Short communication

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Timing of bud burst of smaller individuals is not always earlier than that of larger trees in a cool-temperate forest with heavy snow

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Abstract

Bud-burst timing is one of the key factors to determine tree growth. Smaller trees are known to show earlier bud-bursts, owing to the ontogeny in temperate forests. Snowpack is one of the factors affecting burst timing, especially that of small trees. Because small individuals were buried under snowpack until late spring, we hypothesized although the smaller individuals require less degree-day accumulation for their bud-burst, the bud-burst timing of smaller individuals is not always earlier than that of larger trees. To test this hypothesis, we investigated the relationship between the height of individuals and the sum of degree-days required until the day of bud-burst, as well as the relationship with the bud-burst timings for *Acer mono* and *Quercus crispula* over two years. As hypothesized, both species showed positive relationship between tree height and degree-days for bud-burst in both years. Conversely, there was negative relationship between tree height and the bud burst timing for both species in both years. These results indicate small individuals tended to be late to reach an adequate temperature for bud-burst due to the heavy snowpack, and the day of bud burst was sometime later for the seedlings as compared to the large trees in spite of the less accumulation of degree-day for the bud-burst of smaller trees. These results suggest snow regime changes may influence the phenology not of large trees but of small trees, which could result in a differential influence of winter climate change on tree growth depending on the individual tree height.

Keywords: ontogeny, intraspecific variation, winter climate change, context dependency, ecosystem function

Introduction

Bud burst timing is one of the most important phenological events to determine the growth of trees during the growing season (Seiwa 1999a; Augspurger 2009; Yoshie 2010). The bud burst timing of trees is known to differ depending on species (e.g., Lechowicz 1984; Takahashi et al. 2013). On the other hand, even within the same species, the bud burst timing is known to differ depending on the height due to ontogenetic effects (Borchert 1980; Seiwa 1999a, 1999b; Vitasse 2013; Wang et al. 2013; Osada and Hiura 2019). Specifically, seedlings, saplings and shrubs unfold buds earlier than canopy trees because they physiologically require less accumulation of degree-days of temperature for bud burst (Seiwa 1999a; Augspurger and Bartlett 2003). The early bud burst makes it possible for small trees to acquire more light before canopy closure, and as a result, the small trees can gain carbon efficiently (Seiwa 1998, 1999a, 1999b). In fact, Seiwa (1998) reported that seedlings of *Acer mono* Maxim. showed an earlier leaf emergence than large trees and attained more than half of the annual dry mass gain before canopy closure in the forest with winter snow cover in northern Japan. Conversely, the late bud burst of canopy trees was considered to be beneficial due to a decrease in the risk of leaf damage by frost in the early spring (Sakai and Larcher 1987; Seiwa 1999a; Vitasse et al. 2014). In summary, this ontogenetic determinant of bud burst timing is likely to optimize the growth of individual trees with various heights. However, little is known about how such ontogenetic differences of bud burst timing could be influenced by the local climate (e.g., snow accumulation), which heterogeneously vary in temperate forest ecosystems (see Maruyama 1979; Osada and Hiura 2019).

In temperate forests of northern Japan with heavy snow, snowpack influences the structure and function of tree communities (Makoto et al. 2014). In the snowy biome, snow accumulation and snowmelt timing largely determine the phenological events of plants (Wipf et al. 2009; Wipf 2010; Wheeler et al. 2016). A late snowmelt timing delays the exposure of small plants to air temperatures. If the air temperature is low enough to cause frost damage, the late snowmelt timing allows plants to escape from frost damage in the early spring (Johnson et al. 2004; Coop and Givinish 2008). Conversely, if the air temperature is warm enough to trigger bud burst, the late snowmelt timing delays the accumulation of degree-days of temperature for bud burst, and as a result, the bud burst timing is also delayed even after the adequate exposure to the chilling requirements as well as photoperiod (e.g., Wipf 2010). In forests of northern Japan with heavy snowfall, the snowmelt timing ranges from late April to early May. At that season, the daily mean air temperature reaches higher than 5°C (e.g., the data of Nakagawa meteorological station, Japan Meteorological Agency 2020), which is often regarded as the sufficiently warm temperature for bud development (Clark et al. 2014). In this period, large individuals with buds above the snowpack may be able to advance the leaf phenology, while small individuals (e.g., seedlings and saplings) with buds under the snow cover may not be able to advance bud burst until their buds are exposed to air. These facts make it possible to predict that, although smaller trees require less accumulation of temperature above 5 °C for bud burst, the realized timing of bud burst of smaller individuals is not always earlier than that of larger trees in the temperate forests with heavy snowfall. In fact, Maruyama (1979) reports that smaller trees show a later leaf expansion than larger trees in heavily snowy temperate forests. However, in his study, it is not clear whether the observed timing of later bud burst of smaller trees was due to the necessity of accumulating more degree-days of temperature for smaller trees or environmental factors such as the burial of smaller trees under snow.

We hypothesized that the bud burst timing is not always earlier for smaller trees as compared to larger trees in the temperate forests of northern Japan with heavy snowfall, even though smaller trees need a less cumulative temperature (degree-days) for their bud burst than larger trees because of ontogenetic physiological differences (Vitasse 2013). To test this hypothesis, we investigated the relationship among tree height, bud burst timing, and the temperature experienced by buds together with the information of snow cover over two years in a temperate forest of northern Japan with heavy snowfall. We investigated an oak and a maple species in the forest because the two species are dominant in this region and it is known that these two species have distinct phenological patterns (successive leafing and simultaneous leafing, respectively) due to their differential wood anatomy (Lechowicz 1984).

Materials and Methods

Site description

Field observations were conducted from April to May in 2016 and 2017 in the cool-temperate Nakagawa Experimental Forest of Hokkaido University in northern Hokkaido, Japan (44°52’ N, 142°05’ E). The altitude of the research site is ca. 100 m a.s.l. The forest type is a mixed conifer -broadleaf forest (Tatewaki 1958), and the canopy layer consists of *A. mono*, *Quercus crispula* Blume, *Abies sachalinensis* Masters, *Betula ermanii* Cham. and *Betula platyphylla* var. *japonica* Hara (nomenclature according to Sato 2017). The understory is almost entirely dominated by evergreen dwarf bamboo (*Sasa senanensis* Rehder). According to the FAO-UNESCO classification, the soil type is a Dysteric Cambisol, and the bedrock is Mesozoic sedimentary rock. The annual precipitation in 2016 and 2017 was 1140 mm and 1111 mm, respectively (Nakagawa meteorological station, Japan Meteorological Agency 2020). The precipitation as snowfall from November 2015 to April 2016 was 541 mm. The data of snowfall was obtained in Teshio Experimental Forest of Hokkaido University, which is about 7 km north west of research site. The elevation of the research site is about 100m a.s.l while that of the Teshio Experimental

Forest is 15 m a.s.l.. Although the snowfall data was not the data from the research site, it is known that the two area follow the similar climate conditions (Hiura et al. 2019). Therefore, the data of the Teshio Experimental Forest can be believed to be representative for the research site. Snow covered the forest floor from November to early May, and the maximum snow depth was 1.6 m at the study site.

Observation of bud burst

We observed the bud burst of two species: *A. mono* and *Q. crispula*, both of which have individuals with a wide range of heights in mature forests (Hiura et al. 1998). In 2016, the number of observed trees was 38 and 46 for *A. mono* and *Q. crispula*, respectively. In 2017, the number of observed trees was 63 and 40 for *A. mono* and *Q. crispula*, respectively. The different numbers of individuals were observed between the two year because some individuals were dead and found between the two years. The height ranged from 0.1 to 23.1 m and from 0.1 to 22.6 m for *A. mono* and *Q. crispula*, respectively in both years. The largest trees in both species investigated in our study were high enough to represent the canopy layer of our studied forests. To avoid the influence of the heterogeneous snow depth within the forest, we chose trees that were in relatively flat areas on a south facing slope and not close to evergreen conifer trees, where less snow accumulates than in other parts of the forest. In 2016, half of the snow cover disappeared in the beginning of May almost simultaneously across the research sites (see the Supplement). We also avoided the trees with deer damage from the observation. We observed the bud burst more than twice a week from April to early June in 2016 and 2017. In the beginning of April, the snow depth was about 1.6 m and 1.2 m in 2016 and 2017 respectively. At the beginning of the observation, 9 individuals of *A. mono* and 16 individuals of *Q. crispula.*were buried under snow. We defined the day of bud burst of an individual when more than half of the buds of the crown of the individual started to open (cf. Augspurger 2009). To see the bud burst of canopy trees appropriately by using binoculars, we used ladders to be close to the canopy for large individuals (four individuals of *A. mono* and nine individuals for *Q crispula*, the heights of which were approximately over 15 m, were often difficult to see without ladders).

Temperature measurement and evaluation of degree-days

From 4th April to 26th May in 2016 and 3rd April to 6th June 2017, the air or snow temperature was monitored with thermometers (Thermo Recorder Mini RT-30S, Espec, Japan) at three heights at the site: ground surface (height = 0.1 m above the ground surface), middle layer (height = 7.5 m above the ground surface), and canopy layer (height = 15 m above the ground surface). We hanged the thermometers on the branch by using rope. All the thermometers were placed not near the trunk of trees (about three meters away from the trunk). Furthermore, each thermometer had the shield to avoid the effect of sunshine. At each height, the temperature was recorded once every hour, and the daily mean temperature was calculated (Fig. 1). Degree-day models are often used to quantify advances in phenological events such as bud bursts (Murray et al. 1989). The temperature data obtained at the ground surface were used to calculate the degree-days for seedlings less than 1.9 m in height because the stems of these seedlings were bent under snow due to the precipitation pressure of snow, and after snowmelt they kept bending for approximately a few days at our study site. The data obtained at the middle layer were used for saplings (1.9 m < height ≦ 5 m) and juvenile trees (5 m < height ≦ 10 m), and the data from the canopy layer were used for the canopy trees (10 m < height). We calculated the degree-days until the bud burst day as follows:

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

where DD_x was the value of degree-days with the threshold of x °C (here, the threshold was set at 5 °C as in the previous study, Clark et al. (2014)) for the daily mean temperature. We used t_0 as the initial day to calculate degree-days when a daily mean temperature firstly reached the threshold (> 5 °C). For instance, in 2016, t_0 was DOY (day of the year) 127 at the ground surface (which was used for the calculation of seedlings less than 1.9 m), and DOY 98 at the middle and canopy layer (Fig. 1). Here, *n* was the day of bud burst of an individual. The daily mean temperature of DOY *m* was defined by t_m. When t_m was below 5°C, the data was 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 reached above 0 °C, which was DOY 125 in 2016 and DOY 115 in 2017 respectively.

Statistics

The relations between the degree-days or bud burstrea day (DOY) and tree height were evaluated with Spearman's rank correlation coefficients (ρ). When the *p*-value of the correlation was less than 0.05, we judged the relationship to be significant. All statistical analysis was conducted by using the R software, version 3.3.1 (R Development Core Team 2016).

Results

The degree-days for bud burst showed a positive relationship with tree height for both *A. mono* (Fig. 2a) and *Q. crispula* (Fig. 2b, d), while the relationship was not statistically significant for *A. mono* in 2017 (Fig. 2c). Overall, *Q. crispula* required more degree-days for bud burst as compared to *A. mono* (Fig. 2)

Conversely, there was a negative relationship between the day of bud burst and tree height in both *A. mono* (Fig. 3a) and *Q. crispula* (Fig. 3b, d), while the relationship was not statistically significant for *A. mono* in 2017 (Fig. 3c). Overall, *Q. crispula* showed later bud burst timing as compared to *A. mono* (Fig. 3).

Discussion

The positive relationships between degree-days for bud burst and tree height (Fig. 2) are consistent with the findings of previous studies, which reported that the degree-days required for bud burst had an ontogenetic variation along with the tree height and were smaller in seedlings than in large trees (Augspurger and Bartlett 2003; Vitasse 2013). Conversely, there were negative relationships between the day of bud burst and tree height for both species (Fig. 3). These results support our hypothesis that the bud burst timing is not always earlier for smaller trees, although a later bud burst is disadvantageous for smaller trees to intercept light in the forest understory. Seiwa (1999a) reported that the bud burst of *A. mono* started from seedlings and then proceeded to large trees in temperate forests in northern Japan with snow cover. The present study and Seiwa (1999a) investigated the same species in Hokkaido region. The major differences between the two studies were the snow depth and the snowmelt timing. At our study sites, the maximum snow depth reached approximately 1.6 m, and the snow had melted by early May. In southern Hokkaido, where Seiwa (1999a) conducted the research, the snow depth was approximately 60 cm (the data of Shintoku Meteorological Station, Japan Meteorological Agency 2020), and the snowmelt ended between late March and early April when the study was conducted. Accordingly, there was a large difference in the rate of increasing air temperature among the three heights (especially between the temperature at forest floor and those at upper two heights) at the stands in this study (Fig. 1). A previous study by Maruyama (1979), which shows that the leaf expansion of smaller trees is later than that of larger trees, was also conducted in a heavily snowy temperate forest. Furthermore, based on an intensive literature survey, Osada and Hiura (2019) found that that bud burst occurred earlier in the saplings of most species at sites with less snowfall, whereas budburst occurred earlier in trees at sites with heavy snowfall. Together with our study, these results indicate that the later bud burst of smaller trees compared to larger trees is the result of the plastic response to the temperature regime of the forest floor caused by snow cover, which commonly occurs in snowy temperate forests.

Warm temperatures enough to activate bud occurred later at the ground surface as compared to the middle and canopy layers because the remaining snow cover became less than 50 % at the ground surface around DOY 125 (Supplement). Even after snowmelt, the temperature at the ground surface would be retarded due to the dense dwarf bamboo preventing air circulation and shading the ground surface in northern Hokkaido (Takahashi et al. 2003). These mechanisms suggest that the degree-days at the ground surface accumulated slowly, and the seedlings under snow cover required a longer period for bud burst.

Our results suggest that the height-dependent phenology of bud burst in heavily snowy (1.6 m in the maximum depth) temperate forests differs from those in less snowfall temperate regions (ca 0.5 m in the maximum depth) in Japan and Switzerland (e.g., Seiwa 1999a; Vitasse 2013). Earlier bud-burst of seedlings is beneficial to increase the light capturing, while it is disadvantageous to increase the risk of frost damage (Sakai and Larcher 1987; Seiwa 1999a; Vitasse et al. 2014). In the forest floors with deep snowpack, the establishment and survival of seedlings are known to be difficult (Wada 1993), suggesting that the late bud burst timing of seedlings, which was observed in the present study, might be disadvantageous for their survival. We should be careful about the fact that the degree-days were calculated based on the three height classes for trees of continuous heights. Even within the trees smaller than 1.9 m, relatively larger seedlings were exposed to the atmosphere earlier than the time when the temperature logger at 10 cm were supposed to be exposed to the atmosphere. However, based on our field observation, the difference between the two timings were assumed to be few days. The relatively short difference between the two timings was partly because the snow melted drastically around the snow disappearance date (DOY 116 in 2016, see Supplementary figure

1). Furthermore, before the snow disappearance date (DOY 125 in 2016 and 115 in 2017), the mean daily temperature did not exceed 5 ºC (threshold temperature to calculate degree-days) at all three height, which indicate that the results of the calculation of degree-days do not change even by considering the earlier exposure of relatively larger seedlings by a few days to the temperature similar at middle height. In the future study, by knowing the exact temperature to which each tree was exposed (e.g. by hanging small temperature logger to the canopy of each tree), the clearer relationship between the tree height and degree-days might be shown. It should be further noted that there was large year-to-year variation in the statistical significance of the relationship between the degree-days for bud burst and tree height for *A. mono* (Fig. 2). Furthermore, while the less degree-days are needed for the smaller trees for their bud-burst than larger trees, it is interesting to see the large variation of thermal requirement among small trees. Some seedlings required larger thermal requirement than that of large trees and the bud-burst timing of some seedlings overlapped with that of upper trees. Underlying mechanisms to cause these variations should be clarified in the future study.

Ongoing and predicted winter climate change and the coincidental advance of snowmelt timing (Makoto et al. 2014) could modify the phenology of deciduous trees differently depending on the tree height in northern Japan with heavy snowfall. In future studies, climate change studies (e.g., snow manipulation) with a special reference to height dependency and with detailed measurements of the vertical temperature gradient should be conducted for the accurate prediction of the forest vertical structure, which matters for the maintenance of biodiversity in forest ecosystem (Ishii et al. 2004).

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Legends for figures

Figure 1

Daily mean temperature at three different heights in the studied forest from April to May in 2016 and 2017; ground surface (height = 0.1m, black circle), middle layer (height = 7.5m, black triangle), canopy layer (height = 15m, open circle). The lines of middle layer and canopy layer often overlapped throughout the research periods.

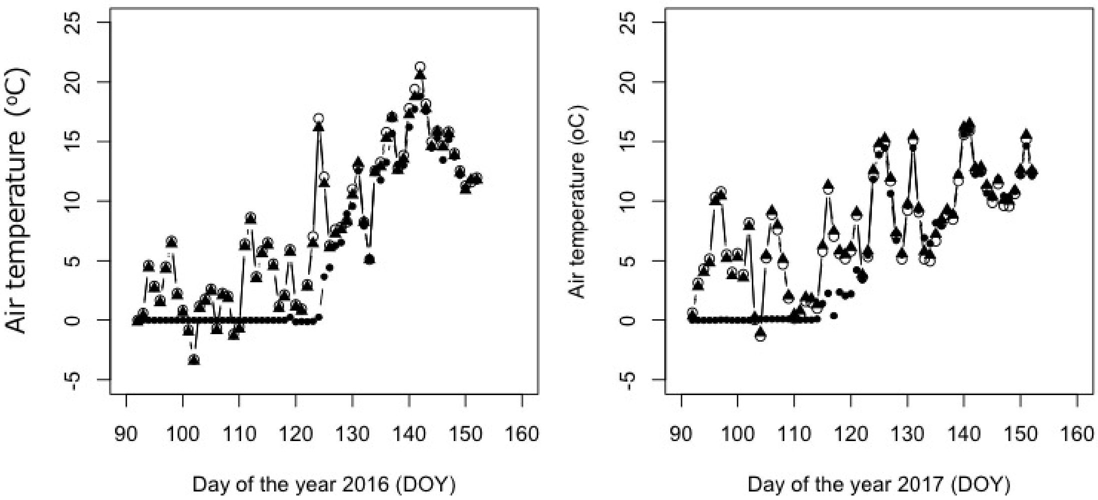
Figure 2

The relationship between tree height and degree-days until bud burst of *Acer mono* in 2016 (a) and 2017 (c) and *Quercus crispula* in 2016 (b) and 2017 (d). The tree individuals smaller than the dot line in each figure are those buried under snow. Correlation coefficient (ρ) and the significance (p) was determined by Spearman's rank correlation. "n.s." was shown when the correlation was statistically not significant ($p \geqq 0.05$).

Figure 3

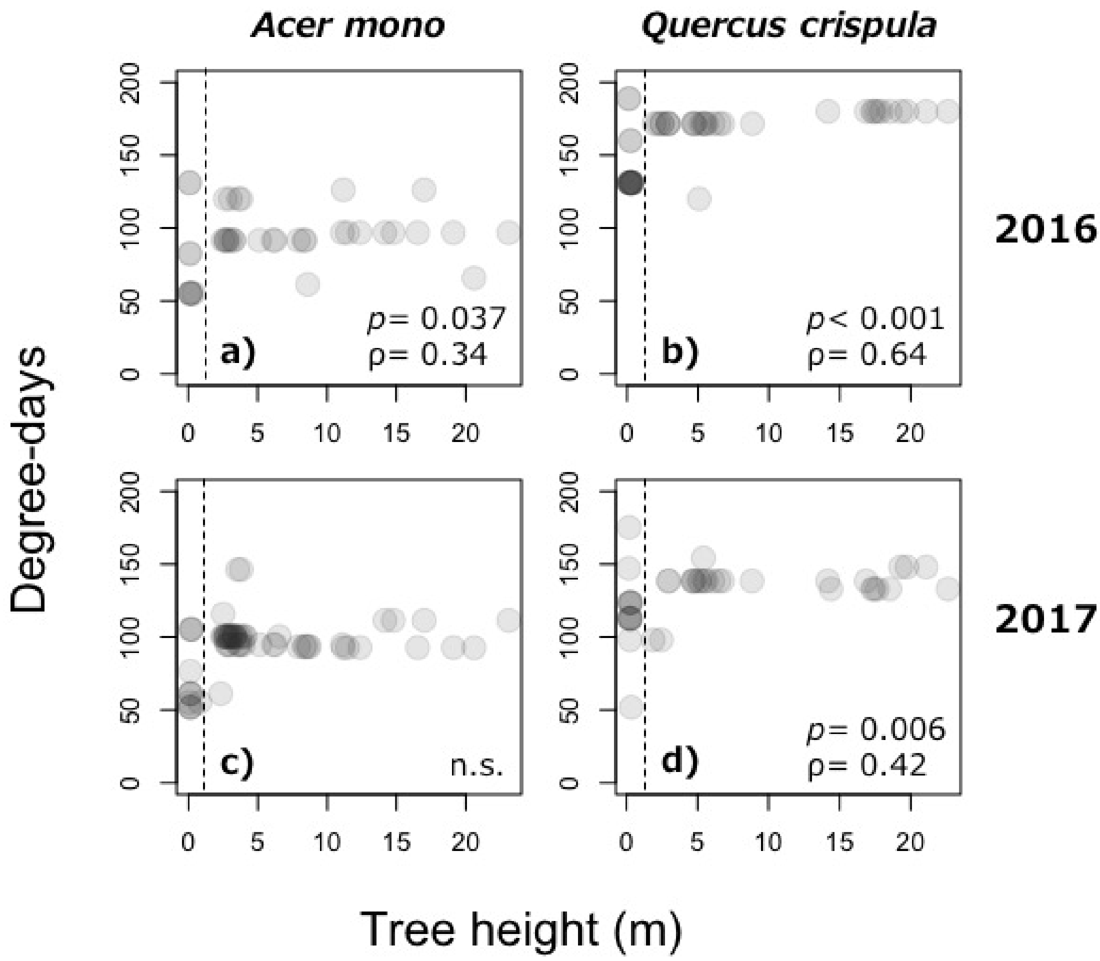
The relationship between tree height and the day of bud burst of *Acer mono* in 2016 (a) and 2017 (c) and *Quercus crispula* in 2016 (b) and 2017 (d). The tree individuals smaller than the dot line in each figure are those buried under snow. Correlation coefficient (ρ) and the significance (p) was determined by Spearman's rank correlation. "n.s." was shown when the correlation was statistically not significant ($p \geqq 0.05$).

Figure 1



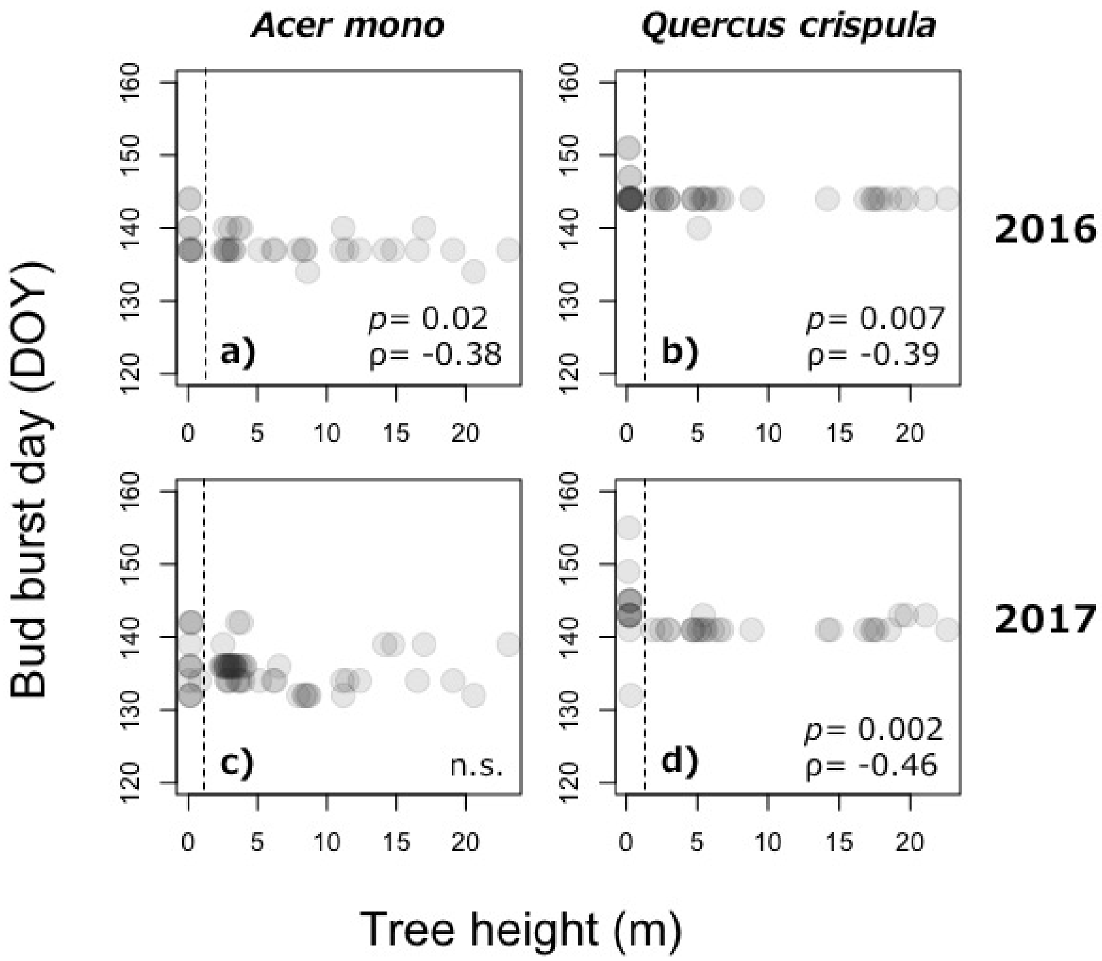
Air temperature (°C)
25
20
15
10
5
0
-5
90
100
110
120
130
140
150
160
Day of the year 2016 (DOY)
Air temperature (oC)
25
20
15
10
5
0
-5
90
100
110
120
130
140
150
160
Day of the year 2017 (DOY)

Figure 2



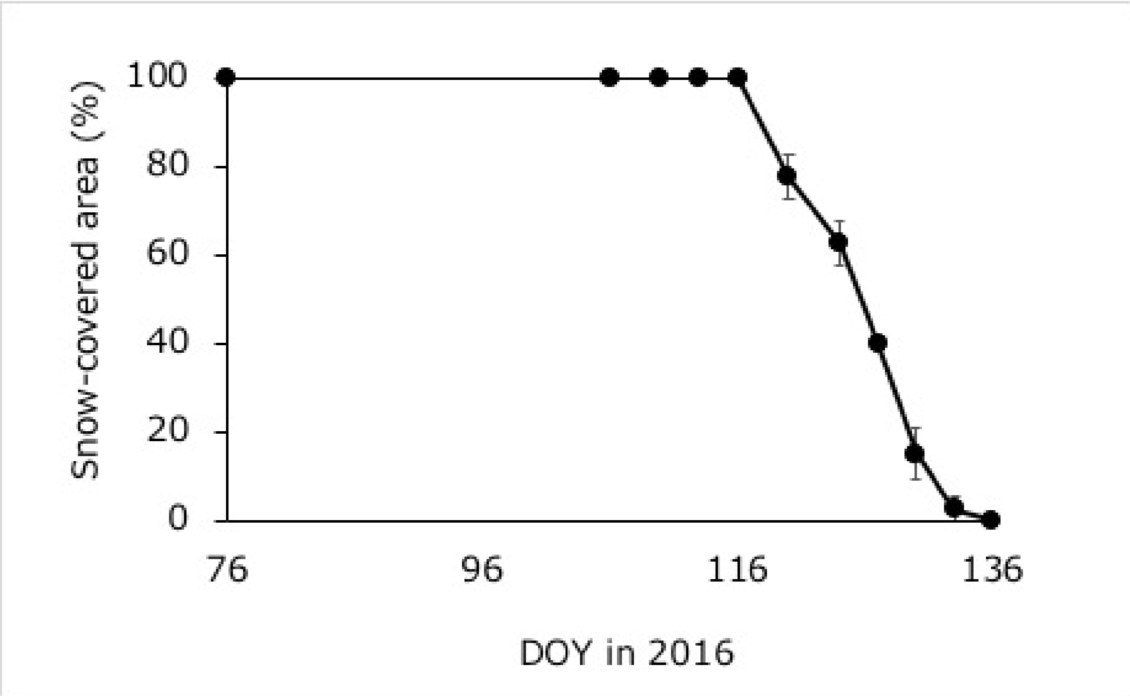
Acer mono
Quercus crispula
2016
2017
Degree-days
Tree height (m)
p= 0.037
ρ= 0.34
a)
p< 0.001
ρ= 0.64
b)
c)
n.s.
p= 0.006
ρ= 0.42
d)
0
50
100
150
200
0
5
10
15
20

Figure 3


Acer mono
Quercus crispula
2016
2017
Bud burst day (DOY)
Tree height (m)
a)
p= 0.02
ρ= -0.38
b)
p= 0.007
ρ= -0.39
c)
n.s.
d)
p= 0.002
ρ= -0.46

Supplementary figure 1:

Spring snow-cover dynamics in the research site in 2016.



Snow-covered area is the relative area within each plot, which is identified visibly. Data in each date is the average of the four plots (the size of each plot is 10 m by 10 m). The error bar is SD of four plots.