

Article

Relationships between Wood Formation and Cambium Phenology on the Tibetan Plateau during 1960–2014

Minhui He ^{1,2,*}, Bao Yang ¹, Vladimir Shishov ^{3,4} , Sergio Rossi ^{5,6}, Achim Bräuning ², Fredrik Charpentier Ljungqvist ^{7,8}  and Jussi Grießinger ² 

¹ Key Laboratory of Desert and Desertification, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou 730000, China; yangbao@lzb.ac.cn

² Institute of Geography, University of Erlangen-Nürnberg, 91058 Erlangen, Germany; achim.braeuning@fau.de (A.B.); jussi.griessinger@fau.de (J.G.)

³ Mathematical Methods and Information Technology Department, Siberian Federal University, L. Prushinskoi Street, 2, Krasnoyarsk 660075, Russia; vlad.shishov@gmail.com

⁴ LE STUDIUM Loire Valley Institute for Advanced Studies, 1 rue Dupanloup, 45000 Orléans, France

⁵ Département des Sciences Fondamentales, Université du Québec à Chicoutimi, Chicoutimi, QC G7H 2B1, Canada; sergio_rossi@uqac.ca

⁶ Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems and Guangdong Provincial Key Laboratory of Applied Botany, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510000, China

⁷ Department of History, Stockholm University, SE-106 91 Stockholm, Sweden; fredrik.c.l@historia.su.se

⁸ Bolin Centre for Climate Research, Stockholm University, SE-106 91 Stockholm, Sweden

* Correspondence: minhuihe16@gmail.com; Tel.: +49-152-3691-7781

Received: 29 January 2018; Accepted: 9 February 2018; Published: 13 February 2018

Abstract: The variability of tree stem phenology plays a critical role in determining the productivity of forest ecosystems. Therefore, we aim to identify the relationships between the timings of cambium phenology, and forest growth in terms of tree-ring width over a long-term scale. A meta-analysis was performed that combined the timings of xylem formation, which were calculated by a tree-ring formation model of the VS (Vaganov-Shashkin)-oscilloscope during the period 1960–2014, and a tree-ring width series at 20 composite sites on the Tibetan Plateau. Both the start and length of the growing season significantly affected the formation of wood at 70% of the 20 composite sites within the study region. A wider tree ring probably resulted from an earlier start and a longer duration of the growing season. The influence of ending dates on tree-ring width was less evident, and more site-dependent. Weak relationships were identified between the start and end of the growing season at 85% of the composite sites. Compared to the monitoring results, which could only detect the relationships between cambium phenology and xylem cell production from a limited number of trees and years, our long-term relationships deepened such connections, and therefore should be used to improve mechanism models for the accurate evaluating and predicting of wood production and carbon sequestration in forest ecosystems under current and future climate change.

Keywords: xylogenesis; growing season; growth; dendroclimatology; conifers; forest ecosystems; tree-ring

1. Introduction

Forests store nearly half of the total carbon accumulated in terrestrial ecosystems [1]. One of the most relevant natural processes for carbon sequestration is wood formation [2], which is a large component of the productivity of a forest stand [3,4]. The understanding of carbon uptake and storage

in trees requires precise knowledge of when and how carbon is sequestered in the form of woody biomass [5].

Seasonal rates of wood formation are significantly influenced by the length of the growing season [6]. In contrast to primary growth (e.g., bud-burst, foliage, and shoots), secondary growth (xylem wood formation) occurs within the plants, and cannot be directly recorded by visual observations or detected by remote-sensing imagery. Presently, microcoring is the most suitable method for detecting and quantifying xylogenesis [7–9]. For example, relationships between the duration of xylogenesis and xylem production were conducted by observing anatomical sections obtained from microcores collected weekly from the stem [10]. Based on the microcoring method, the onset of xylogenesis in black spruce (*Picea mariana* (Mill.) BSP) in the boreal forest of Quebec, Canada, influenced the number of cells produced by the cambium, which in turn had an effect on the ending of cell differentiation [11]. No causal relationship was detected between the onset and ending of xylogenesis [11]. However, differences in tree radial growth in silver fir (*Abies alba* Mill.) in France resulted mainly from differences in the rate of xylem cell production, rather than from the duration of the growing season [12]. Although of great precision, this method needs much field and laboratory work, and the small sampling size limits generalization and the reliability of any long-term trends. In addition, it is more difficult and expensive to conduct such research in remote and harsh environments, such as the Tibetan Plateau (TP), the highest and largest plateau in the world, which is a region especially sensitive to climate changes. Consequently, few results have been reported from this vast region up to now [13–15], limiting our understanding of long-term responses of the cambium phenology to climate changes, and the inherent relationships between wood formation and xylogenesis over time.

Recently, a long time series (1960–2014) of xylogenesis has become available for the TP, which is based on the modification of the process-based tree-ring growth VS (Vaganov-Shashkin)-model [16], i.e., the VS-oscilloscope [17]. The model was developed to quantify tree-ring formation as a function of climate variables to the kinetics of secondary xylem development [16,17]. According to this long phenological series covering the period 1960–2014, the start and end of the growing season have been extended to earlier and later dates, respectively, resulting in a significant extension of the growing season [18]. In parallel, several studies reported increasing trends in tree radial growth in different parts of the TP [19–21]. However, wider tree rings may result from a higher cell production rate during the active growth period, as well as from an extended growing season. Questions are therefore raised on the effect of such phenological changes on tree radial growth. In particular, we would like to know whether there are inherent relationships between the start, end, and duration of the growing season, and the wood formation. Resolving these issues is crucial to thoroughly evaluate the complex dynamics of xylem cell formation, and therefore provide insights to link forest ecosystems and carbon sequestration.

The objective of this meta-analysis is to identify the relationships between the timings of cambium phenology, and growth in terms of tree-ring width. The analysis will test the hypothesis that the start and end of the growing season are correlated to each other. Other studies found that the timing of autumn senescence is affected by the timing of spring phenology in European temperate tree species [22], in northeastern United States (US) temperate forests [23] and in northern hemisphere deciduous forests [24]. In this meta-analysis, we used the timings of cambium phenology produced by the tree growth VS-oscilloscope model at 20 composite sites on the TP. Subsequently, we compared the resulting phenological time series with the respective tree-ring width chronologies during 1960–2014. This approach allows for the first time the investigation of possible relationships between cambium phenology variability and radial growth performance across a wide geographical area and over a long time scale.

2. Materials and Methods

2.1. Study Region

The study region is located on the Tibetan Plateau (TP), which has an average elevation of more than 4000 m above sea level (a.s.l.) (Figure 1). Climate conditions are dominated by the East Asian monsoon, the Indian monsoon, and the Westerlies [25]. The summer season (June–August) is normally wet and moderately warm, while winter (December–February) is generally dry and cold (Figure S1). Based on 20 weather stations in the study region, during the period 1960–2014, the mean annual temperatures ranged from -2.9 to 15.4 °C, while the annual precipitation varied between 87–1183 mm (Table S1). Compared to temperature, precipitation shows slightly lower agreement among the different weather stations (Figure S1).

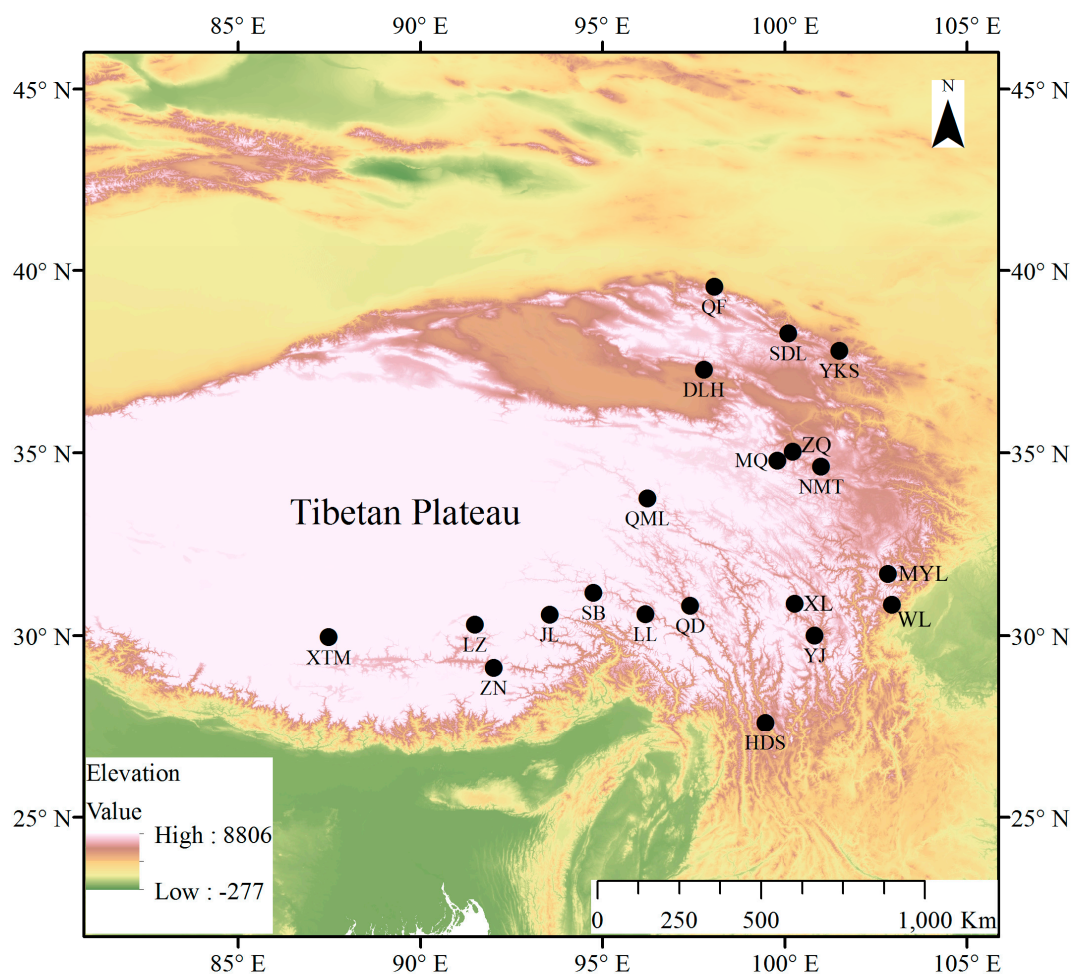


Figure 1. Study region including the 20 composite sites (centroid of the corresponding single sites) on the Tibetan Plateau (TP).

2.2. Tree-Ring Width Chronology

The sampling sites are mainly located in the eastern part of the TP (Figure 1), where the forests are naturally distributed at elevations varying between 2750–4780 m a.s.l. The main studied genus is *Juniperus*. The other genera of *Sabina*, *Cupressus*, *Tsuga*, *Picea*, and *Abies* are also included, and more detailed information (including the number of trees, coordinates, elevations, and so on) is listed in Table S2. While almost all of the tree-ring width chronologies have been published before, we re-checked the quality of all of the raw measurement data, as well as the cross-dating using

the software COFECHA [26]. Then, we developed all of the tree-ring width chronologies following standard dendrochronological practices [27] with the software ARSTAN [28]. Prior to standardization, a data adaptive power transformation was applied to reduce the potential heteroscedasticity that is commonly found in the raw ring-width measurements [29]. To remove the influences of age or other factors unrelated to climate, raw series were detrended conservatively using a negative exponential function. Tree-ring indices were then calculated as the residuals between the measured ring width and the corresponding value of the fitted curve. The detrended tree-ring series were averaged to a standard site chronology using a biweight robust estimate of the mean to minimize the influence of outliers [30]. The obtained standardized tree-ring width chronologies (TRW) were used for further analyses. During this process, we combined 50 single-site chronologies into 20 composite series, due to the co-variability of the tree-ring width records, as indicated by the high values of the inter-series correlation (R_{bar}), and expressed population signal (EPS) in Table S2.

2.3. Timings of Cambium Phenology

Tree-ring phenology data was available from Yang et al. [18], which was derived from results of the VS-oscilloscope model [17]. This model defines the climatic drivers of tree-ring growth through control on the rate and duration of cell-based processes (cell division, enlargement, and maturation) in the developing xylem. The simulated cambial growth rate is determined by using the most limiting factor to scale the component processes of tree-ring formation. This procedure can accurately capture the start (SOS) and end (EOS) of the growing season, and its length (LOS), which is calculated as the difference between the EOS and SOS. Herein, the SOS and EOS are defined as the time of first and last xylem cell differentiation, respectively. The input climate data include daily temperature and precipitation, which were selected from 20 meteorological stations nearest to the 20 composite sites for the modeling (Table S1). Based on the significant correlations between the simulated tree-ring width indices and the actual tree-ring width chronologies over their common period at each composite site ($p < 0.05$), model output of the cambium phenological data were used for the further analyses.

2.4. Statistical Analyses

Relationships between amount of wood and timings of cambium phenology were performed by Spearman correlations, because the cambium phenological data (SOS, EOS, and LOS) did not meet the conditions of normality (Figures S2–S4). Correlations at each composite site were calculated separately over their common period. A two-tailed test was used for determining the significance level. Significant correlations were presented in their respective scatter plots ($p < 0.10$). Statistical Package for the Social Sciences (SPSS) software was used for the statistical analyses.

To investigate the overall significance of the relationships across the metadata, a Fisher z -transformation [31] was used, because z -scores of transformed r follow a normal distribution under the null hypothesis of statistical independence. The inversed r -value from the Fisher z -transformation at each composite site was pooled to represent the final correlation over the TP. The transformed correlation was considered significant when both 95% confidence intervals of the distributions were either higher or lower than zero.

3. Results

3.1. Tree-Ring Width Chronologies

Due to the co-variability of the tree-ring width series and the large sample depth, the expressed population signal (criteria quantifies the degree to which an averaged time series with a limited number of samples approximates the theoretically infinite replicated time series) at each composite site reached the threshold of 0.85. Additionally, the generally high values of the inter-series correlation (R_{bar}) and signal-to-noise ratio (SNR) indicated the coherence of the chronologies. The produced tree-ring width chronologies covered the past hundreds to thousands of years (Table S2). All of the tree-ring width

series were truncated after the year 1960 for further analyses. Accordingly, 70% of the 20 composite chronologies showed significant positive trends over the studied period ($p < 0.05$).

3.2. Timings of Cambium Phenology

The start of the growing season mainly occurred in May and June (day of year (DOY) 120–180) during the period 1960–2014 in the study region (Figure S2). The accumulated frequency of SOS during DOY 120–180 ranged from 83.6% to 100% at the 20 composite sites, with a mean value of 95.9%, and a standard deviation of 4.7%. However, the SOS may also occur in early April or late July, depending on the different composite sites or in specific years. From 1960 to 2014, the SOS showed a significant advancing trend at 75% of the composite sites ($p < 0.10$). Compared to the two months (May and June) of variability for the occurrence of SOS in the whole study region, the ending dates normally focused on September and the first half of October (DOY 240–285, Figure S3). The mean accumulated frequency of the EOS during DOY 240–285 reached 94.4% in the study region. A prominent delaying trend of the EOS was observed at 80% of the study region during 1960–2014. The length of the growing season varied between 60 to 120 days at most of the composite sites (Figure S4), accounting for 80.1% of the LOS variability over the period 1960–2014. A significant extension of the LOS was detected for 80% of the 20 composite sites over their common period ($p < 0.05$). Additionally, another 10% of the composite sites passed the significance level of $0.05 < p < 0.10$, resulting in a total of 90% of the composite sites that lengthened the growing season. However, in total, a spatial pattern for the variability of the cambium phenology (including SOS, EOS, and LOS) in the whole study region could not be clearly identified, which was probably due to the different climate conditions, as well as elevations, of the sampling sites. Namely, compared to the northern region, an earlier (later, longer) SOS (EOS, LOS) is not detectable in the southern part of the TP. Similar results also apply to the relative western and eastern dominated sites of the study region.

3.3. Relationships between Cambium Phenology and Wood Formation

Significant negative Spearman correlations between SOS and TRW were found at 70% of the composite sites over the period 1960–2014 ($p < 0.10$, Figure 2). Thus, a wider tree ring was significantly correlated with an earlier date of cambium activation at 14 composite sites. However, the influence of the ending date on the formation of wood was only small and site-dependent (Figure 3). Prominent positive correlations between the EOS and TRW only occurred at 35% of the composite sites. In accordance with the absolute value of the correlation, TRW was more correlated with the SOS than the EOS, except at three (ZQ, HDS and WL) of the 20 composite sites. Furthermore, significant correlations between the LOS and TRW prevailed at 70% of the composite sites over their full investigated period (Figure 4). A narrower TRW was thus associated with a shorter LOS, and vice versa. More specifically, 94% of the significant relationships occurred in the juniper trees. Additionally, weak relationships between SOS and EOS were identified in the study region except at three composite sites (Figure 5). Thus, no specific pattern can be detected for the relationships between the start and end of the growing season over their common period 1960–2014. In total, the mean values calculated from the Fisher z -transformation and its inverse pooled r over the common period indicated that the SOS and LOS were significantly correlated with TRW, while the EOS was not prominently related with TRW and SOS in the study region (Table 1).

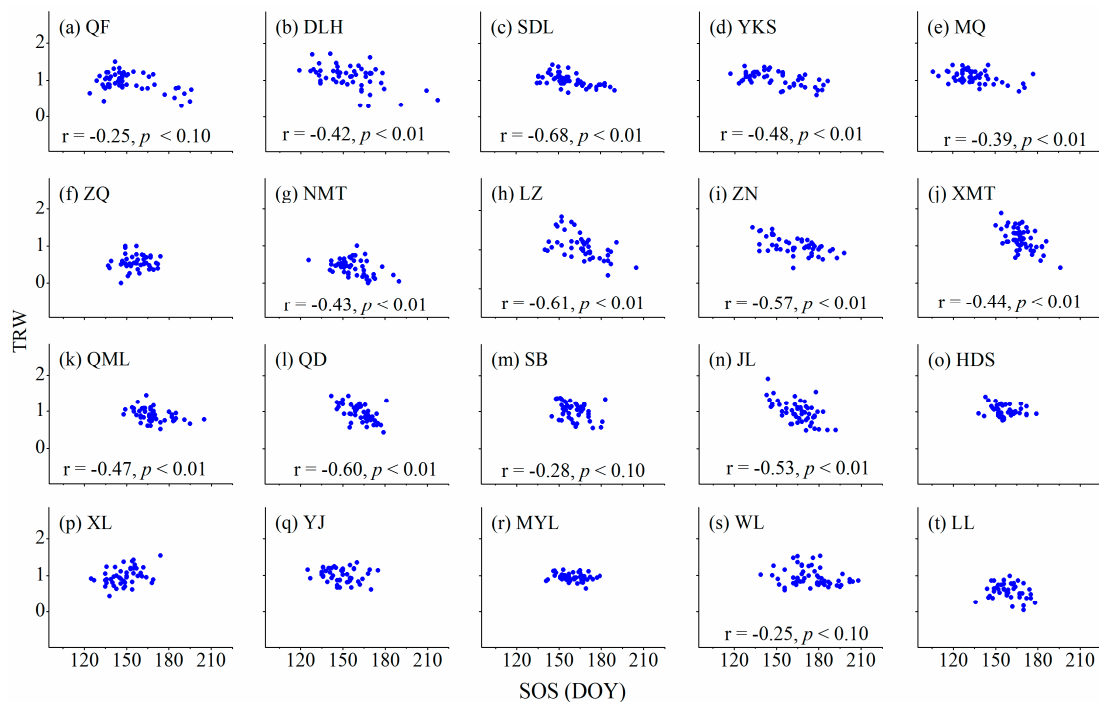


Figure 2. Scatter plots of the tree-ring width chronologies (TRW) and start of the growing season (SOS) at the 20 composite sites during 1960–2014. DOY means day of the year. Significant Spearman correlations are presented at the corresponding plots ($p < 0.10$).

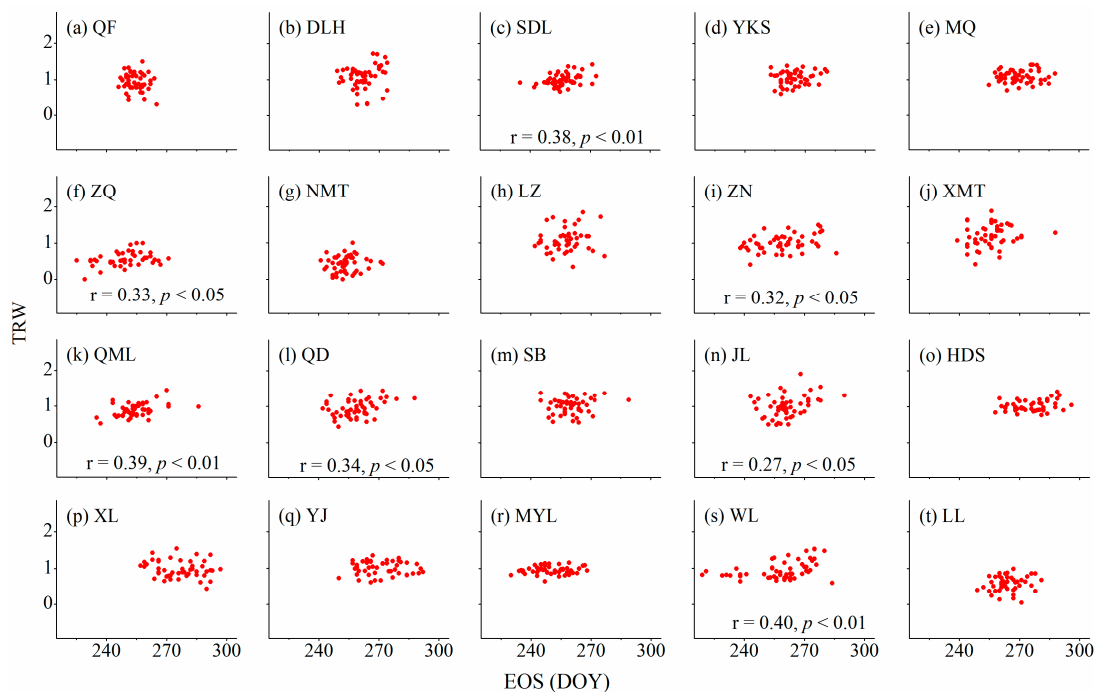


Figure 3. Relationships between the tree-ring width chronologies (TRW) and end of the growing season (EOS) at the 20 composite sites over their common period 1960–2014. DOY means day of the year. Only composite sites that reached the significance level of $p < 0.10$ are shown by their Spearman correlations.

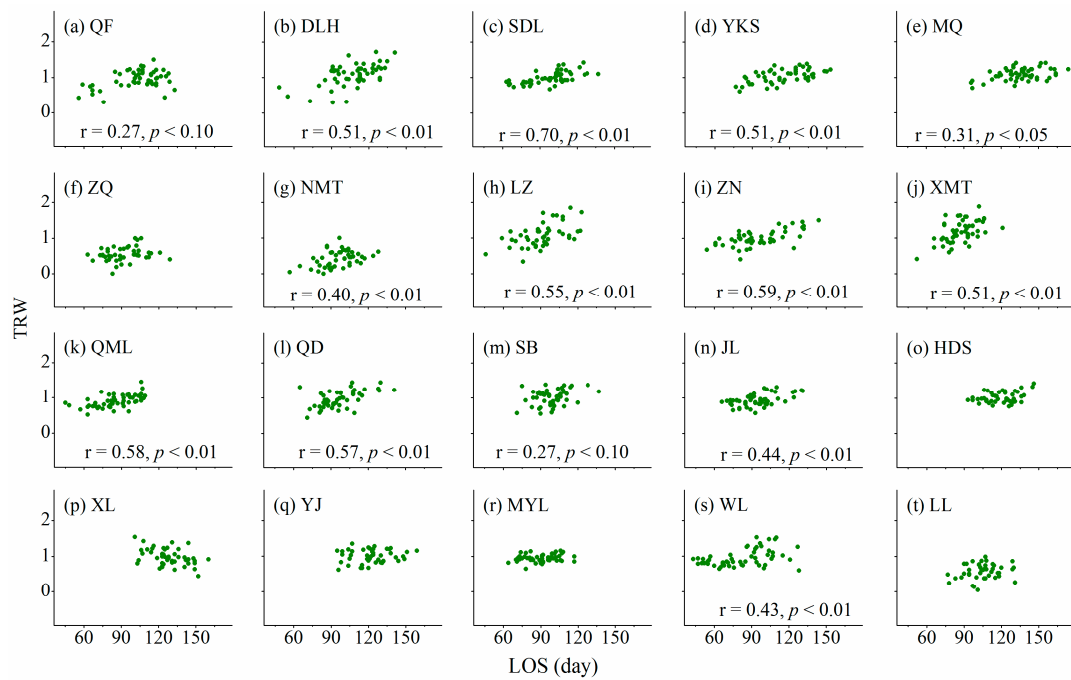


Figure 4. Scatter plots of the tree-ring width chronologies (TRW) and the length of the growing season (LOS) during 1960–2014. Significant relationships are revealed by their respective Spearman correlations ($p < 0.10$).

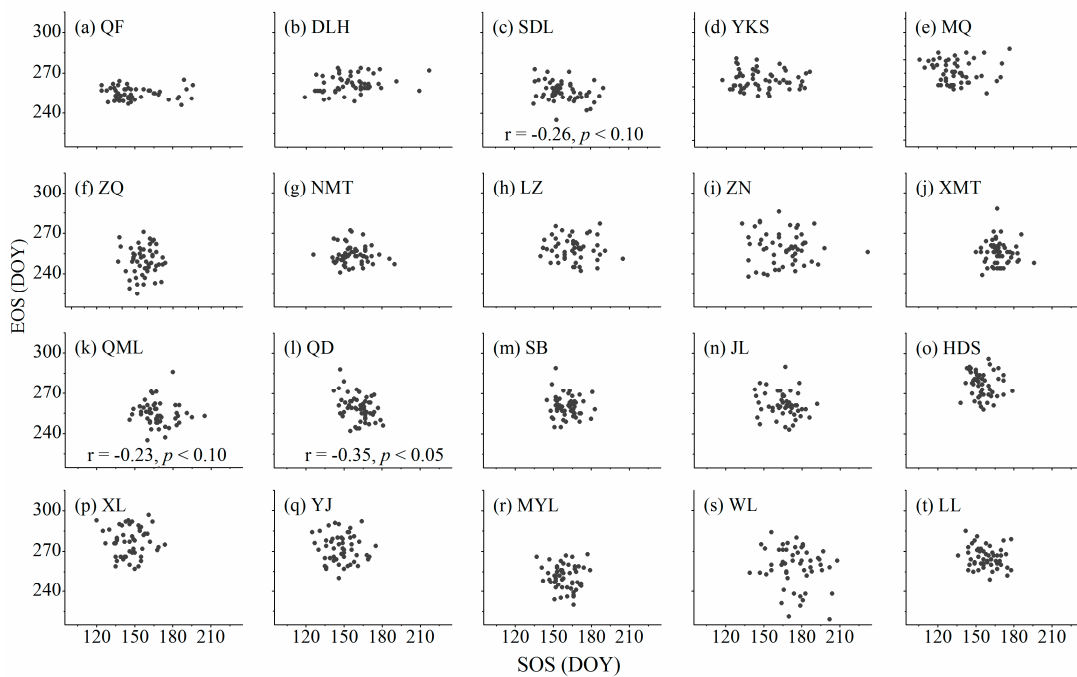


Figure 5. Scatter plots of SOS and EOS at the 20 composite sites during the period 1960–2014. Significant relationships occur in limited composite sites, as detected by their Spearman correlations.

Table 1. Mean correlations between wood formation (TRW) and cambium phenology (including the SOS, EOS, and LOS) calculated from the Fisher z-transformation and its inverse pooled r at the 20 composite sites over the common period 1960–2014 on the Tibetan Plateau (TP).

	TRW–SOS	TRW–EOS	TRW–LOS	SOS–EOS
Mean value	−0.36	0.18	0.38	−0.09
95%	−0.55	0.43	0.57	−0.34
5%	−0.08	−0.09	0.11	0.18

TRW–SOS, TRW–EOS and TRW–LOS indicate correlations between TRW and SOS, EOS as well as LOS, respectively; SOS–EOS means correlation between SOS and EOS. The 95% and 5% in the left hand column mean the upper and lower bound of the 95% confidence interval. The transformed correlation was considered significant when both 95% confidence intervals of the distributions were either higher or lower than zero.

4. Discussion

Based on the large tree sample depth at 20 composite sites from the TP, the consistent and straightforward results from our meta-analyses revealed the good applicability of our approach in the study region. Firstly, the significant correlations between the modeled results and actual tree-ring width chronologies (TRW) suggest that the model performance is robust (95% series reaches the significance level of $p < 0.01$, and the remaining 5% series is significant at the level of $p < 0.03$). Secondly, the derived phenological series are generally consistent with the available monitored results in the study region [18]. Thirdly, the regionally averaged phenological variability closely matches with the vegetation green-up series derived from remote sensing data over their common period 1982–2011, as conducted by Yang et al. [18]. Hence, in comparison to the monitoring results that could only detect connections from a limited number of trees and years [10–12], our analysis is thus able to deepen the understanding of the relationships between the stem radial growth of a tree and the start (SOS), the end (EOS), and the length (LOS) of cambial activity.

4.1. Relationships between Wood Formation and Start (Ending) of the Growing Season

The assumption that an earlier start of the growing season results in a wider tree ring is supported by the significant correlations between TRW and SOS at the majority of the composite sites in our study region (Figure 2). Additionally, we also detected significant correlations between TRW and EOS at 40% of the composite sites (Figure 3). Thus, a wider tree ring is in general associated with an earlier start and a later end of the growing season. Consistent with results applying the microcoring method during the period 1998–2011, the earlier spring phenology and later termination of cell differentiation is associated with increases in the number of cells produced in one annual growth ring in conifers [7]. Specifically, our results further reveal that the correlations between tree growth and SOS are in general higher than with EOS, at 85% of the study region, suggesting the more prominent influence of SOS on wood formation. An earlier start of the growing season would probably produce more earlywood cells, considering that the maximum daily cell production rate in conifers occurs around the summer solstice [32–34]. On the TP, monitoring results also found that the main cell production period occurs between June–July [13,35–37]. The earlywood cells account for a substantial proportion of the whole ring width in conifers, and especially in junipers [38]. The EOS is mainly relevant to the formation of latewood cells, and affects the TRW to a lesser extent. Hence, a narrow tree ring may be formed mainly due to a delayed onset of xylem formation [15]. Such a result is consistent with the intra-annual growth dynamics of the xylem in black spruce (*Picea mariana*) in the boreal forest of Quebec, Canada [11]. Consequently, although we cannot exclude the possibility that an earlier start of the growing season might be associated with an increased risk of frost damage to the cambium [39], we conclude that wood production may benefit more from the earlier dates of onset rather than the later cessation of growth in the future on the TP.

4.2. Relationships between Wood Formation and Length of Growing Season

The significant correlations between TRW and LOS suggest that a longer growing season would result in a wider tree ring in the study region (Table 1 and Figure 4). The relationship between the duration of growth and seasonal cell production has also been observed both in nature and in manipulated experiments (tree stem portion can be locally manipulated by heating with an electric heat tape, or cooling by a circulating pump that pushes cooled water through copper tubes that are wrapped around the stem). Xylem growth is positively correlated with the rate and duration of cell production, with the latter explaining most of the variability in growth in Quebec, Canada [10]. An increased duration of xylogenesis in 2003 resulted in an increased stem biomass production of *Pinus leucodermis* in southern Italy through increases in both ring width and the amount of carbon fixed in the cell walls [40]. Cooling treatments reduced the width of tree rings, and shortened the period of cambial activity in Slovenia [41]. Moreover, both the LOS and TRW show significant positive trends at the majority of the composite sites during the period 1960–2014 in the study region. Based on the long-term relationships between xylogenesis and wood formation, we expect that the extension of the growing season (induced by the warming trend) would definitely result in wider tree rings, and thus increase tree growth, forest productivity, and carbon sequestration on the TP in the future.

4.3. Relationships between Start and Ending of the Growing Season

Our hypothesis affirming that the start and end of the growing season are correlated to each other is not supported by their weak relationships during the period 1960–2014. Thus, the timing of autumn senescence is not affected by the timing of spring phenology in the stem of trees over the study region (Table 1 and Figure 5). However, previous authors found that an earlier leaf flushing resulted in an earlier senescence in two tree species of pedunculate oak (*Quercus robur* L.) and European beech (*Fagus sylvatica* L.) in Belgium [22]. The timing of autumn senescence was related to the timing of spring bud-burst by using two decades of ground and satellite-based observations of temperate deciduous forest phenology in the northeastern US [23]. A positive correlation between the SOS and EOS was detected from a satellite-observed normalized difference vegetation index over 1982–2011 in the southwestern TP [42]. Definitely, the aforementioned relationships between the SOS and EOS were derived from the primary growth of plants. Our study investigated the secondary growth of trees, and was consistent with results from four years of monitored xylogenesis in the boreal forest of Canada [11]. Long-term relationships between the SOS and EOS in the xylem in other study regions are not reported. Herein, the different physiological mechanisms of the primary and secondary growth probably result in the contrary relationships between the SOS and EOS. Additionally, different methods and various time scales from the experimental results or satellite observations may also drive some bias. We therefore expect more studies directly conducting both the primary and secondary growth of plants [43] in the future. Nevertheless, comparison of the different relationships between the start and end of the growing season provide useful information for the modification or adjusting of models, which normally use primary and secondary growth as input to assess or predict forest growth, ecosystem productivity, and carbon equilibrium at various spatial and temporal scales [44,45].

4.4. Other Factors Influencing Wood Formation

Definitely, additional other internal/plant physiological factors may affect the relationships between wood formation and the timings of cambium phenology. For example, tree-ring width is also a function of the rate of radial increment, and the size of the cells formed [16,46]. The effect of a longer growing season on the formation of wood can be biased by a decreased formation rate or reduced cell size [15,47,48]. The different allocation strategies of absorbed carbon by a tree probably result in more complex relationships between wood formation and cambium phenology [7,49]. The variability of tree-ring width is also affected by the climate conditions during previous year(s) [50–52]. Consequently, weak relationships, or the lack of relationships between wood formation and cambium phenology at

some of the composite sites is rational and coherent with our actual knowledge of tree-ring formation. Herein, it is additionally found that the significant correlations are in general consistently associated with the studied juniper trees. Interestingly, 67% of the weak relationships occurred in the other studied genera of Himalayan hemlock, spruce, and fir. However, it should be noted that compared to the juniper trees, the sample sizes for the other genera are limited. We therefore could not systematically define that the relationships between wood formation and cambium phenology are genus-specific on the TP. Investigations on more different sites and/or genera are expected to verify these relationships in the future.

5. Conclusions

In our meta-analysis, we investigated the relationships between wood formation (represented by the standardized tree-ring width chronology) and cambium phenology over the long period between 1960–2014 on the Tibetan Plateau. The results indicated that a wider tree ring is significantly related with an earlier onset, a later cessation, and a longer duration of the growing season in the xylem. Specifically, the influence of initiation on the formation of wood is more prominent than that of the cessation in the xylem. We therefore expect that in the future, wood production will benefit more from the earlier onset, rather than the later cessation. More interestingly, we detect that the timing of autumn senescence is not affected by the timing of spring phenology in the xylem, contrary to the relationships derived from the primary growth of plants. This meta-analysis therefore contributes to a more complete understanding of the growth dynamics of plant ecosystems. To check whether such relationships between cambium phenology and wood formation are specific for the TP or whether they are a more general feature, these relationships need to be tested at other locations with different types of forest and climate. If the relationships between changes in wood formation and cambial phenology are better understood, such knowledge may be useful for developing mechanistic models relating wood production and carbon storage, considering that the active cambium is the main carbon sink in a tree.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1999-4907/9/2/86/s1>, Figure S1: Averaged mean, minimum and maximum temperatures (lines with filled squares) and precipitation (gray histogram) from January to December at the 20 composite sites during the period 1960–2014, Figure S2: Frequency distributions of the start of the growing season (SOS) in the study region. DOY: day of year, Figure S3: Frequency distributions of the ending of the growing season (EOS) in the study region. DOY: day of year, Figure S4: Frequency distributions of the length of the growing season (LOS) in the study region, Table S1: Summer season temperature (including mean, minimum and maximum temperature) and accumulated precipitation at the 20 composite sites during the period 1960–2014 on the Tibetan Plateau. Data inside the bracket is the respective climate conditions in the winter season, Table S2: Tree-ring width chronology used in the study.

Acknowledgments: The authors are grateful to the editor and the two anonymous reviewers for their constructive comments. This study was supported by the National Natural Science Foundation of China (Grant No. 41325008, 41520104005). M.H. appreciates the support by the Alexander von Humboldt Foundation for supporting her research stay in the lab of A.B. V.S. was supported by the Russian Science Foundation (Grant 14-14-387 00219P), Russian Ministry of Education and Science (Project #5.3508.2017/4.6) and LE STUDIUM/Marie Skłodowska-Curie Research Fellowship.

Author Contributions: M.H. and B.Y. conceived and designed the experiments; M.H., B.Y. and V.S. performed the experiments. M.H. analyzed the data. M.H., B.Y., V.S., S.R., A.B., F.C.L., and J.G. discussed the results and implications. M.H., B.Y., V.S., S.R., A.B., F.C.L., and J.G. wrote the manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Bonan, G.B. Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science* **2008**, *320*, 1444–1449. [[CrossRef](#)] [[PubMed](#)]
2. Sass-Klaassen, U. Tree physiology: Tracking tree carbon gain. *Nat. Plants* **2015**, *1*, 15175. [[CrossRef](#)] [[PubMed](#)]

3. Anderegg, W.R.L.; Schwalm, C.; Biondi, F.; Camarero, J.J.; Koch, G.; Litvak, M.; Ogle, K.; Shaw, J.D.; Shevliakova, E.; Williams, A.P.; et al. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science* **2015**, *349*, 528–532. [[CrossRef](#)] [[PubMed](#)]
4. Zweifel, R.; Eugster, W.; Etzold, S.; Dobbertin, M.; Buchmann, N.; Hasler, R. Link between continuous stem radius changes and net ecosystem productivity of a subalpine Norway spruce forest in the Swiss Alps. *New Phytol.* **2010**, *187*, 819–830. [[CrossRef](#)] [[PubMed](#)]
5. Cuny, H.E.; Rathgeber, C.B.; Frank, D.; Fonti, P.; Makinen, H.; Prislan, P.; Rossi, S.; Del Castillo, E.M.; Campelo, F.; Vavrcik, H.; et al. Woody biomass production lags stem-girth increase by over one month in coniferous forests. *Nat. Plants* **2015**, *1*, 15160. [[CrossRef](#)] [[PubMed](#)]
6. McMillan, A.M.S.; Winston, G.C.; Goulden, M.L. Age-dependent response of boreal forest to temperature and rainfall variability. *Glob. Chang. Biol.* **2008**, *14*, 1904–1916. [[CrossRef](#)]
7. Rossi, S.; Anfodillo, T.; Čufar, K.; Cuny, H.E.; Deslauriers, A.; Fonti, P.; Frank, D.; Gričar, J.; Gruber, A.; King, G.M.; et al. A meta-analysis of cambium phenology and growth: Linear and non-linear patterns in conifers of the northern hemisphere. *Ann. Bot.* **2013**, *112*, 1911–1920. [[CrossRef](#)] [[PubMed](#)]
8. Lupi, C.; Morin, H.; Deslauriers, A.; Rossi, S. Xylogenesis in black spruce: Does soil temperature matter? *Tree Physiol.* **2012**, *32*, 74–82. [[CrossRef](#)] [[PubMed](#)]
9. Coccozza, C.; Palombo, C.; Tognetti, R.; La Porta, N.; Anichini, M.; Giovannelli, A.; Emiliani, G. Monitoring intra-annual dynamics of wood formation with microcores and dendrometers in *Picea abies* at two different altitudes. *Tree Physiol.* **2016**, *36*, 832–846. [[CrossRef](#)] [[PubMed](#)]
10. Rossi, S.; Girard, M.J.; Morin, H. Lengthening of the duration of xylogenesis engenders disproportionate increases in xylem production. *Glob. Chang. Biol.* **2014**, *20*, 2261–2271. [[CrossRef](#)] [[PubMed](#)]
11. Lupi, C.; Morin, H.; Deslauriers, A.; Rossi, S. Xylem phenology and wood production: Resolving the chicken-or-egg dilemma. *Plant Cell Environ.* **2010**, *33*, 1721–1730. [[CrossRef](#)] [[PubMed](#)]
12. Rathgeber, C.B.; Rossi, S.; Bontemps, J.D. Cambial activity related to tree size in a mature silver-fir plantation. *Ann. Bot.* **2011**, *108*, 429–438. [[CrossRef](#)] [[PubMed](#)]
13. He, M.; Yang, B.; Wang, Z.; Bräuning, A.; Pourtahmasi, K.; Oladi, R. Climatic forcing of xylem formation in Qilian juniper on the northeastern Tibetan Plateau. *Trees* **2016**, *30*, 923–933. [[CrossRef](#)]
14. Li, X.; Liang, E.; Gričar, J.; Rossi, S.; Čufar, K.; Ellison, A.M. Critical minimum temperature limits xylogenesis and maintains treelines on the southeastern Tibetan Plateau. *Sci. Bull.* **2017**, *62*, 804–812. [[CrossRef](#)]
15. Ren, P.; Rossi, S.; Gričar, J.; Liang, E.; Čufar, K. Is precipitation a trigger for the onset of xylogenesis in *Juniperus przewalskii* on the north-eastern Tibetan Plateau? *Ann. Bot.* **2015**, *115*, 629–639. [[CrossRef](#)] [[PubMed](#)]
16. Vaganov, E.; Hughes, M.; Shashkin, A. Modeling external influence on xylem development. In *Growth Dynamics of Conifer Tree Rings*; Ecological Studies (Analysis and Synthesis); Springer: Berlin/Heidelberg, Germany, 2006; Volume 183.
17. Shishov, V.V.; Tychkov, I.I.; Popkova, M.I.; Ilyin, V.A.; Bryukhanova, M.V.; Kirdeyanov, A.V. VS-oscilloscope: A new tool to parameterize tree radial growth based on climate conditions. *Dendrochronologia* **2016**, *39*, 42–50. [[CrossRef](#)]
18. Yang, B.; He, M.; Shishov, V.; Tychkov, I.; Vaganov, E.; Rossi, S.; Ljungqvist, F.C.; Bräuning, A.; Griesinger, J. New perspective on spring vegetation phenology and global climate change based on Tibetan Plateau tree-ring data. *Proc. Natl. Acad. Sci. USA* **2017**, *114*, 6966–6971. [[CrossRef](#)] [[PubMed](#)]
19. Silva, L.C.; Sun, G.; Zhu-Barker, X.; Liang, Q.L.; Wu, N.; Horwath, W.R. Tree growth acceleration and expansion of alpine forests: The synergistic effect of atmospheric and edaphic change. *Sci. Adv.* **2016**, *2*, e1501302. [[CrossRef](#)] [[PubMed](#)]
20. Huang, R.; Zhu, H.; Liu, X.; Liang, E.; Griesinger, J.; Wu, G.; Li, X.; Bräuning, A. Does increasing intrinsic water use efficiency (iWUE) stimulate tree growth at natural alpine timberline on the southeastern Tibetan Plateau? *Glob. Planet. Chang.* **2017**, *148*, 217–226. [[CrossRef](#)]
21. Wang, W.; Liu, X.; Shao, X.; Qin, D.; Xu, G.; Wang, B.; Zeng, X.; Wu, G.; Zhang, X. Differential response of Qilian juniper radial growth to climate variations in the middle of Qilian Mountains and the northeastern Qaidam Basin. *Clim. Chang.* **2015**, *133*, 237–251. [[CrossRef](#)]
22. Fu, Y.S.; Campioli, M.; Vitasse, Y.; De Boeck, H.J.; Van den Berge, J.; AbdElgawad, H.; Asard, H.; Piao, S.; Deckmyn, G.; Janssens, I.A. Variation in leaf flushing date influences autumnal senescence and next year's flushing date in two temperate tree species. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 7355–7360. [[CrossRef](#)] [[PubMed](#)]

23. Keenan, T.F.; Richardson, A.D. The timing of autumn senescence is affected by the timing of spring phenology: Implications for predictive models. *Glob. Chang. Biol.* **2015**, *21*, 2634–2641. [[CrossRef](#)] [[PubMed](#)]
24. Liu, Q.; Fu, Y.H.; Zhu, Z.; Liu, Y.; Liu, Z.; Huang, M.; Janssens, I.A.; Piao, S. Delayed autumn phenology in the Northern Hemisphere is related to change in both climate and spring phenology. *Glob. Chang. Biol.* **2016**, *22*, 3702–3711. [[CrossRef](#)] [[PubMed](#)]
25. Yao, T.; Masson-Delmotte, V.; Gao, J.; Yu, W.; Yang, X.; Risi, C.; Sturm, C.; Werner, M.; Zhao, H.; He, Y.; et al. A review of climatic controls on $\delta^{18}\text{O}$ in precipitation over the Tibetan Plateau: Observations and simulations. *Rev. Geophys.* **2013**, *51*, 525–548. [[CrossRef](#)]
26. Holmes, R.L. Computer-assisted quality control in tree-ring dating and measurement. *Tree Ring Bull.* **1983**, *43*, 69–78.
27. Stokes, M.A.; Smiley, T.L. *An Introduction to Tree-Ring Dating*; The University of Chicago Press: Chicago, IL, USA, 1968.
28. Cook, E.R.; Krusic, P.J. *Program ARSTAN, a Tree-Ring Standardization Program Based on Detrending and Autoregressive Time Series Modeling with Interactive Graphics*; Tree-Ring Laboratory Lamont Doherty Earth Observatory of Columbia University: New York, NY, USA, 2005.
29. Cook, E.R.; Peters, K. Calculating unbiased tree-ring indices for the study of climatic and environmental change. *Holocene* **1997**, *7*, 361–370. [[CrossRef](#)]
30. Cook, E.R.; Kairiukstis, L.A. *Methods of Dendrochronology*; Kluwer Academic Press: Dordrecht, The Netherlands, 1990.
31. Fisher, R.A. Frequency distribution of the values of the correlation coefficient in samples from an indefinitely large population. *Biometrika* **1915**, *10*, 507–521. [[CrossRef](#)]
32. Gruber, A.; Zimmermann, J.; Wieser, G.; Oberhuber, W. Effects of climate variables on intra-annual stem radial increment in *Pinus cembra* (L.) along the alpine treeline ecotone. *Ann. For. Sci.* **2009**, *66*, 1–11. [[CrossRef](#)] [[PubMed](#)]
33. Heinrichs, D.K.; Tardif, J.C.; Bergeron, Y. Xylem production in six tree species growing on an island in the boreal forest region of western Quebec, Canada. *Can. J. Bot.* **2007**, *85*, 518–525. [[CrossRef](#)]
34. Rossi, S.; Deslauriers, A.; Anfodillo, T.; Morin, H.; Saracino, A.; Motta, R.; Borghetti, M. Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. *New Phytol.* **2006**, *170*, 301–310. [[CrossRef](#)] [[PubMed](#)]
35. Li, X.; Liang, E.; Gričar, J.; Prisljan, P.; Rossi, S.; Čufar, K. Age dependence of xylogenesis and its climatic sensitivity in Smith fir on the south-eastern Tibetan Plateau. *Tree Physiol.* **2013**, *33*, 48–56. [[CrossRef](#)] [[PubMed](#)]
36. Wang, Z.; Yang, B.; Deslauriers, A.; Bräuning, A. Intra-annual stem radial increment response of Qilian juniper to temperature and precipitation along an altitudinal gradient in northwestern China. *Trees* **2014**, *29*, 25–34. [[CrossRef](#)]
37. Zhang, J.Z.; Gou, X.H.; Zhang, Y.X.; Lu, M.; Xu, X.Y.; Zhang, F.; Liu, W.H.; Gao, L.L. Forward modeling analyses of Qilian Juniper (*Sabina przewalskii*) growth in response to climate factors in different regions of the Qilian Mountains, northwestern China. *Trees* **2015**, *30*, 175–188. [[CrossRef](#)]
38. Cuny, H.E.; Rathgeber, C.B.; Frank, D.; Fonti, P.; Fournier, M. Kinetics of tracheid development explain conifer tree-ring structure. *New Phytol.* **2014**, *203*, 1231–1241. [[CrossRef](#)] [[PubMed](#)]
39. Begum, S.; Nakaba, S.; Yamagishi, Y.; Oribe, Y.; Funada, R. Regulation of cambial activity in relation to environmental conditions: Understanding the role of temperature in wood formation of trees. *Physiol. Plant.* **2013**, *147*, 46–54. [[CrossRef](#)] [[PubMed](#)]
40. Deslauriers, A.; Rossi, S.; Anfodillo, T.; Saracino, A. Cambial phenology, wood formation and temperature thresholds in two contrasting years at high altitude in southern Italy. *Tree Physiol.* **2008**, *28*, 863–871. [[CrossRef](#)] [[PubMed](#)]
41. Gričar, J.; Zupančič, M.; Čufar, K.; Oven, P. Regular cambial activity and xylem and phloem formation in locally heated and cooled stem portions of Norway spruce. *Wood Sci. Technol.* **2007**, *41*, 463–475. [[CrossRef](#)]
42. Cong, N.; Shen, M.; Piao, S. Spatial variations in responses of vegetation autumn phenology to climate change on the Tibetan Plateau. *J. Plant Ecol.* **2016**, *10*, 744–752. [[CrossRef](#)]
43. Huang, J.G.; Deslauriers, A.; Rossi, S. Xylem formation can be modeled statistically as a function of primary growth and cambium activity. *New Phytol.* **2014**, *203*, 831–841. [[CrossRef](#)] [[PubMed](#)]

44. Pan, Y.; Birdsey, R.; Fang, J.Y.; Houghton, R.; Kauppi, P.E.; Kurz, W.A.; Phillips, O.L.; Shvidenko, A.; Lewis, S.L.; Canadell, J.G.; et al. A large and persistent carbon sink in the world's forests. *Science* **2011**, *333*, 988–993. [[CrossRef](#)] [[PubMed](#)]
45. Peng, C.H.; Liu, J.X.; Dang, Q.L.; Apps, M.J.; Jiang, H. TRIPLEX: A generic hybrid model for predicting forest growth and carbon and nitrogen dynamics. *Ecol. Model.* **2002**, *153*, 109–130. [[CrossRef](#)]
46. Vaganov, E.A.; Anchukaitis, K.J.; Evans, M.N. How well understood are the processes that create dendroclimatic records? A mechanistic model of the climatic control on conifer tree-ring growth dynamics. In *Dendroclimatology*; Hughes, M.K., Swetnam, T.W., Diaz, H.F., Eds.; Developments in Paleoenvironmental Research; Springer: Berlin, Germany; Dordrecht, The Netherlands, 2011; pp. 37–75.
47. Henttonen, H.M.; Mäkinen, H.; Nöjd, P. Seasonal dynamics of the radial increment of Scots pine and Norway spruce in the southern and middle boreal zones in Finland. *Can. J. For. Res.* **2009**, *39*, 606–618. [[CrossRef](#)]
48. De Micco, V.; Campelo, F.; Cherubini, P.; Battipaglia, G.; Bräuning, A.; Grabner, M.; De Luis, M. Intra-annual density fluctuations in tree rings: How, when, where, and why? *IAWA J.* **2016**, *37*, 232–259. [[CrossRef](#)]
49. Gower, S.T.; Krankina, O.; Olson, R.J.; Apps, M.; Linder, S.; Wang, C. Net primary production and carbon allocation patterns of boreal forest ecosystems. *Ecol. Appl.* **2001**, *11*, 1395–1411. [[CrossRef](#)]
50. Franke, J.; Frank, D.; Raible, C.C.; Esper, J.; Brönnimann, S. Spectral biases in tree-ring climate proxies. *Nat. Clim. Chang.* **2013**, *3*, 360–364. [[CrossRef](#)]
51. Esper, J.; Schneider, L.; Smerdon, J.E.; Schöne, B.R.; Büntgen, U. Signals and memory in tree-ring width and density data. *Dendrochronologia* **2015**, *35*, 62–70. [[CrossRef](#)]
52. Büntgen, U.; Trnka, M.; Krusic, P.J.; Kyncl, T.; Kyncl, J.; Luterbacher, J.; Zorita, E.; Ljungqvist, F.C.; Auer, I.; Konter, O.; et al. Tree-Ring amplification of the early nineteenth-century summer cooling in central Europe. *J. Clim.* **2015**, *28*, 5272–5288. [[CrossRef](#)]



© 2018 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<http://creativecommons.org/licenses/by/4.0/>).