoint analysis and different thresholds in loss of canopy greenness (i.e.10, 20, 30, 40 and 50%) for a plantation of birch in Ås, southeastern Norway, for the years 2018-2020. Same letters indicate no significant difference between years, whereas different letters indicate a significant difference between years (at $p < 0.05$).



Suppl. Figure 3: Day of year of cessation of wood growth (mean ± 1 SE) determined using different thresholds of percentage of xylem cells in the wall-thickening phase (i.e. 0.25, 0.5 and 1.0%) for a natural stand (red) and a plantation (blue) of birch in southeastern Norway for the years 2017-2020. For each stand, same letters indicate no significant difference between years, whereas different letters indicate a significant difference between years (at $p < 0.05$). Asterisks indicate a significant difference between the plantation and the natural stand for each year (*:$p < 0.05$, **: $p < 0.01$ and ***: $p < 0.001$).

Suppl. Table 1: Tree sampling scheme at the natural stand in the years 2017-2020. W_A: wood phenology in autumn (early August till late October); W_S: wood phenology for whole growing season (mid-April till late October); L_A: leaf phenology in autumn (early August till late October); L_S: leaf phenology for whole growing season (mid-April till late October).

Tree	**2017**	**2018**	**2019**	**2020**
B1MC	W_A L_A	W_S L_S	W_S L_S	L_S
B2MC		W_S L_S	W_S L_S	L_S
B3MC	W_A L_A	W_S L_S	W_S L_S	L_S
B4MC		W_S L_S	W_S L_S	L_S
B1BB		L_S	W_A L_S	W_A L_S
B2BB	W_A L_A	L_S	W_A L_S	W_A L_S
B3BB		L_S	W_A L_S	W_A L_S

B4BB	Ls	WA Ls	WA Ls

Suppl. Table 2: Leaf and wood phenological events of birch in a natural stand and plantation for 2018 and 2019 in Ås, Norway. BB: Bud-burst; OFS: Onset of foliar senescence; OLCG: Onset of loss of canopy greenness; CA: Cambium activity; CWG: Cessation of wood growth.

		2017		2018			2019			2020	
		Mean date	range	Mean date	range	Length growing season (days)	Mean date	range	Length growing season (days)	Mean date	range
Natural stand	BB			3 May	1-4 May	144	April 23	April 19-25	124		
	OLCG	5 Sept.	4-6Sept.	24 Sept.	14 Sept – 20 Oct.		Aug. 25	Aug. 20 – Sept. 1		8 Sept.	29 Aug. – 14 Sept.
	CA			26 April	18 April – 11 May	88	May 5	April 30 – May 6	125		
	CWG	19 Sept.	17-24 Sept.	23 July	26 June – 12 Sept.		Sept. 7	Aug. 28 – Sept. 28			
Plantation	BB						19 April	18- 19 April	129		

OLCG	28 Sept.	26 Sept.- 1 Oct.	26 Aug.	19 Aug. – 8 Sept.	6 Sept.	25 Aug. – 17 Sept.
CWG	24 Aug.	13 Aug.- 2 Oct.	26 Sept.	12 Sept. – 3 Oct.		