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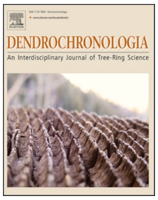

Contribution of Russian dendroanatomical studies to the dendrochronology since the mid-20th century

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ABSTRACT

Russia, the country with the most forested area, significantly influences global climate, carbon, and water dynamics. In addition, a considerable part of the Russian forests is in remote regions with a low direct anthropogenic disturbance, but at the same time, recently experiencing unprecedented warming. This combination of factors makes Russia a hotspot for dendrochronological and dendroanatomical studies, providing a valuable perspective on the consequences of climate change in a global context. Dendroanatomy is a powerful dendrochronological tool that provides a robust insight into xylem traits, their relation to climate conditions during tree-rings formation, and the cell structure-function relationship over time (tree life span). Although dendroanatomy in Russia has been gaining momentum lately, there is a long tradition of characterizing and modeling wood anatomical traits, including the development of novel methodologies, hardware and software since the mid-20th century. Unfortunately, in many cases, these advances have been hidden from the international readership because most of them were published in Russian. This descriptive inventory presents an overview of dendroanatomical studies carried out in Russia since the mid-20th century. It focuses on different periods and topics to facilitate its accessibility and highlight its contribution to the global dendrochronological community.

1. Introduction

Russian forests represent ca. 20 % of the world's forested area (FAO and UNEP, 2020) and 60 % of the world's boreal forests (Kayes and Mallik, 2020). The Russian territory is experiencing an accelerated climate change, with a temperature increase of 0.4 ℃ per decade over the 1976–2021 period (Roshydromet, 2022), which is twice higher than the global rates (IPPC, 2021). Under the expected global and regional climate changes, the influence of climate on Russian forests will significantly increase (Shvidenko and Schepaschenko, 2013), affecting forest productivity (Shuman et al., 2013) but also increasing climate-related disturbances together with declining or dieback phenomena (Gauthier et al., 2015). Therefore, Russia has become a hotspot for dendrochronological studies to assess the ability of woody plants to adapt to rapidly changing conditions across different biomes in the present time. However, the interest of Russian researchers in dendrochronology started earlier and frequently aimed to provide a mechanistic understanding of intra-annual tree-ring growth.

The focus of research has been changing along with the evolution of Russian dendrochronology over time, from the description of tree-ring growth and the understanding of the environmental effect on wood structure and cell anatomy (e.g., Antonova et al., 1983; Vaganov and Sviderskaya, 1990) to the modeling of the process which controls wood formation (e.g., Vaganov et al., 2006) and the use of multiple tree ring proxies (e.g., Kirdyanov et al., 2020a; Churakova et al., 2022, 2023). Thus, a large number of tree ring-related studies have been conducted in Russian forests, covering a wide range of topics, including tree growth response to climate (e.g., Briffa et al., 1998; Hughes et al., 1999; Vaganov et al., 1999; Esper et al., 2010; Kirdyanov et al., 2013; Hellmann et al., 2016; Kharuk et al., 2019; Arzac et al., 2021a, 2022), paleoclimatology (e.g., Naurzbaev et al., 2002; Briffa et al., 2013; Myglan et al., 2015; Büntgen et al., 2020; Hantemirov et al., 2021, 2022,

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2023), tree- and shrubline shifts (e.g., Shiyatov, 1962; Kammer et al., 2009; Kirdyanov et al., 2012; Hagedorn et al., 2014; Devi et al., 2020; Grigoriev et al., 2021), forest productivity estimates (e.g., Knorre et al., 2006; Prokushkin et al., 2006), isotopes (e.g., Churakova et al., 2019, 2022), wood density (e.g., Camarero et al., 2017), wood chemistry (e.g., Kirdyanov et al., 2020a), tree growth modeling (e.g., Vaganov et al., 2006; Shishov et al., 2016, 2023; Tychkov et al., 2019; Arzac et al., 2021b), and other ecological applications as the impact of fires (e.g., Kirdyanov et al., 2020b; Kharuk et al., 2021), or a better understanding of tree growth in permafrost zones (e.g., Bryukhanova and Kirdyanov, 2014; Fonti et al., 2018, 2021). Most of the effort has been carried out by researchers from Moscow (Institute of Geography RAS), Yekaterinburg (Institute of Plant and Animal Ecology), and Krasnoyarsk (Institute of Forest and Siberian Federal University).

The study of wood anatomical traits adopting quantitative metrics (QWA; von Arx et al., 2016) on dated tree-rings time series (dendroanatomy[1]) could potentially allow deciphering the complex species-specific interaction mechanisms between internal and external factors and their influence on xylem formation with a higher temporal resolution (Vaganov and Terskov, 1977; Antonova and Stasova, 1993; Benkova and Benkova, 2006; Vaganov et al., 2006; Babushkina et al., 2010). The secondary xylem is produced from the vascular cambium in a succession of steps (Smirnov, 1964; Antonova et al., 1983; Antonova and Stasova, 1988; Rathgeber et al., 2016), controlled by exogenous and endogenous factors during the growing season (Hsiao and Acevedo, 1974). In conifers, up to 90 % of the xylem is constituted by tracheids (Vaganov et al., 2006; Hacke et al., 2015). Thus, dendroanatomy allows to evaluate the spatial arrangement of cell profiles or tracheidograms within dated tree rings (Vaganov, 1990) and its links with function and environment (Vaganov et al., 1990; De Micco et al., 2019) over time.

The popularity of dendroanatomy is proliferating worldwide, thanks to the improvement in anatomical preparation techniques and the evolution of high-resolution image acquisition and measurement systems (von Arx et al., 2016). However, Russian dendrochronologists have been working on descriptive and morphological wood anatomy since the second half of the 20th century, with pioneering studies in the development of techniques and methodologies (e.g., Moskaleva, 1958; Melekhov, 1979; Vaganov et al., 1983, 1985, 1990) to evaluate the response of wood anatomical traits to environmental factors. During this time, Russian dendrochronologists have adopted specific methods (e.g., staining of forming wood, quantification of cell anatomy, comparison of annual rings with tracheidograms) and developed the Vaganov-Shashkin model (VS-model) to simulate ring growth and structure. Many of these technical advances have been exported worldwide and contribute to the development of dendroanatomy.

Unfortunately, most of these early studies were published in Russian and are still poorly known by the international community due to their difficult access. This work aims to provide an overview of the dendroanatomical studies carried out in Russia, from the pioneering to most recent studies, by showing the evolution of the most common methodologies used in sample preparation and measuring, and the development of new tools and approaches over the last seventy years without forgetting the limitations Russian scientist faced in pioneer studies due to the poor development of dendroanatomy at that time. We also summarize some of the main results obtained in the field during the last decades and provide a prospect for future research in Russia.

2. Evolution in methodology

The evolution of dendroanatomy in Russia has followed a series of steps linked to the focus of research, which has been changing over time, from the description of tree-ring growth and wood formation and its relation to the environmental conditions, to the modeling of wood formation and process that controls it. In this section, we focus on the specific methodologies used or developed by the Russian community which has contributed to the current state of dendroanatomy worldwide.

2.1. Sample preparation

The methodology of sample preparation for dendroanatomical studies in Russia has continuously evolved as for the rest of the world. Although in recent times, thin anatomical preparations are sectioned, stained and fixed following internationally accepted protocols (e.g., Rossi et al., 2006; Gärtner and Schweingruber, 2013; Schneider and Gärtner, 2013; von Arx et al., 2016), Russian pioneer studies differed in this methodology due to the limited knowledge and available technology at that time, pushing the Russian scientist to explore different ways in order to conduct their research and develop forward the dendroanatomy. Thus, for example, instead of sections thinner than 15 μm commonly obtained in the present time using a sliding or rotary microtome and disposable blades, previously, thin sections (20–30 μm thick) were prepared with a well-sharpened knife and a sliding microtome (e.g., Vaganov et al., 2006; Kuzmin et al., 2007; Vaganov et al., 2010), as for example the MC-2 produced in the USSR. Moreover, when the optics allowed it, observations and measurements were performed directly under magnification on polished or flattened (with a microtome) wood surfaces without requiring thin section preparations (Vaganov, 1996).

Similarly, pioneering studies conducted in the mid-20th century followed different techniques for sample fixation and staining, contributing to finding the best approaches for sample processing currently followed. Nowadays, the most common differential staining for thin sections is, as described by Gärtner and Schweingruber (2013), a solution of Alcian blue (or Astra blue) and safranin for observation and measurements. However, previously, other staining solutions were employed. Moskaleva (1958) prepared *Pinus sylvestris* L. sections by fixing wood material in ethanol-formalin, then washing and submerging them into a solution of ethanol, glycerol and water to finally embed them in celluloid and sectioning with a microtome. The staining of sections differed for lignified wood and cambium, being lignified wood stained with a solution of phloroglucinol and sulfuric acid, chlorin-zinc-iodine, safranin, methylene green or malachite green. In contrast, samples for cambium development studies were stained with hematoxylin or ruthenium red. In some cases, sections were submerged in a ferrous sulfate or acetic copper solution to obtain differential staining (Moskaleva, 1958). Other staining solutions, such as Nile blue (Vysotskaya and Vaganov, 1989), cresyl violet (Antonova and Stasova, 1997), or methylene blue (Fonti et al., 2013, 2022), have been or are still in use. Furthermore, different mountain mediums to fix the anatomical preparation have been used. Glycerol is the most used (e.g., Babushkina et al., 2010; Bryukhanova et al., 2013; Darikova et al., 2013), although Canada balsam (Fonti et al., 2015) and Eukitt (Tabakova et al., 2021) are replacing the use of glycerol in recent time primarily due to the way in which sections are digitalized. Thus, all these trials by the Russian community have contributed with solid experience to the set of standards protocols currently in use.

In recent times, the Russian community is still in search of new approaches in order to provide more reliable results for dendroanatomy-related studies. An example of this continuous search is the proposed alternative methodology to microtomy, based on embedding-polishing protocols established for hard tissue preparation (Arzac et al., 2018b). Although it is not commonly used, in this method, wood samples are infiltrated and embedded in a transparent and non-reactive resin as polymethylmethacrylate (PMM), to be then ground and polished to acquire images from stained or unstained polished surfaces of the PMM

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[1] In this review, we consider QWA as the study of wood anatomical traits adopting quantitative metrics (e.g., xylogenesis), whereas dendroanatomy when year-to-year variations of anatomical traits are considered, for example, with time series (e.g., chronologies of anatomical traits).

blocks and sections (thinner than 100 μm). The technique allows the use of a wide range of optical methods for observation, including reflected polarizing microscopy, epifluorescence microscopy, bright-field microscopy with diffuse illumination and circularly polarizing microscopy.

2.2. *Cell structure measurements*

The techniques for xylem cell traits measurements have evolved alongside the advances in image digitalization and analysis. Due to the need of Russian dendroanatomists to understand tree growth year-to-year, initially, cell structural traits were measured for radial files of tracheids (from five to eight per ring) from cross-sections using transmitted light microscopy over several consecutive rings (Antonova and Stasova, 1993, 1997). A researcher generally measured the lumen size and double cell wall thickness by identifying the boundary between adjacent cells along a radial file during a linear movement of the microscope stage (e.g., Vaganov et al., 1983; Vysotskaya et al., 1989). Since this technique was highly time-consuming, it was automatized at the Institute of Forest in Krasnoyarsk by interfacing a video camera with the microscope and connecting it to a computer to improve the accuracy of data collection and analysis, as well as reducing the time needed to obtain reliable results (Vaganov et al., 1985). Moreover, during the 1980s and 1990s, to further speed up the process, the measurements were performed under magnification directly on wood surfaces when the optics allowed it, avoiding the preparation of anatomical sections (Vaganov, 1996).

These advances in measuring systems and the recent development in sample preparation techniques and image digitalization systems (e.g., digital cameras, slide scanners) allowed the creation of new specialized software produced in Russia. For example, Lineyka (Silkin, 2010) and AutoCellRow (ACR) (Dyachuk et al., 2020) facilitate the semiautomatic quantification and measurement of different xylem traits (e.g., cell number, lumen diameter and cell-wall thickness) along individual radial files of tracheids in single rings, and have been widely used in Russian studies (e.g., Belokopytova et al., 2020; Vaganov et al., 2020; Babushkina et al., 2021; Belousova et al., 2021; Zharkov et al., 2021a), but also abroad (Rita et al., 2022).

The data from radial files, obtained either via direct observation or software measurement, has been used for the production of tracheidograms, profiles of cell dimensions across individual tree rings, widely used to evaluate year-to-year variations in cell dimensions and cell wall thickness over the growing season (e.g., Vaganov, 1990; Panyushkina et al., 2003; Popkova et al., 2018). However, since tree-ring width varies yearly, the number of tracheids along radial files also varies within and between rings (e.g., Vaganov and Terskov, 1977; Vaganov et al., 1979, 1985, 1992). Therefore, the tracheidograms needed to be standardized to the same number of tracheids to compare measured traits over radial files between tree rings and different trees (e.g., Vaganov et al., 1985; Vaganov, 1990). Then, the individually standardized tracheidograms for each radial file within a ring are averaged to obtain a mean tracheidogram for a tree ring (e.g., Vysotskaya et al., 1989; Darikova et al., 2013) to finally produce “cell chronologies” that are independent of tree-ring width (Vaganov et al., 1994, 1996). Such an approach allowed the correlations between time series of external factors (e.g., air temperature, soil moisture, defoliation, etc.) and cell size and wall thickness chronologies (Vaganov, 1996). The mean tree-ring tracheidogram data have also been combined with other tree-ring parameters. For example, cell structure data were combined with tree-ring density profiles to produce cell mass chronologies (e.g., Silkin and Kirdyanov, 1999, 2003).

Tracheidograms have also been recently used to describe the dynamics of seasonal variability in tracheid properties (Zharkov et al., 2022). The potential of tracheidograms developed in Russia was exported abroad and a tracheidogram approach is nowadays helpful also to automatically organize cells according to their position within the ring by R packages such as “RAPTOR” (Peters et al., 2018), which allows to analyze extensive output datasets from specialized software such as ROXAS (von Arx and Carrer, 2014).

Depending on the focus of the study, and although most Russian studies are still based on self-developed methodologies, the use of software such as ROXAS by the Russian community is gaining popularity in recent times in order to measure a broader range of anatomical traits (e.g., cell number, lumen diameter, cell-wall thickness, theoretical maximum water conductivity, anatomical wood density, ray parenchyma and estimation of carbon accumulation in cells, among others) over a digitally captured surface of plant tissue (e.g., Fonti et al., 2015; Sviderskaya et al., 2021; Tabakova et al., 2021; Khotcinskaia et al., 2023). Nevertheless, it is crucial to highlight that many of the recent advances in dendroanatomy have a background in the efforts of the Russian community searching for a better understanding of the mechanisms controlling tree growth in boreal environments.

2.3. *Tree growth and wood formation modeling*

The well-known process-based Vaganov-Shashkin model (VS-model), widely used to simulate seasonal growth and tree-ring formation as a function of daily meteorological data (Shashkin and Vaganov, 2000; Vaganov et al., 2006), has been another essential contribution from Russian scientists to dendrochronology and dendroanatomy. As inputs, the model requires daily climate records (mean temperature and total precipitation), site latitude to determine the photoperiod, and an actual tree-ring width residual chronology to calibrate the simulated ring growth (Tychkov et al., 2019; Vaganov et al., 2006). As final outputs, the model provides values of daily growth rates based on day length, soil moisture and temperature limitations and an integral growth rate considering both limiting factors. The accuracy of the model is based on the values of Pearson’s correlation coefficient, the Gleichläufigkeit synchrony and the root mean square error between the simulated and actual chronologies (Shishov et al., 2016). In addition, annual estimations of the date for the start (SOS), end (EOS) and length (LOS) of the growing season are calculated. The SOS is defined when the daily temperature is equal to or higher than the value of the minimum temperature required for tree growth (Tmin; 5 °C), and the temperature sum for the previous ten days reaches some critical level (Tbeg). The EOS is the last day within a year when the growth rate’s value exceeds the critical growth rate (Vcr), and the temperature sum is no longer higher or equal to Tbeg. The LOS is estimated as the number of days between SOS and EOS.

The VS-model has also been a starting point for developing new models. Thus, for example, a visual parametrization of the VS-model, the VS-Oscilloscope (Tychkov et al., 2012, 2015; Shishov et al., 2016), has been commonly used for tree-growth simulations (e.g., Arzac et al., 2018a, 2021b; Tychkov et al., 2019). An online version of the VS-oscilloscope also allows the simulation of tree growth without the requirement of any preinstalled software (http://www.vs-genn.ru/). Moreover, in recent times, supercomputers may carry out the model’s parametrization (e.g., Kirdyanov et al., 2020a). In addition, the devolvement of the monthly resolution version, the VS-lite model (Tolwinski-Ward et al., 2011), has allowed the tree-growth simulation in areas where daily climate data is not easily available. Finally, the VS-Cambium-Developer, based on the cambial block algorithm of the VS-model, reproduces the process of cambial activity of coniferous species (Belousova et al., 2021; Shishov et al., 2021; Popkova et al., 2023).

3. An inventory of the Russian studies

The publications on dendroanatomy in Russia cover a vast geographical extension (Fig. 1), and the number of published works is continuously increasing (Fig. 2). The published articles extend to a broad range of approaches and research topics: quantification of tracheid number and sizes along radial cell rows and tracheidograms (e.g., Silkin and Kirdyanov, 2003; Fonti and Babushkina, 2016; Zharkov

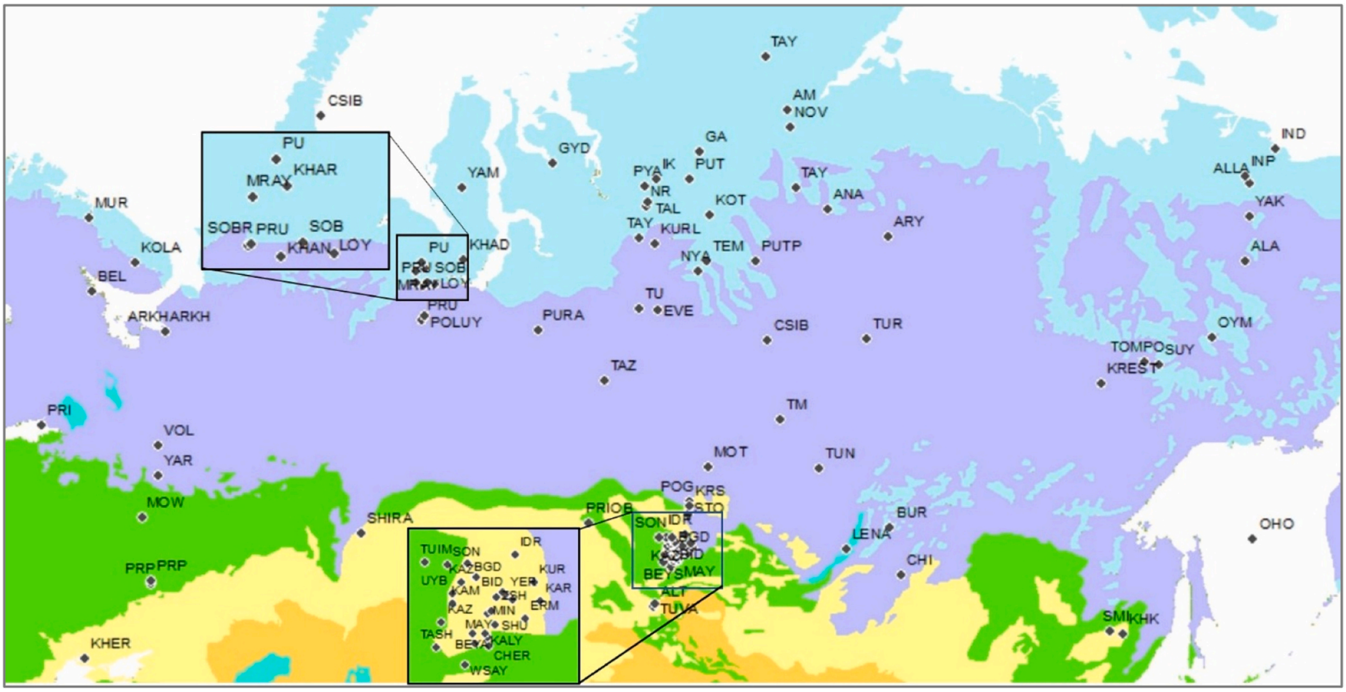

Fig. 1. Distribution of published studies on dendroanatomy within the Russian Federation (also see Supplementary Table A1 for further details). Colors represent different biomes: tundra (blue), lake, rock and ice (cyan), taiga (purple), steppe (yellow), desert (orange), and temperate forest (green).

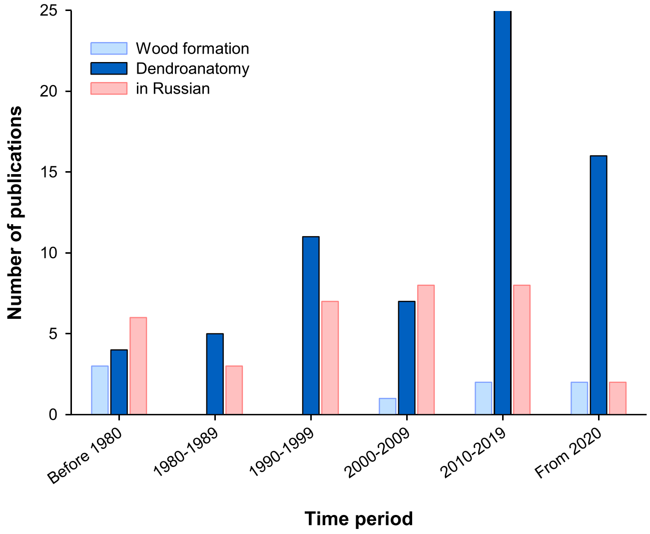

Fig. 2. Number of published manuscripts related to dendroanatomy in the last 40 years over the Russian territory grouped in 10-years period (included in the Supplementary Table A1) and divided by topic (wood formation and dendroanatomy). The pink bar highlights the number of manuscripts published in Russian.

et al., 2021a), measurement of multiple of xylem traits (e.g., Fonti et al., 2015; Belokopytova et al., 2019), seasonal growth studies (e.g., Bryukhanova et al., 2013; Kalinina et al., 2019) and modeling of cambial activity (e.g., Popkova et al., 2020; Shishov et al., 2021), obtaining density profiles (Silkin et al., 2022). In addition, the influence of extraordinary and extreme events on cell characteristics has been studied, including the Tunguska episode in 1908 (Vaganov et al., 2004) and the incident in the Chernobyl nuclear power station in 1986 (Musaev, 1996). Moreover, several methodological books have been published, including basics of dendrochronology (e.g., Shiyatov et al., 2000), seasonal growth dynamics and modeling (e.g., Smirnov, 1964; Antonova, 1999; Vaganov and Shashkin, 2000; Vaganov et al., 2006) and anatomy atlas of Russian woody plants (Benkova and Schweingruber, 2004). The supplementary Table A1 provides a chronological overview of studies conducted in Russia since the mid-20th century, highlighting the relevant contribution of Russian scientists in the development of the field.

A total of 95 studies (i.e., manuscripts, books and book chapters) on Russian dendroanatomy published by Russian scientists (Fig. 2) were considered in this overview, 45 % of them published in Russian and hardly accessible to the broader international scientific community (in the supplementary file A2, we have included the first page of the articles with the most difficult access). However, 91 of them were discussed either throughout the text or described in the supplementary Table S1 to avoid redundancy among published material. Furthermore, the majority of the selected publications (~90 %) focused on wood structure data from conifers (i.e., *Pinus sylvestris* L., *Pinus sibirica* Du Tour, *Picea obovata* Ledeb, *Larix sibirica* Ledeb) and only ~10 % have been conducted on broadleaved species such as *Betula pendula* (e.g., Popkova et al., 2018; Vaganov et al., 2020; Babushkina et al., 2021) and *Betula pubescens* Ehrh. (Fonti and Prokushkin, 2021).

Since dendroanatomical studies started to popularize worldwide during the 2000s due to the improvement in high-resolution image acquisition and software, here we outline the main Russian developments and studies published before and after the year 2000 to provide a better description of the contribution of Russian scientists to the dendrochronological community. Then, we present results on tree-ring growth simulation studies based on dendroanatomical data. Finally, we discuss the further prospects for dendroanatomy in Russia. In general, the Russian scientific community has provided critical insight into the factors controlling wood formation in the boreal forests, highlighting the shift in limitation from temperature in higher latitudes to water availability in lower latitudes, leading to the focus on the study of climate signals in cell anatomical traits and its dependence on environmental conditions. This information has been crucial for modeling the processes controlling wood formation under contrasting environments, which have resulted in the development of different models by the global community.

3.1. Studies published before 2000

The first studies on dendroanatomy in Russia (during the Soviet Union period), published in the late 1950s–early 1970s, were mainly focused on the physiological processes of tree-rings growth. The obtained data were subsequently used to model the kinetics of seasonal growth and the cellular structure of conifer tree rings in different regions of Russia. Moskaleva (1958) observed tree-ring and early/latewood tracheid formation of *Pinus sylvestris* in the Moscow region. Later, Melekhov (1979) showed that the study of seasonal tree-ring dynamics in *Pinus sylvestris* and *Pinus nigra* helped evaluate and predict climate conditions in the Western Soviet Union. During the same period, several efforts were oriented toward identifying the environmental factors triggering cambial activity, showing the critical role of air temperature in northern latitudes (Tyrtikov, 1956; Kandelaki, 1979). In addition, methodological papers (e.g., calculation of tree growth indices; Shiyatov, 1970) and book chapters related to basic principles and methods in dendrochronology (Shiyatov, 1973) were published.

During the 1980s, a novel approach was proposed to quantitatively describe intra- and inter-annual variability of tree-ring cell structure parameters using tracheidograms and "cell chronologies" (e.g., Vaganov et al., 1985; Vysotskaya. et al., 1985; Vaganov, 1990), finding that tracheids number and size depend on the duration of their formation (Antonova et al., 1983) and its dependence on water availability in lower latitudes (Vaganov et al., 1985). Then, in the early1990s, a seasonal tree-ring growth simulation model was developed, and simulated tracheidograms were compared to tree-ring cell structure measurements in pine from central Siberia (Vaganov et al., 1990, 1994; Fritts et al., 1991). Results showed that using a simulation model effectively captures the main meteorological factors influencing the seasonal rate of tracheid production and their sizes (Vaganov et al., 1992). At the same time, it revealed the limitations of the standard statistical approaches, based on response function and multiple regression, to quantify the influence of climate on tree growth (Vaganov et al., 1994).

The effect of temperature on different phases of xylogenesis and accumulation of cell wall biomass, with early and latewood cells forming at different time windows, was shown in trees growing in the forest-steppe ecosystems in southcentral Siberia (e.g., Antonova and Stasova, 1993, 1997) and temperature-limited forest-tundra in Russian subarctic (e.g., Vaganov et al., 1996, 1999; Silkin and Kirdyanov, 1999). Furthermore, the optimal temperature and precipitation values for cell production, radial expansion of cells, and thickening of the secondary wall were identified for forest-steppe conditions in Siberia. These optimal values were similar for cell production and expansion while significantly differed between sites for the secondary wall thickening phase, where dependence on seasonal growth temperature was observed (Antonova et al., 1995; Antonova and Stasova, 1997).

In the earlier stages of dendroanatomy in Russia, a couple of books related to the study of the process of seasonal growth (Smirnov, 1964) and xylem formation (Antonova, 1999) were published, including an overview of the effect of different climate conditions on conifers growth.

3.2. Studies published after 2000

After the year 2000, the field of Russian dendroanatomy has been rapidly expanding (Fig. 2), with about 67 studies been published. Moreover, several books have been released, such as "Anatomy of Russian Woods" (Benkova and Schweingruber, 2004), an illustrated atlas describing the anatomy of 333 Russian species. "Growth and structure of growth rings of conifers" (Vaganov and Shashkin, 2000) and "Growth Dynamics of Conifer Tree Rings Images of Past and Future Environments" (Vaganov et al., 2006), where tree growth and cell production are considered and the process-based VS-model is described. During this period, it has been shown how climate conditions affect tree-ring formation and their cell structure, which determine the hydraulic and mechanical properties of the xylem, including the use of conifers tree-ring parameters as proxies for climate reconstructions (Hantemirov et al., 2000; Babushkina et al., 2003; Sidorova et al., 2012; Churakova et al., 2019; Büntgen et al., 2022).

Thus, cell parameters allowed for obtaining additional detailed information about climate variations during the growing season and identifying the "key" intervals of the season affecting tree radial growth and structure (e.g., Kirdyanov et al., 2003; Benkova and Benkova, 2006; Vaganov et al., 2006; Kuzmin et al., 2007, 2011; Babushkina et al., 2010). This becomes especially important for the permafrost zone considering its possible degradation (e.g., Blokhina et al., 2012; Bryukhanova and Kirdyanov, 2014; Fonti et al., 2018, 2021; Mashukov et al., 2021a). Tracheidograms were used to evaluate the variability of the anatomical characteristics of annual rings formed in graft and rootstock stems (Vaganov et al., 2010). It was demonstrated that tracheidograms of coniferous are an indirect but effective tool for assessing the seasonal influence of internal and external factors on tree growth (e.g., Arzac et al., 2018b; Kalinina et al., 2019; Belokopytova et al., 2020; Babushkina et al., 2021). Furthermore, it has also been proven that climate conditions can significantly affect the formation of rings and their structure, which determines xylem hydraulic and mechanical properties (Fonti et al., 2013; Bryukhanova and Kirdyanov, 2014). A significant outcome proved that, over the last 20 years, annual rings in certain environments had undergone some anatomical changes, such as the thinning of cell walls (e.g., Antonova et al., 2017; Camarero et al., 2017;) and disturbed ray tracheids (e.g., Belokopytova et al., 2019; Mashukov et al., 2021a), highlighting the effect of environmental conditions on the structure-function relationship of the secondary xylem (Bryukhanova et al., 2014). Recently, other xylem traits, such as ray parenchyma, have been studied, suggesting that their formation may be linked to climate depending on the species (Fonti et al., 2015; Tabakova et al., 2021).

Special attention was also paid to the study of different zones of the tree ring, between early and latewood (Sviderskaya et al., 2011; Babushkina et al., 2019) and its relationship with the number of cells within each zone (Fakhrutdinova et al., 2017) and climate (Fonti and Babushkina, 2016; Belokopytova et al., 2019, 2020; Popkova et al., 2020). As well, since the 2000s, several seasonal growth studies have also been conducted, determining the importance of environmental factors (Ostroshenko, 2002; Babushkina et al., 2010; Kalinina et al., 2019) and tree age (Kishchenko, 2014) as limiting factors of tree growth, as well as the start, end and length of the growing season of conifer species (Tishin et al., 2017; Matveev et al., 2020; Zharkov et al., 2021b), and the formation duration of each tree-ring zone within the ring (Bryukhanova et al., 2013). In addition, a recent study based on seasonal growth and in situ monitoring of ecophysiological processes has shown the mechanism of tree decay due to the symbiosis of pine bark beetles and ophiostomatoid fungi in Central Siberia (Barchenkov et al., 2023).

3.3. Modeling

The process-based Vaganov-Shashkin model, originally developed to simulate tree growth under different environments (Shashkin and Vaganov, 2000; Vaganov et al., 2006), has been widely used to understand the main limitations of tree growth as well as temporal changes in these limitations and phenology under contrasting conditions (e.g., Vaganov et al., 2011; Tychkov et al., 2012; Arzac et al., 2021b; Fonti et al., 2021; Babushkina et al., 2022; Shishov et al., 2023). However, it was recently provided the basis to describe the process beyond tree growth limitations, explain seasonal cambium development, and estimate tree-ring cell production (Shishov et al., 2021; Popkova et al., 2023). Thus, based on dendroanatomical data, the simulations of cambium development reproduce the process of cambial activity in conifers based on the hypothesis of the presence of a cytoplasmic inhibitor for cell differentiation, the functioning of which is limited by temperature, moisture, and light (Belousova et al., 2021). Moreover, the VS-model has also been applied to generate synthetic tracheidograms and test its applicability to study the formation of intra-annual density fluctuations

(Popkova et al., 2018), one of the most frequent climatic markers of tree rings in drought-prone areas as southern Siberia (e.g., Arzac et al., 2021a). Recently, dendroanatomical data were used in a new model to assess how tracheids of different sizes can contribute to the hydraulic properties of tree rings (Sviderskaya et al., 2021). Thus, in recent years the VS-model has been widely used beyond its original conceptualization to be applied to dendroanatomy-related studies.

4. Future perspectives for dendroanatomy in Russia

Almost 50 % of Russia, the world's largest country, is forested (FAO and UNEP, 2020), with several tree species inhabiting extensive areas within different climatic zones, from the subtropics to the Arctic. The use of dendroanatomy was proven to be an effective tool for assessing the climate impact on tree radial growth under different conditions. This approach can be effectively applied in Russia in trees growing along a wide range of climatic gradients and extended geographical transects (e.g., latitudinal, longitudinal, altitudinal), where it can reveal changes in the wood structure of trees as an adaptation across climatic and environmental gradients. This becomes especially relevant considering that the projected climate changes may exceed the threshold when tree species are able to adapt to a rapidly changing environment, with significant potential consequences on the structure, age, and composition of forests and, in turn, on forests' contribution to global carbon uptake. For these reasons, it is essential to continue investigating the influence of environmental conditions on tree growth and wood structure in order to better understand the response of trees to environmental changes.

Unfavorable environmental conditions that affect physiological processes reduce the growth of a tree. For example, water deficiency inhibits growth, as the tree closes the stomata, reduces the intensity of photosynthesis, stops cell growth, and creates other unfavorable conditions inside the tree, which can be tracked using dendroanatomy. Future research should focus on the relationship between function and structure, such as mechanical conductivity and structural support, to understand how these functionalities may be affected by ongoing climate change. In addition, the study using dendroanatomy of different tree species with different stem architecture or the same species growing in different climatic conditions will take a huge step ahead in understanding wood functions.

The combination of several disciplines, such as dendrochronology, dendroanatomy and modeling, with tools such as remote sensing and/or on-site study of tree response (e.g., monitoring of seasonal growth, sap flow measurements, Etc.), will contribute more effectively to the forest management decisions in the face of climate change.

5. Conclusions

Russians dendroanatomists, in the search for the understanding the intra-annual dynamics of tree-ring growth, have been pioneers in the development of methodologies and software (e.g., staining, measurements, modeling), many of which have been exported worldwide and contributed to the development of dendroanatomy. This review presented an overview of dendroanatomy-related studies published by Russian scientists over the last 70 years, including a total of 43 manuscripts published in Russian, hardly accessible to the broader international scientific community. Besides providing an overview related to the new methodologies proposed, here we highlighted the critical contribution of Russian investigations for the dendroanatomy of boreal ecosystems. All these researches targeted a wide spectrum of topics: from the study of the environmental effect on the wood structure and cell anatomy (i.e., the shift of limiting factors of tree growth and wood formation, from temperature limitation in the north to water limitation in the south), to wood formation monitoring (i.e., timing of cell productions, growing season length) or the modeling of the process (i.e., cell production, simulation of tracheidograms) which controls wood formation under different environmental conditions. It is important to remember and recognize that many of these studies partially set the basis for the current state of dendroanatomy worldwide.

Declaration of Competing Interest

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dendro.2023.126128.

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