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Blue light advances bud burst in branches of three deciduous tree species under short-day conditions — [Source link](#)

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1 Title: Blue light advances bud burst in branches of three temperate deciduous
2 tree species under short-day conditions.

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14 **Abstract**

15 During spring, utilising multiple cues allow temperate tree species to coordinate their bud burst and leaf out, at the right
16 moment to capitalise on favourable conditions for photosynthesis. Whilst the effect of blue light (400-500nm) has been
17 shown to increase percentage bud burst of axillary shoots of *Rosa* sp, the effects of blue light on spring-time bud burst of
18 temperate deciduous tree species has not previously been reported. We tested the hypotheses that blue light would advance
19 spring bud burst in temperate tree species, and that late-successional species would respond more than early-successional
20 species, who's bud burst is primarily determined by temperature. The bud development of *Alnus glutinosa*, *Betula pendula*,
21 and *Quercus robur* branches, cut from dormant trees, was monitored under two light treatments of equal photosynthetically
22 active radiation (PAR, 400-700 nm) and temperature, either with or without blue light, under controlled environmental
23 conditions. In the presence of blue light, the mean time required to reach 50% bud burst was reduced by 3.3 days in *Betula*
24 *pendula*, 6 days in *Alnus glutinosa*, and 6.3 days in *Quercus robur*. This result highlights the potential of the blue region of
25 the solar spectrum to be used as an extra cue that could help plants to regulate their spring phenology, alongside photoperiod
26 and temperature. Understanding how plants combine photoreceptor-mediated cues with other environmental cues such as
27 temperature to control phenology is essential if we are to accurately predict how tree species might respond to climate
28 change.

29

30 Key Words (4-6 words)

31 Phenology; bud break; leaf flush; spectral composition; spectral quality; photoreceptors.

32

33 Key Message

34 An LED spectrum containing blue light advanced bud burst in branches of *Betula pendula*, *Alnus glutinosa* and *Quercus*
35 *robur* compared with a spectrum without blue light in a controlled environment.

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40 **Introduction**

41 Trees at northern latitudes must time the bud burst and unfolding of their leaves in spring so that they are able to
42 capitalise on favourable conditions for photosynthesis as early as possible, whilst avoiding late frosts which can cause foliar
43 damage (Hänninen 1991, Augspurger 2009, Bennie et al. 2010). Prior to bud-burst, a tree must go through three dormancy
44 periods over winter which can be separated into 1) paradormancy – the inhibition of growth by distal organs, 2)
45 endodormancy - the inhibition of growth by internal bud signals, and 3) ecodormancy – the inhibition of growth based on
46 temporarily-unfavourable light conditions (Samish 1954, Lang et al. 1987,). The dormancy period between endodormancy
47 and ecodormancy is jointly controlled by a chilling requirement and by photoperiod, where the chilling requirement is
48 defined as non-freezing temperatures below 10°C (Battey 2000). After or concomitantly with this period of vernalisation,
49 temperature is the predominant cue affecting bud burst, and to predict bud burst many models calculate the accumulated daily
50 mean temperature above a given minimum threshold (e.g. >0°C) after sufficient vernalisation has occurred (Hänninen 1995,
51 Cesaraccio et al. 2004).

52 Typically, early-successional light-demanding species adopt a risky strategy by timing their bud burst primarily based
53 on temperature (Körner 2007, Caffarra and Donnelly 2010, Körner and Basler 2010), whereas it is more common for later-
54 successional shade-tolerant species to be photoperiod sensitive (Basler and Körner 2012). Körner and Basler (2010) propose
55 that in a warmer climate the absence of a photoperiod requirement in opportunistic early-successional species will probably
56 give them a competitive advantage over later-successional species. However, this may also lead early-successional species to
57 be at greater risk from late spring frosts (Cannell and Smith 1986), since a day-length threshold provides a fail-safe
58 mechanism ensuring that a period of unseasonably warm weather during the winter cannot prematurely fulfil the temperature
59 requirement. The date of bud burst in tree species is considered to have advanced by 2.5 days per decade at temperate
60 latitudes since 1971 due to climate change (Menzel et al. 2006, Körner and Basler, 2010), however this trend for promotion
61 of bud burst date with warmer temperatures has recently started to diminish (Fu et al. 2015). Specifically, leaf unfolding was
62 advanced by fewer days per additional °C of warming in 13 temperate deciduous woody species measured across northern
63 temperate Europe and the USA from 1980-2012. Fu et al. (2015) partially attributed this decline to fewer chilling days, but
64 also to a photoperiod requirement that reduces the influence of warmer springs. Additionally, periods of “global dimming”
65 caused by anthropogenic and volcanic emissions, affect the spectral composition of incident solar radiation reaching the
66 Earth’s surface (Stanhill and Cohen 2001, Mercado et al. 2009), increasing its diffuse/direct fraction and consequently also

67 the relative proportion of blue light (420-490 nm) (Urban et al. 2007). If we are to forecast the response of bud burst to
68 climate change, we will need to improve existing models to include and account for all the mechanisms involved (Way and
69 Montgomery 2014, Yun et al. 2017, Mayshev et al. 2018).

70 The effect that spectral composition has on the timing of bud burst and leaf out in tree species has been studied much
71 less than that of photoperiod. The spectral composition that trees receive changes predictably with time of year, day length,
72 and latitude; and over shorter time-scales with cloud cover and other factors that alter the ratio of direct to diffuse solar
73 radiation (Johnson et al. 1967, Smith 1982, Hughes et al. 1984, Urban et al. 2007). These compositional changes have
74 implications for tree species undergoing range shifts under rising global temperatures where differences in spectral irradiance
75 at higher latitudes will produce novel combinations of phenological cues (Wareing 1956, Saikkonen et al. 2012). Recently,
76 light pollution from street lamps has also been shown to advance the bud burst date of tree species *Acer pseudoplatanus*,
77 *Fagus sylvatica*, *Fraxinus excelsior* and *Quercus robur* across the whole UK (Somer-Yeates et al. 2016). Although the
78 regions of the spectrum produced by street lamps that were responsible for the earlier bud burst were not specified, this study
79 highlights the potential ecological role for light quality influencing bud burst. What little research has questioned which
80 regions of spectral irradiance are likely to provide cues for bud phenology has largely focussed on the ratio of red (R, 655-
81 665 nm) to far-red light (FR, 725-735 nm, Smith 1982). For instance, FR light is enriched during the periods of twilight from
82 dawn to sunrise and between sunset and dusk, and thus the R:FR ratio varies with day length, latitude and the time of year
83 (Holmes and Smith 1975, Smith 1982, Hughes et al. 1984). In a controlled-environment study, simulating twilight with a
84 treatment of FR light caused bud burst to advance in *B.pendula* (Linkosalo et al. 2006), implicating phytochromes in the
85 coordination this response. However, bud burst mediated by R and FR light has been shown to be both species-specific and
86 dependent on the population studied (Erez et al. 1966, Mølmann et al. 2006, Girault et al. 2008).

87 Numerous studies have investigated how R and FR light affect bud burst and yet the mechanisms behind this response
88 are not well understood, far less still is known about the effects of blue light on bud burst. The blue light region of solar
89 radiation is also enriched during the hours before sunrise and after sunset (Robertson 1966, Johnson et al. 1967, Hughes et al.
90 1984). Since cryptochrome photoreceptors, that detect blue and ultraviolet-A radiation (UV-A, 315-400 nm), are known to
91 influence the circadian rhythm and photoperiodic flowering responses (Guo et al. 1998, Somers et al. 1998). This result
92 implies that it could be worthwhile testing whether blue light can serve as a cue for bud burst in temperate deciduous tree
93 species. Of the few studies on the effects of blue light on bud burst, Girault et al. (2008) report that blue light (Philips TL-D

94 18W/18 fluorescent tubes) was as effective as white light (Osram L 18W/77 Fluora fluorescent tubes, 31% blue; both spectra
95 given in SI of Girault et al. 2008) in terms of the percentage of axillary buds reaching bud burst in *Rosa* sp. However, the
96 timing of spring bud burst in trees may not be mediated through the same mechanisms as axillary buds of herbaceous species:
97 for instance, monochromatic blue light (460nm) did not induce bud-burst in the gymnosperm *P.abies* after 6 weeks of 24h
98 photoperiod (Mølmann et al. 2006). To our knowledge, there have been no studies investigating the effects of blue light on
99 the bud burst of temperate deciduous tree species.

100 Given that blue light has been reported to increase the percentage bud burst in the vegetative shoots of angiosperms
101 including *Rosa* sp. and another Rosaceae, *Prunus cerasifera* (Muleo et al. 2000, Girault et al. 2008), we hypothesised that
102 blue light would advance bud burst in temperate deciduous tree species. Additionally, we expected that bud burst of early
103 successional species, which is predominantly affected by temperature (Basler and Körner, 2012), would be less affected by
104 blue light than late successional species. To this end, we tested the effect on bud burst of light treatments that either included
105 or excluded blue light in branches of the three temperate deciduous species *A.glutinosa*, *B.pendula* and *Q.robur*, differing in
106 their functional strategy from early successional to late successional.

107

108 **Methods**

109 **The collection and care of branch material**

110 We collected dormant branches of *A.glutinosa*, *B.pendula* and *Q.robur* from co-occurring populations of local origin
111 in a natural forest stand in southern Finland (60°13'04.2"N 25°00'31.0"E) and kept them in a temperature-controlled
112 environment under different light treatments while monitoring their bud development. Branches were collected from the
113 lower canopy of trees (2-3 m height above the ground) using sterile garden secateurs on 6th February 2017. We selected eight
114 trees per species, taking 10-15 branches from each tree. Only dormant branches, free of pests and symptoms of disease were
115 selected.

116 The use of this approach, putting cut twigs in controlled conditions for the study of bud burst phenology, and its
117 reliability have recently been exemplified in several studies (Basler and Körner 2012, Laube et al. 2014, Polgar et al. 2014,
118 Vitasse and Basler 2014, Primack et al. 2015). We followed a similar protocol to these studies, placing the cut end of twigs

119 immediately into test tubes of water and continuously monitoring their bud development, under two light treatments: a broad
120 spectrum containing blue light, and a broad spectrum of equal PAR and far red but with blue light attenuated (Table S1).

121 All trees received 111 chilling days prior to harvest: this was calculated according to Murray et al. (1989) as the
122 number of days from 1st of November with a mean temperature $\leq 5^{\circ}\text{C}$. All trees were on the east-facing side of a mixed-forest
123 stand, and only branches that were exposed to sunshine for the majority of the day were selected (spectral composition
124 provided in Table S2, monthly precipitation and temperature in Table S3). Branches were selected which presented at least
125 five buds including the terminal bud. Once collected, branches were all immediately taken into a greenhouse kept at ambient
126 outdoor temperature (0°C), and re-cut to a mean length of 28.35 cm (mean \pm 0.34 SE), and then placed into upright sterilised
127 clear-plastic test tubes (10.26cm long – 15ml volume) containing tap water (Table S4, following Basler and Körner 2012 and
128 Polgar et al. 2014). These twigs were directly removed into a temperature-controlled room with six compartments measuring
129 97-x-57-x-57 cm. Branches from individual trees of each species were randomly assigned into each compartment, so that in
130 each compartment there were 16 branches of *Q.robur*, 20 branches of *B.pendula* and 16 branches of *A.glutinosa*. Twigs were
131 rotated inside the compartments every two days to avoid any bias coming from undetected microclimatic variation inside the
132 compartments. Lights were kept at the same distance from the tips of branches in each compartment.

133

134 **Light treatments under controlled conditions**

135 Three of the six compartments received a broad spectrum of irradiance from an array of LED lamps (2 \times Valoya
136 AP67, 400-750 nm, Table S1: mean PAR among compartments of $161 \pm \pm \leq 10 \mu\text{mol m}^{-2} \text{s}^{-1}$, plus $28 \mu\text{mol m}^{-2} \text{s}^{-1}$ far red)
137 including blue light (BL, $21.8 \mu\text{mol m}^{-2} \text{s}^{-1}$, 13.5% of total PAR), and in the other three compartments BL was attenuated (no
138 BL) by wrapping film Rosco #313 Canary Yellow (Westlighting, Helsinki, Finland) around the LED lamps (3 \times Valoya
139 AP67), limiting the spectrum to a wavelength range 500-750nm (Table S1: PAR $156 \pm \leq 10 \mu\text{mol m}^{-2} \text{s}^{-1}$, plus $31 \mu\text{mol m}^{-2} \text{s}^{-1}$
140 far red). Spectral irradiance measurements were taken inside all the experimental compartments with an array
141 spectroradiometer (Maya 2000Pro, Ocean Optics Inc., Dunedin, Florida, USA) to ensure equivalent PAR and R:FR ratios
142 between the treatments (Table S1). Lights were kept on a 12 h light-dark cycle to simulate photoperiod conditions
143 experienced at the beginning of spring in southern Finland ($60^{\circ}13'04.2''\text{N}$ $25^{\circ}00'31.0''\text{E}$), to ensure that photoperiod would
144 not be a confounding factor in the experimental test of light quality (Rinne et al. 1994, Welling et al. 2004, Sjøgaard et al.
145 2008).

146

147

148 **Temperature measurements under controlled conditions**

149 Day/night temperature was thermostatically adjusted to maintain $12.6/9.5 \pm 0.05$ °c. Temperatures were monitored
150 with iButton sensors (Maxim Integrated, San Jose, United States) in each compartment, sampling every one hour for the
151 entire duration of the experiment, with a resolution of 0.065°C. An infra-red thermal thermometer (Optris LS LT, Berlin,
152 Germany) was used to measure the temperature on individual buds of branches inside the compartments, to ensure there was
153 no difference in bud temperature between treatments. The temperature of buds measured with the infra-red thermometer had
154 a strong positive correlation with mean daily air temperature measured with iButton sensors ($R^2=0.83$, Fig. S1, Table S5),.

155

156 **Monitoring bud development**

157 Bud burst was scored until buds reached stage 4 on a scale of 1-7, made by adapting the scales from Teissier du Crois
158 et al. (1981) and Kramer et al. (2017) whereby, 1 = dormant bud, 2 = bud swelling, 3 = bud scales begin to split, green visible
159 on the bud, 4 = bud split, with leaf tip protruding. The experiment lasted 57 days at which point all species in all
160 compartments had reached at least 50% bud burst (stage 4). Degree-days were calculated as the accumulated mean daily
161 temperature > 0°C after the date of December 31st 2016, following methods by Heide (1993), including any degree-days
162 accumulated by the branches from the dates January 1st to February 6th 2017, during the period prior to the experiment.

163

164 **Data analysis**

165 All results are given as the means \pm 1 SE of three replicates, whereby each compartment was treated as one replicate.
166 We followed statistical methods from Guak et al. (1998), Heide (2003), Sogaard et al. (2008), and Olsen et al. (2014), in
167 comparing the days and degree-days needed to reach 50% bud burst in the BL and no BL treatments for each species. The
168 effect of BL on the bud burst of each species was analysed using an ANOVA (R version 3.2.2., R Core Team, 2017).
169 Pearson's correlation was used to test the relationship between bud temperature and recorded air temperature in each
170 compartment. Figs. 1 and 2 were produced in Microsoft Excel (2013).

171

172

173 **Results and Discussion**

174 In all three species, BL decreased the mean number of days until 50% bud burst (Fig. 1). The response to blue light
175 was smallest in the early successional species *B.pendula*, which reached 50% bud burst only 3-days earlier in the BL
176 treatment compared to the no BL treatment ($F_{1,4} = 100$, $p < 0.001$). The later successional *A.glutinosa* and *Q.robur* reached
177 50% bud burst 6 days ($F_{1,4} = 16.20$, $p = 0.016$) and 6.3 days ($F_{1,4} = 90.25$, $p < 0.001$) earlier respectively in the BL treatment
178 compared to the no BL treatment. These results are consistent with other studies showing that early-successional species
179 achieve bud burst sooner than late-successional species (Wesołowski and Rowiński 2006, Basler and Körner 2012).

180 [Insert Fig. 1. here]

181 [Insert Fig. 2 here.]

182 In our experiment, the effect of BL expressed as a degree day difference between treatments was consistent with the
183 days until 50% bud burst (Fig. 2). Our BL light treatment reduced the degree-days required for bud burst in *B.pendula* by
184 17.12 degree-days ($F_{1,4} = 12.3$, $p = 0.025$), in *A.glutinosa* by 28.14 degree-days ($F_{1,4} = 35.8$, $p = 0.04$) and in *Q.robur* by 60.04
185 degree-days ($F_{1,4} = 20.9$, $p = 0.010$): this is the equivalent of a 10.54%, 15.48% and 11.03% reduction due to BL in each
186 species respectively (Table 1). The degree-day requirement for bud burst in *B.pendula* was very similar to that of a natural
187 population in southern Finland (Table S6), and was within the range reported in previous studies (Basler and Körner 2012,
188 Heide 1993), as was *A.glutinosa* (Table S6, Heide 1993). The bud burst of *Q.robur* branches had a lower degree-day
189 requirement than a natural population in southern Finland (Table S6): this discrepancy may derive from the photoperiod
190 sensitivity of bud burst in *Quercus* species (Basler and Körner 2012, Basler and Körner 2014) which could have been
191 activated by the 12h photoperiod we employed. Alternatively, this difference could be due to the reduced number of chilling
192 days that treated branches received prior to February compared with those in forest stands throughout spring (Table S6).
193 When expressed as the difference in the total length of time until bud burst, the effect of BL in days or degree-days was
194 smallest in branches of *B.pendula*: however, because of the three species we compared it required the shortest total period
195 before bud burst, the effect of BL on *B.pendula* was greatest in relative terms when measured as a % difference (Table 1).

196 [insert Table 1 here]

197

198

199 **What are the mechanisms by which blue light advances bud burst?**

200 Our results demonstrate for the first time that blue light advances spring bud burst in temperate deciduous tree species,
201 through a photoreceptor-dependent mechanism which is yet to be elucidated. This result is consistent with studies of plants of
202 the *Rosacea* family, including *Rosa* sp. and *Prunus cerasifera*, where a higher percentage bud burst and more axillary
203 vegetative shoots and branches were produced under blue light compared to red light (Muleo et al. 2001, Girault et al. 2008).
204 The growth rate and number of preformed leaves in the buds of these species were also higher under blue light. The control
205 of bud burst was exercised in part through the photoregulation of sugar metabolism in this case (Girault et al. 2010), whereby
206 the allocation of sugars to the growing bud increased in the light compared to darkness. The authors attribute the regulation of
207 sugar metabolism in the buds to be primarily mediated by the phytochrome photoreceptors, which have an absorption
208 spectrum in blue light and R:FR, but also possibly by cryptochromes in response to blue light (Reed et al. 1993, Girault et al.
209 2010). Interestingly, several tree species including *Q.robur*, *Fagus sylvatica*, *Betula pubescens*, *Fraxinus excelsior* and *Acer*
210 *pseudoplatanus* (Catesson 1964, Barnola et al. 1986, Cottignies 1986, Kelner et al. 1993, Rinne et al. 1994) increase in bud
211 sink strength close to bud burst, resulting in increased mobilization of stem carbohydrates. It appears from these studies that
212 sugar metabolism, at least in part, plays a role in the process of bud burst of tree species.

213 Regulation of flowering time in response to photoperiod by the blue/UV-A cryptochrome and the R:FR phytochrome
214 photoreceptors has been well established in the model plant *Arabidopsis thaliana* (Guo et al. 1998, Somers et al. 1998). In
215 comparison, much less is known about the role of photoreceptors that regulate bud burst in response to spectral composition.
216 In the tree species *P.tremuloides*, the phytochrome gene PHYB₂ was found to be coincident with a quantitative trait locus
217 affecting bud-set and bud burst (Frewen et al. 2000). Similarly, cryptochromes have been shown to facilitate blue-light-
218 mediated phenological responses in other plant species (Guo et al. 1998, Meng et al. 2013), so it is reasonable to speculate
219 that cryptochromes and phytochromes could facilitate bud burst in response to blue light. Conversely, although phototropins
220 also absorb blue light, there is no evidence that they mediate phenological responses (Casal 2000). Considering that UV-B
221 can affect bud burst and bud set in *P.tremula* (Strømme et al. 2015), and that plants possess a UV-B-detecting photoreceptor
222 (Rizzini et al. 2011), we suggest that a productive area of future research would be to determine the relative contribution of
223 different photoreceptors to regulating bud burst in response to spectral composition.

224

225

226 **What is the ecological significance of blue light?**

227 We provide two possible explanations (in italics) for the ecological role of blue light advancing bud burst, and why it could
228 have a greater effect on early-successional species, measured in absolute terms as days (or degree days) until bud burst, as
229 opposed to percentage differences. Firstly, it has been demonstrated that blue light enhances photosynthesis in *B.pendula*
230 plantlets *in vitro* (Sæbø et al. 1995), and among other plant species (Goins et al. 1997, Matsuda et al. 2004, Hogewoning et al.
231 2010). Blue light is often associated with conditions that are favourable to photosynthesis and normal photosynthetic function
232 (Matsuda et al. 2004, Sellin et al. 2011), so it is possible that *blue light advances bud burst in order to allow the plant exploit*
233 *an opportunity for photosynthetic gains whilst conditions are favourable*. Secondly, the ratio of blue:red light is higher during
234 the twilight hours of sunrise and sunset than the middle of the day (Johnson et al. 1967, Hughes et al. 1984). Robertson et al.
235 (1966) proposes that at higher latitudes the extended hours of twilight rich in blue light and FR could have effects on plant
236 growth not found at lower latitudes, such as the delay in bud dormancy exhibited by *P.abies* grown under day extension using
237 blue light (Mølmann et al. 2006). Given that at high latitudes the day length and thus hours of twilight vary drastically
238 throughout the year, *it is possible that blue light provides cues related to lengthening twilight and daylight periods in spring*.
239 Since photoperiod often has a greater effect on the timing of bud burst in late-successional species (Basler and Körner 2012,
240 Basler and Körner 2014), we might infer that blue light should also have a greater effect on later successional species due to
241 its ecological relevance, i.e. changes in spectral composition related to day length and the length of twilight. Since we used a
242 fixed day length in our experiment, we cannot speculate on the possible interactive effects of blue light and day length here.
243 Similarly, we cannot say whether the bud burst response that we report is related to the proportion of blue light received or
244 the total irradiance of blue light. As such, we suggest future research should test whether bud burst in response to blue light
245 is related to diurnal changes in the proportion of blue light.

246 Under controlled temperature and light conditions we found that blue light advances bud burst in the tree species
247 *B.pendula*, *A.glutinosa*, and *Q.robur*. Further research into bud burst and other phenological processes is needed to: establish
248 whether or not the effect of blue light on bud burst is related to diurnal changes in blue light as opposed to a seasonal
249 increase, describe how plants integrate cues from day length and spectral composition (from UV through to far-red) through

250 crosstalk among photoreceptor mediated responses, and combine this information with other environmental cues (e.g.
251 temperature)to produce an environmentally-appropriate response.

252

253 **Author Contributions**

254 CCB conceived, designed and carried out the experiment and statistical analyses. TMR supervised the design, analyses and
255 interpretation of results. Both authors wrote the manuscript.

256

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260

261 **Conflict of Interest Statement**

262 None declared.

263

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270

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- 428

429 **Tables**

430

431 Table 1. The effect of BL on bud burst expressed both as the difference in the mean number of days and mean degree-days

432 until 50% bud burst in *A.glutinosa*, *B.pendula* and *Q.robur*, and the percentage differences in the total number of days or

433 degree-day. Degree-days were calculated as the accumulated daily mean temperature > 0°C starting from 1st January 2017.

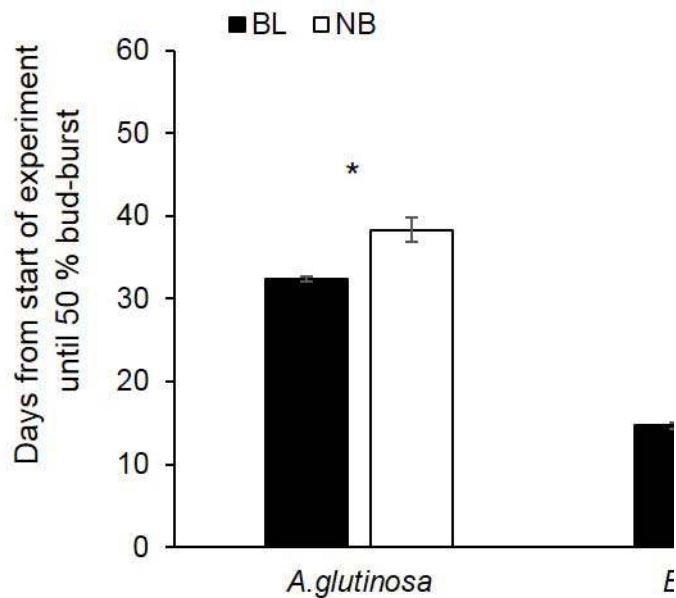
434

BL effect on bud burst expressed in days		
	Number of days earlier with BL	% difference between treatments
<i>A.glutinosa</i>	6.00	15.65
<i>B.pendula</i>	3.33	18.50
<i>Q.robur</i>	6.33	11.30

438

List of Figures

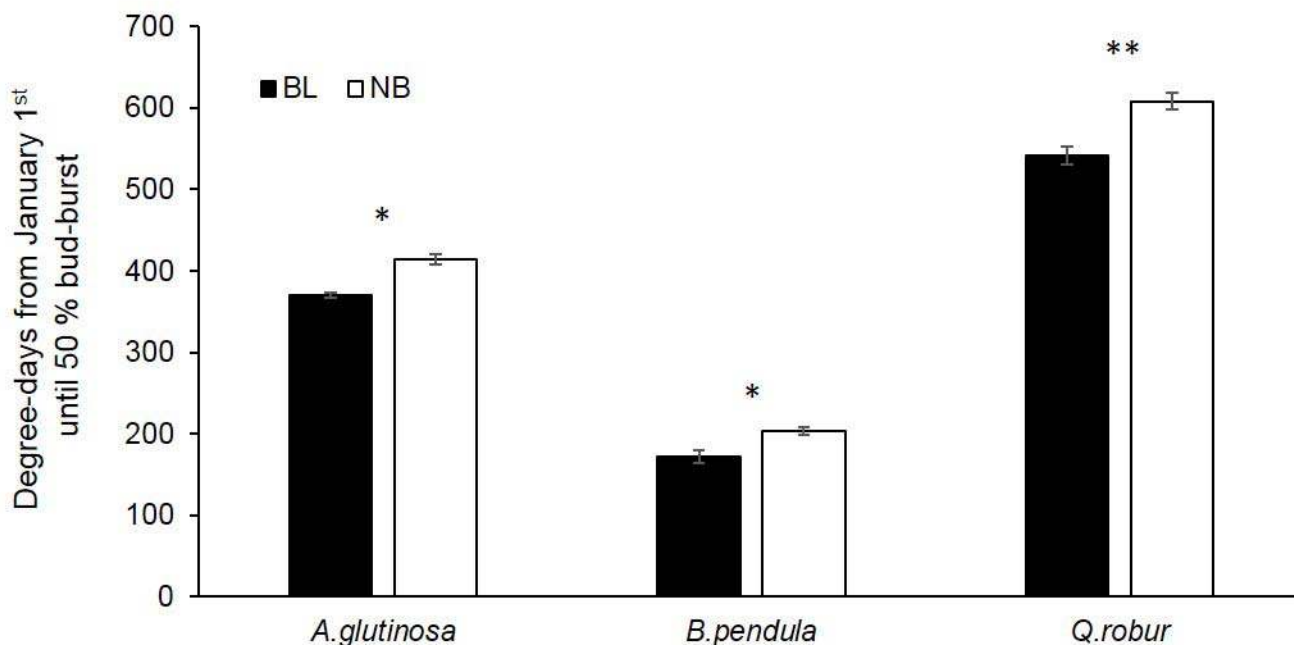
BL effect bud burst expressed in degree-days		
	Number of degree-days earlier with BL	% difference between treatments
<i>A.glutinosa</i>	43.61	10.54
<i>B.pendula</i>	31.45	15.48
<i>Q.robur</i>	67.03	11.03



439

440

441 **Fig. 1.** The mean number of days until 50% bud burst in *A.glutinosa*, *B.pendula* and *Q.robur*, in a broad spectrum treatment
442 with blue light (BL) and without blue light (No BL). Error bars represent standard error (n=3) from three replicate
443 compartments, each containing 16 *A.glutinosa* branches, 20 *B.pendula* branches and 16 *Q.robur* branches. Asterisks represent
444 statistically significant differences between treatments, where * = $p \leq 0.05$, ** = $p \leq 0.010$, *** = $p \leq 0.001$. *A.glutinosa* ($F_{1,4}$
445 = 16.20, $p = 0.016$) *B.pendula* ($F_{1,4} = 100$, $p < 0.001$), *Q.robur* ($F_{1,4} = 90.25$, $p < 0.001$).



446

447 **Fig. 2.** Mean degree-days until 50% bud burst in *A.glutinosa*, *B.pendula* and *Q.robur*, in a broad spectrum treatment with
448 blue light (BL) and without blue light (No BL). Error bars represent standard error (n=3) from three replicate compartments,
449 each containing 16 *A.glutinosa* branches, 20 *B.pendula* branches and 16 *Q.robur* branches. Degree-days calculated as the
450 accumulated daily mean temperature $< 0^{\circ}\text{C}$ after the date of December 31st 2016. Asterisks represent statistically significant
451 differences between treatments, where * = $p \leq 0.05$, ** = $p \leq 0.010$, *** = $p \leq 0.001$. *A.glutinosa* ($F_{1,4} = 35.8$, $p=0.04$)
452 *B.pendula* ($F_{1,4}=12.3$, $p = 0.025$), *Q.robur* ($F_{1,4} = 20.9$, $p= 0.010$).

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454