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Intra-annual dynamics of cambial and xylem phenology in subalpine conifers at Deogyusan National Park in the Republic of Korea

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Abstract

Subalpine conifers are highly sensitive to climatic changes. In these trees, the intra-annual dynamics of cambial activity and phenological process in xylem development are closely associated with climatic conditions. However, these scientific findings have not been verified for subalpine conifers in the Republic of Korea. Therefore, we initiated such a study with four subalpine conifers, viz. *Abies koreana*, *Pinus koraiensis*, *Taxus cuspidata*, and *Picea jezoensis*, growing between 1573 and 1594 m a.s.l. at Deogyusan National Park. Microcores (Ø 2 mm) of these trees were obtained using a mini borer, called as Trephor, every week between April 7 and September 25 in 2017 to monitor their growing seasons, the intra-annual dynamics of the cambial activity, and the number of cells during phenological phases of cell enlargement and cell-wall thickening. For the study, five trees were selected for each conifer species. Results showed that the cambial activity of *A. koreana*, *P. koraiensis*, and *P. jezoensis* required at least 73.8 heat-sum values, whereas the *T. cuspidata* needed 109.6 heat-sum. The durations of cambial activity of *A. koreana*, *P. koraiensis*, *T. cuspidata*, and *P. jezoensis* were 134 (127–144), 113 (92–128), 113 (106–120), and 100 (76–128) days, respectively. The intra-annual variations of the number of cells in the cambium, during the cell enlargement phase and cell-wall thickening phase showed predominantly a bell-shaped curve, with a delay of approximately 2–4 weeks between each other. On the other hand, the number of cumulated mature cells showed an S-shaped curve. Through this study, the first fundamental data on phenological process in xylem development of subalpine conifers in the Republic of Korea have been successfully presented.

Keywords: Cambial activity, Xylem cell development, Phenology, Subalpine conifers, Degree-days

Introduction

The total forest area in the Republic of Korea is 6383000 ha which corresponds to 64% of the total land of Korea (Korea Forest Service 2018). Furthermore, the net absorption of greenhouse gases due to land use, land use change and by the forestry (LULUCF) sector is 41.6 million metric tons CO₂ eq. or 5.9% of the total national emissions in 2017, with forests accounting for 99.9% of the total absorption [1]. Therefore, it can be seen that trees, the main component of forests, play the most vital

role in reducing the vast amount of carbon emissions from the atmosphere [2, 3]. However, the trees growing at high elevations and/or latitudes face mortality risk and extinction threat due to the ever-increasing global warming and drought risks due to climatic changes [4–8].

Subalpine forest, with harsh conditions for tree growth [9, 10], serves as an ecotone between mixed deciduous forest and alpine vegetation communities [11]. In the Republic of Korea, the subalpine forests start from 800 to 1000 m a.s.l. [12], and trees such as *Abies koreana*, *Abies nephrolepis*, *Picea jezoensis*, *Juniperus chinensis*, *Pinus pumila* and *Taxus cuspidata* dominantly occupy the forests [13–16]. Although the conifer species in the subalpine zone can grow under extreme growth conditions, these species are vulnerable to the effect of rapid climate

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change [7, 17–19]. In a recent publication [16], it has been reported that the area of conifers in the subalpine zones of the Republic of Korea had reduced by 25%, from 93.27 to 69.90 km², over the last 21 years (1994–2015).

Deogyusan, the fourth highest mountain peak (1614 m a.s.l.) of the Republic of Korea, is one of the important habitats of plants, containing 811 different plant species [20]. The Deogyusan National park serves as a habitat for subalpine conifers; however, their spread is only restricted within 3 km² [12]. Although the subalpine conifers are under the threat of extinction due to climatic change, surprisingly, only a handful of studies have been done so far on the climatic effect on their growth or growth strategy. Moreover, most of the research focused on the subalpine ecosystem [21–23].

Tree growth mainly occurs due to the activities of meristem tissues, viz. apical meristem and vascular cambium [24, 25]. The growth of shoot is induced by the former and is an externally visible phenology, whereas radial growth is due to the latter and remains hidden [26, 27]. The radial growth integrates exogenous influences as well as endogenous factors, which are archived in each annual ring [28, 29]. Unlike the annual rings, the cambial activity and xylem formation can be monitored in a short time rather than a growing season [30–33]. Based on these advantages, researchers explored the intra-annual dynamics of cambium, the xylem phenology and their growth rates to achieve a deeper insight into the tree-growth strategy depending upon climate [32, 34–37].

Trees at cold temperatures, such as subalpines, are particularly vulnerable to frost damage during winter season at the beginning and cessation of meristem tissue growth [10, 38–40]. Therefore, temperature plays an important role in activating their growth. A large volume of research [41–43] confirmed that trees growing under cold conditions can initiate cambial activity with lower heat-sum value than those in warmer environment. The heat-sum value is the amount of heat accumulated by a plant during its growth or up to its the maturity [44]. Furthermore, the trees in cold environment have a shorter growing season than those at warmer locations [45–51]. Some research groups presented that even if the growing conditions remain the same, the growing seasons do not remain the same and vary according to tree species [32, 46, 50–53]. However, these general findings, have not been verified to-date for the conifer trees in the subalpine zones of the Republic of Korea. Therefore, the present study aimed to monitor the intra-annual variations of the cambial activity and xylem phenology for some dominant subalpine conifer species (*Abies koreana*, *Pinus koraiensis*, *Taxus cuspidata*, and *Picea jezoensis*) at the Deogyusan National Park in the Republic of Korea, which are facing the threat of disappearance due to continuous

climate change. To evaluate the influence of temperature on the initiation of their cambial activities, heat-sum values, the so-called degree-days, were applied. The results are expected to serve as fundamental data to evaluate the growth conditions of subalpine conifer tree species under climate change as well as to understand their growth phenology at the cellular level.

Materials and methods

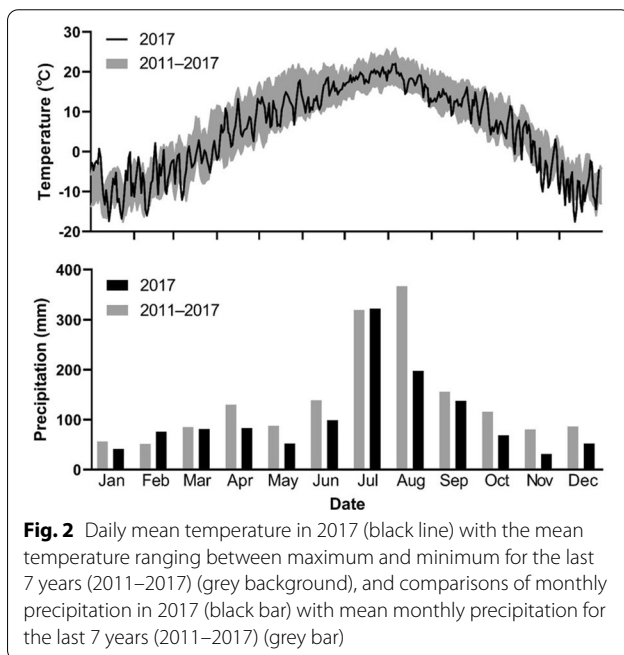
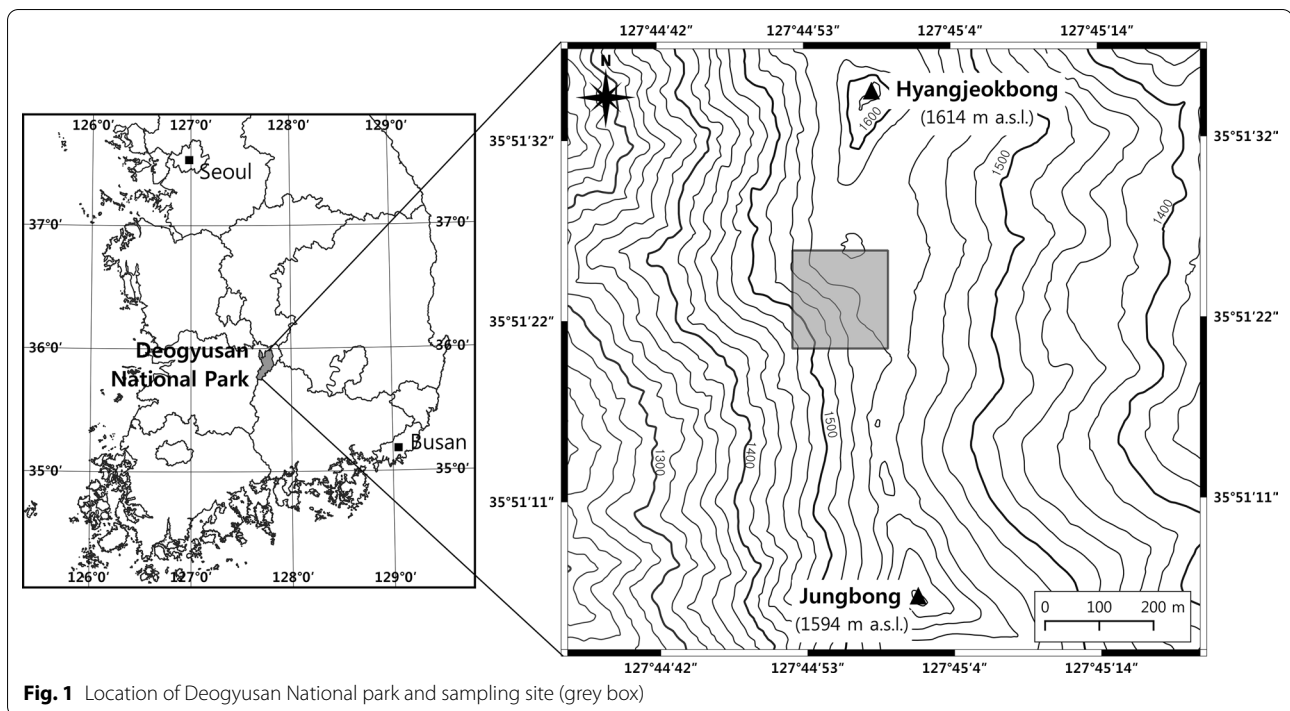
Study sites and tree species

The study site was chosen between the peaks of the Hyangjeokbong (1614 m a.s.l.) and Jungbong (1594 m a.s.l.) in Deogyusan National Park (35°51'N, 127°44'E) (Fig. 1). The natural vegetation between the Hyangjeokbong and Jungbong peaks consists of *Quercus mongolica*, *Pinus koraiensis*, *Taxus cuspidata*, *Abies koreana*, and *Rhododendron schlippenbachii*. Among these, the tree species older than 100 years are *Taxus cuspidata* and *Abies koreana* at Hyangjeokbong [54, 55]. As recorded by a meteorological station close to the study site, the mean annual temperature and total precipitation during 2011–2017 were 5.2 °C and 1677 mm, respectively (Fig. 2). The coldest and warmest months were January (−9.6 °C) and July (17.8 °C), whereas the driest and wettest months were January (54 mm) and August (348 mm), respectively.

In the present study, four conifer tree species, viz. *Abies koreana*, *Taxus cuspidata*, *Picea jezoensis* and *Pinus koraiensis* were selected for experiments. Among these, *A. koreana*, *T. cuspidata* and *P. jezoensis* were the representative subalpine species whose habitats are higher than 1300 m a.s.l. at the Deogyusan National Park. By contrast, the primary habitat of *P. koraiensis* is between low and high altitudes (550–1500 m a.s.l.), and only a few *P. koraiensis* are distributed at the study site [13, 56]. Considering the effect of size and age of the trees on the cambial activity [31, 57], the trees were selected according to their vitality and diameter at breast height. Due to limited population of each species at the study site, only five trees were monitored and no trees of the same age were selected (Table 1). The tree ages were verified using increment cores extracted from portions of the test trees at 1.2 m from the ground after finishing micro sampling at the end of October, 2017.

Microcore sampling and preparation

Microcores were extracted from the trees weekly using a Trephor [58] between April and September in 2017. To minimize any difference between the timings of cambial activity or xylem phenology due to sampling height [59], sampling was done from the same height, 1 m from the ground. Furthermore, to avoid any wounding effect from prior sampling action, the



sampling points were kept separated by at least 2.5 cm horizontally direction in a zigzag pattern (Fig. 3a). Two microcores were weekly extracted from each tree, and a total of 1000 microcores were collected. In general, the microcores comprised the developing tree ring and 2 more previous tree rings.

Immediately after extraction, the microcores were soaked in distilled water and after coming back to the laboratory, they were stored in refrigerator at 8 °C to prevent tissue deterioration before embedding [50]. Within 1 month, all the microcores were embedded within PEG 2000 (Polyethylene glycol) [30], followed by cutting transverse planes from them using a sliding microtome (H/I Sliding Microtome, Hacker, USA) of thickness 6–12 µm (Fig. 3b). The cut sections were next stained with a mixture of safranin (1%) and astra blue (0.5%) [49, 59–61] to visibly observe the cambium and the developing xylem cells under light microscope (Fig. 3c).

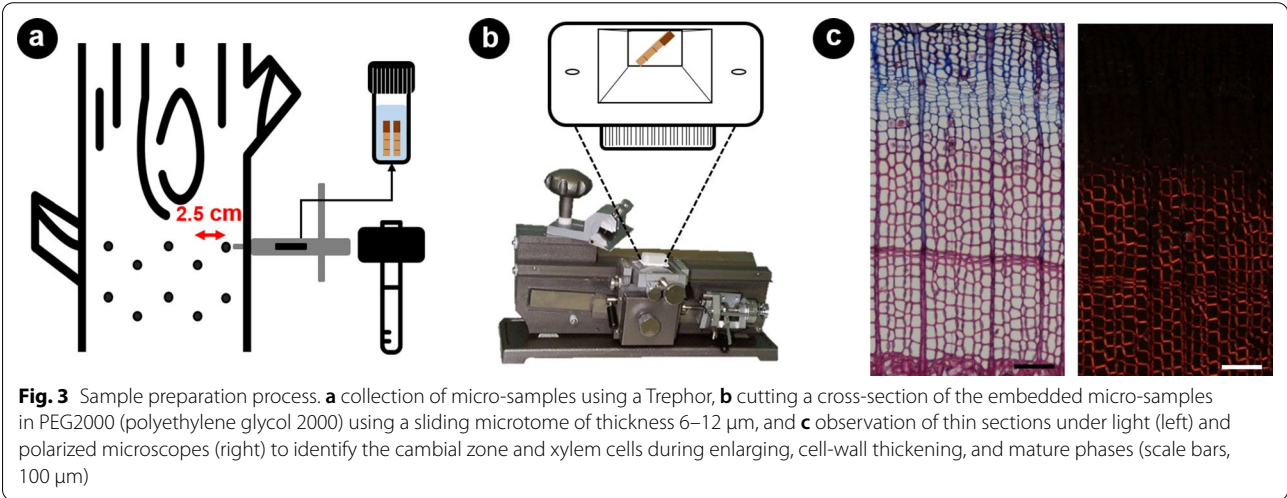
Microscopic observation

The cambial cells and the developing xylem cells were examined under a light and/or a polarized light microscope to observe the criteria reported in literature [30, 36, 37, 52, 62]. A cambial cell has a primary wall and a small radial diameter. Therefore, these cells were blue stained by astra blue due to absence of lignin in the primary wall (Fig. 4). On the other hand, the xylem cells have much larger radial diameter than the cambial cells during their enlargement stage, and possess only primary wall; so, they can be easily distorted and blue stained with astra blue. However, during the cell-wall thickening phase, the xylem cells thicken slightly and the walls become stiffer due to development of secondary walls. These characteristics can be easily observed as purple under light microscope and slightly glistened

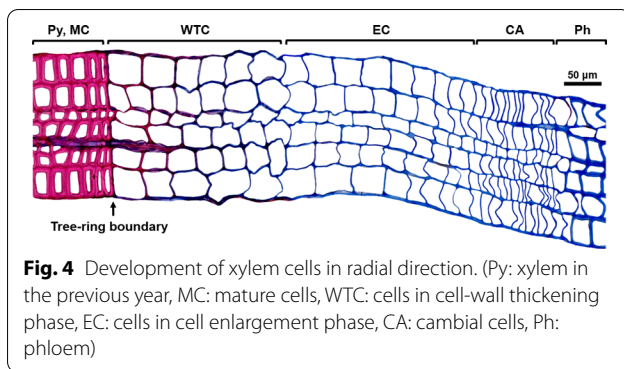
Table 1 Detailed information of the experimental trees

Tree species	ID	DBH (cm)	Altitude (m a.s.l.)	Latitude	Longitude	Tree age (year)	Pith
<i>Abies koreana</i>	AK01	26	1585	35°51'25.8"	127°44'44.8"	47	–
	AK02	16	1587	35°51'25.8"	127°44'45.4"	77	P
	AK03	20	1585	35°51'25.7"	127°44'45.4"	48	nP
	AK04	29	1588	35°51'26.1"	127°44'46.1"	41	–
	AK05	16	1594	35°51'26.8"	127°44'46.4"	40	–
<i>Pinus koraiensis</i>	PK01	22	1581	35°51'25.7"	127°44'47.1"	42	nP
	PK02	19	1589	35°51'26.2"	127°44'46.4"	58	P
	PK03	26	1584	35°51'25.8"	127°44'46.7"	49	–
	PK04	25	1582	35°51'25.8"	127°44'46.0"	41	–
	PK05	27	1587	35°51'26.3"	127°44'47.0"	60	–
<i>Taxus cuspidata</i>	TC01	55	1579	35°51'25.5"	127°44'47.4"	190	nP
	TC02	43	1577	35°51'24.9"	127°44'47.4"	96	nP
	TC03	20	1573	35°51'24.8"	127°44'47.6"	201	–
	TC04	33	1582	35°51'25.9"	127°44'47.0"	173	–
	TC05	21	1583	35°51'25.8"	127°44'46.6"	117	–
<i>Picea jezoensis</i>	PJ01	16	1590	35°51'26.3"	127°44'46.6"	82	P
	PJ02	26	1577	35°51'25.8"	127°44'46.4"	48	P
	PJ03	42	1573	35°51'25.8"	127°44'44.8"	165	–
	PJ04	34	1582	35°51'25.8"	127°44'44.6"	138	–
	PJ05	34	1583	35°51'25.8"	127°44'44.8"	145	nP

DBH: diameter at breast height, a.s.l.: above sea level, P: pith, nP: near pith



under polarized light microscope due to crystalline cellulose microfibrils with biaxial anisotropic structure in the secondary wall [63]. The mature cells are distinctly glistened under a polarized light microscope and normally appear red when stained by safranin, which stains the lignin content [64] formed on complete lignification in the secondary walls. During each developmental phase, the cells were counted every week along five radial files [36, 45, 65]. In the current study, the day of a year (DOY) for the initiation of cambial activity was set when an enlarging cell was first observed in the cross-section under light microscope. The cessation of cambial activity was marked when no more cell division in the cambial zone was observed and the youngest xylem cells start cell-wall thickening phase.



Heat sum

Heat sum, the so-called degree-days (hereafter d.d.), was calculated using the Sarvas model [66], as shown in Eq. 1:

$$d.d. = \sum_{i=j}^{365} (T_{\text{Diff}})_i \quad (1)$$

$$T_{\text{Diff}} = \begin{cases} T_i - 5 & \text{for } T_i > 5 \\ 0 & \text{otherwise} \end{cases}$$

where d.d. is the sum of T_{Diff} , i.e., the sum of the differences between the daily mean temperature (T_i) and the threshold of $+5^\circ\text{C}$; j is the day of year (DOY) when the mean daily temperature is greater than or equal to the threshold for at least five consecutive days [41].

Results and discussion

Effects of degree-day (d.d.) on triggering the cambial activity

Among the experimental tree species, *A. koreana* and *P. koraiensis* initiated the cambial activity between beginning and middle of May (DOY 124–132), *T. cuspidata* in the middle of May (DOY 132) and *P. jezoensis* between

beginning and end of May (DOY 124–146) (Table 2). Based on these observations, it was verified that *A. koreana* (three in five trees), *P. koraiensis* (one in five trees), and *P. jezoensis* (one in five trees) required at least 73.8 d.d. to trigger the cambial activity and *T. cuspidata* (all five trees) 109.6 d.d. (Table 2). To completely start the cambial activity in all the trees of each species, 109.6 d.d. was required for *A. koreana*, *P. koraiensis* and *T. cuspidata*, and 191.2 d.d. for *P. jezoensis* (Table 2).

The cambium cells are vulnerable meristematic tissues under cold condition [39]. Therefore, cambium cell division in the subalpine zones starts later than the trees at low elevations [33, 48, 67]. Prior studies stated that in the Republic of Korea [50, 52, 60], conifer trees, such as *Chamaecyparis pisifera*, *Pinus koraiensis* and *Pinus densiflora*, growing under 600 m a.s.l. at latitudes between $36^\circ30'$ and $37^\circ88'$ begin cell division between middle of March and middle of April. This is almost half a month or one and a half month earlier than the first cambial activities of the subalpine conifers (*A. koreana*, *P. koraiensis* and *P. jezoensis*) used in our study. The cambial activity in *T. cuspidata* begins around one or 2 months later than the conifers at low elevations (Table 2). By comparing with the previous studies, we verified in the present work that a time lag exists between the cambial activities in conifers of subalpine and low altitudes. To improve our understanding of the time lag effect according to altitudes, trees at different altitudes but of the same species were studied. Additionally, tree age was also considered, because it was reported that cambial activity starts later in conifers (*Larix decidua*, *Pinus cembra* and *Picea abies*) older than 200 years at the Alpine timber line than in the same tree species of age 50–80 years [31].

There is only one publication from Korea on the effect of d.d. on cambial activity [50], which reported that 3 of 3 *P. koraiensis* and 5 of 6 *C. pisifera*, located at

Table 2 Day of a year (DOY) for initiation of cambial activity and the corresponding degree-days (d.d.) for *Abies koreana* (AK), *Pinus koraiensis* (PK), *Taxus cuspidata* (TC), and *Picea jezoensis* (PJ) in 2017

ID	AK01	AK02	AK03	AK04	AK05	Mean
DOY	124	132	124	132	124	127
d.d	73.8	109.6	73.8	109.6	73.8	88.1
ID	PK01	PK02	PK03	PK04	PK05	Mean
DOY	124	132	132	132	132	130
d.d	73.8	109.6	109.6	109.6	109.6	102.4
ID	TC01	TC02	TC03	TC04	TC05	Mean
DOY	132	132	132	132	132	132
d.d	109.6	109.6	109.6	109.6	109.6	109.6
ID	PJ01	PJ02	PJ03	PJ04	PJ05	Mean
DOY	132	124	141	132	146	135
d.d	109.6	73.8	160.2	109.6	191.2	128.9

the center of the Republic of Korea (N36°50', E128°03', 520–550 m a.s.l.), initiated the cambial activity between 134 d.d. and 200 d.d, respectively. This indicates that *A. koreana*, *P. koraiensis* and *T. cuspidata* in the sub-alpine require lower d.d. to trigger the cambial activity than those at lower altitudes (Table 2). The trees growing in cold environment must complete all its growth processes within a restricted growing season to survive the winter [41] and it is essential that they adapt to the low winter temperature. Although three out of five *P. jezoensis* initiated the cambial activity at lower d.d. than those at lower altitudes, the other two trees initiated it at higher d.d.. Therefore, to trigger the cambial activity, *P. jezoensis* required a higher d.d. than *A. koreana*, *P. koraiensis* and *T. cuspidata* even at the same altitudes. To confirm this result, the dependence of cambial activity on the age of *P. jezoensis* has to be considered, as done in a previous study which reported that the cambial activity started later in old (200–350 yr) conifers (*Larix decidua*, *Pinus cembra* and *Picea abies*) than the adult (50–82 yr) trees [31]. In the current study, such aging effect did not seem to play any role in triggering the cambial activity of *T. cuspidata*. The variations in the initiation days of cambial activity in the subalpine conifers were smaller than the variations in the cessation days (Fig. 5). This result signified that the conifers in the subalpine have similar strategies for using temperature in triggering their cambial activity but not the cessation. In most publications, the mean daily temperatures between 4 and 6 °C are suggested as critical temperatures for cold-adapted trees [46, 68–70].

Duration of cambial activity

The durations of cambial activity (DCA) of *A. koreana*, *P. koraiensis*, *T. cuspidata*, and *P. jezoensis* were observed as 134 (127–144), 113 (92–128), 113 (106–120), and 100 (76–128) days, respectively (Fig. 6). The difference between the longest and shortest DCAs for *T. cuspidata* was 14 days, followed by *A. koreana* (17 days), *P. koraiensis* (36 days), and *P. jezoensis* (52 days).

The mean DCA of the conifer species at low altitudes in the Republic of Korea lies approximately in the range 145–210 days [50, 52, 60]. The mean DCA of the sub-alpine conifers at the Deogyusan National Park was at least 45 days shorter than that of the conifers at low altitudes. However, the mean DCA of the subalpine conifers was found to be similar to the DCAs of the conifers located higher than 1280 m a.s.l. in the north-western Himalayas in India, which is around 120–150 days [33], and at 3850 m a.s.l. in the south-eastern Tibetan Plateau in China which is around 119 days [71]. Through these comparisons, it was verified that the mean DCAs higher than ~1300 m a.s.l. were not over 150 days.

Observations under polarized light revealed that initiation of cell wall thickening in *A. koreana* and *T. cuspidata* started on DOYs 131 and 153, respectively (Fig. 5), whereas for *P. koraiensis* the DOY was between 131 and 153, and for *P. jezoensis*, the DOY was between 153 and 160. The initiation time of the cell wall thickening showed distinct differences depending upon the species. These differences are due to phenological variations in xylem cell development depending upon the tree species and tree age [31, 51, 71].

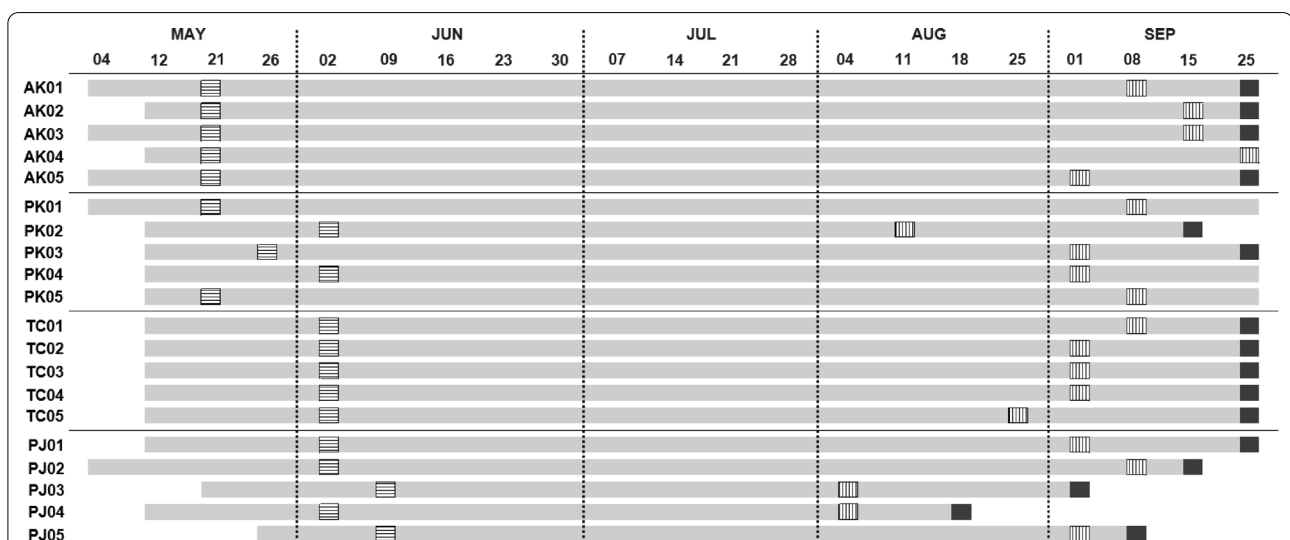
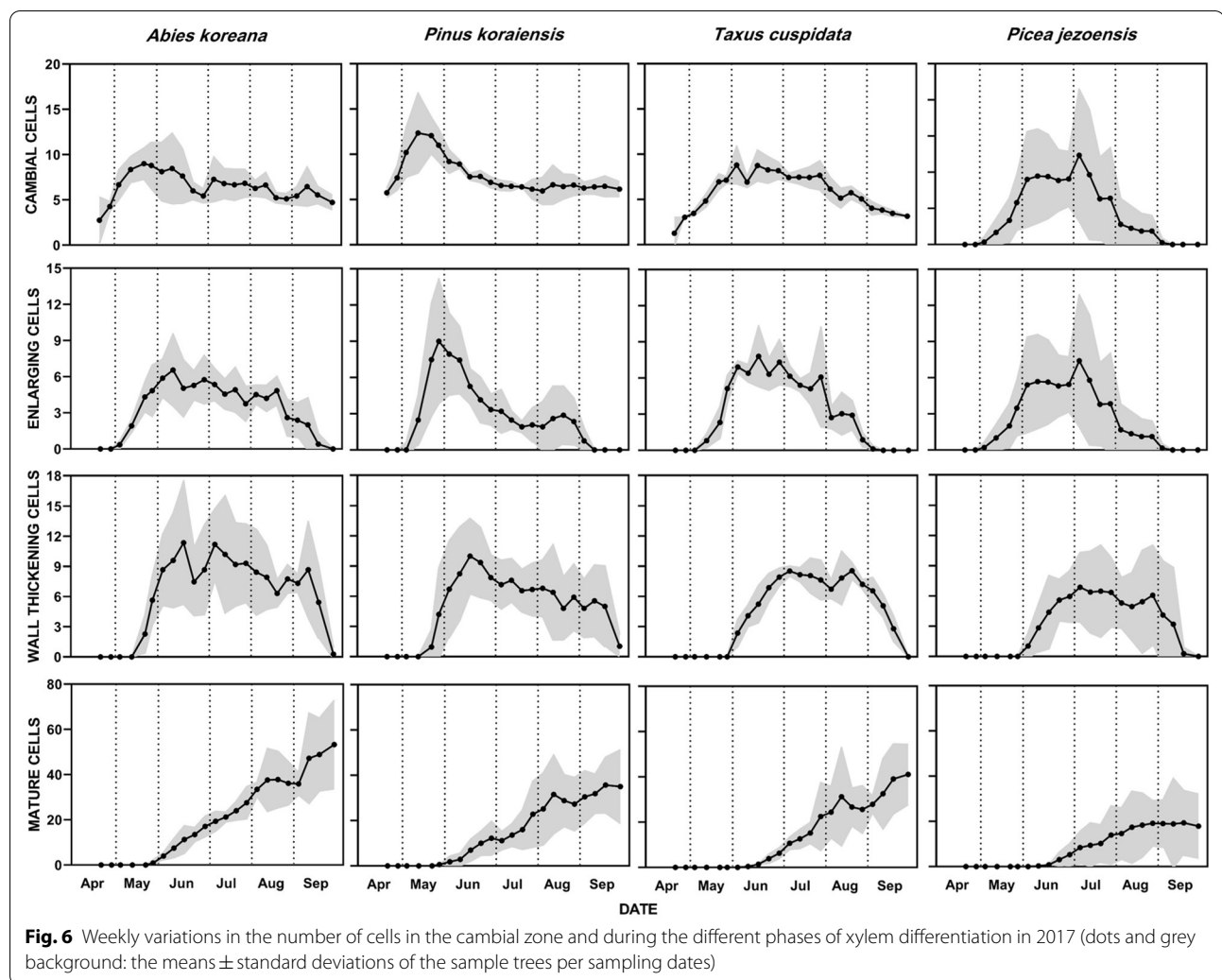


Fig. 5 Durations of cambial activity (grey bars) in *Abies koreana* (AK), *Pinus koraiensis* (PK), *Taxus cuspidata* (TC) and *Picea jezoensis* (PJ). The boxes with horizontal and vertical lines indicate when the cell-wall thickening begun the first time and the cell division ended in the cambial zone, respectively, while the black boxes indicate when cell-wall thickening ended completely



Intra-annual variations of the number of cells in the cambium and at each phenological phase in xylem development

The intra-annual variations in the number of cells in cambium, and the cells in enlargement phase and cell-wall thickening phase showed predominantly bell-shaped curves with the exception of cambial activity and cell differentiation dynamics in *P. koraiensis*, which are right skewed, with delay of approximately 2–4 weeks from each other (Fig. 6). The number of accumulated mature cells showed an S-shaped curve.

According to an earlier report [60], the initiation of cell-wall thickening in *P. densiflora* in western (E129°10'–12', 478–1005 m a.s.l.) and eastern (E126°21', 27–80 m a.s.l.) Republic of Korea was observed around 1–4 weeks later than the initiation of the cambial activity. Such restricted time delay was also reported for conifers at high altitudes [33, 48, 71].

Furthermore, the time delay between the end of cell division and cell-wall thickening, and/or lignification could be relatively larger, because increase in cell-wall thickness and lignification can occur when temperature is warm enough in autumn for xylem development [72]. Therefore, the time delay in initiations between the cambial activity and cell-wall thickening seems to rely more on a biological process than between the cessations of cambial activity and cell-wall thickening and/or lignification.

Several past studies reported that intra-annual xylem formation follows a sigmoid curve [32, 33, 36, 37, 48, 49, 53, 62, 73]. This intra-annual dynamics of wood-formation was confirmed as well in our study of coniferous tree species growing at a subalpine site in the Republic of Korea. However, due to different cambial activities along the stem circumference the number of mature xylem cells may decrease during the growing period.

Conclusions

Past studies confirmed that the area of subalpine conifers has decreased in the Republic of Korea due to climate change. To evaluate the effects of climate change on such decrease, the biological activities of the subalpine conifers were evaluated in the present study. In the current study, the first fundamental data on phenological process involved in xylem development of subalpine conifers in the Republic of Korea has been successfully presented. Based on the experimental results, our understanding on the phenological process in subalpine conifers, as well as their biological strategy to use heat sum value, the so-called degree days (d.d.), to trigger the cambial activity safely was improved. To further improve our understanding on the biological activity, studies considering age classes and altitudes are necessary. Furthermore, to obtain more reliable results, the number of sample trees should also be increased.

Abbreviations

LULUCF: land use change and by the forestry; DBH: diameter at breast height; a.s.l.: above sea level; P: pith; nP: near pith; d.d.: degree-days; DOY: day of year; DCA: duration of cambial activity; AK: *Abies koreana*; PK: *Pinus koraiensis*; TC: *Taxus cuspidata*; PJ: *Picea jezoensis*; Py: xylem in the previous year; MC: mature cells; WTC: cells in cell-wall thickening phase; EC: cells in cell enlargement phase; CA: cambial cells; Ph: phloem.

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Authors' contributions

J-HP was a major contributor to write the manuscript and perform all statistical analyses as well as design the experiment. E-BC contributed to collect samples and prepare the samples for microscopic observation. H-CP and N-YL contributed to collect samples. J-WS managed the research. All authors read and approved the final manuscript.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interest

The authors declares no conflict of interest.

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