Title page:

Does ontogeny matter for the spring temperature requirement for bud burst of two coniferous species in cool-temperate forests?

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Author contribution

K.M. designed the research, conducted the field monitoring, analyzed the data and wrote the entire part of the manuscript.

Abstract: Spring leaf phenology is an important event for trees to determine carbon fixation during the growing season. However, less is understood about the intraspecific variation in spring leaf phenology and its relationship with the spring temperature requirements of conifers, which is problematic for accurately predicting the influence of spring climate warming on conifers. I monitored bud burst timing and the degree days required for bud burst for seedlings and large individuals of *Abies sachalinensis* (fir) and *Larix kaempferi* (larch) over two seasons in northern Japan. Contrary to my expectation, the degree days required for the bud burst of small individuals were similar to or larger than those of the large individuals for fir and larch. Consequently, the bud burst timing of small individuals was similar to or later than that of large individuals for fir and larch. Even when conifer species are in their early stage, the spring temperature requirement for bud burst is not necessarily less than that for large individuals, which is not the case for many broad-leaved species. These results indicate that for these two coniferous species, ontogenetic differences in temperature requirements are not necessary to be considered for the response of communities to spring climate change.

Keywords; ontogeny, phylogeny, winter climate change, gymnosperm, snow

Introduction

Spring leaf phenology, such as bud burst timing, is one of the most important events for trees to determine their survival and carbon fixation during the growing season (Sakai and Larcher 1987; Richardson et al. 2009). The bud burst timing of trees has been intensively studied in the context of climate change (Körner and Basler 2010). This is because climate warming is expected to proceed (IPCC 2021), and a detailed understanding of the driver of the variation in spring phenology and its relationship with air temperature is crucial to predict the carbon fixation by trees acutely under a warming climate. However, surprisingly, a large portion of the bud burst phenological studies were conducted for broad-leaved trees, probably due to the difficulty in observing the bud burst of the small winter bud of large coniferous trees in the field (as cautioned also by Montgomery et al. 2020, but see Bailey and Harrington 2006; Panchen et al. 2014). In particular, the determinant of intraspecific differences in the spring leaf phenology of conifers is poorly understood in the field. The lack of understanding of the relationship between temperature and intraspecific variation in spring phenology makes it difficult to predict the influence of climate warming on carbon fixation in coniferous forests, which dominate at higher latitudes.

For broad-leaved trees, in addition to species differences (Panchen et al. 2014),

56 ontogenetic size differences are known to drive the intraspecific variation in spring leaf
57 phenology (Seiwa 1999; Augspurger and Bartlett 2003; Vitasse 2013; Osada and Hiura
58 2019). Ontogenetically small trees (e.g., seedling and sapling) show earlier bud burst than
59 ontogenetically large trees because smaller trees generally need less accumulation of
60 degree-days for their bud burst (Vitasse 2013; Marumo et al. 2020). Early bud burst due
61 to the lower requirement of degree days makes it possible for small trees to intercept more
62 light before canopy closure of large trees in spring, and consequently, small trees can
63 photosynthesize efficiently in the understory (Seiwa 1999). However, late bud burst is
64 considered beneficial for large trees due to the decrease in the risk of leaf damage by frost
65 in early spring (Sakai and Larcher 1987; Seiwa 1999). Such ontogenetic differences in
66 bud burst timing can contribute to maximizing the growth of trees of various sizes and
67 consequently can determine the size-dependent climate niches in temperate forests (Koide
68 et al. 2021). For Norway spruce (*Picea abies* (L.) Karst), ontogenetic differences in the
69 requirements of photoperiod and chilling temperature during autumn are known to drive
70 intraspecific variation in bud burst timing (Partanen et al. 2005). In addition, spring
71 temperature is important for bud burst timing in Norway spruce (Hannerz 1999). However,
72 for coniferous species, little is known about how size differences impact the intraspecific
73 requirement of spring temperature for bud burst timing. Well-studied broad-leaved

species are phylogenetically distant from coniferous species. Phylogenetic differences in various plant traits, such as wood anatomy and leaf construction costs, might also cause a phylogenetic signal in size-dependent patterns in leaf phenology (Osada and Hiura 2019). In fact, there are significant differences in bud burst timing between gymnosperms and angiosperms (Panchen et al. 2014). Consequently, the relationships between tree height and spring leaf phenology have the potential to differ more for phylogenetically distant species, and earlier bud burst in smaller trees might be detected only for broad-leaved species but not for coniferous species (Osada and Hiura 2019). Therefore, it is worth investigating whether the size-dependent pattern of degree days required for bud burst timing in broad-leaved species is also present for coniferous species.

In addition to the physiological requirement, the environmental condition affects the size-dependent difference in bud burst timing of trees. Importantly, snow accumulation and subsequent snowmelt occur heterogeneously even within a forest. The difference in the leaf habit of canopy trees is linked to differential snow accumulation (Suzuki et al. 2008); snow depth is lower and snowmelt timing is earlier under evergreen conifers than under the canopy of deciduous conifers and open canopy in Hokkaido. There, the dominant evergreen coniferous trees (e.g., *A. sachalinensis*) are shade tolerant and regenerate under the closed canopy (Iijima et al. 2009), while the deciduous larch

species (*L. kaempferi*) are light-demanding species (Ryu et al. 2009) and regenerate in open habitat (Kondo and Tsuyuzaki 1999; Iijima et al. 2009; Kitao et al. 2018). In addition, the bud burst timing of smaller trees is later than that of canopy trees because of the later snowmelt and later start of the accumulation of degree-days for smaller trees compared to large trees despite the lower requirement of degree-days for smaller trees (Marumo et al. 2020). Together, these facts can complicate the size-dependent patterns of bud burst timing of tree species regenerating under the canopy of different leaf habits.

In this study, I hypothesized the following.

1) Similar to broad-leaved trees, smaller trees require less accumulation of degree days for their bud burst than large trees.
2) For bud burst timing, trees that require less accumulation of degree days do not always show earlier bud bursts because of differential snowmelt and the coincidental start of the accumulation of degree days in heterogeneous forests.

To test these hypotheses, I conducted a phenological survey of two coniferous species of Pinaceae that regenerate under different canopy types over two years together with temperature monitoring.

Materials and Methods

I conducted a phenological survey from the beginning of March to the end of May of 2020 and 2021 in a subboreal forest (Teshio Experimental Forest of Hokkaido University) in northern Hokkaido, Japan (44°55′ N, 142°01′ E). The altitude of the research site is 15 m a.s.l. The annual precipitation in 2020 and 2021 was 1041 mm and 980 mm, respectively (Horonobe meteorological station, Japan Meteorological Agency 2022). The precipitation as snowfall from November 2019 to April 2020 was 200 mm and that from November 2020 to April 2021 was 376 mm. Snow covered the forest floor from November to early April, and the maximum snow depth was approximately 0.7 m under the evergreen canopy and 1.2 m in the open canopy at the study site.

I investigated the bud burst of two canopy tree species: *Lamb Carr. kaempferi*. (larch) and *A. sachalinensis* (F. Schmidt) (fir) during the spring of 2020 and 2021. I conducted the observation every 3 or 4 days (twice a week). The large trees of the two species were planted in the botanical garden of Teshio Experimental Forest. The trees were planted every 3 meters linearly, and the ages of the large individuals of the two species were 61.4 (±3.9) years larch and 62.6 (±4.2) years fir. While both species are two of the most dominant coniferous species in Hokkaido, fir is the native species, while larch is a domestically introduced species from the mountain range in central Japan approximately 1 1900 AD. The seedlings of the two species are those that

naturally regenerate on the forest floor. Larch seedlings are distributed under the open canopy because it is a light-demanding species (Ryu et al. 2009), while fir seedlings are distributed under the canopy of large firs due to the difference in shade tolerance (Iijima et al. 2009). Leaf out starts from early to middle May for both larch and fir, while bud formation is completed at the beginning of September for larch and in the middle of October for fir (Makoto et al. 2020). Leaf senescence and litter fall occur from the end of October to the beginning of November for larch, while most of the two occur from September to throughout the winter for firs.

For each species, the number of observed trees was 20 for seedlings and 20 for large trees (a total of 80 individuals). The average height of the seedlings was approximately 30 cm for fir and 28 cm for larch at the beginning of the observation. At the end of the observation, the average height and age of the larch seedlings were approximately 50 cm and 2.4 (±0.5 SD) years old, while those of fir seedlings were 31 cm and 4.8 (±1.6 SD). There was no significant difference in tree age between larch seedlings and fir seedlings. The average height of the canopy individuals was approximately 17 m for fir and 20 m for larch.

I used the bud burst timing of the healthy lowest branch as the phenology of the representative data of the large trees. In the preliminary observation of some individuals (whose whole canopy was easily observed from the trail), the bud burst timing proceeded almost simultaneously across the canopy. Therefore, it was possible to use the bud burst timing of the lowest branch, which is easy to observe, as the proxy of the bud burst timing of each large individual. The average height of the lowest branch (where the observed buds existed) of the large individuals was 6 m for fir*s* and 5 m for larch.

Temperature measurement and degree-days

The observed trees experienced three types of temperature conditions. The large trees of the two species exist in a mixture, so they experience similar air temperatures at the site. There were significant differences in the amount of snow and its melt timing between open canopy and under the canopy, which are known to influence the phenological timing of seedlings (Marumo et al. 2020). Therefore, I observed air temperature at the lowest healthy branch (approximately 5-6 m from the ground surface) for canopy trees, 20 cm from the ground surface in the open canopy (as the proxy for the temperature condition of larch seedlings), and 20 cm from the ground surface under the canopy of fir (Fig. 1).

In each condition, I set three thermometers (Thermo Recorder Mini RT-30S, Espec, Japan) and monitored the temperature every hour from the beginning of March to the end of May 2020 and from the beginning of September 2020 to the end of May 2021, and the daily mean temperature was calculated. Degree-day models are often used to calculate the progress of leaf phenology, such as bud bursts (Murray et al. 1989). The temperature data monitored at the forest understory were used to quantify the degree days for seedlings, while those at the lowest branch of large trees were used for the calculation of large trees. I calculated the degree days until the bud burst day as follows:

$$DD_x = \sum_{m=t_0}^{n} (t_m - x)$$

where DD_x is the value of degree-days with the threshold of x°C (here, the threshold is set at 5 °C as in the previous study, Clark et al. (2014)) for the daily mean temperature. t_0 was used as the initial day to calculate degree-days when a daily mean temperature first reached the threshold in each season (> 5 °C). n is the day of bud burst of a tree. The daily mean temperature of day of the year (DOY) m is defined by t_m. When t_m was below 5 °C, the data were not used for the calculation of *DDx.* The day of snow disappearance was defined as the day when the daily mean temperature at the ground

surface started to fluctuate drastically due to the loss of snowpack insulation. It has been confirmed that the start of the temperature fluctuation matches the date of snow disappearance in the forest floor of northern Hokkaido (Makoto et al. 2022).

Statistical analysis

To meet the assumption of normal distribution and homoscedasticity, the bud burst day and degree-day data were log-transformed. Then, the difference in the degree-days or bud burst day (DOY) between the tree species and size classes was evaluated by two-way analysis of variance (ANOVA) by using the "aov" function in R software. For this ANOVA, the explanatory variables were the tree species, size class and their interaction. When the *p value* was less than 0.05, the difference between groups was considered significant, and Tukey's HSD multiple comparison test was conducted to see the specific difference among the species and size. All statistical analyses were conducted using R software, version 4.1.0 (R Development Core Team 2021).

Results

Size class and the species interactively influence the degree-days required for bud burst ($p<0.001$, ANOVA). For the degree-days, there was no significant difference between the size class for fir ($p<0.05$, Tukey HSD, Fig. 3). However, for larch, the smaller larch individuals required more accumulation of degree days for their bud burst compared to the larger individuals ($p<0.05$, Tukey HSD, Fig. 3). Over the two years of observation, the influence of species and size class on the bud burst day showed similar patterns (Fig. 3).

In addition, size class and the species interactively influenced the bud burst day ($p<0.001$, ANOVA). For the bud burst day, the fir showed later bud burst timing ($p<0.05$, Tukey HSD, Fig. 4). However, the smaller larch individuals showed a later bud burst than the larger larch individuals ($p<0.05$, Tukey HSD, Fig. 4). Over the two seasons of the study period, the influence of species and size class on the bud burst day showed similar patterns (Fig. 4).

Discussion

The results of the present study demonstrated that body size does not always determine the required number of degree days for bud burst or bud burst timing for conifers (Fig.

213 3). The observed patterns of temperature requirement and its relation with conifer bud
214 burst were largely different from those of broad-leaved trees (e.g., Seiwa 1999;
215 Augspurger and Bartlett 2003; Vitasse 2013; Marumo et al. 2020). To the best of my
216 knowledge, for coniferous species, this is the first study to investigate the intraspecific
217 ontogenetic patterns of phenological timing and its relationship with spring temperature
218 requirements under comparable conditions.

219 Contrary to my expectation, the degree days required for the bud burst of small
220 individuals were similar to or even larger than those of the large individuals for fir and
221 larch, respectively (Fig. 3). For fir, this could be partly because a requirement of fewer
222 degree-days for bud burst is not beneficial for smaller individuals. The fir seedlings
223 often regenerate under the canopy of evergreen conifers in Hokkaido owing to their
224 higher shade tolerance (Iijima et al. 2009). Under the canopy of evergreen coniferous
225 species, the light availability is not drastically high in spring (e.g., Bontempo e Silva et
226 al. 2012) because the canopy of evergreen trees keeps the majority of leaves over
227 winter. Logically, this might make it less beneficial for smaller fir seedlings to open
228 their buds in spring due to a larger risk of frost damage. In the temperate forests of
229 North America, saplings of the evergreen *Juniperus virginiana* maximize carbon gain
230 not by changing bud burst phenology but by maximizing their photosynthetic rate in

231 spring and fall (Augspurger and Bartlett 2003). It is also known that the seedlings of fir
232 change leaf thickness drastically and plastically to acclimate to shady conditions in
233 northern Japan (Iijima et al. 2009). In addition, fir is known to be sensitive to
234 photoinhibition immediately before bud burst in spring, which implies a higher risk of
235 early shoot growth in spring for this species (Kitao et al. 2018). Such high plasticity of
236 leaf traits and vulnerability to photoinhibition might be linked to the nonnecessity (or
237 even high risk) of advancing the bud burst timing of fir seedlings.

238 For larch species, to my surprise, more degree-day accumulation was required for
239 the bud burst of deciduous conifer seedlings (Fig. 3b). This could be potentially due to
240 one or both of the following factors: 1) the requirement of more accumulation of
241 degree-days is more beneficial for smaller individuals and 2) other environmental
242 factors are required for the bud burst of larch species. To my knowledge, no plausible
243 explanation for the greater requirement of degree-days for the bud burst of smaller trees
244 exists in the context of increasing the fitness of the smaller trees. However, larch
245 seedlings regenerate mainly after severe disturbance (Kondo and Tsuyuzaki 1999),
246 where the canopy does not exist to inhibit light availability for seedlings. It is possible
247 that smaller individuals do not need to take the risk of suffering from frost damage
248 under open conditions and can therefore delay bud burst timing by requiring less

accumulation of degree-days. In the natural habitat of larch in central Japan, it was observed that larch seedlings showed later bud bursts than large larch individuals (Shirota, T, personal communication). Therefore, the observed patches in this study in northern Hokkaido can highlight those in natural habitats. In addition to spring temperature, spring photoperiod and chilling temperature in winter are known to be determinants of the bud burst timing of trees (Körner and Basler 2010). For the tree species in the southern habitats (in my case, larch), the photoperiod and chilling temperature are known to be important factors for the release from endodormancy and therefore for bud burst (Jewaria et al. 2021; Zhang et al. 2021). In addition, it is known that the shorter exposure of the winter bud to the chilling temperature results in later bud burst (Murray et al. 1989). Additionally, chilling temperature is usually calculated as the sum of days below 10 °C and above 0 °C (Pletsers et al. 2015). At our site, the sum of the days under chilling temperature from autumn to winter was greater for the larch seedlings than for the large individuals (Fig. 2B), which makes it difficult to speculate that the lower accumulation of the chilling temperature resulted in the later bud burst of larch seedlings compared to the larger individuals. The importance of chilling temperature, spring forcing temperature, and photoperiod for bud dormancy

266 should be tested with an experiment to manipulate these factors in combination byn
267 using the cutting of shoots, as conducted by Basler and Körner (2012).

268 The second hypothesis was inconsistent with the results. For bud burst timing, the
269 fact that the fewer requirements for bud burst are so exact resulted in a later bud burst
270 (and *vice versa*). As expected, the snowmelt timing was earlier for fir seedlings under
271 the fir canopy than for larch seedlings under the open canopy (Fig. 2). However,
272 because of 1) the markedly and significantly large difference between the two species
273 for the requirement of degree days and 2) the cold air temperature between the
274 snowmelt under the canopy and open canopy, the larch seedlings showed earlier bud
275 burst than the fir species.

276 In this study, I have not focused on the importance of the leaf habit of the two
277 coniferous species for bud burst timing in relation to their adaptability to their local
278 environment. This is because the larch species is the domestically introduced species to
279 my site from central Japan, and the two species do not coexist naturally. However, it
280 was interesting that the degree days required for bud burst were greater for evergreen
281 conifers than for deciduous conifers (Fig. 3). Panchen et al. (2014) reported earlier bud
282 bursts for evergreen species than for deciduous species without an explanation of the

physiological mechanism. The results of the present study might indicate that the observed difference in bud burst timing by Panchen et al. (2014) between leaf habits is at least partly caused by the differential requirement of the degree days between evergreen and deciduous species. The bud burst timing is earlier for deciduous species, probably for the following reason: spring leaf phenology regulates the growth of deciduous trees because all of their leaves fall during the winter, and they produce new leaves in the spring (Augspurger et al. 2005). In contrast, evergreen trees keep the majority of their leaves over winter (Reich et al. 2014); thus, the overwintering leaves can photosynthesize in early spring, and it is less important to produce new leaves in early spring (Yang et al. 2020). Additionally, it is possible that the difference in natural habitats drove the interspecific difference in the temperature requirement for bud burst between the two species. The tree species in southern milder habitat (in this case, larch species) might require less accumulation of degree days for their bud burst compared to those living in northern colder species because of the lower risk of spring frost from early spring, and the earlier bud burst can result in the benefit of elongating the growing season compared to the northern species. It should be noted that it is difficult to draw conclusions about the performance of coniferous species in general because 1) the studied species is only two and 2) one species is not native to the study sites. For future

studies, it will be beneficial to test the size-dependent pattern of bud burst phenology for many coniferous species with different leaf habits where the species with two types of leaf habits coexist naturally (e.g., Far East Russia, Makoto et al. 2007).

Conclusion

Body size does not always influence the requirement of degree days for bud burst to increase light interception for fir and larch (two coniferous species) in northern Japan. The observed patterns were largely different from those observed in broad-leaved trees. The results of the present study imply that a difference in degree-days based on size might not be necessary for the early stage of *L. kaempferi* and *A. sachalinensis*, and this finding is different from the findings of previous studies of broad-leaved species (Marumo et al. 2020) in Japanese temperate forest. These results indicate that the difference in the spring temperature requirement for the spring leaf phenology of these two coniferous species based on size is not necessary to predict the response of a Japanese temperate forest, which consists of trees of different sizes, to ongoing climate change (as conducted by Koide et al. 2021).

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Statements and Declarations

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Captions to the figures

Figure 1: The graphical overview of the canopy type (Evergreen = the area covered with the canopy trees of fir, Deciduous = the area covered with the canopy trees of larch, Open = the area covered without canopy trees), temperature monitoring system with thermometer, and snowpack distribution.

Figure 2: Temperature dynamics at the study site from March to May 2020 (A), from September to December 2020 (B), and from January to May 2021 (C). The black dotted line indicates the data monitored at the lowest branches of canopy trees, the gray solid line indicates those under the canopy of evergreen trees, and the black solid line indicates those at the open canopy. Each line indicates the average value calculated with three thermometers in each condition. The snowmelt timing was earlier for fir seedlings under the fir canopy than for larch seedlings under the open canopy. In 2020, the snowmelt timing was DOY 73 under the fir canopy and DOY 92 under the open canopy. In 2021, the snowmelt timing was DOY 87 under the fir canopy and DOY 104 under the open canopy. The difference in snowmelt timing between the sites under the evergreen canopy and open canopy was 19 and 17 days in 2020 and 2021, respectively.

Figure 3: The degree days accumulated until the day of bud burst for large fir individuals (large.fir), small fir individuals (small.fir), large larch individuals (large.larch) and small larch individuals in 2020 (A) and 2021 (B). Boxes show the median, 25th and 75th percentiles, error bars show the 10th and 90th percentiles, and points indicate outliers. The different letters indicate statistically significant differences ($p<0.05$) between the categories of the trees analyzed with Tukey's HSD after two-way ANOVA.

Figure 4: The bud burst day for large fir individuals (large.fir), small fir individuals (small.fir), large larch individuals (large.larch) and small larch individuals in 2020 (A) and 2021 (B). Boxes show the median, 25th and 75th percentiles, error bars show the 10th and 90th percentiles, and points indicate outliers. The different letters indicate statistically significant differences ($p<0.05$) between the categories of the trees analyzed with Tukey's HSD after two-way ANOVA.

Figure 1

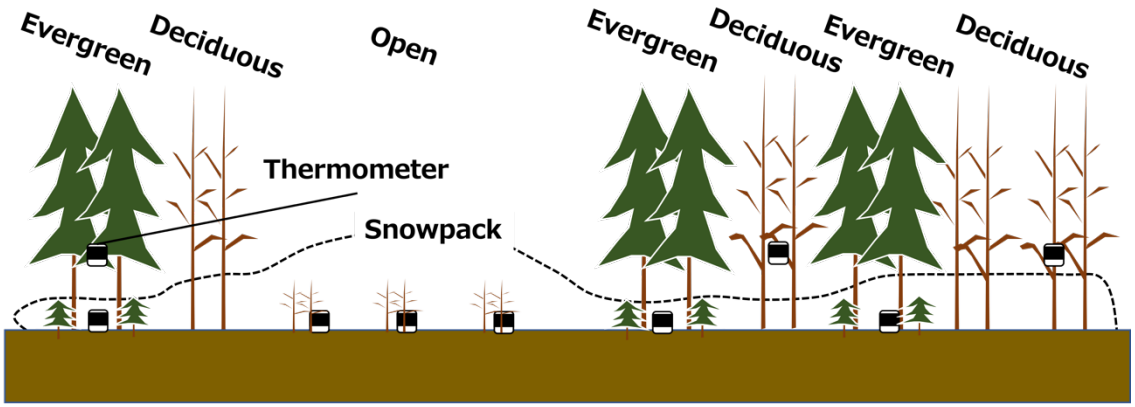

Evergreen
Deciduous
Open
Evergreen
Deciduous
Evergreen
Deciduous
Thermometer
Snowpack

Figure 2

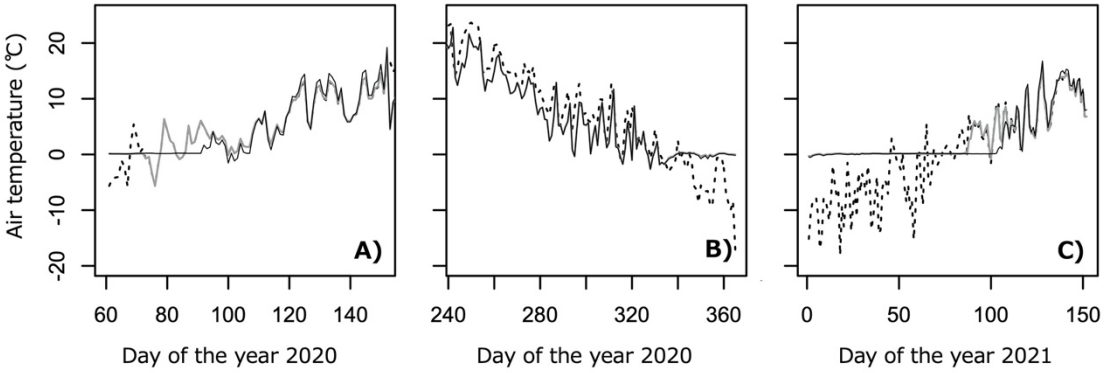

Air temperature (℃)
20
10
0
-10
-20
A)
B)
C)
60
80
100
120
140
240
280
320
360
0
50
100
150
Day of the year 2020
Day of the year 2020
Day of the year 2021

Figure 3

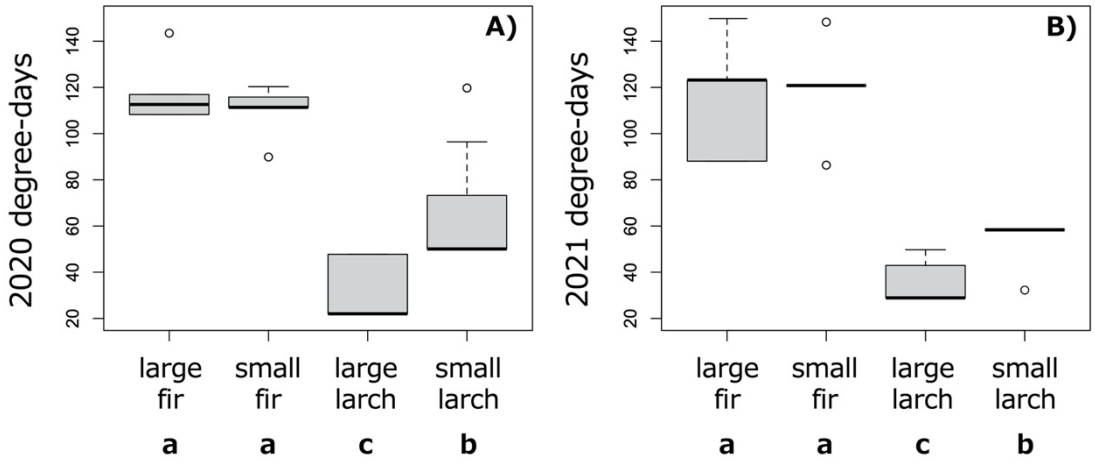
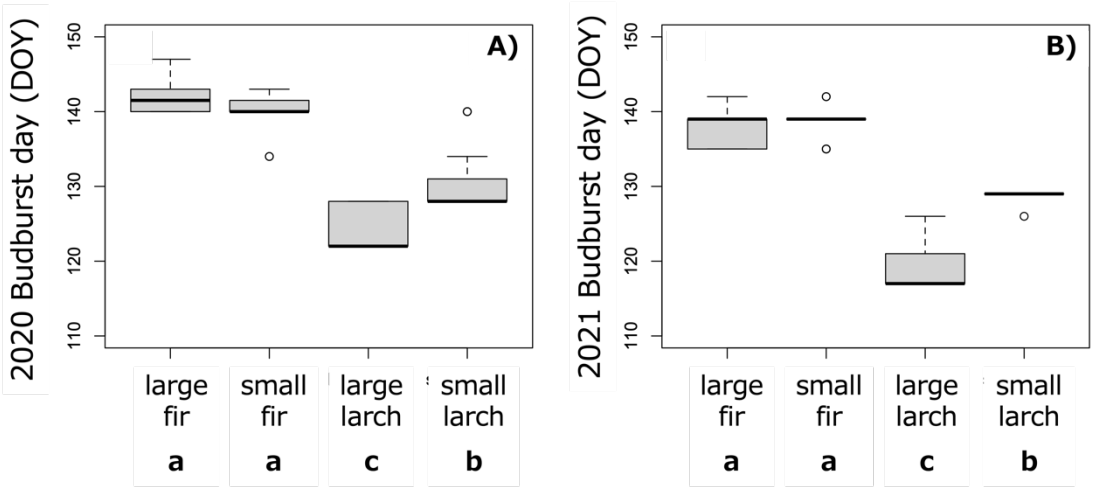

A)
2020 degree-days
20
40
60
80
100
120
140
large fir
small fir
large larch
small larch
a
a
c
b
B)
2021 degree-days
20
40
60
80
100
120
140
large fir
small fir
large larch
small larch
a
a
c
b

Figure 4


2020 Budburst day (DOY)
A)
110
120
130
140
150
large fir
small fir
large larch
small larch
a
a
c
b
2021 Budburst day (DOY)
B)
110
120
130
140
150
large fir
small fir
large larch
small larch
a
a
c
b