Systematic Review: Climate and Non-Climate Factors Influencing Wood Density in the Boreal Zone

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Wood density is a crucial factor in determining the quality of wood in boreal ecosystems within the Northern Hemisphere. Climate variables play a significant role in shaping wood density, posing challenges for forest managers and stakeholders in the wood industry to adapt amidst climate change. However, our current understanding of these effects remains incomplete. This systematic literature review explores the multifaceted influences on wood density in the boreal zone, encompassing both climate-related and non-climatic factors. The findings demonstrate that warmer temperatures can cause both increases and decreases in wood density, primarily due to their impact on tracheid lignification and cell wall thickening. Nonetheless, the outcome depends on various factors, including species type, age, soil conditions, presence of pests and diseases, fire, windstorms, and silviculture practices. The quantification of complex relationships between these factors and wood density has been insufficient in existing literature. Understanding the impacts of both climate and non-climate factors on wood density is essential for fostering a sustainable wood industry, while effectively mitigating adverse effects and maximizing benefits. Forest managers can leverage this knowledge to optimize wood production strategies, ensuring long-term ecological resilience amidst the increasingly variable climate challenges.

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INTRODUCTION

The Boreal Zone (BZ) forms a ring around the North Pole and lies immediately south of the Arctic Circle, encircling the Northern Hemisphere (Brandt 2009; Gauthier *et al.* 2015). This region experiences long, cold winters and short, warm summers. It includes parts of Canada, USA, Norway, Sweden, Finland, Russia, and China (Gauthier *et al.* 2015). The BZ is renowned for its abundant biodiversity, with its forests providing habitats for diverse fauna. The region includes not only forested areas but also other types of woodland and treeless regions, such as alpine regions on mountains, heathlands in maritime regions, grasslands in drier areas, and wetlands (Brandt 2009; Gauthier *et al.* 2015). The tree species composition of the BZ forests varies depending on the specific location within the zone. In general, coniferous trees make up approximately 70% to 80% of the tree population (Brandt 2009; Gauthier *et al.* 2015).

The Boreal Zone covers 17% of the earth's land surface and is crucial for the Earth's ecosystem, as it holds more than 30% of all carbon present in terrestrial biomes (Kasischke 2000; Bradshaw *et al.* 2009). The BZ stores a total of approximately 1095 Pg of carbon, with most of it residing in the soils, peatlands, and forests (Bradshaw and Warkentin, 2015). Additionally, the BZ is essential to the global timber products market, with approximately 33% of lumber and 25% of paper exports originating from the boreal forest (Brecka *et al.* 2018). However, the region is currently facing threats from climate change, which may impact the health of the forest and the quality of wood production (Camarero and Gutiérrez 2017).

Climate change has a profound impact on wood production in boreal ecosystems. Rising temperatures have led to increased precipitation and longer growing seasons (Price *et al.* 2013), resulting in earlier primary growth such as shooting, leafing, and flowering, as well as enhanced secondary growth such as earlier xylem cell production and differentiation (Rossi *et al.* 2007; Lasserre *et al.* 2009; Zhai *et al.* 2012; Hember *et al.* 2017; Boakye *et al.* 2021). However, the benefits of climate change can be eroded due to the increased risk of disturbances such as pests, diseases, and extreme weather events (D'Orangeville *et al.* 2018; Venäläinen *et al.* 2020; Boakye *et al.* 2022, 2023). Furthermore, warmer temperatures have caused drought stress, leading to decreased tree growth and mortality (Hogg *et al.* 2008; Nabais *et al.* 2018; Venäläinen *et al.* 2020). As the pace of climate change accelerates, it is imperative for forest managers to adapt their management strategies to sustain wood production.

Wood quality attributes (WQA) refer to the characteristics of wood that influence its suitability for a particular end use. These attributes are primarily determined by cambium activity, also known as xylogenesis (Mvolo *et al.* 2019; Zhang *et al.* 2020). Of the various WQA, wood density is critical, since it affects the wood's strength, durability, and workability (Rathgeber *et al.* 2006; Romagnoli *et al.* 2014) in addition to its weight, which can have broad applications. Moreover, wood density is closely linked to the amount of water that wood can absorb, which in turn affects its resistance to insect damage and decay (Huang *et al.* 2003). Therefore, comprehending the impacts of climate change on wood density is essential for mitigating any adverse effects on wood quality, which is a key factor in the success of the wood industry.

Wood density is influenced by several factors beyond just climate (Watt *et al.* 2008). These factors include the species of the tree, which is related to its genetics (Rozenberg and Cahalan 1997), the tree's age (Gryc *et al.* 2011), the growing conditions of the soil (Wieruszewski and Mydlarz 2021), the topography of the area (Rossi *et al.* 2015), inter-tree competition (Pretzsch and Rais 2016), disturbances from pests (Brecka *et al.* 2018; Camarero, 2022), windstorms (Sanginés de Cárcer *et al.* 2021), wildfires (McCullough *et al.* 1998), and management practices (Peng and Stewart 2013). For instance, the density of a tree's wood can vary widely depending on its genetic traits. This is because the genetic makeup of a tree influences the size, shape, and chemical composition of its wood cells, which affects the density of the wood (Peltola *et al.* 2009; Soro *et al.* 2022).

The growing conditions of the tree, such as soil fertility, water availability, and sunlight exposure, also have a significant impact on its wood density (Giroud *et al.* 2017; Bouslimi *et al.* 2022). Trees that grow in warmer locations with more sunlight and water generally produce denser wood. Conversely, trees that grow in cooler climates with less sunlight and water tend to produce less dense wood (Camarero and Gutiérrez 2017). Additionally, the fertility and moisture levels of the soil are also important factors in wood density. Wood density is influenced by changes in soil fertility, which can affect tree growth rates, ultimately impacting the accumulation and tightening of wood fibers (Cao *et al.* 2008).

In recent years, significant progress has been made in comprehending the influence of both climate change and non-climatic factors on the boreal zone. Nonetheless, most of the reviews in this field have been primarily centered around the effects of climate change on forest health, ecosystem functioning, forestry adaptation practices, and the overall carbon balance of the forest (Gauthier *et al.* 2015; Brecka *et al.* 2018; Triviño *et al.* 2022), with less attention given to wood quality (Zhang *et al.* 2020). There has not been a comprehensive synthesis of the impact of both climate and non-climatic factors on wood density and its effects on the production of quality wood. The objectives of this review are to integrate existing research on the impact of climate and non-climatic factors on wood density and to assess the implications of these findings for the future impacts of climate change. The apparent focus on conifers in this review is a reflection of the predominance of coniferous species over deciduous ones in the BZ forests and in the studies reported in the literature.

COMPILATION OF REVIEW STRATEGY

Systematic searches of peer-reviewed publications were conducted in three electronic databases (Scopus, ScienceDirect, and Google Scholar) from 1985 to 2023 to ensure the accessibility and inclusion of all relevant publications related to climate change and wood density in the boreal zone. The searches consisted of two steps. Firstly, to generate the most comprehensive list of relevant studies possible, specific keywords were used: ("climate change") AND ("disturbance" OR "biotic" OR "abiotic") AND ("management") AND ("wood quality" OR "wood density") AND ("Boreal zone" OR "Boreal forest" OR "Taiga" OR "Conifer" OR "Deciduous"). These keywords were selected based on their relevance to the research topic. The second search was similar to the first, but specific terms for climate change and wood quality were used to minimize the number of articles excluded and to ensure a thorough investigation of the available literature.

After the removal of duplicates, 66,900 studies were identified, of which 66,600 were excluded based on titles and abstracts. Further assessment excluded 219 studies due to a lack of relevant wood quality and climate assessments, leaving a final selection of 81 studies. In the following sections, the findings based on reviewing of both climate and non-climate factors and their effect on wood density, as well as the implications of these findings to management are discussed. Moreover, the importance of understanding the effects of climate on wood density and the need for further research are emphasized.

FINDINGS

Climate and Wood Density

Climate exerts a significant influence on the characteristics of wood density, including cell count, size, and cell wall thickness (Wang *et al.* 2002; Rossi *et al.* 2008; Lenz *et al.* 2010; Sattler *et al.* 2016; Sun *et al.* 2016). Maximum wood density displays a strong correlation with warm seasonal temperatures in various tree species, such as *Picea* *mariana* (Mill.) B.S.P. (black spruce), *Picea glauca* (Moench) Voss (white spruce), *Pinus banksiana* Lamb. (jack pine) (Kilpeläinen *et al.* 2003; Düthorn *et al.* 2015), *Pseudotsuga menziesii* (Mirbel) Franco (Douglas fir) (Filipescu *et al.* 2014), and *Larix sibirica* Ledeb. (Siberian larch) (Chen *et al.* 2012). Both earlywood density and latewood density of black spruce are positively correlated with summer temperature (Wang *et al*. 2002). Warmer conditions enhance the lignification of tracheids and thickening of cell walls, resulting in higher wood density (Gindl *et al.* 2001). Conversely, elevated temperatures and water deficits during summers may cause a decrease in jack pine wood density in eastern Canada due to reduced photosynthesis (Savva *et al.* 2010). Moreover, Camarero and Gutiérrez (2017) reported a reduction in maximum wood density during colder weather in the late growing season, attributable to decreased lignification and thickening rates of latewood tracheids. Nevertheless, the impact of climate on wood density is complex and species-dependent, with varying responses observed (Franceschini *et al.* 2013; Ramage *et al.* 2017; Harvey *et al.* 2020).

Species and Wood Density

Wood density differs substantially among tree species, which can be attributed to the influence of tree genetics on growth patterns, as demonstrated by various studies (Zhang *et al.* 2003; Lenz *et al.* 2010; Peltola *et al.* 2009; Soro *et al.* 2022), including investigations conducted on jack pine and white spruce in Eastern Canada (Savva *et al.* 2010). Throughout their growth, trees exhibit a wide range of densities due to variations in the compaction and thickness of cell walls, as well as the presence of air-filled vessels (Huang *et al.* 2003; Van Leeuwen *et al.* 2011). Interestingly, these variations in wood density are observed across both broad-leaved and coniferous species. Giroud *et al*. (2017) ranked the dominant boreal tree species in terms of average wood density, revealing the following descending order: *Betula papyrifera* Marshall (white birch) (575 kg/m^3), black spruce (481 kg/m^3), jack pine (469 kg/m^3), *Populus tremuloides* Michx. (trembling aspen) (459 kg/m^3), white spruce (431 kg/m^3), and *Abies balsamea* (L.) P. Mill. (Balsam fir) (403 kg/m^3).

Tree Aging and Wood Density

The variation in wood density follows a radial pattern, which is typically indicated by the number of annual rings counted from the pith outward. This measurement is referred to as the cambial age of the ring (Plomion *et al.* 2001; Mvolo *et al.* 2022). These radial trends assist in classifying wood into two categories: juvenile wood and mature wood zones. Juvenile wood generally forms within the first 15 to 20 years, while mature wood forms later (Zobel and Sprague 1998; Plomion *et al.* 2001).

While not all of these species are native to the boreal region, some boreal species such as Eastern hemlock (*Tsuga canadensis* (L.) Carrière), eastern larch (*Larix laricina* (Du Roi) K. Koch), as well as temperate species such as western larch (*Larix occidentalis* Nutt.), southern hard pines (subgenus Pinus, the diploxylon) including longleaf (*Pinus palustris* Mill.), and slash (*Pinus elliottii* Engelm.) pine, juvenile wood exhibits lower density than mature wood (Schimleck *et al.* 2022) due to its larger lumens, thinner cell walls, and lower lignification (Zobel and Sprague 1998; Plomion *et al.* 2001; Mansfield *et al.* 2009).

As a tree grows and ages, its wood fibers become more compressed and tightly packed within a given volume, and the cell walls thicken, resulting in higher density in mature wood (Park *et al.* 2009; Sillett *et al.* 2010; Mvolo *et al.* 2022). However, exceptions to this phenomenon exist due to species-specific genetic and anatomical characteristics, as well as site-specific environmental factors that influence tree growth. For example, in the case of white spruce (Mvolo *et al.* 2022) and jack pine (Park *et al.* 2009; Savva *et al.* 2010), juvenile wood tends to have higher density than mature wood. Koubaa *et al*. (2005) and Alteyrac *et al*. (2006) investigated the radial variation in wood density with cambial age and found that in black spruce, wood density is high near the pith but decreases significantly with increasing cambial age up to 10 years of tree growth. Schimleck *et al.* (2022) observed a similar trend in various tree species, including jack pine, red pine, the western hard pines, western hemlock, the genera *Pseudotsuga*, *Picea*, and *Abies*. In these species, wood density is initially high at the pith, decreases during the first few years, and then increases as cambial age continues to advance.

A few species such as Atlantic white cedar (*Chamaecyparis thyoides* (L.) BSP), bald cypress (*Taxodium distichum* (L.) Rich.), and eastern red cedar (*Juniperus virginiana* L.) exhibit a general decrease of wood density with the aging of the tree (Schimleck *et al.* 2022).

Overall, the juvenile wood zone exhibits significant variability. Rings closer to the pith can display both very high and very low density. However, they generally have wider ring widths due to their proximity to the living crown during xylogenesis. Consequently, these wider rings during the first 1 to 3 years have minimal impact on bulk wood density, particularly considering the long lifetime of trees in the BZ.

Soil and Wood Density

Nitrogen, phosphorus, and potassium are essential for tree growth and development. Increasing temperatures in the northern boreal forest are accelerating chemical reactions that release these nutrients, thus increasing the growth of trees and microbial populations. However, increasing soil nutrient addition has been linked to decreased wood density in Norway spruce (Cao *et al.* 2008). Increasing nutrient availability leads to increased tree growth rates, which results in less dense wood. Furthermore, higher temperatures in the southern boreal forest are increasing evaporation of soil moisture, making the soil more prone to droughts. The consequence of this is increased stress, stunted growth, and decreased wood density of tree species (Nearing *et al.* 2004; Giroud *et al.* 2017; Pugnaire *et al.* 2019; Bouslimi *et al.* 2022). Additionally, topographical variation causes individual trees to differ in wood density, as terrain slope, aspect, and altitude all modify the availability of light, moisture, and nutrients for growth (Rossi *et al.* 2015).

Pests and Disease and Wood Density

Pests can have varying effects on wood bulk density due to their distinct feeding habits and behaviors. For example, insects such as beetles tunnel into wood to lay their eggs and larvae, weakening the structure and reducing wood density. Termites, on the other hand, feed on wood's cellulose and lignin, leading to a deterioration in density (McCullough *et al.* 1998; Brecka *et al.* 2018). Wood borers also cause physical damage by chewing on the surface, further reducing density. In live trees, pests damage the tree by consuming sapwood and heartwood, resulting in a decrease in density. In dead trees, pests consume softer wood, such as sapwood, which reduces density. Additionally, dead wood is more prone to decay, further lowering wood density (Jacobs and Work 2012).

Infectious diseases can significantly impact wood density, leading to slower growth, structural damage, and premature death. Fungal infections can cause trees to allocate more resources to defense mechanisms, reducing the available resources for growth and resulting in lower wood density (Brecka *et al.* 2008). Fungal root rot can reduce a tree's ability to absorb water and nutrients, resulting in slower growth and lower wood density (Koricheva *et al.* 2006). For instance, brown rot decay in eastern white cedar (*Thuja occidentalis* L.) selectively removes structural carbohydrate components, leading to an increase in the lignin/carbohydrate ratio as decay progresses. This process causes more significant density changes in earlywood compared to latewood tracheids (Bouslimi *et al.* 2014). However, the brown-rot effect on decreasing wood density is less pronounced than that of its counterpart, white-root fungus, especially in spruce trees (Reinprecht *et al.* 2007).

Windstorm and Wood Density

Changes in wood density occur due to the formation of reaction wood in response to wind disturbance. This specialized wood, namely compression wood and tension wood, helps trees adapt and maintain their structural integrity (Sanginés de Cárcer *et al.* 2021). Compression wood is predominantly found in conifers, whereas tension wood is predominantly found in broadleaf trees. This distinction arises from the varying structural needs and growth patterns exhibited by these two types of trees (Schweingruber *et al.* 2018). Compression wood develops on the lower side of branches or leaning stems, becoming denser and stiffer than normal wood. It contains higher lignin content, smaller cell lumens, and thicker cell walls. This wood provides support against compressive stress caused by wind and gravity. On the other hand, tension wood forms on the upper side, exhibiting less density but greater flexibility. It has higher cellulose content, larger cell lumens, and thinner cell walls. Tension wood absorbs and dissipates tensile forces induced by wind, preventing breakage (Sanginés de Cárcer *et al.* 2021; Potterf *et al.* 2022). The changes in wood density associated with compression wood and tension wood enable trees to balance the effects of wind disturbance. Compression wood supports the compressed side, while tension wood counters tensile stress on the opposite side. This adaptive mechanism helps trees withstand wind-induced stresses and ensures their growth and survival in varying environmental conditions (Potterf *et al.* 2022).

Wildfire and Wood Density

Wildfires significantly impact wood density by causing physical changes in its structure (Bravo 2010). A study analyzed post-fire scars on North American conifers to understand the effects of fire on wood density (Arbellay *et al.* 2014). The findings revealed that Douglas fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), and ponderosa pine (*Pinus ponderosa*) species experienced the strongest impact on wood density within the first year after fire injury. Tracheid density increased by 21% to 53% for these species, while Douglas fir and western larch also exhibited a rise in ray density by 19% to 36%. The increased density of tracheids is linked to ethylene synthesis, which occurs as a response to fire-induced injuries and interferes with auxins flow during tracheid formation. On the other hand, ponderosa pine generally did not display an increase in ray tissue (radial parenchyma) after fire injury. Changes in ray density vary not only among species of different genera but also among species within the same genus.

Silviculture Practices and Wood Density

Silvicultural practices, such as thinning and spacing, have a direct impact on wood density by regulating the growth conditions of trees (Mörling 2002). Thinning improves the wood density of individual trees by promoting their growth rate through decreased competition (Zhai *et al.* 2012; Diao *et al.* 2022). However, despite the initial increase, thinning has been observed to decrease wood density in Quebec black spruce stands (Vincent *et al.* 2011) and jack pine stands in New Brunswick, Canada (Schneider *et al.* 2008). Excessive thinning diminishes the wood density of Norway spruce as it accelerates growth rates, resulting in a shorter duration for tracheid lignification (Cao *et al.* 2008).

Although low-intensity spacing, characterized by widely spaced trees, is advocated for reducing establishment costs and accelerating the diameter growth of individual trees, a study by Zhang *et al*. (2021) observed that such low spacing intensity actually reduces wood density in black spruce. However, Mvolo *et al*. (2022) found that except for extreme spacing, increasing the spacing intensity had no effect on wood density in white spruce. Silvicultural effects on wood density in lodgepole pine were relatively small and mostly masked by random variation at the tree level (Peng and Stewart 2013). These findings suggest that the impact of spacing on wood density is variable and dependent on the tree species. Silvicultural practices can have both positive and negative impacts on wood density, which are influenced by management objectives, tree species, and local environmental conditions.

Implications to Wood Industry

The enhancement of wood density can be achieved through various management implications, considering both climate-related and non-climatic factors. It is crucial to select suitable tree species based on local climate and soil conditions to achieve higher wood density. Additionally, silvicultural practices, such as thinning and spacing management, play a key role in optimizing wood density by ensuring trees have sufficient resources and reduced competition. Furthermore, genetic selection of tree varieties with higher wood density traits can provide advantages for future generations. By managing forests with different age classes, it becomes possible to optimize wood density variation, utilizing juvenile wood with lower density for specific applications and mature wood with higher density for others.

Adapting management strategies to climate change impacts involves altering rotations, adjusting planting times, and considering resilient species. Furthermore, the adoption of proper harvesting techniques plays a crucial role in preventing tree damage and mitigating factors that reduce wood density, thereby preserving structural integrity. Continuous monitoring of forest health and wood quality is vital for identifying emerging issues and adapting practices accordingly. Additionally, investing in research and technology to understand wood density relationships with climate and other factors facilitates informed decision-making for sustainable wood quality improvement. By implementing these implications, wood density can be enhanced, leading to valuable and sustainable timber resources.

Summary of Future Directions

Understanding the complex relationship between climate and non-climate factors is crucial for comprehending the impact of climate change on wood density in boreal ecosystems. Wood density serves as a significant indicator of forest health and productivity, making it necessary to unravel the multiple influencing factors. Climate change directly affects wood density through temperature and precipitation pattern alterations. Tree genetics, aging, soil condition, pest and disease infestations, windstorms, wildfires, and silvicultural practices also substantially shape wood density. By delving into the intricate interactions between these factors, researchers and policymakers can formulate effective strategies to mitigate climate change's adverse effects on boreal ecosystems.

Identifying genetic traits that enhance wood density resilience, implementing sustainable silvicultural practices, and developing resilient forest management approaches can help maintain healthy and productive forests amidst changing climate conditions. Ultimately, a comprehensive understanding of both climate and non-climate drivers of wood density will inform policies and practices, fostering the long-term sustainability of boreal ecosystems in a changing climate.

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