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Climatic influence on tree wood anatomy: a review

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Abstract

Wood anatomical traits of xylem are the characteristics of tree rings at cellular and subcellular scales providing important insights on structural features and their linkage to the environment. Therefore, studying the relationship between anatomical traits and environmental changes not only provide physiological explanations, but also provide a new vision of studying the adaptation process and response strategies of tree growth to climate. In this paper, I review and synthesize literature on the influence of climatic parameters on wood anatomy from the different geographical regions using recent (2015–2020) published articles on the topic. This paper discusses the relationship between the anatomical features of angiosperm and gymnosperm xylem with climatic factors. Based on the literature, I then purpose to explore the temporal and spatial variations in the anatomical characteristics of xylem tree rings with environmental changes. Also, more studies can be conducted to assess the synergetic and antagonistic effects among different tree-ring proxies and to determine the specific roles and contributions of major climatic factors during different periods of tree-ring formation.

Keywords: Angiosperm, Environmental change, Gymnosperm, Wood anatomical traits, Xylem

Introduction

Climate change is the biggest challenge of this century and is exerting pressure on both plants and animals [1, 2]. An increase in global temperature (≈0.2 °C/decade) along with the rise in CO_2 (2.5 + / − 0.8 ppm/year) in the atmosphere with the change in precipitation regime may have effects on the structure and function of trees [3–5]. This climatic change interacts with trees during their life leaving a permanent imprint in the woody tissues. Therefore, trees are considered as the most valuable natural archives of past environmental conditions [6–8] showing a unique source for annual variability in forest biomass and carbon allocation [9, 10]. Thus, there is an increasing interest of researcher in analyzing tree-ring characteristic to better understand tree growth responses to environmental variability and extreme events [11–15].

Recent advancements in dendroecology, namely dendroanatomy aim at deciphering the effects of climate on the whole xylogenetic process, i.e., complex process of differentiation and division of cambium with environmental input and formation of new woody tissues [16–18]. Dendroanatomy is defined as the analysis of xylem-cell features along dated tree rings which provide a long-term perspective on the wood formation process [19]. The advancement in sample processing and image analysis allows studying the detailed measurement of multiple traits in wood at decadal to centennial time scales [20, 21]. This allows the researcher in studying inter-annual variability of vessels/tracheids lumen area or cell wall thickness retrospectively analyzing the cambium phenology with changing environment [14, 22, 23].

Afterwards, many studies have explored the long-term effects of climate variability on the corresponding year-to-year change in wood anatomical traits and its consequence for gymnosperm [13, 24, 25] and angiosperm [15, 26] physiology and growth. For instance, some authors reported a drought decreases the lumen area leading to

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decline in stem hydraulic conductivity [27, 28], whereas others found the opposite [29, 30]. Two dominant Mediterranean shrub species, *Erica multiflora* and *Globularia alypum* grown in the same drought conditions showed contrasting phenology indicating its effects to be species-specific [31, 32]. Researchers also found some tree species in extreme drought conditions produce intra-annual density fluctuation [24, 33] or distorted and collapsed cells [34], early cessation of cell division [35] and light rings characterized by narrow latewood brand [36]. Drought stress is related to missing rings formation in Himalayan (*Betula utilis* D. Don) [15, 37] and Tibetan species (alpine Juniper shrub) [38] providing compelling evidence of moisture-triggered xylogenesis. Restricted water availability is not only a limiting factor for growth in warm and dry areas, but also low-temperature control growth at high latitudes and elevation [39]. Elevated carbon dioxide in ring-porous species showed an increase conduit size in earlywood and wood density due to a higher proportion of latewood [40], whereas in coniferous species there is an increase in radial growth but not a large change in wood density and tracheids dimensions [41, 42]. This shows climatic parameters impact in xylem anatomy of trees and ultimately determine its future scenario. Yet, more studies are needed focusing on different species from different geographical regions.

In this review, I briefly present an overview of inter- and intra-annual variation in wood structure in response to climatic parameters. This focuses on dendroecology-based xylem anatomy to assess the state of the art in the emerging field and future research. The paper discusses how changing climatic parameters have interactive effects on the xylem anatomy of angiosperm and gymnosperm trees from different geographical regions. Lastly, it gives an idea about the research conducted till now and way forward specifying the research gaps.

Materials and methods

The literature search was done using an electronic database, google scholar and web of science using the term xylem anatomical traits and climate; climate change and wood anatomy as keywords. The original articles collected from different search engines were compiled. Only peer-reviewed articles based on climatic influence and trees at a different geographical zone with specific methods and result were selected. The printed and online journals registered on the journal website were included for study. Valuable sources of information from news articles, case studies, technical notes, educational materials were excluded as they are not peer-reviewed. To make a concise and systematic review, we choose only articles published in English between 2015 to 2020 (Table 1). I also consider articles that include at least one tree-ring chronology and analyze the relationship with instrumental climate data. The searched articles were imported into Mendeley reference management software (Mendeley Desktop version 1.19.4).

Result

A total of 240 articles were found through databases and 45 duplicates were removed. The first screening of the articles consisted of reading the title and abstracts and 70 articles were identified as eligible for full text. Also, references to the analyzed paper were accessed to identify other studies that had not been found in the consulted databases. From the 70 articles, 20 of them were selected to make an equal representation of angiosperm and gymnosperms with climatic parameters from different geographical region.

The studies included 19 species (12 angiosperms and 8 gymnosperms) from 8 families (Table 2). Twenty articles from 12 countries were reviewed to understand the response of xylem anatomical traits with changing climate. Studies showed climatic parameters, i.e., temperature and precipitation as main driving factors for the growth and development of plants. The response differs based on origin, climatic condition and the orientation of tree species.

Discussion

Climatic influence on wood anatomy of trees

Wood is a porous and fibrous structural tissue found in the stems and roots of trees and woody plants. A tree is composed of a bundle of vessels (for transporting water

Table 1 The inclusion and exclusion criteria

S no.	Criterion	Eligibility	Exclusion
1	Literature type	Research articles (journal)	Review journal articles, book, book chapter, book series, conference paper, report, proceeding
2	Language	English	Non-English
3	Timeline	Between 2015 and 2020	< 2014
		Full-length paper peer-reviewed journal	Published abstract

Table 2 Articles included in the study

Country	Name of plant	Family	Plant type	Measured parameter	Environmental parameter considered	References
Italy	*Picea abies*	Pinaceae	Gymnosperm	Tracheids	Temperature and precipitation	[23]
North America (Alaska and Canada)	*Picea glauca* (Moench) Voss	Pinaceae	Gymnosperm	Lumen area and cell wall thickness	Drought	[25]
Canada	*Picea mariana*	Pinaceae	Gymnosperm	Cell wall thickness and tracheids size and number	Temperature and precipitation	[13]
Norway	*Picea abies*	Pinaceae	Gymnosperm	Cell wall thickness	Drought	[50]
Slovenia	*Picea abies*	Pinaceae	Gymnosperm	Cell lumen area	Temperature and precipitation	[52]
Italian Alps	*Picea abies*	Pinaceae	Gymnosperm	Cell lumen area	Temperature and precipitation	[51]
Italian Alps	*Larix decidua* Mill. and *Picea abies* (L.) Karst	Pinaceae	Gymnosperm	Xylem anatomy	Temperature	[14]
Portugal	*Pinus pinaster*	Pinaceae	Gymnosperm	Cell wall thickness, lumen diameter	Water availability and temperature	[53]
Italy	*Robinia pseudoacacia L.* and *Quercus robur L*	Fabaceae	Angiosperms	Vessels	Temperature and precipitation	[54]
Italy	*Quercus ithaburensis* and *Quercus boissieri*	Fagaceae	Angiosperms	Vessels	Drought	[26]
Greenland	*Betula nana L*	Betulaceae	Angiosperms	Vessels	Temperature and precipitation	[55]
Greenland	*Betula nana L*	Betulaceae	Angiosperms	Vessels	Temperature and precipitation	[56]
Nepal	*Betula utilis* D. Don	Betulaceae	Angiosperms	Vessels and fibers	Temperature and precipitation	[15]
Chile	*Nothofagus pumilio* (Poepp. et Endl.) Krasser	Nothofagaceae	Angiosperms	Vessels	Temperature and moisture	[58]
Chile	*Embothrium coccineum* (Evergreen) and *Nothofagus antarctica* (Deciduous)	Proteaceae Nothofagaceae	Angiosperms	Vessels	Precipitation	[57]
Switzerland/Italy	*Ilex aquifolium* L	Aquifoliaceae	Angiosperms	Vessel area, number	Temperature and precipitation	[59]
Canada	*Populus tremuloides*	Salicaceae	Angiosperms	Vessel diameters	Temperature and precipitation	[60]
Spain	*Quercus robur* and *Quercus pyrenaica*	Fagaceae	Angiosperms	Vessels	Temperature	[61]
Poland	*Quercus robur*	Fagaceae	Angiosperms	Vessel area and number	Temperature	[62]
Brazil	*Tectona grandis*	Lamiaceae	Angiosperms	Earlywood vessels (EWV)	Temperature and precipitation	[63]

within trees) and its wall composed of cellulose glued together with lignin. These woods are classified based on cellular structure as softwood (derived from conifer tree—gymnosperm) and hardwood (derived from broad-leaved trees—angiosperm) (Fig. 1). These cellular structures are commonly known as xylem which is complex tissues composed of tracheids (narrow cells), vessels (wider cells), xylem parenchyma (live cells) and xylem fibers (dead cells) [10, 22]. Out of these four, tracheids and vessels are chief conducting dead cells in the xylem. Xylem anatomical features of gymnosperm are relatively simple composed of earlywood and latewood tracheids, whereas angiosperm has more complex structures with specialized structures called vessels for conducting sap upward.

Studies showed the anatomy of the xylem affects functional properties such as hydraulic safety and efficiency [43, 44]. Therefore, changes in xylem anatomy strongly determine trees performance, survival and capacity to fix carbon [45, 46]. Xylem shape is affected by the synergic

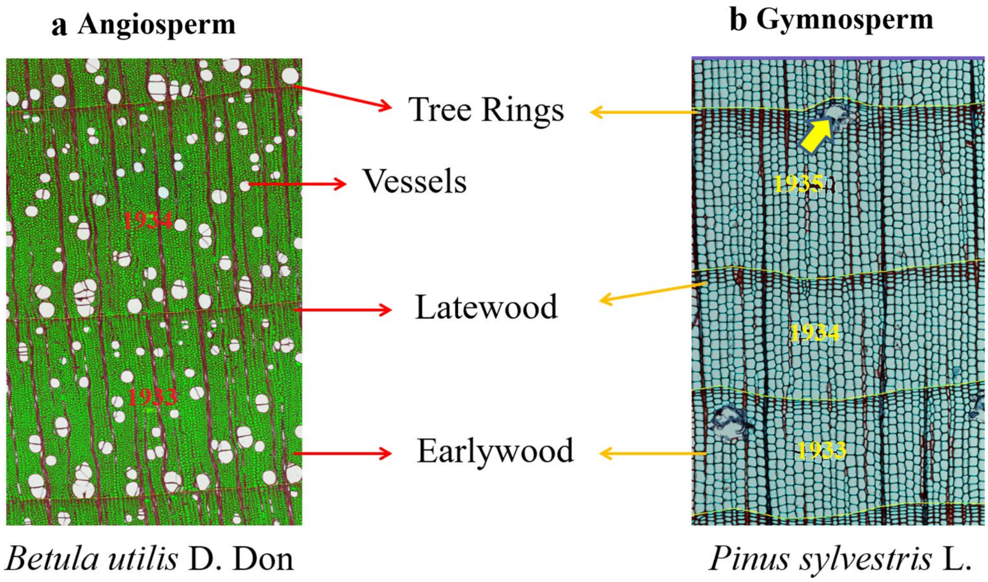

Fig. 1 Cut-out image showing xylem anatomical features (vessels, latewood, earlywood, tree rings) **a** Image of *Betula utilis* D. Don, Angiosperm **b** Image of *Pinus sylvestris* L., Gymnosperm. The arrow in **b** depicts a parenchyma cell of a resin duct

effects of endogenous (genetic) and exogenous (environmental) factors [47, 48]. Therefore, it is necessary to critically evaluate and discuss the effects of ongoing environmental changes to wood anatomical traits.

In gymnosperm, most of the wood is composed of tracheids, which simultaneously provide vascular transport and mechanical support [49]. The tracheid size of *Picea abies* from the Italian Alps has been influenced by climate conditions in the growing season. They found that early-summer temperature affects cell enlargement at higher elevation, whereas at lower elevation water availability helped in the enlargement of the cell [23]. A similar study was conducted by Rosner et al. [50] on Norway spruce (*Picea abies*) which showed trees from the coldest site was smaller with the largest lumen area indicating the species to be probably less resistant under extreme climatic events.

Also, Norway spruce from Italian Alps, Slovenia and the Czech Republic showed lumen dimension of earlywood tracheids to be positively affected by precipitation in the previous autumn and early summer of the current growing season [51, 52]. In white spruce [*Picea glauca* (Moench) Voss] lumen area and cell wall thickness were found higher sensitive to drought indicating a plastic adaptation to shift in growth-limiting conditions mainly stabilizing latewood cells [25]. A similar study conducted on black spruce (*Picea mariana*) from the boreal forest of Canada showed cell number (CN) and cell wall thickness (CWT) to be positively affected by spring and summer daily mean and maximum temperature at northern sites. Moreover, they found latent impacts of water availability on xylem traits [13].

Carrer et al. [14] investigated wood anatomical traits of two high-elevation conifers (*Larix decidua* Mill., *Picea abies* (L.) Karst.) and found xylogenesis in the species benefits from warm temperature depending on the timing of cell production. A study on CWT and LD of *Pinus pinaster* from Portugal showed a crucial role of water availability on cambial activity and wood formation. They found that *P. pinaster* under water-limited environments appears to adjust LD, while in temperature-limited environments the species adjust CWT [53]. This shows that even though conifer wood at first glance is a rather uniform material at the microscopic and functional levels, it is quite varied and gives rise to important differences in capabilities of woody parts in response to change in climatic parameters.

Woody angiosperm is widely divergent in its xylem cellular makeup. For example, xylem hydraulic traits of native *Quercus robur* L. was more sensitive to previous-summer drought than those of alien *Robinia pseudoacacia* L. This suggests that *R. pseudoacacia* L. might be more competitive under future drier conditions [54]. Two deciduous species namely *Quercus ithaburensis* and *Quercus boissieri* from the southeastern Mediterranean showed abundant precipitation and low temperature from November to April benefit the xylem formation [26]. The dry years strongly limit vessels size and number in *Q. ithaburensis* compared to *Q. boissieri*, making one highly resilient and the other highly resistant.

Betula nana L. vessel lumen area from western Greenland showed influence by spring and summer temperature, whereas vessel grouping was driven by winter temperature [55]. Similarly, Hollesen et al. [56] documented that *Betula nana* growth is positively influenced by winter temperature as important as summer.

High-altitude angiosperm, *Betula utilis* D. Don of Nepal showed vessel area to be positively associated with March precipitation and fiber area negatively correlated with temperature during the previous and current season [15]. This showed that the fibers get narrower when the vessels are wider. Wood anatomy of southern Chilean species *Embothrium coccineum* (Evergreen) and *Nothofagus antarctica* (Deciduous) showed an increase in vessels density with dryness without changes in estimated hydraulic conductivity [57]. Similarly, another Chilean deciduous broadleaf tree *Nothofagus pumilio* (Poepp. et Endl.) Krasser showed an increase in vessels density and a decrease in vessels composition with lower temperature, however, the xylem-specific hydraulic conductivity remained constant across elevation and latitude [58]. Rita et al. [59] study xylem traits of *Ilex aquifolium* L. from Switzerland (mesic site) and Italy (drought-prone site). They found the species from Switzerland were primarily affected by temperature; however, precipitation had the greatest effects at the Italian site showing a positive relationship with potential hydraulic conductivity (Ks) and negative with xylem vulnerability (Vx). This concludes that compared with the drought-prone site, the mesic climatic condition favored xylem traits associated with hydraulic efficiency showing the stronger influence on anatomical traits.

Populus tremuloides, a deciduous Canadian species vessel diameter showed strong relationships primarily with mean annual precipitation and less association with temperature. Also, vessels diameters were highly plastic in response to different environments and varied with summer moisture availability [60]. The temperate *Quercus robur* earlywood vessels were exclusively affected by temperature whereas they were more independent in the sub-Mediterranean *Quercus pyrenaica* [61]. A similar study was conducted in *Q. robur* from northern Poland and found vessel area to have a significant positive correlation to minimum winter temperatures to reduce damage to the root systems [62]. *Tectona grandis* earlywood vessels from Brazil showed a significant correlation with summer season temperature and precipitation for efficient water transport. They found spring conditions to have a direct influence on the formation of earlywood vessels suggesting warmer temperature to favor efficient water transporting system [63]. This concludes that the whole xylem formation process including earlywood and latewood might be most affected by the climate during the current growing season. Temperature seems to be the most influencing factor for the timing of earlywood and latewood formation during the xylem formation process according to the physiological status of the trees.

Conclusion

Climate warming is shown to be more apparent impacting tree growth and xylem anatomical traits. Wood xylem traits, therefore, help to understand and predict woody plant responses to global environmental change and provide an opportunity for understanding the hydraulic safety margin of trees. This review showed that the xylem is more sensitive to environmental factors and depends on species, e.g., deciduous species did not show a significant difference in wood structure, however, evergreen species showed higher variation indicating a higher sensitivity to varying climatic conditions. Moreover, it provides great potential for a multidisciplinary approach in wood science to provide an answer to a question related to tree performance under changing environmental conditions [64]. In addition to wood anatomical traits study, there is a promising research avenue of investigating spatial and temporal variation in wood anatomy to understand genetic and phenotypic variation. Lastly, a better understanding of the mechanisms on how climate affects wood anatomical traits facilitate the prediction of climate change impacts at a local regional and global level.

Abbreviations

CO_2: Carbon dioxide; CWT: Cell wall thickness; CN: Cell number; Ks: Potential hydraulic conductivity; LD: Lumen diameter; Vx: Xylem vulnerability.

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Authors' contributions

SP conceptualized the research, conducted a literature review and wrote the manuscript. The author read and approved the final manuscript.

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Availability of data and materials

The dataset analyzed during the current study are available from the corresponding author on request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

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Competing interests

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