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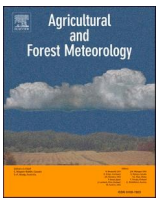

How tree stand phenology determines understorey senescence - a case study from boreal forests

Maxime Durand [a,*], Arthur Daviaud [a,b], T. Matthew Robson [a,c]

[a] Organismal and Evolutionary Biology (OEB), Viikki Plant Science Centre (ViPS), Faculty of Biological and Environmental Sciences, University of Helsinki, 00014, Finland
[b] UniLaSalle Polytechnic Institute, 60000 Beauvais, France
[c] National School of Forestry, Institute of Science & Environment, University of Cumbria – Ambleside, LA22 9BB, United Kingdom

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ABSTRACT

Leaf fall in the autumn opens the forest canopy, allowing more solar radiation to be transmitted to the forest floor. Those understorey species that remain physiologically active into the autumn may benefit from the sunlight received by extending their growing season, to assimilate additional carbon while conditions remain favourable. We monitored leaf water and pigment content, as well as photosynthetic capacity in understorey species growing in adjacent stands differing in their canopy tree species. Leaf fall, transmitted light, and microclimate were monitored in each stand. We found that overstorey leaf fall started earlier in the birch (*Betula pendula*, L.), than in the oak (*Quercus robur*, L.) stand, and light transmission changed accordingly. Concurrently, understorey leaf senescence was generally earlier in the birch than in the oak stand, itself earlier than in the evergreen spruce stand (*Picea abies*, L. H. Karst.). Neither atmospheric CO_2, humidity, nor temperature differed between stands. A change in light quality and/or increase in quantity following leaf fall drove the difference in the timing of senescence in the understorey. Understorey species with later senescence were able to use the increased light more after leaf fall. Together these findings help to provide a mechanistic foundation to predict how ecosystem functioning and ultimately carbon balance will be impacted by phenological shifts in response to global changes.

1. Introduction

Although autumn senescence is a highly visible seasonal event occurring in many of the worlds' plant canopies, it remains an under-researched field in plant science, especially compared to spring phenology (Gallinat et al., 2015). Leaf discoloration and eventual fall at the end of the growing season is the counterpart to leaf out in spring. They each define the duration of photosynthetic activity. As such, their respective timings are interlinked with potential cumulative or compensatory effects on productivity (Barichivich et al., 2012; Fu et al., 2014; Panchen et al., 2015). For example, an extended growing season might compensate for a late start in spring, or extend an already long summer. Shifts in the timing of these phenological (early start in spring, later end in autumn) events have been found to alter carbon balance at the ecosystem scale (Richardson et al., 2010), shown not only in spring but also in autumn (Taylor et al., 2008; Jeong et al., 2011; Wu et al., 2013; Lu and Keenan, 2022). These shifts can impact carbon uptake, both positively *via* increases in carbon uptake and plant growth (Myneni et al., 1997), and negatively due to a rise in ecosystem respiration in autumn (Piao et al., 2008; Richardson et al., 2010). In turn, leaf phenology can also feedback on climate, by governing the seasonality of surface roughness, albedo, and water cycling (Richardson et al., 2013). It then follows that understanding the determinants of autumn phenology will provide the knowledge to improve global climate models.

Unlike spring phenology, which is now recognized to be principally dictated by temperature and to a lesser degree photoperiod (Polgar and Primack, 2011), autumn phenology is influenced by a complex variety of factors (Gallinat et al., 2015; Gill et al., 2015). These include, though are not limited to, drought (Wu et al., 2022), temperature (Menzel et al., 2006), photoperiod (Vitasse et al., 2011), spectral composition of sunlight (Brelsford et al., 2019, 2022), soil fertility (Keskitalo et al., 2005), wind (Staelens et al., 2003), and rainfall (Travers and Eldridge, 2013). Two corollaries can be deduced from this. Firstly, the timing of leaf out is

* Corresponding author.
E-mail addresses: maxime.durand@helsinki.fi (M. Durand), arthur.daviaud@etu.unilasalle.fr (A. Daviaud), matthew.robson@cumbria.ac.uk (T.M. Robson).

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not necessarily correlated with leaf senescence (Panchen et al., 2015). Secondly, senescence is dependent on both the local microenvironment and latitude (Gill et al., 2015).

Among forests in the northern hemisphere, boreal forests may be under particular pressure from climate change. A shorter photoperiod in autumn and faster seasonal transition may limit the scope for warm temperatures to extend the growing season at high latitudes (Fracheboud et al., 2009; Gill et al., 2015; O'Connell and Savage, 2020). In boreal forests, the timing of senescence may be critical; too early and the already-short growing season will potentially be reduced beyond a minimum threshold required for some species to reach a positive annual carbon balance (Lee and Ibanez, 2021), while senescing too late risks frost damage causing valuable nutrients to be lost before they can be reabsorbed (Näsholm et al., 1998).

Leaf fall creates a unique seasonal environment in the understorey of deciduous forests. The canopy opens allowing more radiation to be transmitted. Researchers have considered the possibility that understorey species may take this opportunity to extend their growing season (Gill et al., 1998; Fridley, 2012). However, this capacity appears species-specific, and less widespread than accelerated leaf expansion in spring (Augspurger and Bartlett, 2003; Augspurger et al., 2005). Besides, leafy forests provide a buffer to the understorey against diurnal and seasonal fluctuations in temperature and humidity when compared to open environments. De Frenne et al. (2019) found that the forest microclimate kept maximum temperatures on average 4.1 °C cooler, and minimum temperatures 1 °C warmer than adjacent non-forest systems. After leaf fall, this buffering effect is greatly diminished (von Arx et al., 2013; Zellweger et al., 2019). The capacity for some understorey species to extend their growing season further in the autumn after overstorey leaf fall may have large consequences for the boreal ecosystem functioning. Although the understorey compartment represents a relatively small part of the standing biomass, it contributes a significant fraction of the litterfall because of the high turnover rates of understorey species litter (Nilsson and Wardle, 2005). They can also affect seedling seedlings' establishment and growth (Jäderlund et al., 1997), and modify soil mineral composition, litter decomposition, and nutrient availability (Wardle and Zackrisson, 2005). Although the contribution of understorey plants to carbon gain at the ecosystem level is limited, these indirect impacts feedback to the overstorey and drive ecosystem function (Nilsson and Wardle, 2005).

Light itself is a complex cue that can either promote (Cavender-Bares et al., 2000; Lee et al., 2003) or delay senescence (Biswal and Biswal, 1984). Shading (often severe, or complete darkening) can also trigger a senescence response (Okada et al., 1992; Janečková et al., 2018). There is still a debate as to whether this process is induced by carbon starvation (Biswal and Biswal, 1984), or by a photosynthesis-independent signal mediated by phytochromes through the ratio of red to far-red light (R: FR; Hidema et al., 1992), or both (Liebsch and Keech, 2016). Reactive oxygen species (ROS) are important mediators of senescence (Zimmermann and Zentgraf, 2005) as they cause the oxidation of pigments, proteins, and lipids, needed for the mobilization of nutrients (Juvany et al., 2013; Renner and Zohner, 2019). ROS need to be tightly regulated in both space and time, otherwise nutrient resorption will be thwarted and leaf death induced prematurely (Kitao et al., 2022). Flavonoids and anthocyanins provide a mechanism for effective regulation both as antioxidants scavenging for ROS, and by slowing ROS formation through the attenuation of solar UV radiation in the leaf epidermis (Agati et al., 2021).

In natural conditions however, there is no consensus on the effect of an increase in radiation on the canopy understorey in autumn (Okada et al., 1992; Cavender-Bares et al., 2000; Lee et al., 2003; Špundová et al., 2005). We monitored meteorological conditions and senescence traits (relative water content, pigment concentration, and quantum yield of Photosystem II) of six species from three functional types (saplings, deciduous perennials and evergreen perennials) during the autumn of 2021 in three adjacent boreal forest stands. Such stands located in close vicinity provided a similar climate and soil conditions, allowing us to isolate the effects of temperature and light on understorey plants during and after leaf senescence. We aimed to: (1) contrast these stands' canopy and understorey phenological development and their environmental conditions, (2) evaluate the dynamics of traits related to senescence in the understorey, and (3) test whether earlier leaf fall of the overstorey was associated with extended photosynthetic activity in the understorey.

2. Materials and methods

2.1. Study site and sampling

All data was collected from three forest stands near Lammi Biological Research Station (61°3′14.6″ N, 25°2′13.8″ E, southern Finland). Extensive stand information can be found in Hartikainen et al. (2018; 2020) and Brelsford et al. (2022). Briefly, the three stands were dominated respectively by silver birch (*Betula pendula,* L.), pedunculate oak (*Quercus robur,* L.), and Norway spruce (*Picea abies* L. H. Karst.). No other tree species at a mature stage were found in either stand. The understorey and ground vegetation are typical of Finnish forests. From the September 1st to November 30th, the daily average temperature was 5.3 °C, average PAR irradiance was 8.06 mol m^{-2} d^{-1}, and precipitation summed to 156.7 mm (see Fig. A1 for more details on the local meteorological conditions).

2.2. Sampling and stand measurements

Six measuring points per stand were set up, each at equal distance from the surrounding trees (Fig. A2). Stand measurements were performed once per day at these locations. Canopy light transmission was calculated as the percent of below-to-above-canopy irradiance, using a ceptometer (Accupar LP-80, Meter Group, Pullman, USA), under an overcast sky. Before measuring in each stand, the above-canopy photosynthetically active radiation (PAR, 400–700 nm) was measured in a nearby open field ($n = 10$). Every 3–4 days depending on weather, 20 below-canopy recordings were made per measuring point (*i.e.* 120 per stand), between September 6th and November 29th, 2021. Atmospheric CO_2 concentration, air temperature, and humidity were recorded at a seventh measuring point, located among the other six within each stand, with sensor probes (GM70 and HMP76, calibrated in January 2020, Vaisala Oy., Vantaa, Finland). Three times a week, all probes were left to acclimate to the surrounding conditions, 30 cm above the ground, for at least 30 min, away from the operator before logging the data. Leaf nets (60×40 cm, 0.24 m^2 area) fixed to the ground were surveyed to count the number of fallen leaves belonging to the dominant canopy species. There were seven leaf nets (at each measuring point) in the birch and oak stands, and two nets in the spruce stand. Unless otherwise stated, "leaf fall" refers only to overstorey leaves.

During the spring of 2020, spectral photon irradiance was recorded at each stand before (May 22nd) and after leaf out (June 10th), to compare the understorey light conditions between a leafless and fully flushed canopy. These measurements were made with a CCD array spectroradiometer (Maya 2000 Pro, Ocean Optics, Dunedin, FL, USA – calibrated in April 2019 by the Finnish Radiation and Nuclear Safety Authority), attached to a cosine diffuser (D7-H-SMA, Bentham Instruments Ltd., Reading, UK) by way of a fiber-optic cable (FC-UV400–2 400-µm, Avantes, Leatherhead, UK). Additional corrections followed Hartikainen et al. (2018), involving matching measurements with a polycarbonate cap (blocking solar UV radiation) and a dark cap (blocking all radiation), to correct for stray-light, and dark noise, respectively (Aphalo and Ylianttila, 2022). At four locations in each stand, sets of 100 scans were recorded with the diffuser held horizontal on a tripod 30 cm above the ground. At each location measurements were taken at three positions (at most 20 cm away from each other), in the shade of a tree trunk, in the middle of a sunfleck, and in the

semi-shade (or penumbra, defined as the irradiance in between shade and sunflecks). We manually adjusted the integration time to allow for maximum precision (between 100 ms and 2 s). All data were recorded within three hours of solar noon, and processed using the "*ooacquire*" and "*photobiology*" R packages (Aphalo, 2015; Aphalo and Ylianttila, 2022). The following spectral photon ratios were calculated: UV-A:PAR, blue:red (B:R), blue:green (B:G), and red:far-red (R:FR) (UV-A: 315–400 nm; PAR: 400–700 nm; blue: 420–490 nm; green: 500–570 nm; red: 620–680 nm; far-red: 700–750 nm).

2.3. Leaf-level measurements

Every week from September 1st to November 29th, five leaves were sampled in each stand from each focal understorey species, at or near the measuring points described above. We selected the lily-of-the-valley (*Convallaria majalis*, L.) and wild strawberry (*Fragaria vesca*, L.), two deciduous perennials, as well as two evergreen perennials: the common hepatica (*Anemone hepatica* L. syn. *Hepatica nobilis*) and the wood sorrel (*Oxalis acetosella*, L.). Additionally, we selected two deciduous saplings, rowan (*Sorbus aucuparia*, L.) and Norway maple (*Acer platanoides*, L.). Species were selected first for their abundance in all three stands, and second for their representativeness of typical Finnish understorey vegetation. The period of measurement was determined by the timing of their senescence. Due to the high inter-individual variability in senescence, we made a visual assessment of the stand before sampling to make sure selected leaves were representative of the stand phenological stage. Sampled leaves were labelled, placed in a sealed plastic bag, themselves in a polystyrene box containing an ice pack, and taken immediately to the adjacent laboratory for further analyses (within 20 minutes).

When leaves were unevenly senescing, the greenest part of the leaf lamina was selected for analyses, avoiding major veins. The initial quantum yield of Photosystem II, Φ_{PSII}, was measured by performing the light curve protocol of the MINI-PAM-II (Heinz-Walz, Effeltrich, Germany) with a leaf-clip holder (2030-B, Heinz-Walz) on the adaxial side of the leaves. The protocol had 11 light steps, in increasing order from 0 to 2000 μmol $m^{-2} s^{-1}$, with a 30 s period between the modulated actinic light change and the saturating pulse (5000 μmol $m^{-2} s^{-1}$, 654 nm for 0.8 s). Leaf pigment content (chlorophyll, and epidermal flavonoids and anthocyanins) were measured non-destructively (Cerovic et al., 2012), using an optical leaf clip Dualex Scientific^{+} (Force-A, University Paris-Sud, France) on the adaxial side of the leaf at the same location as the light curves. An assessment of Dualex readings and spectrophotometric pigment absorbance from leaf extracts of these species found a good agreement between the two methods for flavonoids (Hartikainen et al., 2020). All leaves were weighed fresh, then placed in a drying oven for three days at 65 °C, and weighed again. The percent difference between dry and fresh mass was used to calculate the relative water content (RWC).

2.4. Modeling electron transfer rate during senescence

We modelled potential electron transfer rate (ETR) during senescence using the following equation:

$$ETR = PAR_{top} * \Phi_{PSII} * \alpha * 0.5 * \tau_{canopy} \quad (1)$$

PAR_{top} is the PAR irradiance above the canopy that we multiply by τ_{canopy} (the canopy light transmission) to obtain an estimate of the understorey PAR. α is the leaf absorptance (0.84), and the factor 0.5 accounts for the energy partitioning between PSI and PSII (Maxwell and Johnson, 2000). The PAR above the canopy was measured continually every 10 min with a PAR sensor (PQS1 PAR Quantum Sensor, Kipp & Zonen, OTT HydroMet B.V., Delft, Netherlands) in an open field adjacent to the stands at Lammi Biological Research Station. We interpolated both the canopy light transmission in each stand using bi-weekly ceptometer measurements, and Φ_{PSII} between September 6th to November 29th (DOY 250 – 333), corresponding to the first and last measurement of Φ_{PSII}. ETR was calculated for each day with a single value of Φ_{PSII} and τ_{canopy}, and the daily sum of PAR_{top} (converted to mol $m^{-2} d^{-1}$). ETR was then summed over the whole period (ETRc, cumulated ETR) to assess how changes in light transmission and Φ_{PSII} affected the overall photosynthetic activity. This simple calculation did not account for more complex dynamic processes. The estimated parameters PAR_{top}, Φ_{PSII}, and τ_{canopy} vary diurnally and with the weather faster than we could measure them. Moreover, leaf absorption can also change dynamically with the composition of pigments within the leaf. Finally, the applied interpolation included some measurement noise which reduces the precision of the calculation. Therefore, one should consider the obtained calculations as an indicative synthesis of the measurements conducted in this study.

2.5. Statistical analysis

Statistical analyses were made with R 4.2.1 (R Core Team, 2022) using the R packages: "*car*" (Fox and Weisberg, 2019), "*emmeans*" (Searle et al., 1980) and "*multcomp*" (Hothorn et al., 2008). Type II analyses of variance were used to test for differences in pigment content, chlorophyll fluorescence parameters, and RWC between stands and day of the year. Differences in canopy light transmission and leaf fall between stands and day of the year were assessed with repeated measures ANOVAs, using the measuring point as within-subjects identifier (selecting a different leaf each time prevented us from using repeated-measures ANOVAs for the leaf-level data). We used the same design in an ANCOVA form, by using numeric values of the day of the year, to assess temporal trends between days. Partial R^2 was calculated as the proportion of the overall variance explained by each effect. We checked for normality, and homoscedasticity or sphericity, of the residuals graphically. To test for differences among stands, a *post-hoc* pairwise contrast analysis was done, and we adjusted *p* values to control the false discovery rate. We considered differences significant when $p < 0.05$ for all tests.

3. Results

3.1. Understorey environment during canopy leaf fall

The timing and rate of overstorey leaf fall differed greatly between stands (Fig. 1a). From September 8th to October 1st (DOY 251–274), leaf fall proceeded faster in the birch stand than in the oak stand. On October 1st, 46 % of all leaves had fallen in the birch stand, compared to only 18 % in the oak stand. Only by October 6th (DOY 279) had canopy leaf fall in the oak stand advanced significantly beyond that of the evergreen spruce canopy ($p = 0.02$). Continued leaf fall in the oak stand from then on allowed its percentage leaf fall to reach parity with the birch canopy by November 3rd (DOY 307, $p = 0.17$, Fig. 1a). For birch and oak respectively, 50 % of leaf fall was achieved on October 2nd and October 7th. Since the spruce is evergreen, many needles remained on the trees, so cumulated leaf fall from the spruce stand in Fig. 1a is a percentage of all the needles fallen during the measurement period, and reflects the day-to-day environmental factors driving leaf fall (*e.g.* wind and precipitation) rather than a seasonal pattern.

The earlier leaf fall in the birch stand resulted in increased canopy light transmission compared to the oak stand (Fig. 1b). Until September 9th (DOY 252), light transmission was similar in the birch and oak stands, ($p = 0.52$). But for the period that followed, until October 27th (DOY 300), canopy light transmission in the birch stand was regularly found to be significantly higher than that of the oak canopy (on five out of eight measurement days). By contrast, there was no temporal change in canopy light transmission to the spruce understorey.

Overall, daily average air temperature from the weather station was in good agreement with the air temperature measured within the canopy (within-canopy temperature = above-canopy temperature × 0.93 +

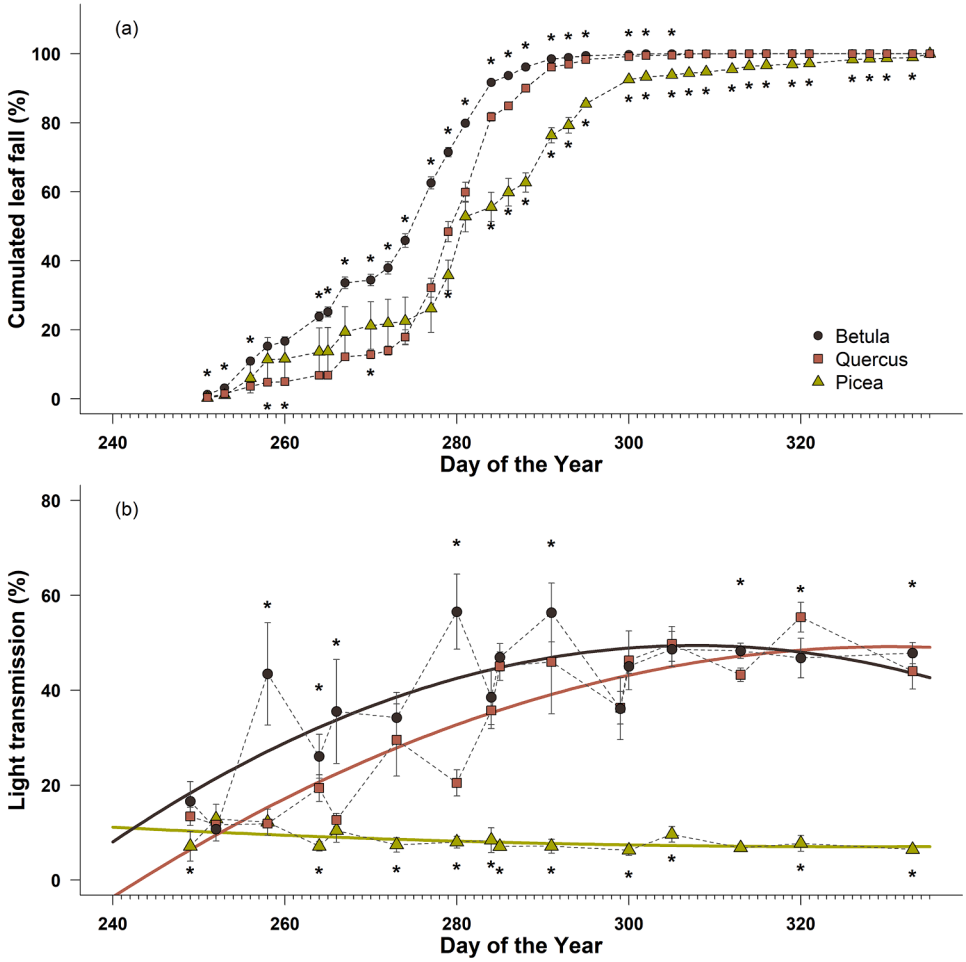

Fig. 1. Cumulative progression of overstorey leaf fall (a) and canopy light transmission (b) through the autumn in stands of birch (circles in brown, *Betula pendula*, L.), oak (squares in red, *Quercus robur*, L.) and spruce (triangles in green, *Picea abies*, L.). In (a), cumulated leaf fall was calculated as a percentage of all leaves fallen during the measurement period. For birch and oak this corresponded to complete leaf fall, but not for spruce. In (b), coloured curves give a polynomial fit for data from each stand. Asterisks above the highest points (or below the lowest) indicate when these data are significantly higher (or lower) than the other two stands. When there is an asterisk both above the highest point and below the lowest point, all three are significantly different from each other.

0.86; $R^2 = 0.92$, $p < 0.001$). We did not find differences in within-canopy atmospheric CO_2 concentration, relative humidity, or air temperature among stands during our measurement period ($p > 0.64$, Fig. A3).

3.2. Spectral composition in the understorey of leafless and fully flushed canopies

Fig. 2 shows the normalized spectral composition in each stand before and after spring leaf-out in 2020. Spectral composition before and after leaf-out differed most in the shade and to a lesser extent in the semi-shade, but did not vary in sunflecks (Fig. A4). UV-A:PAR decreased by about 30 % after leaf-out in the birch and oak stand ($p < 0.004$), but not in the spruce stand ($p = 0.52$).. Both B:G (blue:green) and B:R (blue:red) generally decreased in the shade after leaf-out. This reduction was greater in oak, followed by birch (for which the trend was non-significant for B:R) and lastly spruce (for which no trend was found for B:R). As for R:FR (red:far-red), it generally declined in the shade after leaf-out; more strongly in the oak stand (73 %, $p < 0.001$), than in the birch (54 %, $p < 0.001$), or the spruce stand (26 %, $p = 0.04$). R:FR also decreased in semi-shade in the oak stand, by 50 %. Overall, shorter wavelengths were reduced more strongly after leaf-out, especially in the oak and birch stands, and to a much lesser extent in the spruce stand.

3.3. Temporal changes in leaf water content and photosynthetic capacity of understory species during senescence

Changes in leaf relative water content (RWC) were highly species-specific, but generally RWC decreased through the autumn for deciduous species in the understorey (Fig. 3). The strongest effect of stand type on RWC was found in *Convallaria*. On September 20th (DOY 263), RWC for this species decreased by 80 % in the birch stand, significantly more than the 50 % decrease in the oak stand ($p = 0.003$, Fig. 3a). In the spruce stand the RWC of *Convallaria* declined later on October 5th (DOY 278). A similar trend of higher RWC, and delayed decline, in the spruce stand was recorded in *Fragaria* and *Acer* leaves (Fig. 3b-c). The RWC of *Fragaria* leaves declined faster in the oak stand than in the birch stand - both faster than in the spruce stand - starting on October 13th (DOY 278, $p < 0.009$. Similar to *Convallaria* leaves, *Acer* leaves reached their lowest RWC in the birch stand, with differences between stands becoming more pronounced later in the season (Fig. 3c). On the other hand, *Sorbus* leaves had a consistently higher RWC in the oak stand compared to the other stands (Fig. 3d). In both evergreen perennials, *Anemone* and *Oxalis* (Fig. 3e-f), we found no significant change of RWC through the season, nor consistent differences between stands.

The initial quantum yield of Photosystem II, Φ_{PSII}, declined through the autumn (Fig. 4). Among species, this decline followed similar patterns to those identified in RWC. Thus, *Convallaria* leaves had lowest

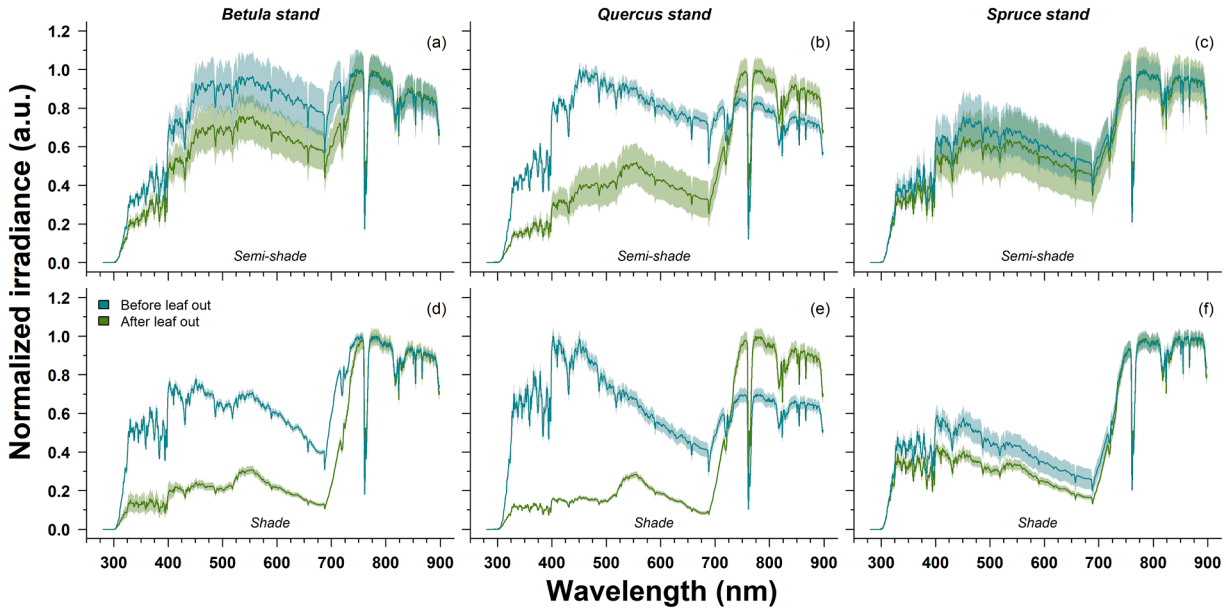

Fig. 2. Normalized spectral irradiance in the understorey of birch (a-d, *Betula pendula*, L.), oak (b-e, *Quercus robur*, L.) and spruce (c-f, *Picea abies*, L.) stands before and after leaf-out (May 22nd and June 10th 2020, respectively). Spectra were normalized with regard to the highest irradiance per scan. Measurements were taken in semi-shade (a, b, c) or in the shade (d, e, f) at 30 cm above the ground. The band around the curves represents the standard error from the mean of four locations in each stand.

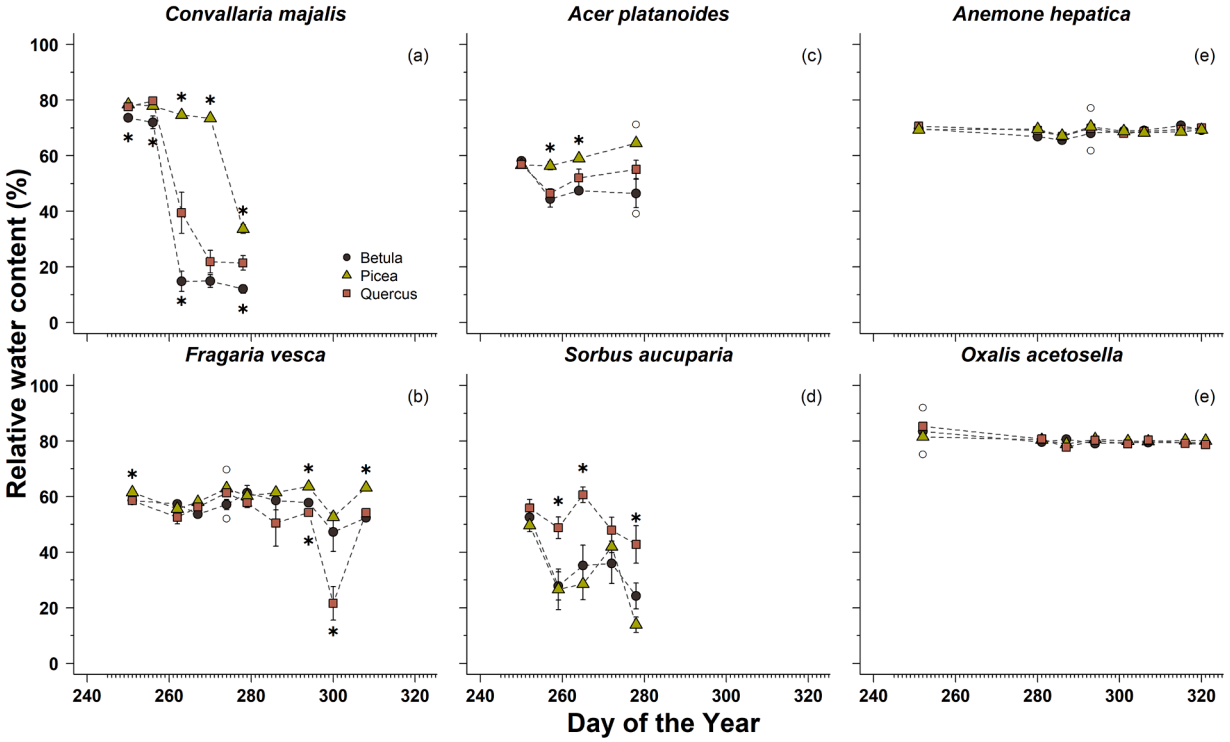

Fig. 3. Relative water content in two deciduous perennials (a, *Convallaria majalis* L. and b, *Fragaria vesca* L.), two tree seedlings (c, *Acer platanoides* L. and d, *Sorbus aucuparia* L.), and two evergreen perennials (e, *Anemone hepatica* L. and f, *Oxalis acetosella* L.). Colours represent the stand from which they were sampled (circles in brown, *Betula pendula*, L; squares in red, *Quercus robur*, L.; triangles in green, *Picea abies*, L.). Data shown are means ± standard error. Asterisks above the highest points (or below the lowest) indicate when these data are significantly higher (or lower) than the other two stands. When there is an asterisk both above the highest point and below the lowest point, all three are significantly different from each other. Circles above the highest point and below the lowest point show they are significantly different from each other, but not from the middle point.

Φ_{PSII} in the birch stand ($p < 0.008$), and highest in the spruce strand ($p < 0.03$).

These differences were recorded on September 13th, a week before the decline in RWC became apparent (September 20th, Figs. 3a & 4a). After September 13th, light curves could not be produced from *Convallaria* leaves from the birch and oak stands, due to the lack of a

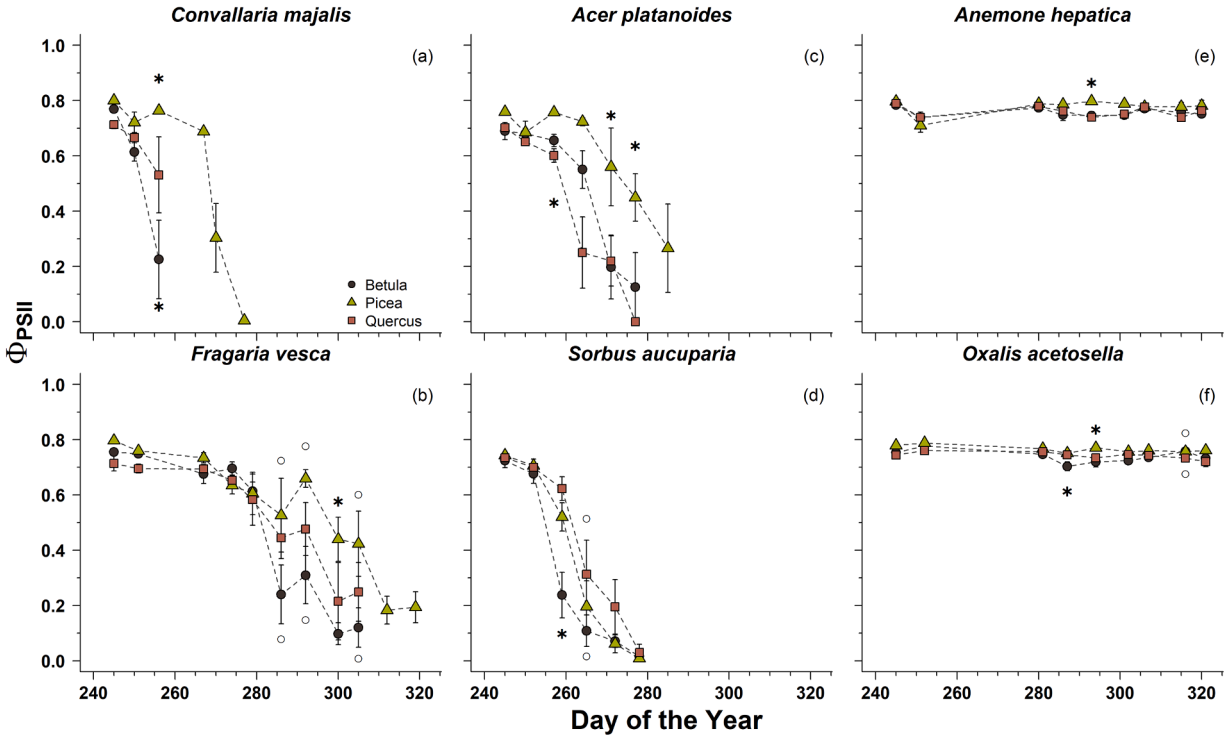

Fig. 4. Initial quantum yield of PSII (Φ_{PSII}) in two deciduous perennials (a, *Convallaria majalis* L. and b, *Fragaria vesca* L.), two seedlings (c, *Acer platanoides* L. and d, *Sorbus aucuparia* L.), and two evergreen perennials (e, *Anemone hepatica* L. and f, *Oxalis acetosella* L.). Colours represent the stand from which they were sampled (circles in brown, *Betula pendula*, L; squares in red, *Quercus robur*, L.; triangles in green, *Picea abies*, L.). Data shown are means ± standard error. Asterisks above the highest points (or below the lowest) indicate when these data are significantly higher (or lower) than the other two stands. When there is an asterisk both above the highest point and below the lowest point, all three are significantly different from each other. Circles above the highest point and below the lowest point show they are significantly different from each other, but not from the middle point.

chlorophyll fluorescence signal. However, in the spruce stand Φ_{PSII} only declined after September 27th. The same general trend of earlier Φ_{PSII} decline in the birch, followed by oak, then the spruce stand was repeated, in the other deciduous perennial *Fragaria* (Fig. 4b). In *Acer* leaves, the decline in Φ_{PSII} was clearly delayed in the spruce stand (Fig. 4c). Similar to our RWC results, the decline in Φ_{PSII} of *Sorbus* leaves was delayed in the oak stand, compared to the birch stand, and spruce stand. For the two evergreen perennials, no change could be detected

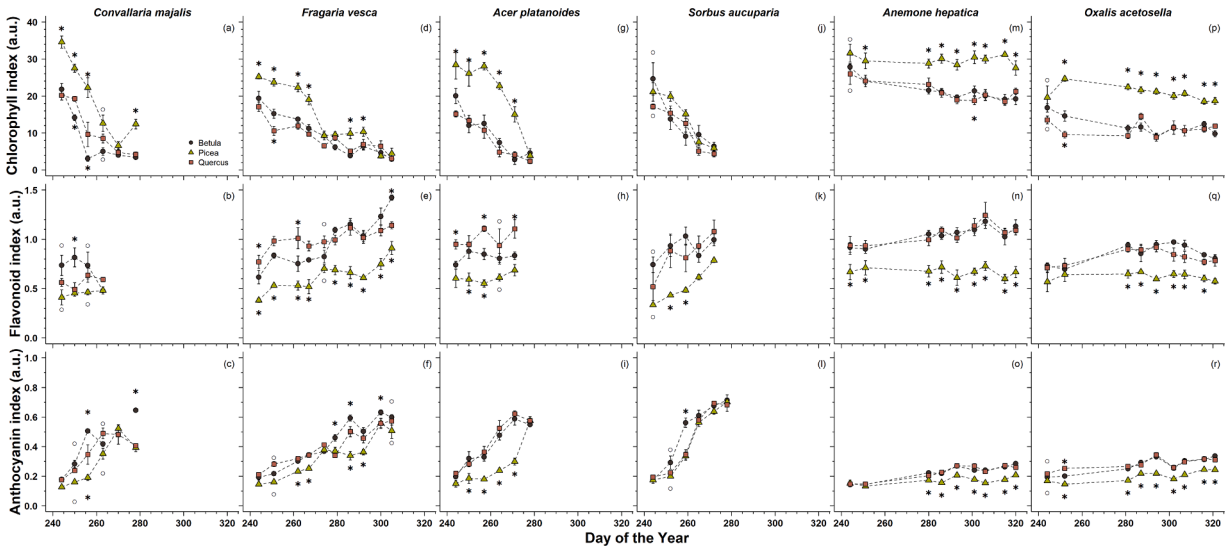

Fig. 5. Pigment content in two deciduous perennials (a-c, *Convallaria majalis* L. and d-f, *Fragaria vesca* L.), two seedlings (g-i, *Acer platanoides* L. and j-l, *Sorbus aucuparia* L.), and two evergreen perennials (m-o, *Anemone hepatica* L. and p-r, *Oxalis acetosella* L.). Chlorophyll (a, d, g, i,m, p), flavonoids (b, e, h, k, n, q), and anthocyanins (c, f, i l, o, r) content measured optically are shown (relative absorptance units). Colours represents the stand from which they were sampled (circles in brown, *Betula pendula*, L; squares in red, *Quercus robur*, L.; triangles in green, *Picea abies*, L.). Data shown are means ± standard error. Asterisks above the highest points (or below the lowest) indicate when these data are significantly higher (or lower) than the other two stands. When there is an asterisk both above the highest point and below the lowest point, all three are significantly different from each other. Circles above the highest point and below the lowest point show they are significantly different from each other, but not from the middle point.

through the autumn, but overall, Φ_{PSII} was significantly higher in the spruce stand than in the other two stands (by about 3.2 % for *Oxalis*, and 2.3 % for *Anemone*). In essence, senescence defined through changes in RWC and Φ_{PSII} generally progressed fastest in the birch stand and was delayed in the spruce strand, except for evergreen understorey species and *Sorbus*.

3.4. Temporal change in pigment content during senescence

On the whole, changes in pigment content through the autumn followed a relatively consistent pattern between species, and according to their deciduousness. Chlorophyll content declined, while epidermal flavonoid and anthocyanin content rose (Fig. 5). Even in the two evergreen species we found a small decline in chlorophyll ($p < 0.001$, partial $R^2 = 0.20$ and 0.12 for *Anemone* and *Oxalis*, respectively) and an accumulation of anthocyanins ($p < 0.001$, partial $R^2 = 0.58$ and 0.53 for *Anemone* and *Oxalis*, respectively) through the season (Fig. 5m-r).. In *Convallaria* leaves, pigment change was faster in the birch stand than in the oak stand. On September 7th and 13th, chlorophyll declined by 35 % and 86 % in the birch stand, but only by 4 % and 52 % in the oak stand, respectively, compared to their September 1st value (Fig. 5a) The epidermal flavonoid and anthocyanin contents followed similarly stand-specific patterns in *Convallaria* leaves. The latter rose on September 13th to 3 times its value on September 1st in the birch stand, but only by twice its value in the oak stand over the same period (Fig. 5c). *Fragaria* leaves behaved through senescence in a comparable way to *Convallaria* among the stands (Fig. 5d). Conversely, flavonoid and anthocyanin content tended to be higher in the oak stand at the start of autumn, but lower at the end of it. For example, flavonoid content was 20 % lower in the birch than in the oak stand on September 1st (DOY 244), but 24 % higher on November 1st (DOY 305). In *Acer* and *Sorbus* leaves, there was a similar trend of delayed senescence in the spruce stand, as defined here through changes in pigment content, but differences between the oak and birch stands were less pronounced (Fig. 5 g-l). In summary, declines in chlorophyll content, and associated increases in flavonoids and anthocyanins happened first in the birch, then the oak, and finally the spruce stand.

4. Discussion

4.1. Differential timing of canopy senescence primarily affects plants through changes in the understorey light environment

At our site in southern Finland, we found that birch trees started their senescence about one week before oak trees. This sequence is consistent with Marchand et al. (2020), who used a leaf color-scale to record senescence in Belgian birch canopies starting 20 days earlier than oak canopies. Elsewhere, various other indices and models have likewise determined senescence in birch to start between 10 and 30 days earlier than oak canopies (Marien et al., 2019; Liu et al., 2020). Perhaps a faster seasonal transition at high latitudes, explains the shorter period between senescence in the birch and oak canopies that we report. Nevertheless, the most original finding of our study resulted from this difference in the timing of canopy openness between stands, which likely led to distinct senescence dynamics in their understoreys.

One might have expected this differential timing in canopy senescence to drive a divergence in temperature microclimate between understorey canopies. With an earlier leaf fall, the buffering effect of the overstorey canopy on diurnal fluctuations in temperature is expected to diminish (von Arx et al., 2013; De Frenne et al., 2021). The extend of this effect is difficult to test experimentally as it requires simultaneous measurements in equivalent leafless and fully leaved canopies. In our study, several factors may explain the lack of a temperature trend. First, the measured stands were not very dense (plant area index, the one-sided area of canopy element per unit ground surface area in all three stand is between 3.5 and 4.0; Hartikainen et al., 2020), which would favor relatively close coupling between the atmosphere and the canopy (Martin, 1989). Second, while leaf fall started later in the oak canopy, it was also faster, resulting in senescence ending at similar times (Fig. 1). Third, a more comprehensive assessment may have revealed microclimate differences between stands,

but the lack of difference in temperature at noon across stand (Fig. A3), despite distinct canopy transmission (Fig. 1) suggests that temperature varied relatively little according to canopy openness. For these reasons, we infer that irradiance more likely to be the primary differentiating environmental factor among stands.

The year 2021 was near the average amount of yearly precipitation received at this site (662 mm in 2021 compared to 640 mm on average between 1990 and 2021). Therefore, it is unlikely that water stress contributed significantly to promote leaf senescence. Moreover, the stands were near one another (Fig. A2), which limited variability in soil type (the whole area is classed as sandy moraine by a geological survey of Finland). Although we did not measure soil moisture in this experiment, it is possible that differences in species composition across stand may feedback into soil structure via *e.g.* rooting patterns, and affect soil water dynamics through the autumn. While intense droughts can affect autumn phenology at northern latitudes (Dox et al., 2022), senescence in boreal forests is generally found to be much less susceptible to water stress than in drier biomes (Peng et al., 2019; Wu et al., 2022).

Other factors induced by overstorey leaf fall, such as litter accumulation or a reduction in the insulation from wind, could also have contributed to the differences in understorey senescence between stands. Therefore, our study does not allow us to establish a firm causal relationship between a change in irradiance as a result of leaf fall, and understorey senescence. Still, our experimental design allowed us to detect stand-specific timings of understorey senescence, which were most likely related to a change in canopy openness. To our knowledge, no other study of autumn phenology reported such local dynamics of senescence, which were only possible by our intensive monitoring of the understorey.

4.2. Dynamics of leaf epidermal flavonoids during canopy senescence

The accumulation of anthocyanins in leaves during senescence is a common occurrence that has been heavily investigated (Wheldale, 1916; Hoch et al., 2001). Yet, their function, particularly in the understorey, is still debated today (Renner and Zohner, 2019; Agati et al., 2021; Hughes et al., 2021). Other flavonoids have also been found to accumulate during leaf senescence (Torras-Claveria et al., 2012; Mattila et al., 2018). The trends we report for increased epidermal flavonoid (based on the flavonol glycoside absorption spectrum) and anthocyanin content during leaf senescence are congruent with the above literature. Moreover, in the same boreal forest, Hartikainen et al. (2020) found that epidermal flavonoids were responsive to seasonal trends in irradiance reaching the understorey. Furthermore, long-term filter treatments attenuating blue light, and/or UV radiation, produced large reductions in flavonoids and anthocyanins during leaf senescence of understorey species and tree seedlings (Brelsford et al., 2022). Moreover, although correlations between traits were generally weak due to differences in the temporal dynamics of each trait during senescence, anthocyanin content was strongly correlated with Φ_{PSII} ($R^2 = 0.84$, Fig. A5), suggesting that the more easily obtainable and scalable optical measure of anthocyanin content (compared to fluorescence data) may be a better proxy than chlorophyll-related indices (Walther et al., 2016), for evaluating photosynthetic activity during senescence. Nevertheless, our finding that flavonoids and anthocyanins increased in the spruce stand as well as in the deciduous stands, indicates that additional factors to spectral irradiance affect pigment accumulation (*e.g.* cold; Pescheck and Bilger, 2019). Building on previous studies, we can surmise that distinctions we found among stands in the dynamics of flavonoid and anthocyanin accumulation are largely driven by changes of spectral irradiance following leaf fall.

4.3. Species-specific dynamics of leaf senescence

Differences in senescence dynamics between stands varied among the species considered. In deciduous species, *Convallaria* generally showed the largest differences between stands while only minor differences between stands were detected in *Sorbus*. This indicates that while in some species the induction of senescence may be more closely related to changes in the environment (*e.g.* light) between stands, in other species senescence may be triggered by more consistent environmental cues, such as daylength. This segregation may occur according to the specific ecological strategy of species. For example, the delayed senescence in *Fragaria* compared to the other species might suggest that the production of wintering leaves requires nutrient redistribution (Alpert, 1996). Although the two evergreen species did not have senescing leaves, they also displayed a trend for reduced chlorophyll and increased epidermal flavonoid and anthocyanin content (Fig. 5), which may indicate fine-tuning of leaf physiology to lower metabolic activity in the frozen understorey of boreal winters (Solanki et al., 2022).

4.4. Light as a senescence trigger for boreal understorey species

Whether a change in the quantity or quality of irradiance is responsible for inducing senescence is difficult to determine, and could not be distinguished using our approach, as both change simultaneously with leaf fall. In our forest stands, attenuation of blue light and UV radiation has previously been found to delay leaf senescence in several boreal understorey species (Brelsford et al., 2022). In contrast, bud set of spruce seedlings is reported to be delayed by supplemental blue light, although the 24 h photoperiod used by Opseth et al. (2016) make the interpretation of this finding in natural conditions difficult. Plants perceive blue light and UV radiation through cryptochromes and UVR8 respectively; photoreceptors which are involved in the regulation of senescence (cryptochromes in *Glycine* max (L.) Meng 2013), as well as mediating flavonoid and anthocyanin accumulation (Rai et al., 2019). With these consideration in mind, the change of light quality following overstorey leaf fall may have accelerated senescence, first in the birch, then in the oak, compared with the spruce stand. However, we did find that the difference in spectral composition before and after leaf-out were larger in the oak stand than in the birch stand (Fig. 2). If spectral composition affects leaf senescence in these understorey species, a larger change is likely to have a greater impact on timing, which we did not find in our experiment. Potentially, if the change in the spectral composition of sunlight after leaf fall induced leaf senescence, this would occur in association with other factors such as the concurrent change in the amount of incident radiation.

We expected understorey species to use the increased radiation received after canopy leaf fall, to extend their photosynthetic activity, and delay senescence. We instead found that it accelerated senescence. In support of our finding, leaf senescence of red oak seedlings (*Quercus rubra*, L.), growing in controlled conditions in low light created by a neutral shade cloth, was delayed compared with those in natural sunlight (Cavender-Bares et al., 2000). Likewise, Lee et al. (2003) found delayed senescence under low irradiance in four of five species tested (including red oak), using *in situ* shading of branches in Harvard Forest. Similarly, chlorophyll degradation was delayed by shading in greenhouse-grown rice leaves (*Oryza sativa*, L.). The studies cited above used a low irradiance treatment of 10–20 % of full sun, which corresponds to the light transmission to the understorey when our stands were fully leaved (Fig. 1). Evidence for shade inducing leaf senescence is weaker, and rests mainly on findings that total darkness can induce senescence (Okada et al., 1992; Ananieva et al., 2008; Janečková et al., 2018). Light triggering senescence is counterintuitive, as dark forest understoreys are a testament to the vital importance of light for growth. Nevertheless, if the change of spectral quality and quantity associated with leaf fall is responsible for triggering senescence, it would provide a clear and reliable signal in the understorey.

4.5. Extended photosynthetic activity after leaf fall?

To synthesize our findings regarding changes in canopy light transmission and Φ_{PSII}, we calculated a cumulative ETR (ETRc) between September 6th to November 29th (DOY 249 - 333). In the light-limited understorey of forest canopies, ETR may give us some insight into photosynthesis activity (Guan et al., 2016). ETRc was strongly species-specific (Fig. 6), because those species that senesced later could benefit from additional days of photosynthetic activity, especially in September when incident irradiance was still relatively high (Fig. A1). In the evergreen species, *Oxalis* and *Anemone*, ETRc is similar in each stand, because only canopy light transmission differed, while a similar Φ_{PSII} was maintained through the measurement period (Fig. 4e-f). As such, they can be considered to potentially gain the most from extended photosynthetic activity. The ETRc was 54 % higher in the birch stand than in the oak stand for these two species, due to earlier leaf fall in the birch. In comparison, there was more variability in the ETRc of the deciduous species and the senescing summer leaves of *Fragaria*. While *Fragaria* responded similarly to *Oxalis* and *Anemone* in the birch stand, in that its ETRc was 52 % higher than in the oak stand, this difference was only 6 % and 2 % in *Convallaria* and *Sorbus*, respectively. This is because *Fragaria* leaves senesced later, thus they were more able to use the increased light arising from earlier leaf fall in the birch, in contrast to *Convallaria* and *Sorbus* which had early senescence (Fig. 4a,d). *Acer* was singular, in that its Φ_{PSII} was maintained higher in the birch than in the

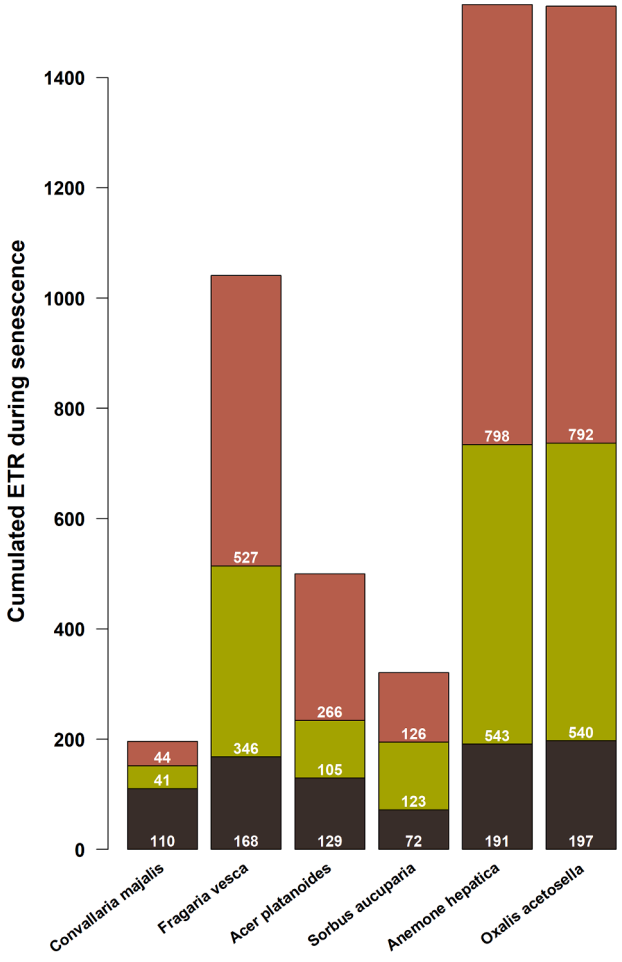

Fig. 6. Electron transport rate cumulated from September 6th to November 29th in six understorey species growing in adjacent forest stands (top in brown, *Betula pendula*, L; middle in red, *Quercus robur*, L.; bottom in green, *Picea abies*, L.).Please see Eqn.1 and associated text for more information on the calculation of ETR. Values for each stand and species are shown in white.

oak stand (Fig. 4c), which combined with the increased irradiance in the birch stand led to a 150 % higher ETRc. It should be noted that these calculations do not account for diurnal variations in canopy transmittance and Φ_{PSII}. Canopy transmittance is dependent on sun angle and weather patterns. The main purpose of this calculation was to highlight relative differences between species, which were located under the same canopy, and would experience the same diurnal changes in PAR and canopy transmission. Leaf absorptance can also vary temporally and between species, which we did not account for, thus some caution should be used when interpreting small differences between groups. Nevertheless, this calculation indicates that although there were species-specific differences, some species were able to benefit from the canopy opening after leaf fall, even though this also led to earlier senescence. This is important because it means that understorey species will likely be differently affected by an extension of the growing season under climate change (Gill et al., 2015).

Extended photosynthetic activity (or phenological avoidance) of understorey plants in autumn has been reported in various forested ecosystems, although most often when comparing invasive species with natives (Fridley, 2012; O'Connell and Savage, 2020). These species are inclined to be adapted to warmer environments where the growing season is longer, compared to native species adapted to conditions which characterized the environment before global warming. It has also been suggested that phenological avoidance may be more advantageous in spring, compared to winter (Augspurger et al., 2005). Temperature and irradiance are often higher in spring, due to the season starting near the summer solstice when daylength is close to its maximum (Hutchison and Matt, 1977). In autumn, soil water reserves are more likely to be depleted, leading to early senescence (Wu et al., 2022). Leaves are also older, with reduced photosynthetic capacity (Augspurger et al., 2005), and a warmer autumn may increase respiration more than photosynthesis (Piao et al., 2008). Photoperiod is known to control senescence via phytochromes (Olsen, 2010), but cold nights seem to play a larger role at northern latitudes (Lang et al., 2019). In boreal forests, where seasonal transitions are rapid and acute, perhaps it is more valuable for deciduous species to conserve resources, than to gain a few extra days-worth of carbon accumulation, thus "safety first" in autumn may be a more reliable phenological strategy.

4.6. Conclusion

While there was evidence of extended photosynthetic activity after canopy leaf fall, we also found for the first time that canopy opening in autumn, leading to increased transmittance of solar radiation, stimulated understorey senescence. More work is needed to decipher the photoreceptors mediating a spectral cue (*e.g.* UV, blue or red light photoreceptors; Meng et al., 2013), or whether the amount of radiation itself is driving oxidative stress (Juvany et al., 2013). With global changes delaying the onset of tree senescence (Gill et al., 2015), our findings postulate that understory senescence would be delayed similarly. Species-specific reactions to environmental cues related to senescence may alter the competitive balance between species in the future (Fridley, 2012), which could have consequences for the biodiversity of plant and animal species within the ecosystem, and affect ecosystem functioning (Nilsson and Wardle, 2005). In any case, those tree seedlings and understorey species that exploit favourable spring conditions prior to canopy flush (*e.g., Convallaria, Acer* and *Sorbus*; Hartikainen et al., 2020; Brelsford et al., 2022) typically senesced upon canopy opening in the autumn. On the contrary, the senescing summer leaves of wintergreen species (*e.g., Anemone, Fragaria* and *Oxalis*) showed some capacity to exploit the available light in autumn. Consequently, prolonged canopy leaf retention due to climate warming may differentially affect the viability of species growing in the understorey according to their light-capture strategy (*i.e.* evergreen, summer leaves, spring ephemerals). Although leaf phenology can have far-reaching consequences for ecosystem functioning (Richardson et al., 2013), there are few models of autumn phenology (Vitasse et al., 2011), partly due to the complexity of the factors involved. By assessing how the local environment affected the phenology of common boreal understorey species, our study addresses this knowledge-gap. Still, there is much more to learn about autumn senescence before we can produce an accurate picture; one in living colours.

5. Author contribution

A.D. contributed to the data collection and analysis. M.D. and T.M.R. contributed to the experimental design, data collection, data analysis, and interpretation. All authors contributed to the writing of the manuscript.

6. Data and materials availability

The data that supports the findings of this study will be available in a public repository. More information is available upon request.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2023.109807.

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