# The influence of spectral composition on spring and autumn phenology in trees

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## Abstract

Several recent reviews highlight the molecular mechanisms which underpin phenological responses to temperature and photoperiod, however these have mostly overlooked the influence of solar radiation and its spectral composition on these processes. For instance, solar radiation in the blue (B) and ultraviolet (UV) regions of the spectrum, as well as the red/far-red ratio (R:FR), can influence spring and autumn phenology. Solar radiation reaching the Earth changes diurnally and seasonally, however rising global temperatures, latitudinal range shifts and light pollution are likely to produce novel combinations of phenological cues for tree species. Here, we review the literature on phenological responses to spectral composition. Our objective was to explore the natural variation in spectral composition using radiative transfer models, and to reveal any species-specific or ecotype-specific responses relating to latitudinal origin. These responses are likely to be most pronounced at high latitudes where spectral composition varies most throughout the year. For instance, trees from high latitudes tend to be more sensitive to changes in R:FR than those from low latitudes. The effects of blue light and UV radiation on phenology have not been studied as much as those of R:FR, but the limited results available suggest both could be candidate cues affecting autumn leaf colouration and senescence. Failure of more-southern species and ecotypes to adapt and use spectral cues during northwards range shifts could result in mistimed phenology, potentially resulting in frost damage, reduced fitness and limited range expansion. Future areas for research should look to establish how consistently different functional types of tree respond to spectral cues, and identify photoreceptor-mediated mechanisms which allow plants to combine information from multiple light cues to coordinate the timing of phenological events. It should then be feasible to consider the synchronous or sequential action of light cues within a hierarchy of environmental factors regulating phenology.

## Introduction

Seasonal cues allow trees to time their bud burst and leaf-out to exploit conditions in spring and summer that are favourable for photosynthesis (Hänninen 1991, Augspurger 2009, Bennie et al. 2010). Another set of cues induce autumn leaf senescence and bud set as conditions become unfavourable again, and trees enter dormancy until the next spring (Lang et al. 1987, Hänninen 1995, Cesaraccio et al. 2004). Once sufficient chilling has occurred during dormancy in winter, rising temperature is the predominant cue affecting bud burst in tree species (Körner 2007, Caffarra and Donnelly 2010, Körner and Basler 2010). In addition, late-successional species are often sensitive to the increase in photoperiod during spring, more so than early-successional species (Basler and Körner 2012). On balance, temperature explains less variation in the timing of bud set and autumn leaf senescence, than it does for spring bud burst (Gallinat et al. 2015). Whilst for some species, average autumnal temperature or accumulated chilling (cold) temperatures have been found to largely predict the date of leaf senescence, photoperiod is a better predictor for other species, such as *Fraxinus excelsior* (Delpierre et al. 2009, Vitasse et al. 2011). Experimental manipulations have also confirmed that decreasing photoperiod to short days (SD) can serve as an autumnal cue for several tree species (Li et al. 2003, Welling and Palva 2006, Lagercrantz 2009).

Phenology of tree species has become a critical field of interest with respect to climate change and rising global temperatures (Bilger and Bugmann, 2018, Post et al. 2018, Richardson et al. 2018). The average date of bud-burst in temperate deciduous species is advancing (Menzel 2006, Körner and Basler, 2010), and the date of autumn leaf senescence is expected to occur later each year in accordance with rising temperatures (Menzel et al. 2006, Ibáñez et al. 2010[a]). However, relatively few studies have investigated the potential effect of climate change on autumn phenology (Gallinat et al. 2015, Panchen et al. 2015). Day length, temperature and numerous other environmental cues have been found to affect autumn phenology (Panchen et al. 2015 and references therein), leaving great potential for complex interactions between them. This is one reason why the timing of autumn senescence is more difficult than that of leaf out to explain with process-based models (Panchen et al. 2015, reviewed by Chuine and Régnière 2017).

Simple process-based bud burst models which incorporate chilling and photoperiod, can outperform linear regression of bud burst against temperature. However, further increasing the complexity of these process-based bud burst models by attempting to simulate the physiological processes by which multiple cues interact, has to-date failed to improve their power (Basler 2016, but see also Olsson and Jönsson 2014). Nevertheless, as our knowledge of the cellular, molecular and physiological mechanisms underlying the response to multiple cues continues to increase, we should be able to make models that are better able to predict tree phenology (Basler 2016, Chuine and Régnière 2017). Not only do changes in tree phenology have potential to create asynchrony with the timing of pollinators and seed dispersers, but they could also have implications for ecosystem processes such as carbon assimilation and leaf decomposition which are affected by the growing season length and the timing of leaf senescence (Cleland et al. 2007, Basler 2016). In turn, reliable models of these ecosystem processes are needed to incorporate feedbacks between vegetation and climate, as well as carbon sequestration into long-term forecasts of phenological events (Leinonen and Kramer 2002, Richardson et al. 2013).

Recently, several detailed reviews have examined the molecular mechanisms that allow trees to integrate cues from temperature and photoperiod to time their seasonality (Ding and Nilsson 2016, Singh et al. 2017, Maurya and Bhalerao 2017). *Populus trichocarpa* was the first tree to have its genome mapped, establishing *Populus* trees as a model tree species (Tuskan et al. 2006). The pathway that mediates growth cessation and bud dormancy through temperature and photoperiodism in *Populus* shows similarities with the pathway that regulates flowering in the other model plant species *Arabidopsis thaliana* (Böhlenius et al. 2006). In *Arabidopsis thaliana*, pathways triggered by blue/UV-A-detecting cryptochromes (CRYs) and R:FR-detecting phytochromes (PHYs) entrain the circadian clock (Somers et al. 1998, reviewed by Oakenfull and Davis 2017), controlling the activity of proteins such as CONSTANS (CO), which activate FLOWERING LOCUS T (FT) under long-days to induce flowering (Valverde et al. 2004). Similarly, in *Populus*, FT overexpression prevents growth cessation and bud set in response to SD conditions (Böhlenius et al. 2006), and temperature modulates the rate at which bud set and growth cessation occur in response to SD conditions (Rohde et al. 2011).

The spectral composition of solar radiation reaching the Earth's surface changes diurnally over the course of a day, seasonally over the course of a year, as well as with latitude (Johnson et al. 1967, Smith 1982, Hughes 1984, Nilsen 1985). There is mounting evidence that these changes in spectral composition can influence spring and autumn phenology in tree species (Juntilla and Kaurin 1985, Linkosalo and Lechowicz 2006, Mølmann et al. 2006, Strømme et al. 2015, Opseth et al. 2016). Whilst the aforementioned reviews (Ding and Nilsson 2016, Singh et al. 2017, Maurya and Bhalerao 2017) summarise the molecular mechanisms underlying temperature- and photoperiod-mediated phenological responses in tree species, they do not consider the effects of spectral composition. The mechanistic responses associated with spectral cues for phenological processes are yet to be elucidated; but may have the potential to help us better predict and model future phenological responses.

Initial research identified an important role for PHYs in facilitating photoperiodic responses during the annual life cycle of trees (Olsen and Juntilla 2002, Mølmann et al. 2006; Taulavuori et al. 2010). However, the mechanism by which PHYs affect bud burst and bud set, as facilitated by changes in red:far-red (R:FR) light, has not been well defined. Although, both blue light and UV-B radiation (280-315 nm) have been shown to affect bud set (Mølmann et al. 2006, Strømme et al. 2015), it is not clear whether these effects act together with R:FR or not. It could be argued that just as blue and R:FR, detected by CRYs and PHYs, affect the circadian clock and flowering in *Arabidopsis thaliana* (Somers et al. 1998), certain regions of the spectrum are likely to affect both the circadian clock and phenological responses in tree species. In addition, light pollution has been shown to advance the date of bud burst of several tree species across the UK (ffrench-Constant et al. 2016), through a photoreceptor-mediated mechanism which has yet to be elucidated.

Given the recent progress towards identifying spectral regions which affect spring and autumn phenology, we have sought to create a comprehensive review and synthesis of studies into the effects of spectral composition on tree phenology. Our aims were to: 1) provide a description of the natural variation in spectral composition that may be utilised by trees as seasonal cues, and the corresponding photoreceptors which detect these changes in spectral composition; 2) critically compare the methodology and results of studies examining phenological responses to spectral cues; 3) assess whether any trends have emerged among species, or ecotype-

specific responses across different latitudes, and 4) identify promising areas for future research into phenological responses to spectral composition, such as photoreceptor-mediated pathways which have yet to be elucidated, and candidate regions of the spectrum which may affect phenology but are yet to be thoroughly tested.

In compiling this review, we compared 21 studies which have investigated the effects of spectral composition on spring phenology (bud burst) (Table 1) and/or autumn phenology (leaf senescence or bud set) (Table 2). Studies demonstrating an effect of spectral composition on the bud burst of axillary shoots of non-tree species (Muleo et al. 2001, Girault et al. 2008) were also included in Table 1. Although this process differs from the spring bud burst of tree species, parallels in the effects of spectral composition and mechanisms involved may be relevant to tree species. Similarly, we included research on the effects of spectral composition on growth cessation (Juntilla and Kaurin, 1985, Tsegay et al. 2005) which has parallels with autumn phenology, and likewise the effects of light pollution on both spring and autumn phenology (Matzke et al. 1936, Saarala et al. 2013, ffrench-Constant et al. 2016). Studies were separated according to the regions of solar radiation they considered, either R/FR, blue light, or UV radiation. To allow a comparison of the different irradiances used in different studies, we give both the original units from each experiment and an estimate of irradiance following conversion to units of energy irradiance in W $m^{-2}$ based on the spectra provided in the studies (Tables 1, 2), and using the *photobiology* package in R (Aphalo, Pedro J., ed., 2013-2018, www.r4photobiology.info ISSN 2343-3248, Helsinki; Aphalo 2015).

To exemplify how spectral composition varies throughout the year and across a latitudinal gradient, we modelled spectral composition using the radiative transfer model libRadtran which allows solar radiation at any location on the Earth's surface to be simulated, using solar angle and atmospheric conditions (following Emde et al. 2016 and Brelsford 2017, further details provided in SI). Our aim was to use these simulations to corroborate and elaborate upon measurements of natural variation in spectral composition from some of the reviewed studies, rather than to provide a comprehensive database of variation in spectral composition (Johnson et al. 1967, Smith 1982, Hughes et al. 1984, Chambers and Spence 1984, Lee and Downum 1991, López-Figueroa 1992, Ragni and D'Alcalà 2004).

## Detection of changes in spectral composition

Phytochromes (PHYs) are plant photoreceptors that detect red (R) and far-red (FR) light and compositional changes between these regions. In the dark, PHYs are synthesized in their red light-absorbing form (Pr, λ=660nm), and upon exposure to light PHYs are converted to their far-red light absorbing form (Pfr, λ=730nm, Smith 1982; Smith & Morgan, 1983). The phytochrome equilibrium refers to the proportion of Pfr/Total Phy, and is thus reflective of the relative ratio of R:FR received, whereby high ratios of R:FR produce a higher phytochrome equilibrium (ϕ), due to the interconversion of PHYs in response to R and FR light (Holmes and Smith, 1977). The model species *Arabidopsis thaliana*, has five types of PHYs, whereby PHY A is the predominantly involved in detecting light/dark transitions, PHY B is the predominant R:FR photoreceptor, and PHYs C-E play a lesser role in R light sensing (Whitelam and Devlin 1997). The tree species *Populus tremula*, has one PHY A gene and two PHY B genes (Howe et al. 1998), whereas *Picea abies* has two genes resembling PHY A and PHY B (PHY N and PHY P) and one gene resembling PHY C/PHY A (PHY O, Clapham et al. 1998). In addition, phyA and phyB have an important role in regulating flowering in *A. thaliana* in response to photoperiodic changes, as well as changes in R:FR (Somers et al. 1998, Mockler et al. 2003).

There are two main groups of photoreceptors that mediate responses to changes in the blue/UV-A region: cryptochromes (CRYs) (max A at λ=450nm) and phototropins (phots) (max A at λ=450nm) (Pudasaini and Zoltowski 2013, Banerjee and Batschauer 2005, Briggs and Huala 1999). CRYs 1 and 2 have a role in entraining circadian rhythms, hypocotyl elongation, and seedling development, as well as the accumulation of flavonoids and anthocyanins (Shalitin et al. 2002, Casal 2000, Somers et al. 1998, Kubasek et al. 1992). Most notably in the context of this review, CRYs also mediate photoperiodic controls on flowering time together with PHYs in *A. thaliana* (Guo et al. 1998). However, in the tree species *Picea abies*, only partial CRY sequences have been found to date (Opseth et al. 2016). There is no evidence that phots modulate phenological responses, but they do maintain the circadian rhythm of oscillations in PSII operating efficiency under blue light (Litthaeur et al. 2015).

Although PHYs are primarily R:FR photoreceptors, they do also have an absorption spectra in the blue/UV-A spectral region (Ohgishi et al. 2004).

Many plant responses to UV-B radiation are mediated by the photoreceptor UV RESISTANCE LOCUS 8 (UVR8) which was first identified in *Arabidopsis thaliana* (Rizzini et al. 2011) but is thought to be ubiquitous among plants, having now been described in many species including bryophytes and the tree species *Betula platyphylla* (Soriano et al., 2018, Li et al. 2018). UVR8 regulates the accumulation of flavonoids in response to UV-B radiation, endowing protection against high irradiances of UV-B (Brown et al. 2005). It also has a role in mediating shade responses (Hayes et al. 2014), and possibly the accumulation of certain phenolic compounds in [Insert Table 1][Insert Table 2]

## Ecological role of R:FR light

The most common calculation of the R:FR ratio is the ratio of λ 660:730nm (defined by Smith 1982, used in studies shown in Table 1 and Table 2). During twilight hours, between dawn and sunrise, and between sunset and dusk (Goldstein 1976, Forsyth et al. 1995, Aphalo 2016), a drop in the ratio of R:FR due to the enrichment of FR light in the atmosphere is reported to occur (Figures 1 and 2, Smith 1982, Hughes et al. 1984, Chambers and Spence 1984). Other studies report a sharp brief increase in the R:FR ratio during sunrise and sunset but confirm that R:FR drops during twilight (Lee and Downum 1991, López-Figueroa 1992, Ragni and D'Alcalà 2004). Increased refraction of light entering the atmosphere during periods when the sun angle is between -18° and 0°, preferentially enhances longer wavelengths of the spectrum causing the reduction in R:FR during twilight (Holmes and Smith, 1977). The annual variation in twilight duration, (and thus the duration of a lowered R:FR ratio during twilight) increases at higher latitudes (Figures 1 and 2, Linkosalo and Lechowicz, 2006, Franklin and Whitelam 2007).

The involvement of PHYs in the detection of photoperiodism was originally inferred from the reversible effects of R and FR light on flowering when applied during night breaks (corresponding to a reversible change from the red $P_r$ to far-red $P_{fr}$ -absorbing forms of phytochrome) (Kasperbauer et al. 1963, Fredericq 1964, Lane et al. 1965). For instance, plants that normally only flower under SD conditions, can be stopped from flowering

by exposure to short night breaks of low-fluence R light, an effect which is reversed by subsequent exposure to FR light (Kasperbauer et al. 1963, Fredericq 1964). Furthermore, mutants of *Arabidopsis thaliana* lacking functional PHYs do not exhibit a photoperiodic flowering response (Guo et al. 1998, Mockler et al. 2002). Plants growing at higher latitudes tend to exhibit greater sensitivity to photoperiodic responses, whereas photoperiodic changes are less relevant for plants at low latitudes which tend not to display this capacity (Stinchcombe et al. 2004, Zhang et al. 2008, Way and Montgomery 2015). An alternative explanation is that there are latitudinal differences in how plants respond to R and FR light, whereby the length of the night is detected by short-day plants and southern ecotypes of plant species, whereas the FR-enriched twilight period at the end of the day is the determining factor for the response of long-day plants and northern ecotypes of plant species (Howe et al. 1996, Olsen 2010). This divergence in the use of R:FR-related cues allows those variations in the R:FR ratio associated with day-length, the time of year and latitude to be exploited by plants as a cue to time their phenology (Nilsen 1985).

[Insert Figure 1]

Figure 1. The change in daylength, twilight length and night length throughout the year 2017, along a latitudinal gradient of locations including Oulu (65.01° N, 25.47° E), Helsinki (60.17° N, 24.94° E) and Madrid (40.42° N, 3.70° W), calculated from the *photobiology* package in R (Aphalo, 2016 ). Twilight length was defined as civil twilight, including solar angles from -6° and 0°.

[Insert Figure 2]

Figure 2. Modelled spectral ratios for B:R and R:FR of incident solar radiation at solar angles of 0° to -6° for civil twilight, and at solar zenith for noon. Locations along a latitudinal gradient shown in Figure 1.Values are shown for spring equinox, summer solstice, autumn equinox, and winter solstice. Here B:R defined as (410-500/610-700nm, Johnson et al. 1967), R:FR Sellaro as(650 – 670/720 – 740 nm, Sellaro et al. 2010) and R:FR Smith as ((655 – 665/725 – 735 nm, Smith, 1982). Spectral irradiance was modelled using the radiative transfer

model libRadtran following Emde et al. 2016, Brelsford 2017). Water column data was taken from Kållberg et al. (2005), ozone column thickness data from Experimental Studies Unit, Environment Canada (http://exp-studies.tor.ec.gc.ca/e/index.htm).For twilight values, the solver sdisort was used, and for noon values, the solver disort was used. Further details provided in SI.

## R:FR effects on bud burst

One of the most widely-cited examples of R:FR ratio affecting bud burst, is from an experiment where natural twilight in southern Finland was simulated in a growth chamber and compared with a twilight treatment enriched in FR light created using incandescent and fluorescence lights (Linkosalo and Lechowicz 2006). This low R:FR ratio treatment advanced bud burst of *Betula pendula* plantlets by 4 days compared with the control simulating natural twilight. Many responses of bud burst to R and FR are particular to specific species or populations (Erez et al. 1966, Mølmaan et al. 2006, Girault et al. 2008). Seedlings of *Picea abies* produce ecotype-specific responses of bud burst to R:FR (Mølmaan et al. 2006): a population from a northern latitude (69˚N) did not reach bud-burst when grown under 12 h of white light (30–35 W $m^{-2}$, Phillips TLD 15 W/840) followed by 12 h daylight extension using R LED lights (660 nm) to provide 24 h total day length. However, the seedlings did achieve bud-burst when grown under 12 h day-length extension using FR LED lights (730 nm). Conversely, the % bud burst of populations from a more-southerly latitude exposed to the same treatments (59˚N and 64˚N) was higher under R light than FR light. Such differences along a latitudinal cline show that some plants may be adapted to use changes in R:FR and spectral composition as cues to regulate the timing of bud burst.

Unlike these results, Erez et al. (1966) found that neither a FR treatment nor a combined R + FR treatment increased the percentage of bud burst in *Prunus persica*. It is interesting to consider whether this difference could be due to the latitude of origin of the plant species/ecotype studied. Bud burst in mid-latitude and northern-latitude ecotypes of *Picea abies* is more responsive to FR than that of southern ecotypes (Mølmaan et al. 2006), and likewise bud burst of *Betula pendula* of Finnish origin responds to FR treatment (Linkosalo and Lechowicz

2006). Considering that *Prunus persica* does not grow at high latitudes, this supports the hypothesis that at high latitudes changes in spectral composition as opposed to changes in day length may regulate plant phenology, whereas at low latitudes the predominant cue is changes in day length rather than changes in spectral composition (Nilsen et al. 1985, Juntilla and Kaurin 1985, Lüttge and Hertel 2009).

The role of PHYs integrating light input into the circadian clock has been well studied in *Arabidopsis thaliana*, and there are several homolog regions of the circadian clock in the model tree species *Populus tremula* (Frewen et al. 2000, Kozarewa et al. 2010, Ibáñez et al. 2010[b]). However, we still do not fully understand the possible mechanisms by which PHY photoreceptors mediate bud-burst in response to R:FR. Expression of PHY homologs PHY B1 and PHY B2 in *Populus tremula*, as well as concentrations of the signalling molecule abscisic acid (ABA), have been reported to increase during bud burst (Frewen et al. 2000). Similarly, PHY-A-mediated FR-signalling has been reported to control expression of homolog regions of the circadian clock, such as LATE ELONGATED HYPOCOTYL (LHY) in *Populus tremula* (Kozarewa et al. 2010). In a separate study, expression of LHY delayed bud burst (Ibañez et al. 2010), suggesting that phytochrome-mediated expression of LHY, as well as ABA signalling, may be good candidate mechanisms to examine with respect to the response of bud burst to R:FR.

## R:FR effects on autumn phenology

Only one study thus far has examined the effects of R:FR on autumnal leaf senescence (Lee et al. 2003). There, an experiment in Harvard Forest USA failed to detect a response of autumn leaf senescence to different R:FR ratios at different PAR irradiances in six woody species. However, a treatment that used a neutral shade cloth to reduce irradiance evenly across the spectrum delayed the decline in leaf chlorophyll content in all six species, and in anthocyanin content in five of the six species, throughout leaf senescence compared with all the R:FR treatments (Lee et al. 2003). In agreement with this, the leaf senescence and degradation of chlorophyll in leaves of *Quercus robur* was also delayed when subjected to shade (Cavender-Bares et al. 2000). Whilst the existing evidence suggests that R:FR ratios may not affect the rate of leaf senescence in woody species, there is

opportunity to study the consistency of this response at different latitudes and in different species. We also recommend further research to identify the regions of the spectrum causing delayed leaf senescence under shaded conditions (Cavender-Bares et al. 2000, Lee et al. 2003).

Interestingly, R:FR has been shown to affect bud set in the gymnosperms *Picea abies* and *Abies lasiocarpa*, (Mølmaan et al. 2006, Opseth et al. 2016, Chiang et al. 2018) FR light delayed bud set most effectively in two experiments with *Picea abies*, however the ecotype-specific effects of FR and R light differed between the studies. Mølmann et al. (2006) demonstrated that FR (730 nm) was more effective at delaying bud set in northern (69˚N) and mid-range ecotypes (64˚N), whereas red light (660 nm) was more effective at delaying bud set in the southern ecotype (59˚N). Similarly, FR has been reported to delay the growth cessation of a northern ecotype more than a southern ecotype of *Salix pentandra* (Kaurin and Juntilla, 1985) However, using a very similar experimental set up to that of Mølmann et al. (2006), with equivalent spectral irradiance and temperature between treatments, Opseth et al. (2016) report that FR was consistently the more-effective light treatment at delaying bud set regardless of the latitudinal origin of the ecotype of *Picea abies*. Opseth et al. (2016) note that their inclusion of a fan to regulate temperature in the experimental compartments could have affected the microclimate of the experimental units, thus contributing to a difference in bud set from the previous experiment. It has been suggested that different mechanisms may regulate bud dormancy and bud set in gymnosperms and angiosperms (Olsen 2010), however given the paucity of studies, specifically on angiosperms, nothing definitive can be concluded.

Surprisingly, all of the above studies describing an effect of R and FR light on bud set express their treatments in terms of equal energy irradiance (W $m^{-2}$). Photons of light at smaller wavelengths possess more energy per photon, thus when expressed in spectral irradiance (PPFD), the trees will be receiving different treatments in terms of spectral photon irradiance. This would mean that shorter wavelength treatments of equal energy irradiance will have a lower value of spectral photon irradiance. This unintended discrepancy in perceived irradiance between treatments could affect photoreceptor-mediated processes differently, and thus

future experiments could be improved by ensuring equal treatments when expressed as spectral photon irradiance.

Of the PHYs that have been characterized in tree species, PHY A overexpression in *Populus tremula* causes insensitivity of apical-growth cessation to changes in photoperiod (Olsen et al. 1997) and the PHY B2 gene is coincident with a quantitative trait locus affecting bud set (Frewen et al. 2000). Beyond this, the specific role of individual phytochrome photoreceptors in tree species is not well defined, nor is the mechanism by which how they mediate bud set and growth cessation in response to R:FR ratio (Olsen 2010). Because northern ecotypes of woody species require prolonged FR treatment to delay bud set, it has been proposed they are most likely to have a predominantly PHY A-based system (Clapham et al. 1998, 1999, 2002). Whereas southern ecotypes of woody species typically respond to night breaks in a R:FR reversible manner, which is typical of the low-fluence R:FR reversibility of PHY B. However, most of the accumulation of transcripts from PHY genes in *P. abies* has been done after growth cessation and bud set (Opseth et al. 2016), making it difficult to distinguish whether transcript accumulation from PHY is a consequence of bud set rather than a causal factor. Although the effects of FR light delaying bud set in *Picea abies* are consistent among studies, its effects on ecotypes and species differs between studies (Table 1, Table 2). These inconsistencies further exemplify the need to identify the photoreceptor-mediated pathways which facilitate species- and ecotype-specific responses to R:FR signals.

## Natural variation in the blue region of the spectrum

Blue light is most often defined as radiation within the spectral range of 400-500 nm (Table 1, Table 2). In a recent review, Olsen (2010) proposed that the ecological role of the phenological response to blue light remains unclear because clines in the relative proportion of blue light within global radiation received by plants in nature, e.g. over latitudinal gradients, have not been well described. Blue light is enriched during twilight because of Chappuis absorption by the ozone layer in the yellow-red regions of the spectrum ($\lambda$ = 575 and $\lambda$=

603nm, Hulbert 1953, Johnson 2012). Measurements in northern Europe fail to show a latitudinal pattern in the mean monthly percentage of total radiation received as blue light throughout the growing season (Kvifte et al. 1983). However, a comparison of monthly means may not be the most ecologically-meaningful approach to detect patterns in blue light. For instance, both Johnson et al. (1967) and Hughes et al. (1984) describe blue light relative to the amount of red light (defined as 410-500/610-700nm by Hughes et al. 1984). The ratio of B:R has been shown to be highest in the mornings during twilight (measured in Loughborough, Leicestershire, U.K. 52.8 "N, 1.2"W by Hughes et al. 1984) and to rise again after sunset at dusk (originally measured in Washington, Kansas, 39°49'22.4"N 97°02'28.5"W by Johnson et al. 1967) (Figures 1,2). As with the R:FR ratio, these differences are due to the low sun-angle and long path-length of sunlight through the atmosphere; however enrichment of shorter wavelengths is due to the increasing proportion of scattered incident radiation. This means that the B:R ratio will be more variable at higher latitudes, due to the larger variation in photoperiod and twilight hours throughout the year (Figure 1,2). The use of the B:R ratio to describe photoperiodic light signals during twilight may provide a physiologically-relevant light ratio as CRYs (blue light/UV-A photoreceptors) and PHYs (R:FR photoreceptors) in tandem regulate the timing of flowering in response to photoperiod (Guo et al. 1998). The irradiance of blue light is higher at low latitudes than high latitudes throughout the year (Figure 3); it also increases with total solar irradiance, photoperiod, and daily insolation.

[Insert Figure 3]

Figure 3. The modelled spectral photon irradiance for blue light (420 – 490nm) and UV-A radiation (315-400nm) at the locations given in Figure 1 along a latitudinal gradient. Spectral photon irradiance was modelled as described in Figure 2. Further details provided in SI.

## Blue light effects on bud burst

Until recently, the effects of blue light on spring bud burst had only been studied in two tree species; the gymnosperm *Picea abies* and the angiosperm *Prunus persica* (Mølmann et al. 2006, Okie and Blackburn 2011).

In *Picea abies*, a 6 week treatment of 12h white light and a day extension of a further 12h blue light (460nm) did not induce bud burst in any of three provenances tested (Mølmann et al. 2006). This suggests that blue light is not involved as a cue for the detection of day length increasing during spring in *Picea abies***.** For *Prunus persica*, blue light ( $\lambda = 475$nm) produced the lowest % bud burst in both cultivars used in the experiment after 27 days, in comparison to red light ($\lambda = 640$nm) and yellow light ($\lambda = 590$nm) (Okie and Blackburn 2011). However, the treatments used by Okie and Blackburn (2011) all differed in their irradiance, meaning that the percentage of bud burst also correlated with the total irradiance used in different treatments.

A recent experiment reported that blue light advanced bud burst in the dormant branches of *Alnus glutinosa*, *Betula pendula* and *Quercus robur* (Brelsford and Robson, 2018), in a comparison of broad spectrum treatments of equal PAR with a 12-h photoperiod which either included or excluded blue light. Interestingly, the time until 50% bud burst was advanced most in the later successional *Quercus robur* (6.6 days), followed by *A. glutinosa* (6.3 days) then *Betula pendula* (4 days), supporting the suggestion that temperature is the primary cue for bud burst in early successional species (Basler and Körner 2012, Brelsford and Robson 2018). Blue light has been found to enhance photosynthesis in several different plant species (Sæbø et al. 1995, Goins et al. 1997; Matsuda et al. 2004; Košvancová-Zitová et al. 2009, Hogewoning et al. 2010). One potential hypothesis for the ecological role of blue light, is that it acts as a cue for conditions that are favourable for photosynthesis (e.g. sunny conditions which have higher irradiance of blue light), hastening bud burst and leaf out once other criteria such as suitable temperature have been met. One other proposed hypothesis is that enriched blue light during twilight may provide the cue (Figure 2; Johnson et al. 1967), and as the period of day length between twilight increases, this diurnal change in the timing of blue light is detected by the plant. It could be argued that this second hypothesis is less likely, because Mølmann et al. (2006) found that day-light extension using blue light did not produce bud burst in *Picea abies.* However, considering those few studies summarised above, it is hard to draw any strong conclusions on the effects of blue light on bud burst of tree species, especially given the unrealistic nature of the light treatments employed. A more-realistic treatment could be created, for instance, by partially attenuating blue light from received solar radiation, as has been done in studies of plant growth and

360 metabolism (Siipola et al. 2015), rather than using monochromatic blue light or blue LEDs in controlled
361 environments.

362 In *Rosa* sp. and another *Rosaceae*: *Prunus cerasifera* (Muleo et al. 2001, Girault et al. 2008), blue light
363 also induced higher % bud burst of vegetative shoots when grown under monochromatic blue light. The growth
364 and number of preformed leaves in buds of *Rosa* sp. was higher under blue light (435 nm) after 12 days (Girault
365 et al. 2008). After 15 days, the bud burst of axillary shoots was highest in *Prunus cerasifera* buds exposed to
366 blue light ($\lambda$ = 435 nm) and a broad spectrum of white light (centred $\lambda$ = 545nm), but lowest under red light (660
367 nm) (Muleo et al. 2001). Whilst the mechanisms underpinning the advance of bud burst in response to blue light
368 in *Betula pendula*, *Alnus glutinosa* and *Quercus robur* remain to be determined, evidence from *Rosaceae*
369 provides a clue as to potential future lines of enquiry.

370 Bud burst of vegetative shoots in response to blue light is in part controlled through the photoregulation of
371 sugar metabolism (Girault et al. 2010). Given that the bud burst of many temperate deciduous tree species is also
372 associated with sugar metabolite accumulation towards the buds (Catesson 1964, Barnola et al. 1986, Cottignies
373 1986, Kelner et al. 1993, Rinne et al. 1994), it could be interesting to investigate the effects of blue light on the
374 sugar metabolism and spring bud burst in temperate deciduous tree species. Although PHYs absorb in both the B
375 and R spectral regions (Ohgishi et al. 2004), Girault et al. (2008) do not rule out the possibility that CRYs could
376 mediate the bud burst of vegetative shoots. Further work on gene expression and transcriptome analysis may
377 begin to unravel which photoreceptors trigger this response.

378

379 **Blue light effects on autumn phenology**

380 Whilst a 6-week day-length extension with blue light (12 h white light + 12 h blue light -460nm) did not
381 induce bud burst in any of three provenances of *Picea abies* along a latitudinal gradient (Mølmann et al. 2006),
382 the same experiment found that autumnal bud-set of *Picea abies* did respond to blue light. Experimental day-
383 length extension with blue light delayed the number of days until 50% bud-set by 4 days, 7 days and 3 days in

provenances from latitudinal origins of 69˚N, 64˚N, and 59˚N respectively, but the time until 100% bud set was only delayed in the latter (by 7 days) (Mølmann et al. 2006). Using a very similar experimental design, with equivalent spectral irradiance and temperature treatments, Opseth et al. (2016) also found a delaying effect of blue light in *Picea abies*, whereby 100% bud set was induced after 30, 24 and 21 days (for population latitudinal origins of 69˚N, 64˚N, and 59˚N ) respectively. In both these experiments, R and FR light were more effective at delaying bud set than blue light (Table 2). However, it is not clear what an appropriate control for the effect of blue light would be: for instance, is the result just an effect of increased PAR irradiance *per se* acting as a day extension delaying bud set rather than a blue-light specific response? Interestingly, the expression of CRYs increased after bud set (Opseth et al. 2016), possibly suggesting the involvement of blue light and CRYs during autumn phenology in *Picea abies.*

There have been a few studies examining the effects of blue light on leaf senescence (Field et al. 2001, Lee et al. 2003, Table 2). Leaf senescence in response to blue light and photoperiod has been shown to occur in soya bean *Glycine max* (Meng et al. 2013, Zhang et al. 2008, Han et al. 2006). Meng et al. (2013) demonstrated a blue light-dependent interaction between cry2 and CIB 1, which regulates leaf senescence in *Glycine max*, and found that cry2 mediated the rate of chlorophyll resorption during senescence. There is also a latitudinal cline in the photoperiodic control of flowering time among accessions of *Glycine max* (Zhang et al. 2008). Interestingly, cry1 expression is strongly correlated with this latitudinal cline (Zhang et al. 2008). Lee et al. (2003) found no R:FR effect on chlorophyll resorption, or on the concentration of anthocyanins and flavonoids in leaves throughout autumn senescence, but the effect of blue light on these processes during autumn senescence has yet to be investigated. Given the role of CRYs in mediating the induction of flavonoids, anthocyanins and chlorophyll in response to blue light (Lin et al. 1996, Wade et al. 2001, Brelsford et al. 2018), the study of blue-light effects on these important processes during autumn senescence could be an interesting line of research.

## Ecological role of UV radiation

UV-B radiation varies naturally with latitude, elevation, season and time of day, as well as with differences in the ozone-layer's thickness, solar angle, and cloud cover across geographical regions (McKenzie et al. 2011; Bais et al., 2018). Generally, this leads to high UV-B irradiance close to the equator and with increasing elevation (Figure 4, Caldwell et al., 1980; Blumthaler et al., 1997; McKenzie et al., 2001a, 2001b). The atmosphere is thought to be entering a period of recovery from the ozone depletion, leading incident UV-B radiation to return to similar or lower levels than those during the mid-late 20$^{th}$ Century (Bais et al., 2018). However, interactions with other climate changes still cause complex variation in the ozone column and localised severe depletion, as occurred in the spring of 2016 over the Nordic countries (Manney and Lawrence, 2016). Furthermore, periods of global dimming and global brightening would lead to changes in the proportion of diffuse to direct radiation reaching the biosphere through increases in aerosols and cloud cover (reviewed by Wild 2009). Such changes would reduce total UV radiation exposure but cause potentially large increases in the UV:PAR ratio due to the relative UV-enrichment of diffuse radiation (reviewed by Calbo and González 2005).

Depending on their exposure to UV-A and UV-B radiation, plants may produce stress and/or regulatory responses (Hideg et al. 2013, Verdaguer et al. 2017 and references there in). UV radiation is recognised as an important environmental cue modulating plant growth and development (Rozema et al. 1997; Jansen & Bornman 2012). Often UV-A and UV-B radiation produce distinct effects on the accumulation of phenolic compounds, photosynthesis and growth (Verdaguer et al. 2017). One underlying reason for this may be that different photoreceptors are responsible for coordinating plant responses to wavelengths in the UV-A and UV-B regions (Lin 2000, Briggs and Christie 2002, Rizzini et al. 2011). In *Arabidopsis thaliana*, UV radiation has also been implicated in day-length sensing (Fehér *et al.* 2011). In addition, diurnal changes in leaf epidermal transmittance of UV radiation mediated by epidermal flavonoids (Barnes et al. 2016), are likely to be modulated by a spectral cue, of which UV radiation is the most likely candidate (Barnes et al. 2017).

[Insert Figure 4]

Figure 4. The modelled spectral irradiance for UV-B (280 – 315nm) at the given locations in Figure 1 across a latitudinal gradient. Irradiance was simulated using the methods described in Figure 2. Further details provided in SI.

## Little evidence that UV radiation is important for spring phenology

There are only a handful published studies on the effect of UV radiation on plant phenology. Most of our knowledge originates from three field studies designed to test the effects of UV-B radiation on the seasonal phenology of the same clones of *Populus tremula*. In a modulated-UV-enhancement field experiment in Joensuu, Finland, Strømme et al. (2018a), found that a supplemental UV-B treatment (30 % increase compared with ambient) received in the previous growing season advanced the bud-burst date by 2.0 days in male (but not female) *Populus tremula* saplings. This effect was significant, but varied considerably from year to year, over three years of growth in plants that were 1-4 years old (Sivadasan et al. 2017, Strømme et al., 2015; 2018a).

In a separate experiment, the same clones were planted along an elevational gradient in Norway, with UV-B attenuating and UV-B transparent filters used to manipulate the spectral composition over one growing season. This solar-UV-B manipulation found no significant effect of UV-B on bud burst (Strømme et al. 2018b). This may suggest that the effects of UV-B radiation on the bud burst of *Populus tremula* are small and short-lived. However, this is a response that has yet to be assessed more widely among species or functional types, being limited to one set of clones of *Populus tremula*.

## UV radiation advances autumn leaf senescence

In the same experiments described above, 30% UV-B-supplementation advanced autumnal bud set by 1 day in the first growing season (Strømme *et al.* 2015), but again, there was no effect during the two subsequent years except when axillary buds were removed, suggesting that hormonal regulation by ABA or auxin could be involved in this response (Sivadasan et al. 2017). Bud set in the first year of growth in the UVB-attenuation

study, however, was advanced by 13 days under near-ambient UV-B compared with reduced UV-B radiation in *Populus tremula* at a high elevation site (830m a.s.l) but not at low altitude sites (237m and 575m a.s.l., Strømme et al. 2018b). The authors of this study suggest that increased UV-B irradiance at higher elevations could be the reason that an effect was only seen at the highest elevation in their study, however differences in UV-B irradiance along their elevation gradient are minute (from lowest elevation to highest elevation UV-B irradiance differs by less than $0.1 Wm^{-2}$ in spring, and no difference in autumn), suggesting that other environmental factors at higher elevations may be interacting with UV-B radiation.

Leaf senescence in *Fagus sylvatica* is also accelerated in response to supplemental UV-B exposure. Zeuthen et al. (1997) grew 5-year-old seedlings of *Fagus sylvatica* in an open-top chamber in Denmark (55.41°N, 12.06°E), with a UV-B treatment equivalent to 15% ozone reduction between 1st July and October 1993. In leaves exposed to supplemental UV-B radiation, the $F_v/F_m$ of PSII (maximal photosynthetic yield of photosystem II) and chlorophyll concentration both declined more rapidly than under near-ambient UV-B. Ultimately, leaf senescence was advanced by 12 days, a response that the authors attributed to stress. Further evidence for this conclusion was provided by the even faster autumn leaf senescence (27 days earlier), and decline in $F_v/F_m$, and chlorophyll degradation, produced when a tropospheric-ozone treatment was combined with supplemental UV-B radiation (Zeuthen et al. 1997).

Strømme et al. (2015, 2018) suggest possible mechanisms by which UV-B radiation could affect bud burst and bud set in tree species. UV-B radiation has been reported to down regulate the plant hormone gibberellic acid (GA) which is involved in apical bud formation in *Salix pentandra* and *Populus tremula*. (Olsen *et al.* 1995a, b, 1997a, b, Mølmann *et al.* 2006). This presents a possible explanatory mechanism for the delay in bud-set reported above, and the difference between the response of intact clones and those with lateral buds excised. UV-B detection by *Arabidopsis thaliana* antagonises shade-avoidance responses mediated by auxin together with GA (Hayes *et al.* 2014). If GA in *Populus tremula* is affected by UV-B radiation through a similar signalling pathway to that of *Arabidopsis thaliana*, it is possible that a UV-B-attenuation treatment, like that of Strømme et al. (2018), would interfere with this response. Increased ABA concentrations in the apical meristem

481 are associated with autumnal bud formation in *Populus* during short days (Ruttink *et al.* 2007), hence bud
482 formation in *Populus tremula* may be affected by UV-B radiation through increases is ABA.

483 Similarly to the effects of UV-B radiation on bud burst, its reported effects on bud set tend to be small and
484 short-lived (not beyond one season). Furthermore, many other studies have reported long-term acclimation to
485 UV-B radiation treatments. For instance, 3 years of supplemental UV-B treatment produced no difference in
486 growth or photosynthesis of *Psuedotsuga menziesii* (Bassman et al. 2002). Likewise, responses of leaves to UV-
487 B radiation often decrease over time (Kakani et al. 2004, Klem et al. 2012, Robson and Aphalo 2012), partly due
488 to the production of UV-B-absorbing phenolic compounds that reduce transmittance of UV-B radiation to the
489 mesophyll (e.g. Jansen et al. 1996). Such UV-B protection also develops in buds and bud scales (Sivadasan et al.
490 2015) and could moderate the true dose of UV-B radiation received by inside the bud in spring-phenology
491 experiments. UV-B screening by phenolics in buds of *Populus tremula* was not checked in the attenuation study
492 by Strømme et al. (2018), but the relative composition of phenolic compounds in leaves did change between
493 plants grown under their different treatments. In this way, we might also expect that the diminishing effects of
494 UV-B radiation on bud burst and bud set may be due to *Populus tremula* acclimating to UV-B radiation.

495 [Insert Figure 5]

496 Figure 5. A schematic representing the different environmental cues which can affect (A) spring bud burst and
497 (B) autumn senescence in tree species, based on mean and median responses in Tables 1 and 2 (further details in
498 Tables S1 and S2). For spring bud burst, chilling during dormancy, forcing temperature and light-derived cues
499 such as photoperiod, irradiance and spectral composition can influence spring bud burst. Phytochrome (PHY)
500 expression can be associated with bud burst (Frewen et al. 2000), although not directly in response to R:FR.
501 Temperature, photoperiod and spectral composition have been shown to influence bud set and autumn leaf
502 senescence. Expression of phytochromes (PHYs) and cryptochromes (CRYs) has been shown to increase during
503 bud set (Frewen et al. 2000, Opseth et al. 2016), suggesting that either twilight or end-of-day (EOD) blue light
504 may also play a role in regulating bud set.

## Future research on responses to spectral composition

Given that autumn leaf senescence is influenced by environmental cues other than temperature to a greater extent than spring phenology, it is surprising that relatively few studies have considered spectral quality in this context. Lee et al. (2003) found that shading reduced the rate of chlorophyll and anthocyanin degradation in several tree species, and yet R:FR had no effect. This leaves open the possibility that regions of the spectrum other than R and FR could act as cues for these responses. For instance, supplemental UV-B radiation can advance leaf senescence, e.g in *Fagus sylvatica* (Zeuthen et al. 1997), and also promotes the accumulation of anthocyanins in leaves (Hoch et al. 2001). Blue light is another candidate cue, shown to advance leaf senescence in *Glycine max* through a cry-dependent response (Meng et al. 2013), and to enhance anthocyanin accumulation in leaves (Hoch et al. 2001).However, experimental studies that use realistic manipulations spectral composition are needed to properly consider the role of these regions as phenological cues, in order to quantifying the magnitude of responses and to assess their importance relative to other environmental cues.

The view that green light (500-600nm) is less important than other wavelengths of the spectrum still persists to some extent (Smith et al. 2017). However, green light not only contributes to photosynthesis deep within canopy profiles (Murchie and Horton 1998, Sun et al. 1998, Nishio 2000), but also conveys information to plants about their light environment producing signalling cascades (Bouly et al. 2007). With respect to its potential involvement in phenological processes, green light has been shown to inhibit blue light/UV-A responses detected by CRY photoreceptors (Banerjee et al. 2007, Bouly et al. 2007, Sellaro et al. 2010). As CRYs have been implicated in regulating phenological responses, we should also consider the role of green light and its natural variation in tree phenology.

## Understanding the integration of multiple spectral cues

Other fields of plant photobiology, have been building an integrated picture of photoreceptor crosstalk, and how plants combine multiple light signals. For example, PHYs and CRYs have antagonistic effects on the light input into the circadian clock and flowering in *Arabidopsis thaliana* (Somers et al. 1998). UV-B radiation perceived by UVR8 delays flowering time in *Arabidopsis thaliana* (Dotto et al. 2018), and inhibits the low R:FR-mediated acceleration of flowering which is characteristic of shade avoidance in *Arabidopsis thaliana* (Hayes et al. 2014). There is potential to investigate similar interactive effects between different regions of the solar spectrum on the spring and autumn phenology of tree species, and this would be more ecologically relevant than looking at individual regions in isolation. We now know that both CRYs and PHYs affect bud set in tree species (Böhlenius et al. 2006, Opseth et al. 2016). Furthermore PHYs, CRYs and UVR8 have all been shown to interact with candidate signalling molecules which can affect phenology such as the plant hormones GA and ABA (Frewen et al. 2000, Xu et al. 2010, Song et al. 2013, Hayes et al. 2014, Dotto et al. 2018). These plant hormones provide a promising focus of study in attempting to reveal the mechanisms by which different light cues and their corresponding photoreceptors combine information to control the timing of leaf and bud phenology

## How important is spectral composition compared to other environmental cues for bud burst?

The mean and median effect sizes of enriched blue light and twilight R:FR on spring bud burst were of a similar range to those reported for long-day photoperiodic treatments conducted on the same species (2.1 days advanced bud burst per hour photoperiod increase, and 4-6 days earlier bud burst in treatments of enriched blue light and twilight R:FR Table 3, S1 and S2). In comparison, the mean effect sizes of chilling and forcing temperatures were 1.0 days advanced bud burst per 1 chilling day increase (Table 3), and 2.0 days advanced bud burst per 1 °C increase in forcing temperature (Table 3). Considering the relatively large responses to an increase in chilling days or forcing temperatures compared with photoperiod and spectral composition, we might expect variation in these cues to have a greater potential to affect the bud burst of trees (Fig S1). However, comparing the mean and median effect size does not take into account all of the different treatment conditions used in these experiments. Like photoperiod, the larger variation in spectral composition at higher latitudes, and the population specific responses seen in these regions, could be but one reason why current process-based models do not perform well at high latitudes in continental scale models (Olsson & Jönsson 2013, Basler 2016). It has been suggested that the effects of photoperiod and chilling on bud burst and leaf-out can compensate for each other, i.e. when chilling is low, there is a greater effect of photoperiod and vice versa (Flynn and Wolkovich 2018). In this sense, different environmental cues e.g. chilling, temperature, photoperiod, irradiance etc. are likely to interact and in doing so affect the treatment response. This likelihood supports a call for future experiments to investigate the interactive effects and importance of these environmental cues and spectral composition. Further understanding of how these environmental cues integrate across different latitudes, will be integral to predicting how trees will adapt and migrate in response to climate change.

## We still lack the experimental evidence to rank the environmental drivers of bud set and leaf senescence

The only experimental studies on bud set in response to spectral composition, temperature and photoperiod are on *Populus tremula* and *Picea abies* (Table S2). In comparison, for *Alnus glutinosa* and *Quercus robur* we were

568 unable to find any studies describing the environmental cues which affect their bud set. For both *Betula pendula*
569 and *Picea abies*, SD conditions induce bud set, and northern ecotypes are most sensitive to changes in
570 photoperiod (Ekberg et al. 1979, Li et al. 2003). Interestingly, in *Betula pendula* temperatures between 15-18 °C
571 have been shown to advance bud set, whilst higher temperatures > 21 °C, and low temperatures between 9-12
572 °C, delay bud set (Li et al. 2003). This indicates adaptation to an optimal temperature range for bud set in *Betula*
573 *pendula*, complicating forecasts of how climate change could affect bud set in *Betula pendula.* Similarly,
574 temperature and photoperiod have an interactive effect on bud-set in *Populus tremula*, whereby short days, cold
575 nights and warmer days have all been shown to hasten bud set (Rhode et al. 2011).

576

577 The biological effect sizes of FR were much greater on bud set than for bud burst. The mean and median
578 percentage of bud set after exposure of trees to end of day FR was 2.4% and 0% (Table S2). There is little
579 evidence to suggest that UV radiation strongly affects bud set, which had a mean and median effect of 2.9 days
580 and 0 days advanced bud set. Day extension with blue light delayed bud set, but was not able to prevent it, as
581 plants reached 100% bud set by the end of the experiments (Table S2). The mean and median effect of UV-B on
582 bud set is also negligible (2.9 days delay, and 0 days). There are insufficient studies to compare the effects of FR
583 light against other environmental drivers affecting bud set, but since in some cases FR is able to prevent bud set
584 altogether this would suggest that FR is potentially an important environmental cue regulating bud set.

585

586 The two experimental studies we found investigating the effects of spectral composition on autumn leaf
587 senescence in trees (Table 2), remain too few to allow us to make generalisations (Gallinat et al. 2015),
588 especially since we were unable to compare the size effects of spectral composition against other environmental
589 cues affecting leaf senescence in the same species. Nevertheless, in experimental studies, both a shortening
590 photoperiod and decreasing temperatures have been shown to advance leaf senescence in *Populus tremula*
591 (Fracheboud et al. 2009). However, a more recent study comparing two common gardens of *Populus tremula*,

found the difference in photoperiod between the locations of the two common gardens not to have an effect on leaf senescence (Michelson et al. 2018). The authors suggest that another light-derived signal, for instance chloroplast-signalling related to a decline in photosynthetic performance may trigger senescence. The effects of UV-B could be advancing the leaf senescence of *Fagus sylvatica* in a similar manner, triggered by a decline in photosynthetic performance (Zuethen et al. 1997). If accumulated photodamage through a growing season can advance leaf senescence, then daily insolation could be a valid parameter to include when examining the main environmental drivers of leaf senescence (Liu et al. 2016). A meta-analysis of studies on leaf senescence found that overall, the most important factors affecting leaf senescence in the northern hemisphere were temperature in October, accumulated cold-degrees, latitude, photoperiod, then lastly, precipitation (Gill et al. 2015), but it did not consider daily insolation or spectral cues. The main cues differed between high and low latitudes. Temperature alone may be a reasonable predictor of 50% leaf senescence at low latitudes ($R^2$=0.49 across both high and low latitudes, Gill et al. 2015). In contrast, the date of leaf senescence at higher latitudes has remained fairly constant between 1993-2010 despite large changes in temperature (Jones et al. 2012, Gill et al. 2015), possibly due to a photoperiodic constraint (Way and Montgomery, 2014). However, the most important environmental factor associated with a change in leaf colour, as opposed to 50% senescence, was latitude (Gill et al. 2015). This begs the question, how are changes in leaf colour and final leaf senescence/leaf fall related, and why is this relationship different at different latitudes? As trees from higher latitudes tend to demonstrate greater sensitivity of bud burst and bud set to changes in spectral composition, it would also be of great interest to test the response of leaf colour as well as leaf senescence to changes in spectral composition. Understanding the environmental cues which govern both bud set and leaf senescence will be important if we are to predict whether these two aspects of autumn phenology will respond differently to climate change (Way, 2011).

## Interaction of phenology with climate change and with other ecosystem processes

Could northward range shift due to increasing average temperatures in the northern hemisphere be limited by spectral composition? It has been reported that bud burst in tree species from southern latitudes is more

sensitive to changes in photoperiod, and more northern ecotypes leaf out earlier when grown in common garden experiments (Kriebel et al. 1957, Olson et al. 2013, Zohner et al. 2016, Osada et al. 2018). Many other studies show the opposite effect, that is that spring bud burst of more northern ecotypes are more sensitive to changes in photoperiod, and that more southern ecotypes tend to leaf out earlier when grown in common garden experiments (Vaartaja 1959, Myking and Heide 1994, Robson et al. 2013, Review by Way and Montgomery 2015, Cooper et al. 2018). According to the latter, photoperiod has been proposed to limit the poleward range shift in tree species (Way and Montgomery, 2015), and may be contributing to a decline in the advance of spring bud burst in response to increasing global temperatures (Fu et al. 2015). Like photoperiod, spectral composition becomes more variable at higher latitudes. Given that most of those tree species and ecotypes tested from high latitudes exhibit greater sensitivity in changes to spectral composition than those from low latitudes, we may expect the importance of spectral composition as a cue for timing phenology to be greater at higher latitudes. Failure of more-southern species and ecotypes to adapt and use these cues during northwards range shifts could result in mistimed phenology in either spring or autumn, which can in turn cause frost damage and potentially reduce fitness and limit range expansion (Hänninen 1991, Chuine and Beaubien 2008). However, factors such as ozone, water vapour and aerosols in the atmosphere affect spectral composition (Emde et al. 2016), and vary by location around the globe. This means that it's possible for two locations that are far apart at different longitudes, but on the same latitude to have different spectral composition but the same photoperiod. This gives all the more reason for studies on both changes in spectral composition and trees responses to these changes, to be expanded beyond Europe and North America (Tables 1 and 2) to other regions and biomes around the globe.

Another driver of autumn leaf senescence is drought (Chen et al. 2015, Estiarte and Peñuelas 2015, Xie et al. 2015). Under climate change, drought is expected to increase, especially in mid-latitude and sub-tropical dry regions (Trenberth et al. 2014), with a poleward expansion of subtropical dry zones (Seager et al. 2010). An increase in drought has been reported to advance leaf senescence in several species (Chen et al. 2015, Estiarte and Peñuelas 2015), however moderate drought can delay leaf senescence (Xie et al. 2015). To varying degrees, drought is expected to advance leaf senescence whilst increasing temperatures under climate change are

642 expected to delay leaf senescence. The combined effects of drought and spectral cues on phenology are yet to be
643 explored. Given the higher UV-B irradiances found at mid-low latitudes compared with high latitudes, and the
644 concurrent higher occurrence of drought, it would be of interest to investigate the interactions between UV-B
645 radiation and drought on leaf senescence for tree species growing at mid-to-low latitudes.

646 Shifts in the timing of canopy development can bring about a change of 20% or more in temperate and
647 boreal forest net photosynthetic production (Myneni et al. 1997). A study in Harvard Forest found that ±10 days
648 variation in bud-burst date led to ±5% difference in annual gross primary productivity (Migliavacca et al. 2012),
649 and over the course of a 34-year record in the tundra region of Alaska, there was a weakening correlation
650 between temperature and spring carbon assimilation over the last 17 years (Piao et al. 2017). One possible
651 explanation for the declining effect of temperature, is the lower irradiance received and shorter days earlier in the
652 year when trees leaf-out (Stine and Huybers, 2014). Considering that spectral composition affects both the
653 timing of bud burst and the rate of photosynthesis in plants (Sæbø et al. 1995, Matsuda et al. 2004; Hogewoning
654 et al. 2010), and can act as a signal for the amount of light available (Casal 2013, Moriconi et al. 2018),
655 understanding the influence of spectral composition is important if we are to assess the phenological impacts on
656 carbon capture during spring in a warming world.

657 Not only can spectral composition affect the timing of leaf out and leaf senescence, but it can also affect
658 the leaf chemistry throughout autumn and during senescence (Biswal 1995, Kotilainen et al. 2010). The
659 increased recalcitrance of litter with high phenolic content, for instance, has cascade effects on the
660 decomposition of the leaf litter, nutrient cycling, and the microbial community (Kotilainen et al. 2009, King et
661 al. 2012).

662

663 **Tackling the problem of light pollution**

664 Whilst it is intriguing to consider the ecological role of spectral cues, and how plants integrate these and
665 temperature cues, studying these processes could also be of practical importance since light pollution presents a

global problem in the 21st Century (Davies and Smyth, 2017). Artificial light has been linked with advancing the date of bud burst in several tree species across the UK (ffrench-Constant et al. 2016), and delaying leaf senescence in trees (e.g. New York, USA - Matzke et al. 1936; also photographed in Exeter, UK, - Bennie et al. 2016), and yet we still know little about how its effects on the phenology of tree species around the globe are mediated. The increased adoption of 'white' LED street lamps enriched in the blue region will expose trees to a broad spectrum of light at twilight and at night (Davies et al. 2013). If we are to tackle the issue of light pollution around the globe, we must build a comprehensive understanding of how a shift in the spectrum of street lamps can affect tree phenology.

## Conclusions

To our knowledge, this is the first attempt to synthesize the effects of spectral composition on spring and autumn phenology on trees. Our findings show that the bud burst and bud set of trees growing at high latitudes exhibit a greater sensitivity to changes in R:FR than those from low latitudes, whilst there is no evidence for R:FR affecting autumnal leaf senescence. Both blue light and UV-B radiation can influence bud set in tree species, and both are candidate regions that could be affecting leaf senescence in trees. We are unaware of any studies which test the effects of green light on spring and autumn phenology. Light pollution presents a practical challenge, and exemplifies why understanding the effects of spectral composition is a priority. Focusing on photoreceptor-mediated ABA and GA hormone signalling may be a promising area of research to investigate how trees integrate multiple spectral cues to time their phenology. Improving our understanding of the spectral cues that affect the phenology of trees across multiple scales is also essential if we are to predict how temperate forest ecosystems will respond to the novel combinations of environmental cues that climate change will produce.

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**Table 1**: Breakdown of studies investigating the effects of spectral composition on bud burst. Studies are separated according to the regions of solar radiation they considered, either R/FR, blue light, or UV radiation. To allow a comparison of the different irradiances used in different studies, we give both the original units from each study and an estimate of irradiance following conversion to standard units of energy irradiance in W $m^{-2}$ based on the spectra provided in the studies, and using the *photobiology* package in R (Aphalo, Pedro J., ed., 2013-2018, www.r4photobiology.info ISSN 2343-3248, Helsinki; Aphalo 2015).

| Study | Test(s) | Process | Species | Biological significance | Irradiance | Spectrum | Photoperiod | Temperature |
|---|---|---|---|---|---|---|---|---|
| Linkosalo and Lechowicz (2006) | ↓R:FR | ↑ Bud burst timing | *Betula pendula* | 4 days bud burst advance with decreased ratio of R:FR in twilight hours. | R:FR of 1.3 and 180 PPFD (32.14 W $m^{-2}$)* in day light treatment, and twilight treatment having 0.58 and 72 PPFD (12.47 W $m^{-2}$)*. | R:FR calculated according to 630nm:730nm | Light treatments starting with 17h dark, 5h20 twilight, 40 min day light, and at spring equinox increasing to 12h day/night, 1h20 twilight. | Starting day/night temperature of 7˚C/0˚C, increasing to 7˚C/3˚C. |
| Møllman et al. | Red & FR latitu | ~ Bud burst % | *Picea abies* | Intermediate populations showed 100% bud burst under Far-red light treatments, but southern | 12 h PAR (30–35 W m−2, Phillips | Red λ = 660nm. FR λ =730nm. | 24h photoperiod | Temperature constant at 18 ˚C. |

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| (2006) | dinal gradient<br><br>Blue | = Bud burst | | populations showed higher bud break under red light treatments, whereas the northern population was not effected by red light. Day light extension with BL had no effect on the percentage bud burst. | TLD 15 W/840), then 12 h day extension with monochromatic R and FR LEDs with treatments of either 0.1, 0.2 or 0.7 W $m^{-2}$. Blue light treatment was 12h PAR 30-35 W $m^{-2}$,with 12 hour day extension with monochromatic BL (1.5 W $m^{-2}$)*. | Blue λ = 460nm. | | |
| Erez (1966) | ↑ Red | ↑Bud burst % | *Prunus persica* | Percentage of bud burst in red light was as high as white light after 21 | 5.65 W $m^{-2}$white light. R was | Red treatment filtered | 8h + 16h photoperiod | 23˚C |

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|---|---|---|---|---|---|---|---|---|
| | ↑ FR | = Bud burst % | | days. Bud burst did not occur without light. Flowering did occur without light. FR light did not increase % bud burst. | 1.35 W m−2. | out any light below 590nm on a broad spectrum white lamp (400-800nm). | | |
| Brelsford and Robson (2018) | ↑ Blue | ↑Bud burst timing | *Alnus glutinosa* *Betula Pendula* *Quercus robur* | Broad spectrum enriched with blue light advanced bud burst by 3.3 days in *B. pendula*, 6 days in *A. glutinosa*, and 6.3 days in *Q. robur*. | 159 PPFD PAR (30 $m^{-2}$)- | Broad spectrum LED Lamp containing FR light. Blue = 400-500nm. Red = 620-680nm FR = 725-735nm | 12h photoperiod | 12.6/9.5 ± 0.05 °C Day/Night. |

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| Girault et al. (2008) | ↑Blue | ↑ Bud burst % | *Rosa* sp. | Measuring the bud burst for axillary shoots. A higher percentage of grafted rose plants had burst their buds after 12days in white and blue light.<br><br>Red light was less efficient than white light in terms of the percentage of plants reaching bud burst after 12 days, however the red light vs blue light were not compared at the same energy irradiance. | White light at 2, 20, 200 PPFD (0.4, 4, 400 W $m^{-2}$)*, BL at 200 PPFD (53.168 W $m^{-2}$)*, R at 20 PPFD (3.625 W $m^{-2}$)*. | Red λ = 660nm FR λ = 710nm Blue λ = 450nm<br><br>R/FR ratios were the following: (1) 4.39 for white light; (2) 0.78 for blue light; (3) 20.27 for red; and (4) 0.25 for FR. | 16h photoperiod | 23˚C |
| | ↑Red | ↓ Bud burst % | *Rosa* sp. | | | | | |
| Okie and Blackburn (2011) | ↑Blue | ↑ Bud burst %<br>↑ Bud burst timing<br>↑>Blue | *Prunus persica* | After 27 days, bud burst in the twigs of *P.persica* had a higher percentage and faster development under Red LED's, followed by Yellow then Blue. However, this | B: 18.9 PPFD (4.76 W $m^{-2}$)* Yellow: 21.2 PPFD (4.298 W $m^{-2}$)* | Blue λ = 475nm Yellow λ = 590nm Red λ = 640nm | 12h photoperiod | 18.3 ˚C |
| | ↑Yellow | | | | | | | |

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| | | Bud burst % ↑>Blue Bud burst timing | | could also be due to the difference in PAR used in treatments. | Red: 27.2 PPFD (5.084 W $m^{-2}$). | | | |
| | ↑Red | | | | | | | |
| | | ↑>Blue , Yellow Bud burst % ↑>Blue, Yellow Bud burst timing | | | | | | |
| Mule o et al. (2001) | ↑% Blue ↑% Red ↑% FR | ↑ > Red, FR Bud burst % ↑ > Red, FR Bud burst timing ↑> FR Bud burst % ↑ > FR Bud burst timing | *Prunus cerasifera* | Measuring the bud burst for axillary shoots. In vitro culture of *P.cerasifera*. Experiment conducted for 15 days. W and B light had the highest percentage of bud burst, followed by R and then FR. | White, Blue, Red, FR and darkness (D). Photon fluence rates for the different treatments were 40 PPFD for W (8.72 W $m^{-2}$)*, | Red λ = 660nm FR λ = 745nm Blue λ = 435nm | Photoperiod not given. | 21 ˚C |

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| | | ↑ Bud burst % ↑ Bud burst timing | | | 41 PPFD for B (11.275 W $m^{-2}$)*, 38:5 PPFD for R (6.978 W $m^{-2}$)* and 41 PPFD for FR (6.584 W $m^{-2}$)*. Using monochromatic LED's. | | | |
| Strømme et al. (2015) | ↑UV-B | ↑ Bud burst timing | *Populus tremula* | UV-B advanced time until 100% bud burst in male *Populus tremula* by 0.14 days. | Supplemental UV-B treatment was given with +30% ambient UV-B at 62°60′ N, 29°75′ E, ranging from a total dose of 6kJm-2d-1 | UV-B = 290-315nm | Natural photoperiod at 62°60′ N, 29°75′ E. | Natural temperature range at 62°60′ N, 29°75′ E. |

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| | | | | | to 1kJm-2d-1 (11.5 Wm2 to 69.4 W $m^{-2}$)*. | | | |
| Sivadasan et al. (2017) | ↑ UV-B | = Bud burst timing | *Populus tremula* | UV-B did not advance bud burst in second and third year of UV-B treatment *in Populus tremula*. Continuation of the study conducted by Strømme et al. (2015). | Supplemental UV-B treatment was given with +30% ambient UV-B at 62°60′ N, 29°75′ E. | UV-B = 290-315nm | Natural photoperiod at 62°60′ N, 29°75′ E. | Natural temperature range at 62°60′ N, 29°75′ E. |
| Strømme et al. (2018) | ↓ UV-B + altitudinal gradient | = Bud burst timing | *Populus tremula* | Attenuation of ambient UV-B along an altitudinal gradient had no effect on bud burst. | UV-B ranged from 1.4 W $m^{-2}$ to 0.2 W $m^{-2}$ | UV-B = 290-315nm | | |
| ffrench-Constant et al. (2016) | ↑ night light | ~Bud burst timing | *Acer pseudoplatanus, Fagus sylvatica,* | Light pollution had no significant effect on the earlier successional *A.pseuodplatanus*, but advanced bud burst in the later successional *Fagus sylvatica,* | Range of typical irradiances coming from street lamps provided in | No spectra for lamp provided in this study. Typical | Natural photoperiod across UK sites. | Natural temperature across UK sites. |

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| | *Fraxinus excelsior*, *Quercus robur* | *Fraxinus excelsior*, and *Quercus robur*. Largest effects reported in *F.excelsior*, where the brightest areas advanced bud burst by 7.5 days. | Bennie et al. (2016). At 11m ground 4800 lx (14.47 W $m^{-2}$)*, and 0m ground 30 lx (9.045 W $m^{-2}$)*. | street lamp spectra provided in Bennie et al. (2016). |

*: W $m^{-2}$ calculated using photobiology package in R.

↑: Increase in the light treatment (column"Test(s)"), or increase/advance in bud burst (column "Process").

↓: Decrease in the light treatment (column"Test(s)"), or decrease/delay in bud burst (column "Process").

~: Interactive effect between treatments

=: No effect of treatment(s)

**Table 2**: Breakdown of studies investigating the effects of spectral composition on bud set and leaf senescence in autumn Studies are separated according to the regions of solar radiation they considered, either R/FR, blue light, or UV radiation. To allow a comparison of the different irradiances used in different studies, we give both the original units from each study and an estimate of irradiance following standardisation to energy irradiance in W $m^{-2}$. Units were converted to W $m^{-2}$ based on the spectra provided in the studies, and using the *photobiology* package in R (Aphalo, Pedro J., ed., 2013-2018, www.r4photobiology.info ISSN 2343-3248, Helsinki; Aphalo 2015).

| **Study** | **Test(s)** | **Process** | **Species** | **Biological significance (Effect size)** | **Irradiance** | **Spectrum** | **Photoperiod** | **Temperature** |
|---|---|---|---|---|---|---|---|---|
| Lee et al. (2003) | ↑↓R:FR | =Senescence<br><br>=Senescence | *Cornus alternifolia*, *Acer rubrum*, *Acer saccharum*, *Quercus rubra*, *Viburnum alnifolium* and *Fagus grandif* | Authors don't report any changes in phenological dates of leaf fall in autumn, but rather the pigment degradation, which forms an important part of the process.<br><br>*In situ* R:FR treatments of 1.15, 0.25, and shade cloth. Shading retarded anthocyanin in 5 out of 6 species, and retarded chlorophyll loss in all 6 during autumn. Reduced R and FR had no effect. | Spectrum for shade cloth not given. Conducted at three different irradiances of 92.4% of solar PAR, 18% of solar PAR, and 3% of solar PAR. | R:FR defined as 660:730nm (Methods Following Lee et al. 1996). | Natural photoperiod at 42˚32′N, 72˚11′W. | Ambient temperature at 42˚32′N, 72˚11′W. |

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| | | | *olia* | | | | | |
| Tsegey et al. (2005) | ↑↓R:FR | = growth cessation | *Betula pendula* | Demonstrated in ecotypes from southern Norway (59ºN), the middle of Norway (64ºN) and northern Norway (67ºN).<br><br>R:FR day light extension does not prevent growth cessation in different ecotypes of *B.pendula* | 110 PPFD PAR with Phillips TLD 58/840 for 12 hours. 12 hours day extension (to provide 24 hours in total) with either monochromatic R or FR at intensities of 0.5, 1, 9.5, and 25 PPFD (0.09/0.08, 0.17/0.16, 1.7/1.5, 4.4/4.0 W | Red λ = 667nm FR λ = 739nm | 24 hour photoperiod. | 18 ˚C. |

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| | | | | | $m^{-2}$ for R/FR respectively )* or R:FR treatments of 1, 1.5, 2, 2.5, 3, 5, and 7.5 at 25 PPFD (4-4.5 W $m^{-2}$)*. | | | |
| Mølmann et al. (2006) | Red & FR latitudinal gradient<br><br>↑Blue | ↓Bud set<br><br>↓Bud set | *Picea abies* | 1:1 ratio of R:FR day extension delayed bud set by at least 25 days.<br><br>Authors suggest there is different regulation for bud set in gymnosperms and angiosperms.<br><br>24 h a day with 12h blue light day extension delayed the number of days until 50% bud set by 3 days, 7 days and 4 days in the three different provenances (latitudinal origins of | 12 h PAR (30–35 W m−2, Phillips TLD 15 W/840), then 12 h day extension with monochromatic R and FR LEDs (spectra provided in Mølmann et al. 2005), | Red=660 nm, FR=730nm, Blue=460 nm. | 12 + 24 hour photoperiod. | 18 ˚C. |

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| | | | | 59˚, 64˚, and 69˚ respectively), but only delayed the time until 100% bud set by 7 days in the southern provenance (59˚) Northern populations require higher irradiance of monochromatic FR and R light than southern populations to prevent bud set. | with treatments of either 0.1, 0.2 or 0.7 W $m^{-2}$. Blue light treatment was 12h PAR 30-35 W $m^{-2}$,with 12 hour day extension with monochromatic BL (1.5 W $m^{-2}$)*. | | | |
| Opseth et al. (2016) | ↑FR<br>↑Red<br>↑Blue | ↓Bud set<br>↓ Bud set<br>↑Bud | *Picea abies* | FR delays bud set, BL advances bud set more than red light in *P.abies.* BL induced 100% bud set in three provenances, and red light only induced 100% bud set in two provenances, after 42 days. | 12 h PAR (35 W $m^{-2}$, Phillips TLD 15 W/840)*. B, R or FR over 24 hour period 3.3 W $m^{-2}$. | Red=660 nm, FR=730nm, Blue=460 nm. | 12 + 24 hour photoperiod. | 18 ˚C. |

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| | | set | | All provenances showed close to 30% more growth with FR day extension in comparison to R:FR day extension<br><br>Expression of CRY and PHY light receptor genes increased after bud set. | | | | |
| Chiang et al. (2018) | ↑FR<br>↑Red<br>↑Blue | ↓Bud set<br>=Bud-set<br>=Bud-set | *Abies lasiocarpa (Hook.)* | The bud set was less developed in trees grown with 12h FR day extension, in comparison to 12h short-day conditions without light extension. Blue and Red light treatments with day extension did not show any significant difference from 12h short-day conditions. | 12 h high pressure sodium lamo ( Lucalox 400 W, General electric, New York, NY, USA).at 160 PPFD (32.16 W $m^{-2}$). | Red=660 nm, FR=730nm, Blue=460 nm. | 12 + 24 hour photoperiod. | 18 °C and 24 °C |
| Juntilla and Kaurin | ↑Blue +R:FR latitudinal | = growth cessation | *Salix pentandra* | Growth cessation and bud set of northern ecotype *S.pentandra* was more sensitive to | 12-20h photoperiod treatment consisting | Red=660 nm. FR=730nm. | 12-20h photoperiod | 18 ˚C. |

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| (1985) | gradient | | | different treatments of spectral composition, whereas southern ecotype was more sensitive to changes in photoperiod. End of day treatment with FR was most effective at delaying growth cessation, white + BL had an intermediate effect, and R light delayed the least. | white light and a 15 minute end of day treatment with either R (6 W $m^{-2}$) or FR light (0.2W $m^{-2}$). In a separate experiment, W light = ~20 W $m^{-2}$. | W=400-700nm and blue undefined. | | |
| Meng et al.(2013) | ↑Blue | ↑Senescence | *Glycine max* | BL advances leaf senescence in via *CRY2a*. CRY2a mutants had increased chlorophyll content measured at 3, 6 and 8.5 weeks after sewing, grown under long day photoperiods and continuous illumination. | White light as 200 to 300 PPFD (43.6-65.4 W $m^{-2}$)*, however no details on irradiance of blue and red irradiance given. | Blue λ = 436nm Red λ = 658nm | Long day photoperiod as 16h light and 8h dark, and continuous illumination as 24h light. | 25 to ~28°C |
| Strøme et | ↑UV-B | ↑Bud set | *Populus* | UV-B advanced time until 100% bud set in | Supplemental UV-B | UV-B = 290- | Natural photoperiod | Natural temperature |

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| al. (2015) | | | *tremula* | both males and females, by an average of 1 day. | treatment was given with +30% ambient UV-B at 62°60′ N, 29°75′ E, ranging from a dose of 6kJm-2d-1 to 1kJm-2d-1 (11.5 W $m^{-2}$ to 69.4 W $m^{-2}$)*. | 315nm | at 62°60′ N, 29°75′ E. | range at 62°60′ N, 29°75′ E. |
| Sivadasan et al. (2017) | ↑UV-B | =Bud set | *Populus tremula* | UV-B does not advance bud set in years 2 and 3 of treatment in *Populus tremula*<br><br>Continuation of the study conducted by Strømme et al. (2015). | Supplemental UV-B treatment was given with +30% ambient UV-B at 62°60′ N, 29°75′ E. | UV-B = 290-315nm | Natural photoperiod at 62°60′ N, 29°75′ E. | Natural temperature range at 62°60′ N, 29°75′ E. |
| Strømme et al. (2018 | ↓ UV-B + altitudinal | ~Bud set | *Populus tremula* | Attenuation of UV-B delayed bud set at high altitude, but not at low altitude. | UV-B ranged from 1.4 W $m^{-2}$ to 0.2 W | UV-B = 290-315nm | Natural photoperiod at 61°27′ N, 10°11′ E. | Natural temperature range at 61°27′ N, |

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| ) | gradient | | | | $m^{-2}$ | | | 10°11′ E. |
| Zueth en et al. (1997) | ↑UV-B | ↑ Leaf senescence | *Fagus sylvatica* | Supplementary UV-B radiation from a lamp advanced final leaf senescence by 12 days. | UV-B treatment provided under 15% ozone depletion, with ambient treatments ranging from 6.9 – 2.29 W $m^{-2}$ from Sep-July and UV-B treatment ranging from an additional + 1.7-0.58 W $m^{-2}$. | UV-B = 280-320nm | Natural photoperiod at 55°4'N, 12°06'E | Natural temperature range at 55°4'N, 12°06'E |
| Matzke (1936) | ↑ night light | ↓ Leaf senescence | *Populus canadiensis*, *Platan* | Street lamp light delays leaf fall in tree species in New York, USA. Leaves on trees facing | Light intensity from street lamps varied from | No spectra available for the street | Natural photoperiod in New York, USA. | Natural temperature range in New York, USA. |

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| | | | *us occidentalis*, *Salix fragilis*. | the street lamp fell at least one month later in comparison to leaves facing the other side. | 1-2 foot candles at the tips of branches (0.017-0.032 W $m^{-2}$)*. | lamps. Street lamps ranged from 76 W 11-volt bulb to a 200 Watt 120-volt bulb. | | |
| Saral a et al. (2013) | ↑ night light | = Leaf senescence | *B.pendula* | Street lamp light does not delay autumn leaf colouration in *B.pendula.* | 250 W high pressure mercury lamps, KolorluxTM, General Electrics, New York, USA. Conducted under low irradiance street lamps (1.3 PPFD 1m down from lamp, | No spectra available. Red = 655-665 nm, FR = 725-735nm. | Natural photoperiod at 65°00"N 25°27"E. | Natural temperature range at 65°00"N 25°27"E. |

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| | | | | | 1.3 W $m^{-2}$)* with low irradiance of R:FR( 0.013PPFD 1m down from lamp, 0.003 W $m^{-2}$)*. | | | |
| Mass etti (2018) | ↑ night light | ↑ Leaf Senescence | *Platanus x acerifolia* | Trees in 3 areas under street lamps, had leaf senescence delayed by 20 days compared to one area of trees which were not under street lamps. | Mean street lamp irradiance of 12.6 W $m^{-2}$ measured at 2m height. | No spectra available. | Natural photoperiod a 43°77 "N 11°26"E | Natural temperature range a 43°77 "N 11°26"Et |

*:$Wm^2$ calculated using photobiology package in R.

↑: Increase in the light treatment (column"Test(s)"), or increase/advance in bud set or leaf senescence (column "Process").

↓: Decrease in the light treatment (column"Test(s)"), or decrease/delay in bud set or leaf senescence (column "Process").

~: Interactive effect between treatments

=: No effect of treatment(s)

Table 3 The mean (± 1 SE) and median (± inter-quartile range) effect sizes and treatment sizes reported in experimental studies investigating the influence of chilling, forcing temperatures and photoperiod on the bud burst of tree species. Further details provided in Table S1.

| | Mean bud burst | | | Median bud burst | | |
|---|---|---|---|---|---|---|
| **Species** | **Days advanced per 1 chilling day increase** | **Days advanced per 1°C increase** | **Days advanced per 1 hr photoperiod increase** | **Days advanced per 1 chilling day** | **Days advanced per 1°C increase** | **Days advanced per 1 hr photoperiod increase** |
| *A. glutinosa* | 0.49 ± 0.11 | - | 3.22 ± .36 | 3.75 ± 0.43 | | 3.33 ± 2.66 |
| *B. pendula* | 0.35 ±0.16 | 1.52 ± 0.24 | 0.66 ± 0.37 | 0.14 ± 0.47 | 1.94 ±1.66 | 0.0 ± 3.33 |
| *P. abies* | 0.76 ± 0.13 | 5.56 ± 0.84 | 2.19 ± 0.85 | 0.94 ± 0.59 | 1.69 ± 3.95 | 0.5 ± 2.04 |
| *P. tremula* | 1.75 ± 0.73 | 1.88 ± 0 | 3.16 ± 2.61 | 1.45 ± 2.04 | 1.88 ± 0 | 1.33 ± 0 |
| *Q. robur* | 35.13 ± 0 | 7.39 ± 2.44 | 0.0 ± 0 | 3.55 ± 0 | 6.52 ± 10.78 | 0.0 ± 0 |
| Mean effect | 1.1 ± 0.15 | 2.04 ± 0.37 | 2.11 ± 0.64 | 0.92 ± 0.86 | 1.92 ± 2.35 | 0.5 ±3.5 |

Figure 1. The change in daylength, twilight length and night length throughout the year 2017, along a latitudinal gradient of locations including Oulu (65.01° N, 25.47° E), Helsinki (60.17° N, 24.94° E), and Madrid (40.42° N, 3.70° W), calculated from the *photobiology* package in R (Aphalo, 2016 ). Twilight length was defined as civil twilight, including solar angles from -6° and 0°.

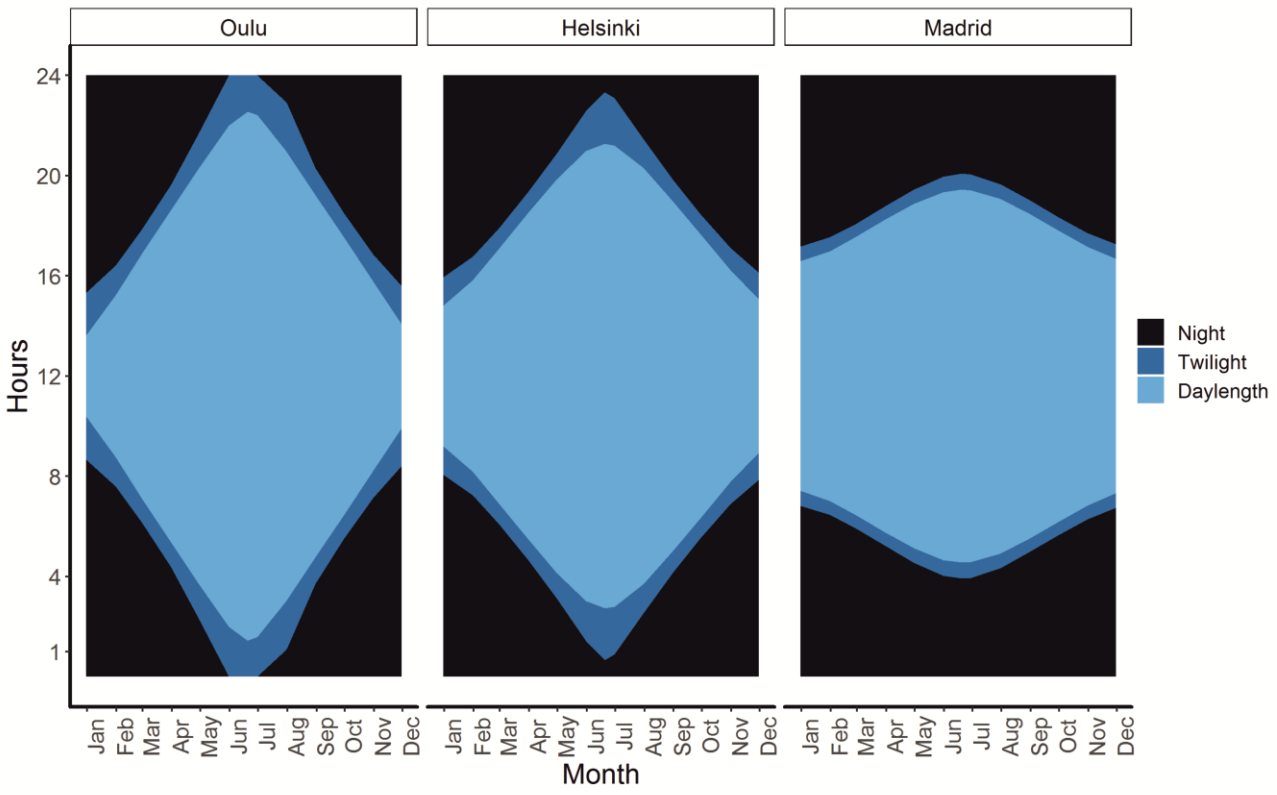


Figure 2. Modelled spectral ratios for B:R and R:FR of incident solar radiation at solar angles of 0° to -6° for civil twilight, and at solar zenith for noon. Locations along a latitudinal gradient shown in Figure 2.Values are shown for spring equinox, summer solstice, autumn equinox, and winter solstice. Here B:R defined as (410-500/610-700nm, Johnson et al. 1967), R:FR Sellaro as(650 – 670/720 – 740 nm, Sellaro et al. 2010) and R:FR Smith as ((655 – 665/725 – 735 nm, Smith, 1982). Spectral irradiance was modelled using the radiative transfer model libRadtran following Emde et al. 2016, Brelsford 2017). Water column data was taken from Kållberg et al. (2005), ozone column thickness data from Experimental Studies Unit, Environment Canada (http://exp-studies.tor.ec.gc.ca/e/index.htm).For twilight values, the solver sdisort was used, and for noon values, the solver disort was used. Further details provided in SI.

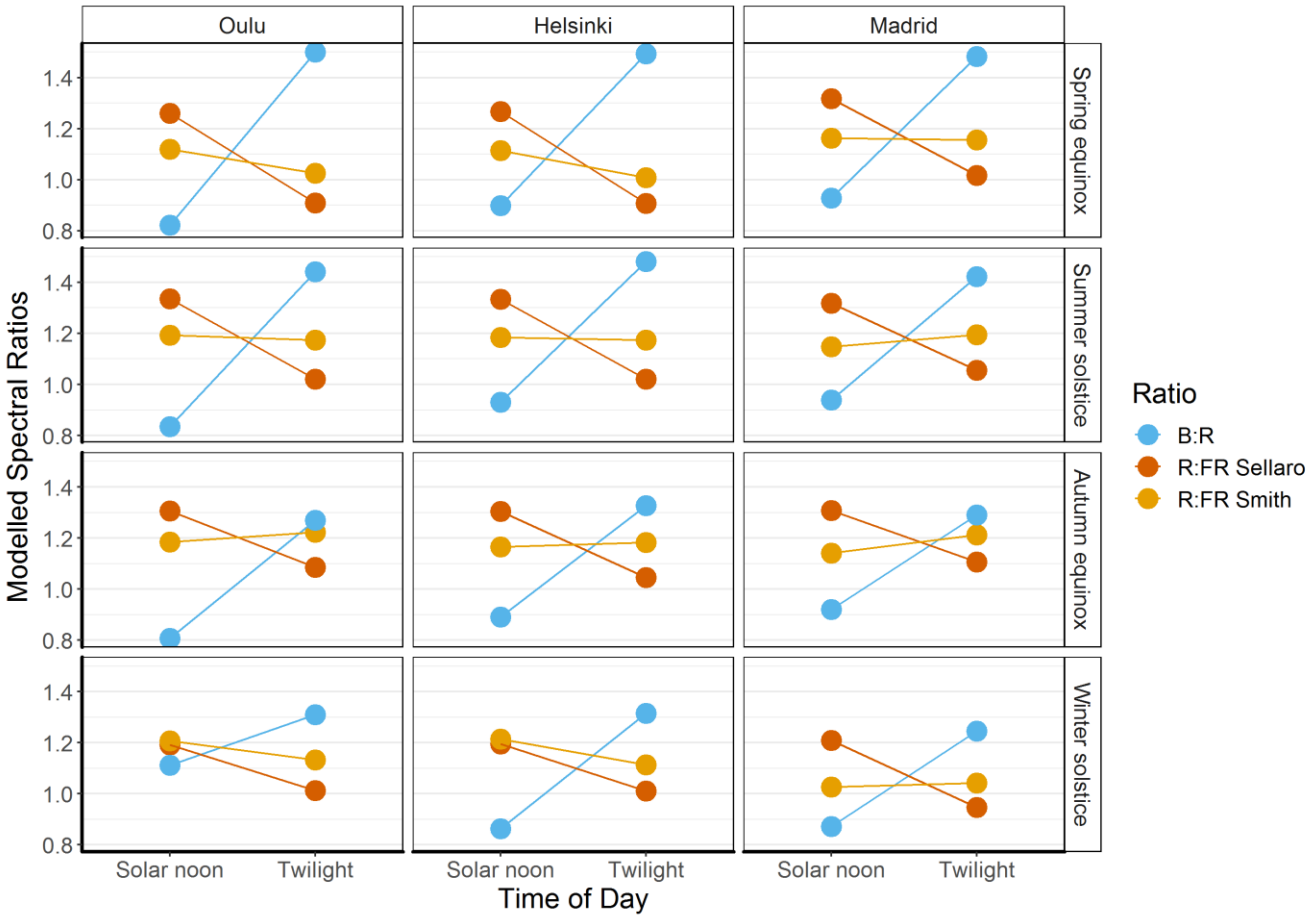
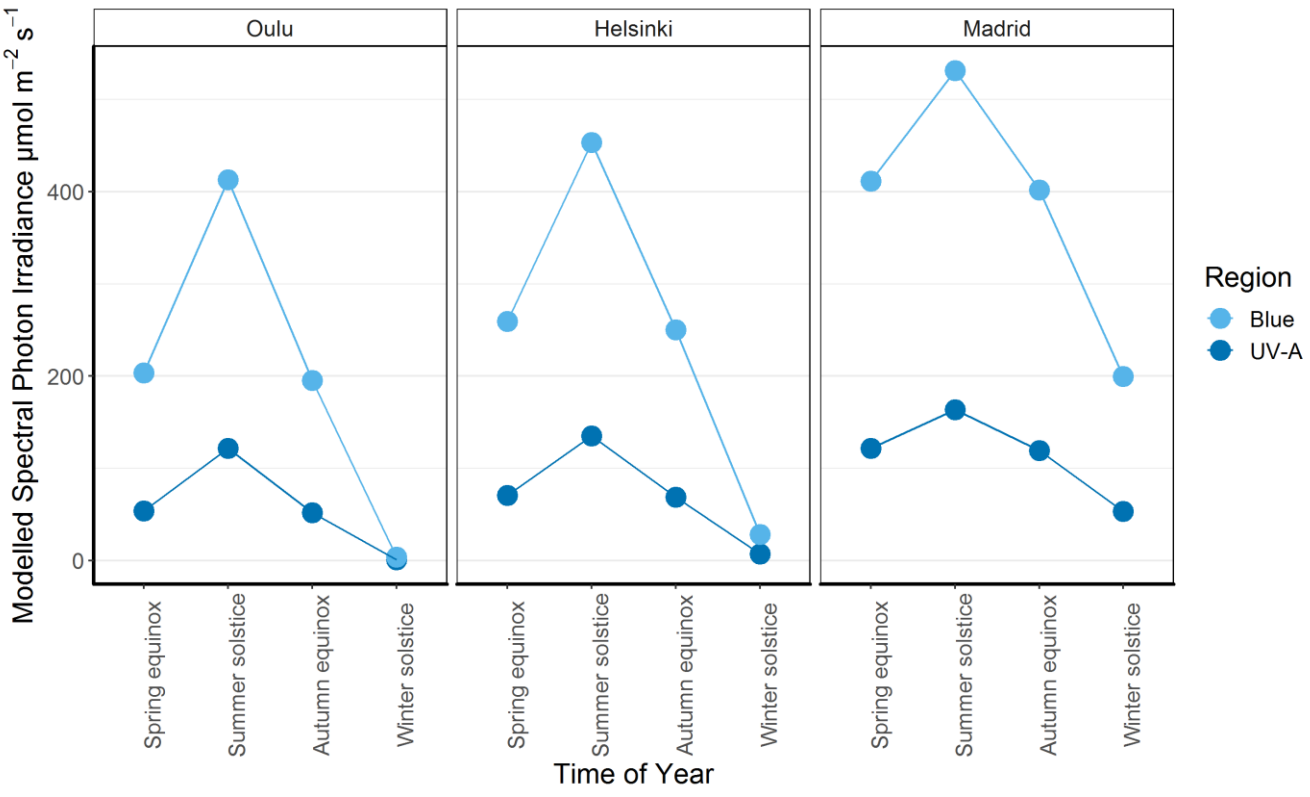


Figure 3. The modelled spectral photon irradiance for blue light (420 – 490nm) and UV-A radiation (315-400nm) at the locations given in Figure 2 along a latitudinal gradient. Spectral photon irradiance was modelled as described in Figure 3. Further details provided in SI.



1249 Figure 4. The modelled spectral irradiance for UV-B (280 – 315nm) at the given locations in Figure 2 across a
1250 latitudinal gradient. Irradiance was simulated using the methods described in Figure 3. Further details provided
1251 in SI.

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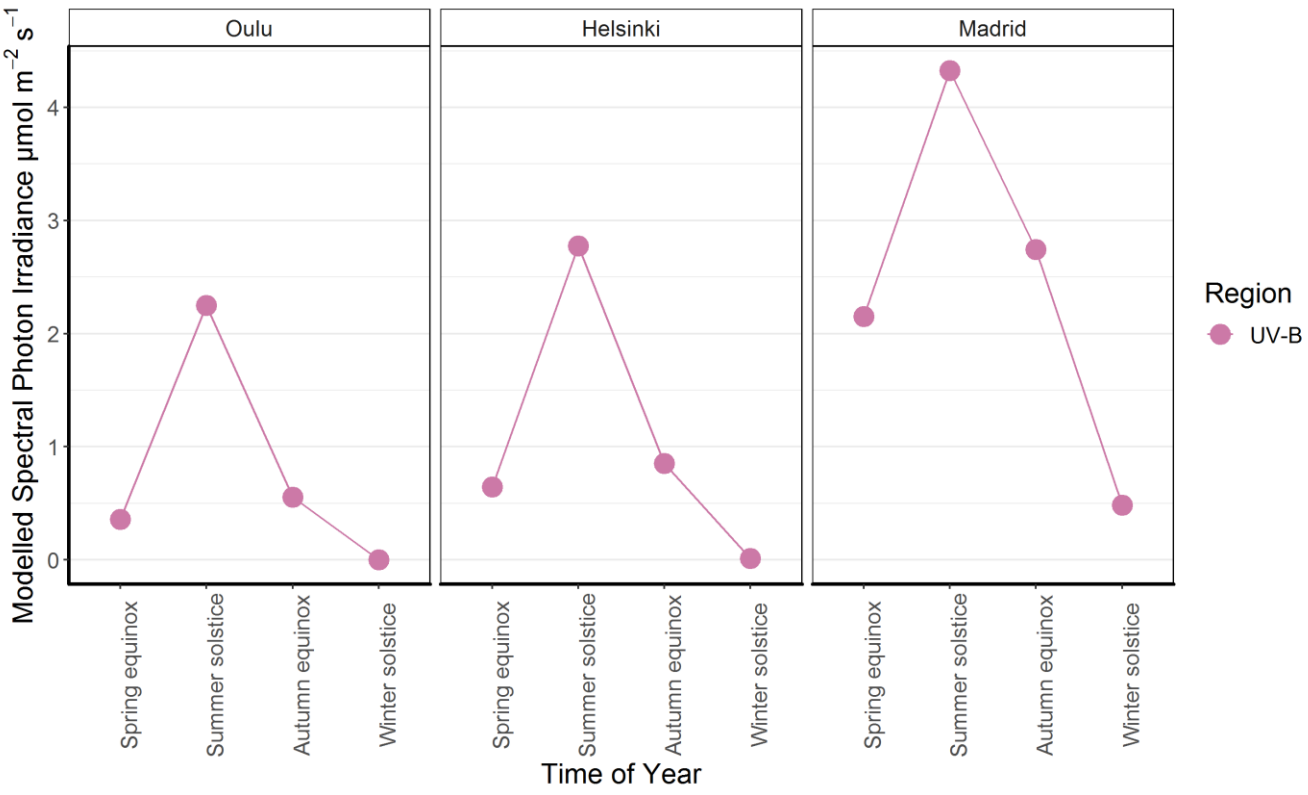


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Figure 5. A schematic representing the different environmental cues which can affect (A) spring bud burst and (B) autumn senescence in tree species, based on mean and median responses in Tables 1 and 2 (Further details in Tables S1 and S2). For spring bud burst, chilling during dormancy, forcing temperature and light derived cues such as photoperiod, irradiance and spectral composition can influence spring bud burst. Phytochrome (PHY) expression can be associated with bud burst (Frewen et al. 2000), although not directly in response to R:FR. Temperature, photoperiod and spectral composition have been shown to influence bud set and autumn leaf senescence. Expression of phytochromes (PHYs) and cryptochromes (CRYs) has been shown to increase during bud set (Frewen et al. 2000, Opseth et al. 2016), suggesting that either twilight or end-of-day (EOD) blue light may also play a role in regulating bud set.