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Microfibril Angle as a Determinant of Wood Physical and Mechanical Properties Across Commercial Tree Species: A Systematic Review and Meta-analysis

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Running Title

Microfibril Angle and Wood Quality

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Abstract

Microfibril angle (MFA), defined as the orientation of cellulose microfibrils within the S2 layer of the secondary cell wall, is one of the most important anatomical characteristics influencing wood mechanical performance and utilisation. Despite extensive research conducted over the past several decades, published evidence remains dispersed across different tree species, geographical regions, and experimental approaches, limiting comprehensive understanding of the role of MFA in determining wood quality. This systematic review synthesised published evidence on the relationships between microfibril angle and the physical and mechanical properties of commercially important tree species following the **Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA 2020)** guidelines. A structured literature search was conducted using major scientific databases, including Web of Science, Scopus, ScienceDirect, SpringerLink, Wiley Online Library, and Google Scholar. Eligible peer-reviewed studies investigating the influence of MFA on wood density, modulus of elasticity (MOE), modulus of rupture (MOR), stiffness, shrinkage, dimensional stability, and related wood-quality attributes were critically evaluated using predefined inclusion criteria and methodological quality assessment procedures.

The verified evidence base comprised **17 primary studies** published between **2000 and 2013**, representing **seven countries** and multiple commercially important hardwood and softwood species. Softwoods accounted for **64.7%** of the included studies, while hardwoods represented **35.3%**. SilviScan-based analytical systems and conventional X-ray diffraction were the dominant methods used for MFA determination. Across the included studies, a consistent inverse relationship was observed between MFA and wood stiffness, with lower microfibril angles associated with higher modulus of elasticity and improved mechanical performance. Predictive models incorporating both wood density and MFA consistently outperformed models based solely on wood density, demonstrating that these variables provide complementary rather than interchangeable information regarding wood quality. Juvenile wood was consistently characterised by higher MFA and lower stiffness than mature wood, highlighting the importance of developmental stage in determining timber performance. Although relationships between MFA and modulus of rupture, shrinkage, and dimensional stability were generally supportive, they were more variable because of additional influences from density, fibre morphology, spiral grain, moisture content, and other anatomical characteristics.

The review further demonstrated that genetic factors and silvicultural practices, including spacing, thinning, fertilisation, and irrigation, influence MFA development and associated mechanical properties. Moderate-to-high heritability estimates reported in several studies indicate that MFA represents an important trait for tree improvement programmes aimed at enhancing structural timber quality. Advances in non-destructive technologies, particularly SilviScan, X-ray diffraction, and acoustic assessment, have substantially improved opportunities for rapid wood-quality evaluation in breeding programmes and commercial forestry.

Despite the generally high methodological quality of the reviewed studies, inconsistent statistical reporting limited opportunities for formal quantitative meta-analysis. Many studies failed to report effect sizes, variance estimates, or analysis-specific sample sizes required for quantitative evidence synthesis. Future investigations should therefore adopt standardised reporting protocols to improve reproducibility and facilitate robust meta-analyses.

Overall, this review confirms that microfibril angle is a fundamental determinant of wood mechanical performance and should be integrated with density and other wood-quality traits in future breeding programmes, plantation management, and timber engineering applications. The findings provide a comprehensive evidence base for researchers, forest managers, and the wood-products industry while identifying priorities for future research on sustainable wood quality improvement.

Keywords: Microfibril angle; wood density; wood quality; modulus of elasticity; modulus of rupture; SilviScan; X-ray diffraction; forest genetics; wood mechanics; systematic review.

1. Introduction

1.1 Global Importance of Wood and Wood Quality

Wood is among the most important renewable biological materials on Earth and has supported human civilization for thousands of years through its extensive use in housing, transportation, furniture manufacturing, pulp and paper production, energy generation, and numerous industrial applications (Bowyer, Shmulsky & Haygreen, 2007; Walker, 2006; Forest Products Laboratory, 2021). In recent decades, the global importance of wood has increased further owing to growing concerns regarding climate change, environmental sustainability, depletion of non-renewable resources, and the transition towards low-carbon and circular bioeconomies (FAO, 2022; IPCC, 2022; Leskinen *et al.*, 2018; Hurmekoski *et al.*, 2021). Unlike energy-intensive construction materials such as steel, aluminium, and concrete, wood is produced through biological processes that capture atmospheric carbon dioxide via photosynthesis while storing carbon throughout the service life of wood products (IPCC, 2022; FAO, 2022). Consequently, sustainable forest management and efficient utilisation of wood resources are increasingly recognised as important strategies for climate change mitigation and sustainable development (Leskinen *et al.*, 2018; Pretzsch *et al.*, 2018).

The global demand for wood and wood-based products has continued to increase because of population growth, urbanisation, industrial development, and expanding markets for engineered wood products such as glued laminated timber (glulam), laminated veneer lumber (LVL), cross-laminated timber (CLT), and mass timber construction systems (Hurmekoski *et al.*, 2021; FAO, 2022). Plantation forestry has become the principal source of industrial timber in many countries, with fast-growing species such as *Pinus radiata*, *Pinus taeda*, *Eucalyptus globulus*, *Eucalyptus grandis*, *Acacia mangium*, *Populus* spp., and *Larix kaempferi* contributing substantially to global timber production (Evans, 2009; Lasserre *et al.*, 2009; Hein *et al.*, 2013). Although plantation forests provide high productivity and shorter harvesting rotations, they also present challenges related to wood quality because rapidly grown trees frequently contain larger proportions of juvenile wood, which often differs significantly from mature wood in terms of density, stiffness, dimensional stability, fibre morphology, and anatomical structure (Zobel & Sprague, 1998; Donaldson, 2008; Apiolaza, 2009).

Wood quality has therefore emerged as one of the central themes in modern forest science, wood technology, and tree improvement programmes. Broadly, wood quality refers to the combination of anatomical, physical, chemical, and mechanical characteristics that determine the suitability of timber for specific end uses (Zobel & Jett, 1995; Barnett & Jeronimidis,

2003). Depending on the intended application, desirable wood properties may include high density, superior stiffness, high bending strength, dimensional stability, favourable machining characteristics, long fibre length, resistance to biological degradation, or high pulp yield (Kollmann & Côté, 1968; Ross, 2010; Forest Products Laboratory, 2021). These characteristics influence not only the engineering performance of timber but also processing efficiency, product recovery, economic value, and long-term durability (Walker, 2006).

Unlike manufactured engineering materials, wood is a naturally heterogeneous and anisotropic biological composite whose properties vary among species, provenances, families, individual trees, annual growth rings, and even different positions within the same stem (Panshin & de Zeeuw, 1980; Zobel & van Buijtenen, 1989). This variability reflects complex interactions among genetic inheritance, cambial age, climatic conditions, soil properties, water availability, silvicultural practices, stand density, tree physiology, and environmental stress (Downes *et al.*, 1997; Plomion, Leprovost & Stokes, 2001; Donaldson, 2008). Consequently, understanding the biological mechanisms responsible for variation in wood quality remains a major objective of wood science because such knowledge underpins tree breeding, sustainable forest management, and industrial wood utilisation.

One of the most significant advances in wood science has been the recognition that the mechanical performance of wood originates from its hierarchical structure extending from the whole tree to annual growth rings, individual cells, cell walls, and ultimately the molecular organisation of cellulose within the secondary cell wall (Cave, 1968; Barnett & Bonham, 2004; Donaldson, 2008). Among these structural characteristics, the **microfibril angle (MFA)**—the angle between cellulose microfibrils in the S2 layer of the secondary cell wall and the longitudinal axis of the wood fibre—has emerged as one of the most influential determinants of wood physical and mechanical behaviour (Evans, 1999; Evans & Ilic, 2001; Donaldson, 2008). A substantial body of research has demonstrated that MFA strongly influences modulus of elasticity, modulus of rupture, stiffness, dimensional stability, shrinkage, acoustic velocity, and other indicators of timber quality (Hein *et al.*, 2013; Ivković *et al.*, 2009; Yamashita *et al.*, 2009).

Despite the rapid expansion of research on microfibril angle over the past three decades, findings remain dispersed across numerous tree species, geographical regions, experimental designs, and measurement techniques. Differences in analytical methodologies, including X-ray diffraction, SilviScan, microscopy, synchrotron imaging, and acoustic assessment, together with variation in sampling procedures and statistical analyses, have made it difficult to compare results across studies and establish general conclusions regarding the role of MFA in determining wood quality (Evans, 2006; Downes *et al.*, 2014; Donaldson, 2008). A rigorous systematic review is therefore needed to integrate the available evidence, evaluate methodological quality, identify consistent patterns, and highlight remaining research gaps.

1.2 Wood Cell Wall Structure and the Biological Basis of Microfibril Angle

Wood is an exceptionally complex biological composite material whose remarkable engineering performance arises from its hierarchical organisation spanning multiple structural scales, from the whole tree to the molecular arrangement of cell-wall polymers (Niklas, 1992; Barnett & Jeronimidis, 2003; Gibson, 2012). This hierarchical architecture enables wood to

achieve an unusual combination of low density, high specific strength, stiffness, toughness, and durability that has made it one of the most valuable renewable structural materials available to humanity (Kollmann & Côté, 1968; Rowell, 2013). Understanding the biological basis of these properties is fundamental for explaining variations in timber quality among species, individual trees, and different growth environments (Donaldson, 2008; Plomion, Bastien, Bogeat-Triboulot & Bouffier, 2021).

Wood originates from the vascular cambium, a lateral meristem responsible for secondary growth in woody plants (Larson, Kretschmann, Clark & Isebrands, 2001). During xylogenesis, cambial initials divide to produce immature xylem cells that subsequently undergo cell expansion, secondary wall deposition, lignification, programmed cell death, and maturation before becoming functional wood tissue (Plomion, Leprovost & Stokes, 2001; Rathgeber, Cuny & Fonti, 2016). These developmental processes are tightly regulated by genetic, physiological, and environmental factors, including hormonal signalling, water availability, nutrient status, temperature, and mechanical loading (Plomion *et al.*, 2001; Donaldson, 2008; Cuny *et al.*, 2014). Variations occurring during these stages ultimately influence the anatomical, physical, and mechanical properties of wood.

The principal conducting and supporting cells of wood differ between gymnosperms and angiosperms. In softwoods (gymnosperms), approximately 90–95% of the wood volume consists of longitudinal tracheids that simultaneously perform water conduction and mechanical support (Panshin & de Zeeuw, 1980; Bowyer, Shmulsky & Haygreen, 2007). Hardwood species (angiosperms), by contrast, possess specialised vessels for water transport together with fibres that primarily provide mechanical support, as well as axial and ray parenchyma responsible for storage and physiological functions (Barnett & Jeronimidis, 2003). Although these anatomical differences influence overall wood properties, the mechanical behaviour of both softwoods and hardwoods is fundamentally governed by the organisation of their secondary cell walls (Donaldson, 2008).

Each mature wood cell consists of three principal structural components: the **middle lamella**, the **primary wall**, and the **secondary cell wall** (Kollmann & Côté, 1968; Barnett & Bonham, 2004). The middle lamella, composed predominantly of lignin, acts as an adhesive layer binding neighbouring cells together and contributing to tissue cohesion (Donaldson, 2008). Surrounding the lumen is the primary wall, a relatively thin and flexible layer deposited during cell expansion that contains randomly arranged cellulose microfibrils embedded within a matrix of hemicellulose and pectin (Cosgrove, 2005). Although essential during cell development, the primary wall contributes relatively little to the stiffness of mature wood compared with the much thicker secondary cell wall (Barnett & Jeronimidis, 2003).

The secondary cell wall is deposited after cell expansion ceases and represents the major structural component responsible for wood strength and stiffness (Kollmann & Côté, 1968). It comprises three distinct layers, designated **S1**, **S2**, and **S3**, each differing in thickness, chemical composition, and cellulose microfibril orientation (Cave, 1968; Donaldson, 2008). Among these, the **S2 layer** is the most important from a mechanical perspective because it constitutes approximately 70–85% of the total wall thickness and contains highly ordered cellulose microfibrils aligned in a predominantly longitudinal direction (Barnett & Bonham, 2004; Donaldson, 2008). Consequently, the orientation of cellulose microfibrils within the S2 layer exerts a dominant influence on the mechanical properties of wood.

The wood cell wall is composed principally of **cellulose**, **hemicellulose**, and **lignin**, together forming a naturally engineered fibre-reinforced composite (Rowell, 2013). Cellulose, the most abundant organic polymer on Earth, consists of long linear chains of β-(1→4)-linked glucose molecules aggregated into highly crystalline microfibrils possessing exceptional tensile strength and stiffness (Somerville, 2006; Burgert & Fratzl, 2009). Individual cellulose microfibrils exhibit elastic moduli exceeding 130 GPa, making them among the stiffest biological materials known (Burgert & Fratzl, 2009). These microfibrils are embedded within an amorphous matrix of hemicellulose and lignin, which together provide compressive resistance, flexibility, energy dissipation, and protection against biological degradation (Donaldson, 2008; Rowell, 2013). The remarkable mechanical behaviour of wood therefore depends not only on its chemical composition but also on the spatial arrangement of these polymers within the cell wall.

One of the most influential structural characteristics of the secondary cell wall is the **microfibril angle (MFA)**, defined as the angle formed between the orientation of cellulose microfibrils in the S2 layer and the longitudinal axis of the fibre or tracheid (Cave, 1968). Although this angle is measured at the microscopic scale, it has profound implications for the macroscopic behaviour of wood because it determines the efficiency with which tensile forces are transmitted along the cell wall (Donaldson, 2008). Small MFAs indicate that cellulose microfibrils are closely aligned with the fibre axis, allowing mechanical loads to be transferred efficiently and producing wood with high stiffness and dimensional stability (Evans & Ilic, 2001; Burgert & Fratzl, 2009). Conversely, larger MFAs permit greater shear deformation within the lignin–hemicellulose matrix, reducing longitudinal stiffness while increasing flexibility and longitudinal shrinkage (Donaldson, 2008; Hein *et al.*, 2013).

Microfibril orientation is established during secondary wall formation through the coordinated activity of cellulose synthase complexes located within the plasma membrane of differentiating xylem cells (Baskin, 2001; Somerville, 2006). These enzyme complexes move along cortical microtubules, depositing cellulose microfibrils in highly regulated orientations that ultimately determine the microfibril angle of the mature cell wall (Cosgrove, 2005). Because this process is genetically regulated yet responsive to environmental signals, MFA is influenced by both hereditary factors and external conditions, including wind loading, stem inclination, growth rate, water availability, nutrient supply, and silvicultural management (Plomion *et al.*, 2001; Apiolaza, 2009; Donaldson, 2008). This interaction between genotype and environment contributes substantially to variation in wood quality among species and plantations.

Several analytical techniques have been developed to quantify MFA. Early investigations relied on **polarised light microscopy** and **X-ray diffraction**, which remain important reference methods for examining cellulose orientation (Cave, 1968; Donaldson, 2008). More recently, technologies such as **SilviScan**, **synchrotron X-ray diffraction**, **Raman spectroscopy**, **near-infrared spectroscopy (NIR)**, and **acoustic methods** have enabled rapid, high-resolution, and often non-destructive assessment of MFA and associated wood properties (Evans, 1999; Evans, 2006; Downes *et al.*, 2014). Among these methods, SilviScan has become one of the most widely used research platforms because it simultaneously measures MFA, wood density, fibre dimensions, and predicted mechanical properties from increment cores, thereby providing comprehensive information for tree breeding and wood quality assessment (Evans, 2006).

Accumulating evidence demonstrates that MFA is a central determinant of wood performance because it links cell-wall ultrastructure with whole-wood mechanical behaviour (Donaldson, 2008; Hein *et al.*, 2013). Variations in MFA influence stiffness, bending strength, longitudinal shrinkage, creep, acoustic velocity, fracture behaviour, and dimensional stability across a broad range of commercially important tree species (Evans & Ilic, 2001; Ivković *et al.*, 2009; Yamashita *et al.*, 2009). Consequently, MFA has become a key trait in forest genetics, plantation management, wood science, and timber engineering. Understanding its biological basis provides the foundation for interpreting the relationships between wood ultrastructure and engineering performance that are examined throughout this review.

1.3 Wood Density as a Determinant of Wood Quality

Wood density is one of the most widely investigated and frequently used indicators of wood quality because of its close association with numerous physical, mechanical, anatomical, and technological properties of timber (Zobel & van Buijtenen, 1989; Walker, 2006; Forest Products Laboratory, 2021). Density represents the amount of wood substance contained within a given volume and reflects the relative proportions of solid cell-wall material and void spaces within the wood structure (Kollmann & Côté, 1968; Siau, 1995). Because the cell wall constitutes the primary load-bearing component of wood, density has historically been regarded as one of the strongest predictors of timber performance and has therefore become a fundamental selection criterion in forest genetics, tree breeding, wood processing, and timber grading systems (Zobel & Jett, 1995; Barnett & Jeronimidis, 2003).

Several definitions of wood density are recognised in wood science depending on the moisture condition under which measurements are obtained. These include **basic density**, defined as oven-dry mass divided by green volume; **oven-dry density**, calculated using oven-dry mass and oven-dry volume; **air-dry density**, determined at equilibrium moisture content under standard atmospheric conditions; and **green density**, representing freshly harvested wood before drying (Siau, 1995; Walker, 2006). Among these, **basic density** is the most widely reported parameter in forestry research because it provides a standardized measure that facilitates comparisons among species, sites, and silvicultural treatments (Downes *et al.*, 1997; Zobel & van Buijtenen, 1989).

The density of wood is determined by the proportion of solid cell-wall material relative to the volume occupied by cell lumina, vessels, resin canals, and intercellular spaces (Panshin & de Zeeuw, 1980; Barnett & Jeronimidis, 2003). At the microscopic level, density is strongly influenced by cell-wall thickness, lumen diameter, fibre dimensions, vessel frequency in hardwoods, tracheid characteristics in softwoods, and the relative proportions of earlywood and latewood formed during each growing season (Donaldson, 2008; Rowell, 2013). Species producing thick-walled fibres or tracheids with relatively small lumina generally exhibit higher wood density than species characterised by thin-walled cells and larger lumina (Kollmann & Côté, 1968). Consequently, wood density integrates multiple anatomical characteristics and serves as an indirect indicator of cell-wall development and structural investment.

Density is also influenced by numerous biological and environmental factors operating throughout tree development. Genetic inheritance plays a major role, with moderate to high heritability reported for wood density in several commercially important species, including *Pinus radiata*, *Pinus taeda*, *Picea abies*, and *Eucalyptus* species (Apiolaza, 2009; Grattapaglia *et al.*, 2009; Lasserre *et al.*, 2009). However, environmental variables—including climate, precipitation, temperature, soil fertility, nutrient availability, water stress, stand density, and silvicultural management—also influence xylem formation and therefore modify density within and among sites (Plomion, Leprovost & Stokes, 2001; Donaldson, 2008). Cambial age further contributes to density variation, as juvenile wood frequently differs from mature wood because of changes in cell dimensions, wall thickness, and annual ring characteristics (Zobel & Sprague, 1998).

The engineering importance of wood density arises from its strong association with numerous mechanical properties. Higher-density wood generally exhibits increased modulus of elasticity (MOE), modulus of rupture (MOR), compressive strength, hardness, shear strength, abrasion resistance, and nail-holding capacity because greater quantities of cell-wall material are available to resist applied mechanical loads (Ross, 2010; Forest Products Laboratory, 2021). Numerous investigations have reported significant positive relationships between density and stiffness across both hardwood and softwood species (Evans & Ilic, 2001; Walker, 2006; Hein *et al.*, 2013). Consequently, density has long served as one of the principal variables incorporated into timber grading standards and predictive models used by the forest products industry.

Despite its importance, density alone cannot fully explain variation in wood mechanical performance. Trees with similar densities may exhibit substantially different values of stiffness, bending strength, longitudinal shrinkage, and dimensional stability because density does not directly account for differences in cell-wall ultrastructure (Donaldson, 2008). In particular, cellulose microfibril orientation within the secondary cell wall exerts a profound influence on mechanical behaviour independent of density (Cave, 1968; Evans & Ilic, 2001). As a result, two wood samples possessing nearly identical densities may differ considerably in modulus of elasticity if their microfibril angles differ substantially (Hein *et al.*, 2013; Yamashita *et al.*, 2009). This observation has become one of the central themes in modern wood science and has prompted increasing interest in integrating anatomical and physical indicators when assessing timber quality.

Numerous experimental studies have demonstrated that combining wood density with microfibril angle substantially improves the prediction of mechanical properties compared with models based solely on density. Evans and Ilic (2001) reported that both density and MFA contributed significantly to explaining variation in stiffness in *Pinus radiata*, with MFA accounting for additional variation not explained by density alone. Similar findings have been reported for *Eucalyptus globulus* (Raymond, Muneri & MacDonald, 2006), *Eucalyptus urophylla* × *grandis* (Hein *et al.*, 2013), *Larix kaempferi* (Yamashita *et al.*, 2009), and *Picea abies* (Gräns *et al.*, 2009), where integrated models consistently outperformed single-variable approaches. These findings indicate that density and MFA provide complementary information concerning wood structure and should therefore be considered jointly when evaluating timber quality.

Technological advances have further strengthened the integration of density and MFA in wood quality assessment. Modern platforms such as **SilviScan** simultaneously determine density, microfibril angle, fibre dimensions, and predicted mechanical properties from

increment cores with high spatial resolution (Evans, 2006; Downes *et al.*, 2014). These systems have transformed wood quality research by enabling rapid, non-destructive evaluation of standing trees and facilitating early selection in breeding programmes (Apiolaza, 2009). Likewise, near-infrared spectroscopy, acoustic methods, and X-ray densitometry have expanded opportunities for large-scale wood quality assessment in both research and operational forestry (Schimleck *et al.*, 2019). The integration of these technologies has improved understanding of the interactions among density, MFA, and mechanical performance while supporting more efficient genetic improvement programmes.

Although density remains one of the most practical and informative indicators of timber quality, accumulating evidence clearly demonstrates that it should not be interpreted in isolation. Rather, wood density interacts with microfibril angle, fibre morphology, moisture content, chemical composition, and growth characteristics to determine the final engineering performance of timber (Donaldson, 2008; Hein *et al.*, 2013). Understanding these interactions is essential for developing accurate predictive models of wood quality and provides the foundation for examining the direct influence of microfibril angle on wood mechanical behaviour, which forms the central focus of this systematic review.

1.4 Mechanical Properties of Wood and the Influence of Microfibril Angle

The mechanical properties of wood determine its ability to resist external forces without excessive deformation or structural failure and therefore represent one of the principal criteria used to evaluate timber quality for structural and industrial applications (Bodig & Jayne, 1982; Forest Products Laboratory, 2021). Mechanical performance influences the suitability of wood for beams, columns, bridges, flooring, utility poles, engineered wood products, and modern mass timber construction systems, where reliability, safety, and long-term dimensional stability are essential (Walker, 2006; Ross, 2010; Ramage *et al.*, 2017). As global demand for sustainable construction materials increases, understanding the biological factors controlling wood mechanics has become increasingly important for forest genetics, timber engineering, and wood science (Hurmekoski *et al.*, 2021; IPCC, 2022).

Unlike isotropic engineering materials such as steel and aluminium, wood is an **orthotropic biological composite**, exhibiting different mechanical properties along the longitudinal, radial, and tangential directions because of the orientation of its cellular structure and cell-wall polymers (Bodig & Jayne, 1982; Barnett & Jeronimidis, 2003). The longitudinal direction, parallel to the grain, exhibits the greatest strength and stiffness because cellulose microfibrils within the secondary cell wall are predominantly aligned with the fibre axis (Cave, 1968; Donaldson, 2008). In contrast, radial and tangential properties are substantially lower because loads are transferred across cell walls and middle lamellae rather than directly through cellulose microfibrils (Kollmann & Côté, 1968). Consequently, the anisotropic nature of wood must be considered when evaluating its mechanical behaviour and engineering performance.

Among the numerous mechanical properties of timber, the **modulus of elasticity (MOE)** is widely recognised as one of the most important indicators of structural quality because it quantifies the stiffness of wood and its resistance to elastic deformation under applied loads (Ross, 2010; Forest Products Laboratory, 2021). High MOE values indicate that timber can

support greater loads while undergoing relatively small elastic deflections, making this property particularly important in structural applications such as beams, roof trusses, bridge decks, and laminated timber products (Walker, 2006). Numerous investigations have demonstrated that MOE is influenced by wood density, moisture content, fibre morphology, juvenile wood proportion, and, most importantly, microfibril angle (Evans & Ilic, 2001; Donaldson, 2008; Hein *et al.*, 2013).

The **modulus of rupture (MOR)** represents the maximum stress sustained by wood immediately before failure during static bending and is commonly used as an indicator of ultimate bending strength (Bodig & Jayne, 1982; Ross, 2010). While MOE describes the elastic response of wood under loading, MOR reflects its capacity to resist catastrophic structural failure. Both properties are fundamental for structural timber grading and design because they directly influence allowable design stresses and safety factors incorporated into engineering standards (Forest Products Laboratory, 2021). Previous research has shown that although MOR is positively associated with density, variation in cellulose microfibril orientation also contributes to differences in bending strength through its influence on stress distribution within the secondary cell wall (Evans & Ilic, 2001; Hein *et al.*, 2013).

Wood mechanical performance is also characterised by compressive strength, tensile strength, shear strength, hardness, toughness, impact resistance, fatigue resistance, creep behaviour, and fracture toughness (Kollmann & Côté, 1968; Bodig & Jayne, 1982). These properties collectively determine the ability of timber to withstand diverse loading conditions encountered during manufacturing and service (Barnett & Jeronimidis, 2003). Their expression depends on interactions among cell-wall chemistry, fibre dimensions, moisture content, annual ring characteristics, density, and cellulose orientation (Rowell, 2013). Consequently, no single property provides a complete description of wood performance, emphasising the need to evaluate multiple anatomical and physical characteristics simultaneously.

Among the structural determinants of wood mechanics, **microfibril angle has emerged as one of the strongest predictors of longitudinal stiffness** because it directly governs the orientation of cellulose, the primary load-bearing component of the cell wall (Cave, 1968; Burgert & Fratzl, 2009). Cellulose microfibrils possess exceptionally high tensile strength and elastic modulus, and their alignment relative to the longitudinal axis determines how efficiently tensile forces are transmitted through the secondary cell wall (Somerville, 2006; Burgert & Fratzl, 2009). When the microfibril angle is small, cellulose microfibrils are nearly parallel to the fibre axis, resulting in efficient load transfer, increased stiffness, and higher MOE (Evans & Ilic, 2001; Donaldson, 2008). Conversely, larger microfibril angles permit greater shear deformation within the lignin–hemicellulose matrix, reducing stiffness while increasing flexibility and longitudinal shrinkage (Donaldson, 2008; Hein *et al.*, 2013).

The relationship between MFA and mechanical performance has been consistently demonstrated across a wide range of commercially important species. In *Pinus radiata*, Evans and Ilic (2001) reported strong inverse relationships between MFA and MOE, demonstrating that reductions in microfibril angle were associated with substantial increases in wood stiffness. Similar relationships have been reported in *Eucalyptus globulus* (Raymond, Muneri & MacDonald, 2006), *Eucalyptus urophylla* × *grandis* (Hein *et al.*, 2013), *Larix kaempferi* (Yamashita *et al.*, 2009), *Picea abies* (Gräns *et al.*, 2009), and *Pinus taeda* (Jordan *et al.*, 2005). Although the magnitude of reported relationships varies among species, the overall

evidence consistently indicates that decreasing MFA is associated with increasing stiffness and improved structural performance.

Microfibril angle also influences several other wood properties relevant to engineering applications. Larger MFAs have been associated with greater longitudinal shrinkage during drying, reduced dimensional stability, increased creep deformation, lower acoustic velocity, and greater susceptibility to distortion (Walker & Butterfield, 1996; Donaldson, 2008). These characteristics are particularly important for structural timber because dimensional instability may reduce serviceability, increase maintenance requirements, and compromise product performance over time. Consequently, the influence of MFA extends beyond stiffness to encompass multiple aspects of timber quality that affect manufacturing, drying, grading, and long-term utilisation.

Advances in non-destructive evaluation have further highlighted the practical importance of MFA. Technologies including SilviScan, X-ray diffraction, acoustic resonance, ultrasonic testing, and near-infrared spectroscopy now permit rapid estimation of wood stiffness in standing trees and increment cores without destructive harvesting (Evans, 2006; Downes *et al.*, 2014; Schimleck *et al.*, 2019). Because MFA strongly influences acoustic velocity and dynamic stiffness, incorporating MFA into predictive models has substantially improved the accuracy of wood quality assessment and facilitated earlier selection of superior genotypes in tree breeding programmes (Apiolaza, 2009; Ivković *et al.*, 2009). These developments demonstrate the increasing value of MFA as both a biological trait and an operational tool for sustainable forest management.

Despite extensive research demonstrating the importance of microfibril angle, considerable variability remains among published studies regarding the magnitude of reported relationships, the relative contribution of MFA compared with density, and the influence of genetics, environment, cambial age, and silvicultural management (Donaldson, 2008; Apiolaza, 2009). Differences in measurement techniques, sample preparation, moisture conditions, statistical analyses, and experimental design further complicate direct comparison among investigations (Evans, 2006; Hein *et al.*, 2013). Consequently, a comprehensive systematic review is required to synthesise available evidence, evaluate methodological quality, identify consistent trends, and clarify the overall contribution of microfibril angle to wood mechanical performance across commercially important tree species.

1.5 Juvenile and Mature Wood: Implications for Microfibril Angle and Wood Quality

The formation of juvenile and mature wood represents one of the most important developmental processes influencing wood quality in forest trees. As trees grow, the vascular cambium undergoes physiological and developmental changes that alter xylem structure, resulting in systematic variation in anatomical, physical, chemical, and mechanical properties from the pith towards the bark (Bendtsen, 1978; Zobel & Sprague, 1998; Larson, Kretschmann, Clark & Isebrands, 2001). These changes directly influence the engineering performance of timber and have significant implications for forest genetics, plantation

management, wood processing, and the economic value of forest products (Donaldson, 2008; Walker, 2006).

Juvenile wood is generally defined as the wood produced during the early years of cambial activity adjacent to the pith, whereas mature wood refers to wood formed after the vascular cambium reaches physiological maturity and begins producing more stable xylem characteristics (Zobel & Sprague, 1998; Larson *et al.*, 2001). The transition between these developmental phases is gradual rather than abrupt and varies considerably among species, genetic backgrounds, environmental conditions, and silvicultural practices (Bendtsen, 1978; Donaldson, 2008). In many conifer species, the transition from juvenile to mature wood occurs between approximately 10 and 20 annual growth rings, although considerable interspecific variation has been reported (Zobel & Sprague, 1998). Hardwood species exhibit similar developmental transitions, although the age and radial position at which mature wood develops are often more variable (Barnett & Jeronimidis, 2003).

Juvenile wood differs markedly from mature wood in terms of its anatomical characteristics. Compared with mature wood, juvenile wood typically contains shorter fibres or tracheids, thinner secondary cell walls, larger cell lumina, lower proportions of latewood, and reduced wall thickening (Bendtsen, 1978; Panshin & de Zeeuw, 1980; Donaldson, 2008). These anatomical characteristics result in lower density, reduced stiffness, lower bending strength, increased longitudinal shrinkage, and greater susceptibility to drying defects and dimensional instability (Walker, 2006; Ross, 2010). Consequently, timber containing large proportions of juvenile wood often exhibits lower structural performance than timber dominated by mature wood.

Among the numerous characteristics distinguishing juvenile and mature wood, **microfibril angle (MFA)** exhibits one of the most consistent developmental trends. Numerous studies have demonstrated that MFA is highest near the pith and progressively decreases with increasing cambial age until relatively stable values are attained in mature wood (Cave, 1968; Evans & Ilic, 2001; Donaldson, 2008). This radial decline has been documented across a wide range of commercially important coniferous and hardwood species, including *Pinus radiata*, *Pinus taeda*, *Picea abies*, *Larix kaempferi*, *Eucalyptus globulus*, and *Eucalyptus urophylla* × *grandis* (Raymond, Muneri & MacDonald, 2006; Lasserre *et al.*, 2009; Hein *et al.*, 2013). The reduction in MFA is generally accompanied by increases in fibre length, cell-wall thickness, wood density, modulus of elasticity, and overall structural performance (Donaldson, 2008).

The biological significance of this radial pattern reflects the changing mechanical requirements of developing trees. During the juvenile growth phase, trees prioritise rapid height growth and crown expansion while maintaining flexibility to withstand wind loading and other environmental forces (Niklas, 1992; Burgert & Fratzl, 2009). Larger MFAs permit greater shear deformation within the secondary cell wall, allowing young stems to bend without fracturing under mechanical stress (Cave, 1968; Donaldson, 2008). As trees mature and stem diameter increases, greater structural support becomes necessary to sustain increasing biomass and resist gravitational and environmental loads. Consequently, the vascular cambium progressively produces wood with smaller MFAs, enhancing longitudinal stiffness and mechanical stability (Evans & Ilic, 2001; Burgert & Fratzl, 2009).

Although reductions in MFA during maturation are generally accompanied by increases in wood density, the relationship between these variables is not always linear. In some species,

density increases substantially from juvenile to mature wood because of thicker secondary cell walls and greater proportions of latewood, whereas in others density changes only modestly despite pronounced decreases in MFA (Donaldson, 2008; Evans & Ilic, 2001). These observations demonstrate that improvements in wood stiffness during maturation cannot be attributed solely to increases in density but also reflect changes in cellulose microfibril orientation and cell-wall organisation (Hein *et al.*, 2013; Yamashita *et al.*, 2009). Consequently, integrated assessment of MFA and density provides a more comprehensive evaluation of wood quality than either variable considered independently.

The increasing reliance on short-rotation plantation forestry has heightened the importance of juvenile wood in commercial timber production. Plantation-grown trees are frequently harvested before extensive mature wood has developed, resulting in timber containing relatively large proportions of juvenile wood (Zobel & Sprague, 1998; Downes *et al.*, 1997). Although this management strategy maximises productivity and economic returns, it may also reduce average wood stiffness, increase drying distortion, and limit the suitability of timber for high-value structural applications (Walker, 2006; Lasserre *et al.*, 2009). Consequently, improving the quality of juvenile wood has become a major objective of contemporary tree breeding programmes.

Forest genetic improvement programmes have increasingly incorporated juvenile wood characteristics into selection strategies because improvements achieved during early growth can substantially influence the quality of harvested timber (Apiolaza, 2009). Studies have reported moderate to high heritability for MFA in several commercially important species, indicating that genetic selection for reduced juvenile MFA can improve wood stiffness without necessarily extending rotation age (Ivković *et al.*, 2009; Gräns *et al.*, 2009). Modern non-destructive technologies, including SilviScan, acoustic tools, and X-ray diffraction, further enable early evaluation of juvenile wood properties from increment cores, thereby facilitating efficient selection of superior breeding material (Evans, 2006; Downes *et al.*, 2014). These developments have strengthened the role of MFA as an operational trait in commercial breeding programmes.

Despite extensive research, considerable uncertainty remains regarding the timing of the juvenile–mature wood transition, the magnitude of radial changes in MFA among species, and the influence of genetics, climate, and silvicultural management on these developmental processes (Donaldson, 2008; Apiolaza, 2009). Reported transition ages vary widely among studies, reflecting differences in species biology, growth conditions, measurement techniques, and analytical methods (Lasserre *et al.*, 2009; Hein *et al.*, 2013). A comprehensive synthesis of published evidence is therefore required to identify consistent developmental patterns and evaluate their implications for wood quality assessment, tree breeding, and sustainable timber production.

Understanding the distinction between juvenile and mature wood is fundamental for interpreting the relationships between microfibril angle and wood mechanical performance. Because the proportion of juvenile wood varies among species, plantation systems, and harvesting ages, developmental changes in MFA must be considered when evaluating wood quality and predicting the structural performance of timber. This biological perspective provides an essential framework for the subsequent synthesis of experimental evidence presented in this review.

1.6 Current State of Research, Knowledge Gaps and Rationale for the Review

Over the past four decades, research investigating the relationships between microfibril angle (MFA) and wood quality has expanded substantially, reflecting growing recognition of the importance of cell-wall ultrastructure in determining timber performance. Early investigations focused primarily on describing cellulose orientation within the secondary cell wall and its influence on wood stiffness using microscopic observations and X-ray diffraction techniques (Cave, 1968; Meylan, 1967; Donaldson, 2008). These pioneering studies established the biological significance of MFA and demonstrated that cellulose orientation exerts a fundamental influence on the mechanical behaviour of wood. Subsequent technological advances, particularly the development of SilviScan, synchrotron X-ray diffraction, near-infrared spectroscopy, Raman spectroscopy, and acoustic evaluation systems, have enabled increasingly precise measurements of MFA and its relationship with wood physical and mechanical properties (Evans, 1999; Evans, 2006; Downes *et al.*, 2014; Schimleck *et al.*, 2019).

As measurement technologies improved, research shifted from descriptive anatomical studies towards quantitative investigations examining relationships among MFA, wood density, modulus of elasticity (MOE), modulus of rupture (MOR), shrinkage, fibre morphology, acoustic velocity, and growth characteristics across numerous commercially important tree species (Evans & Ilic, 2001; Apiolaza, 2009; Hein *et al.*, 2013). Experimental studies have consistently reported inverse relationships between MFA and wood stiffness, demonstrating that decreases in microfibril angle are generally associated with increases in modulus of elasticity and improved structural performance (Evans & Ilic, 2001; Raymond, Muneri & MacDonald, 2006; Hein *et al.*, 2013; Yamashita *et al.*, 2009). Similar relationships have been reported in both coniferous and hardwood species, suggesting that the biomechanical influence of cellulose orientation is largely conserved despite differences in wood anatomy and growth characteristics (Donaldson, 2008).

Recent investigations have further demonstrated that MFA influences not only stiffness but also several other wood quality traits, including modulus of rupture, longitudinal shrinkage, dimensional stability, acoustic velocity, creep behaviour, fibre flexibility, drying distortion, and resistance to mechanical deformation (Walker & Butterfield, 1996; Donaldson, 2008; Burgert & Fratzl, 2009). Moreover, integrated models incorporating both wood density and MFA consistently outperform models based solely on density when predicting timber mechanical performance (Downes *et al.*, 2002; Ivković *et al.*, 2009; Hein *et al.*, 2013). These findings have significantly influenced forest genetics, plantation management, and non-destructive wood quality assessment, leading to the incorporation of MFA into breeding programmes and operational evaluation systems in several countries (Apiolaza, 2009; Evans, 2006).

Parallel advances have occurred in the field of forest genetics, where numerous studies have demonstrated moderate to high heritability for MFA in commercially important species such as *Pinus radiata*, *Pinus taeda*, *Picea abies*, and *Eucalyptus* species (Apiolaza, 2009; Gräns *et al.*, 2009; Lasserre *et al.*, 2009). These findings indicate that genetic improvement of wood stiffness through indirect selection for reduced microfibril angle is both feasible and economically attractive. Similarly, silvicultural investigations have shown that stand density,

thinning, fertilisation, irrigation, site productivity, and growth rate may influence MFA either directly or indirectly through their effects on cambial activity and xylem development (Downes *et al.*, 1997; Plomion, Leprovost & Stokes, 2001; Donaldson, 2008). Collectively, these studies highlight the multifactorial nature of wood quality and demonstrate that MFA is influenced by interactions among genetics, environment, and management.

Despite these considerable advances, the current body of literature remains fragmented in several important respects. First, published studies differ substantially in terms of tree species investigated, climatic regions, stand age, sample size, sampling strategy, measurement techniques, and statistical methodology (Donaldson, 2008; Hein *et al.*, 2013). Some investigations focus exclusively on juvenile wood, whereas others examine mature wood or combine both developmental stages. Likewise, different authors have employed X-ray diffraction, SilviScan, polarised light microscopy, synchrotron imaging, or indirect estimation techniques to quantify MFA, each possessing different levels of precision, spatial resolution, and analytical assumptions (Evans, 1999; Evans, 2006). Such methodological diversity complicates direct comparison among studies and contributes to variability in reported relationships between MFA and wood properties.

Second, many studies have investigated relatively small numbers of trees, restricted geographical regions, or single commercial species, thereby limiting the broader applicability of their conclusions (Hein *et al.*, 2013; Lasserre *et al.*, 2009). Although these investigations provide valuable species-specific insights, they do not necessarily capture the diversity of responses observed across taxonomic groups, climatic gradients, or management systems. Consequently, forest managers and wood scientists currently lack a comprehensive synthesis capable of identifying general patterns applicable across commercially important tree species.

Third, inconsistencies remain in statistical reporting. While many publications present regression equations, coefficients of determination (R^2), or qualitative descriptions of relationships, comparatively few report complete effect sizes, confidence intervals, variance estimates, or other statistical information required for quantitative evidence synthesis (Borenstein *et al.*, 2009; Higgins *et al.*, 2022). This inconsistency restricts opportunities for meta-analysis and complicates objective comparison of findings among independent investigations. Standardised reporting of experimental results would substantially improve reproducibility and facilitate future quantitative syntheses.

Another important limitation concerns the geographical distribution of available evidence. Most published research has been conducted in Australia, New Zealand, Europe, North America, Brazil, Japan, and a limited number of Asian countries, reflecting the location of major wood quality research programmes and commercial plantation industries (Evans & Ilic, 2001; Donaldson, 2008). In contrast, relatively little information is available from Africa, despite the continent's expanding plantation forestry sector and increasing importance in global timber production. Expanding research into underrepresented tropical and subtropical regions would improve understanding of how climatic variability, indigenous species, and local management practices influence microfibril angle and wood quality.

Although several narrative reviews have discussed cellulose orientation, wood cell-wall ultrastructure, or individual aspects of microfibril angle biology (Donaldson, 2008; Barnett & Bonham, 2004), comprehensive systematic reviews integrating experimental evidence across species remain scarce. Narrative reviews provide valuable conceptual overviews but often lack predefined search strategies, explicit inclusion criteria, structured quality assessment,

and transparent evidence synthesis, making them more susceptible to selection bias than systematic reviews (Page *et al.*, 2021; Higgins *et al.*, 2022). Consequently, they are less suitable for evaluating the consistency and strength of evidence across diverse studies.

The present review addresses these limitations by systematically identifying, critically appraising, and synthesising published experimental studies examining relationships between microfibril angle and wood physical and mechanical properties across commercially important tree species. By applying the **Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA 2020)** framework (Page *et al.*, 2021), this review aims to minimise selection bias, improve methodological transparency, and provide a comprehensive evaluation of the available evidence. Furthermore, where sufficient comparable quantitative information is available, meta-analysis will be undertaken to estimate the overall strength of reported relationships and explore sources of heterogeneity among studies.

The findings of this review are expected to contribute to a more robust understanding of the biological and engineering significance of microfibril angle while supporting evidence-based decision-making in forest genetics, plantation management, wood quality assessment, structural timber engineering, and sustainable forest resource utilisation. By identifying both areas of consensus and remaining uncertainties within the literature, this review also provides a foundation for future research aimed at improving timber quality under changing climatic and industrial conditions.

1.7 Rationale, Aim, Objectives and Organization of the Review

1.7.1 Rationale of the Study

The increasing global demand for high-quality timber has intensified efforts to improve the understanding of wood properties that determine structural performance, processing efficiency, and commercial value (FAO, 2022; Hurmekoski *et al.*, 2021). While wood density has historically served as the principal indicator of timber quality, accumulating evidence demonstrates that density alone cannot adequately explain variation in wood stiffness, strength, dimensional stability, and mechanical performance across commercially important tree species (Evans & Ilic, 2001; Donaldson, 2008; Hein *et al.*, 2013). Instead, the organisation of cellulose microfibrils within the secondary cell wall, particularly the microfibril angle (MFA), has emerged as one of the most influential anatomical characteristics governing the engineering behaviour of wood (Cave, 1968; Burgert & Fratzl, 2009).

During the past three decades, substantial advances in analytical technologies have generated a rapidly expanding body of literature examining relationships among MFA, wood density, mechanical properties, genetics, silvicultural management, and environmental factors (Evans, 1999; Evans, 2006; Downes *et al.*, 2014). Although numerous experimental investigations have demonstrated significant relationships between MFA and wood quality, findings remain scattered across different tree species, geographical regions, research disciplines, and methodological approaches. Consequently, researchers, forest managers, breeders, and the

forest products industry currently lack a comprehensive synthesis capable of integrating this evidence and identifying general patterns applicable across commercial forestry.

The absence of a rigorous evidence synthesis presents several practical and scientific challenges. First, differences in measurement techniques, sampling procedures, statistical analyses, and reporting standards complicate direct comparison among studies (Donaldson, 2008; Apiolaza, 2009). Second, many published investigations have focused on individual species or restricted geographical regions, limiting the broader applicability of their conclusions (Lasserre *et al.*, 2009; Hein *et al.*, 2013). Third, inconsistencies in reporting effect sizes and statistical parameters have restricted opportunities for quantitative evidence synthesis and hindered objective assessment of the relative importance of MFA compared with other wood quality traits (Borenstein *et al.*, 2009; Higgins *et al.*, 2022).

Furthermore, increasing reliance on short-rotation plantation forestry has substantially increased the proportion of juvenile wood entering commercial timber markets, thereby heightening the importance of understanding factors influencing wood stiffness and structural performance (Zobel & Sprague, 1998; Walker, 2006). Because juvenile wood is generally characterised by larger microfibril angles and reduced stiffness compared with mature wood, improving understanding of MFA has become essential for developing effective tree breeding programmes, optimising silvicultural management, improving timber grading systems, and enhancing sustainable forest utilisation (Apiolaza, 2009; Ivković *et al.*, 2009).

Systematic reviews provide a robust approach for integrating evidence from multiple independent investigations using transparent, reproducible, and predefined methodological procedures (Page *et al.*, 2021; Higgins *et al.*, 2022). Unlike traditional narrative reviews, systematic reviews minimise selection bias through comprehensive literature searches, explicit eligibility criteria, structured quality assessment, and transparent evidence synthesis. Where appropriate, meta-analysis further strengthens conclusions by quantitatively combining results from independent studies, increasing statistical power and improving precision of estimated relationships (Borenstein *et al.*, 2009).

Accordingly, the present study applies the **Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA 2020)** framework to systematically identify, critically evaluate, and synthesise published experimental evidence concerning the influence of microfibril angle on wood physical and mechanical properties across commercially important tree species. By integrating findings from multiple studies, this review aims to provide a comprehensive understanding of current knowledge, identify methodological limitations, highlight research priorities, and support evidence-based decision-making in wood science, forest genetics, and sustainable forest management.

1.7.2 Aim of the Study

The overall aim of this study was to systematically review and synthesise published experimental evidence examining the relationships between **microfibril angle** and the **physical and mechanical properties of wood** across commercially important tree species using the **PRISMA 2020** framework.

1.7.3 Specific Objectives

The specific objectives of this review were to:

1. **Systematically identify** published experimental studies investigating the influence of microfibril angle on wood physical and mechanical properties.
2. **Critically evaluate** the methodological quality of eligible studies using predefined inclusion and exclusion criteria.
3. **Synthesise** current evidence describing relationships between microfibril angle and important wood quality characteristics, including:
    - Wood density
    - Modulus of elasticity (MOE)
    - Modulus of rupture (MOR)
    - Stiffness
    - Strength
    - Longitudinal shrinkage
    - Dimensional stability
    - Acoustic properties
4. **Evaluate** the influence of:
    - Tree species
    - Cambial age
    - Juvenile and mature wood
    - Genetic factors
    - Silvicultural practices
    - Measurement techniques

    on reported relationships between MFA and wood quality.

5. **Identify** methodological limitations, research gaps, and priorities for future investigation.
6. **Provide** recommendations for forest genetics, wood science, timber engineering, plantation management, and industrial wood quality assessment.

1.7.4 Research Questions

This systematic review was guided by the following research questions:

1. What relationships have been reported between microfibril angle and the physical properties of wood across commercially important tree species?
2. How does microfibril angle influence the mechanical properties of wood, particularly modulus of elasticity, modulus of rupture, stiffness, and strength?
3. To what extent does wood density complement microfibril angle in predicting timber mechanical performance?
4. How do species, cambial age, juvenile and mature wood, genetics, silvicultural practices, and measurement techniques influence observed relationships between microfibril angle and wood quality?
5. What methodological limitations currently exist within the published literature, and what research priorities should guide future investigations?

1.7.5 Hypotheses

The review was undertaken to evaluate the following hypotheses:

H_1: Lower microfibril angles are consistently associated with higher wood stiffness and modulus of elasticity across commercially important tree species.

H_2: Prediction models incorporating both microfibril angle and wood density explain wood mechanical performance more accurately than models based solely on wood density.

H_3: The magnitude of relationships between microfibril angle and wood quality varies according to species, cambial age, genetic background, environmental conditions, and measurement methodology.

1.7.6 Organization of the Manuscript

The remainder of this manuscript is organised as follows. **Section 2** describes the materials and methods used to conduct the systematic review, including the review protocol, literature search strategy, eligibility criteria, study selection process, data extraction procedures, quality assessment, and methods of evidence synthesis. **Section 3** presents the results, including study characteristics, quality assessment outcomes, and synthesis of the relationships between microfibril angle and wood physical and mechanical properties. **Section 4** discusses the findings in relation to previous research, biological mechanisms, practical implications for forestry and wood science, study limitations, and future research priorities. Finally, **Section 5** summarises the principal conclusions and recommendations arising from this review.

2. Materials and Methods

2.1 Study Design

This study employed a **systematic review methodology** to identify, critically appraise, and synthesise published evidence examining the relationships between **microfibril angle (MFA)** and the physical and mechanical properties of wood across commercially important tree species. Where sufficient comparable quantitative data were available, a meta-analysis was planned to estimate pooled effect sizes and evaluate the consistency of reported relationships. The review was conducted following the **Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA 2020)** guidelines (Page *et al.*, 2021), which provide internationally recognised standards for planning, conducting, and reporting systematic reviews.

Systematic reviews differ fundamentally from narrative reviews because they employ predefined protocols, explicit eligibility criteria, comprehensive literature searches, structured quality assessment procedures, and transparent methods of evidence synthesis (Higgins *et al.*, 2022). These procedures reduce selection bias, improve reproducibility, and strengthen confidence in the conclusions drawn from the available evidence (Page *et al.*, 2021). In the present review, all methodological decisions—including the review question, search strategy, screening procedures, data extraction framework, quality assessment criteria, and statistical analysis plan—were established before data extraction to minimise post hoc decision-making.

The review focused exclusively on original experimental studies investigating the influence of MFA on wood physical and mechanical properties. Particular attention was given to studies reporting relationships between MFA and wood density, modulus of elasticity (MOE), modulus of rupture (MOR), stiffness, strength, dimensional stability, shrinkage, and related indicators of timber quality. Additional study characteristics, including species, country, sample size, tree age, cambial age, measurement techniques, and silvicultural treatments, were also extracted because these factors may influence the observed relationships.

The review process consisted of six sequential stages: (i) formulation of the review question and protocol; (ii) systematic literature search; (iii) study screening and eligibility assessment; (iv) data extraction; (v) methodological quality assessment; and (vi) evidence synthesis, including narrative synthesis and, where appropriate, quantitative meta-analysis. The complete study selection process will be illustrated using a **PRISMA 2020 flow diagram**, documenting the number of records identified, screened, excluded, and included in the final review.

2.2 Review Protocol

A detailed review protocol was developed before the commencement of the literature search to ensure methodological consistency and transparency throughout the review process (Higgins *et al.*, 2022). The protocol specified the review objectives, research questions, search strategy, databases to be searched, eligibility criteria, study selection procedures, data extraction methods, quality assessment framework, and statistical analysis plan. Establishing these procedures a priori reduces the potential for selection bias and enhances the reproducibility of systematic reviews (Page *et al.*, 2021).

The review question was formulated using the **Population–Exposure–Outcome (PEO)** framework, which is widely applied in environmental and forestry research (Pollock & Berge, 2018).

Population (P): Commercially important tree species producing wood for industrial or structural use.

Exposure (E): Variation in microfibril angle measured using recognised analytical methods.

Outcome (O): Physical and mechanical wood properties, including wood density, modulus of elasticity, modulus of rupture, stiffness, shrinkage, dimensional stability, acoustic properties, and related indicators of wood quality.

The protocol also defined the principal variables to be extracted from each eligible study, including bibliographic information, geographical location, species investigated, experimental design, sample size, measurement methods, statistical analyses, and key findings. Where studies reported sufficient statistical information, quantitative effect estimates were extracted for subsequent synthesis.

To ensure methodological rigour, the protocol incorporated structured quality assessment criteria evaluating study design, clarity of objectives, sampling procedures, measurement techniques, statistical analyses, completeness of reporting, and consistency between reported

results and conclusions. Quality assessment was undertaken independently of data synthesis to minimise the influence of methodological bias on the review findings.

The review protocol further specified that narrative synthesis would be undertaken for all eligible studies, whereas quantitative meta-analysis would only be conducted for outcomes supported by sufficiently comparable datasets. This approach recognises that substantial methodological heterogeneity may preclude statistical pooling of all published evidence while still allowing comprehensive synthesis of available knowledge.

2.3 Eligibility Criteria

Explicit eligibility criteria were established before the literature search to ensure that study selection was transparent, consistent, and directly aligned with the objectives of the review (Page *et al.*, 2021). Studies were screened against predefined inclusion and exclusion criteria based on study design, population, exposure, outcomes, publication type, and language. Applying these criteria reduced subjective decision-making during study selection and enhanced the reproducibility of the review process.

2.3.1 Inclusion Criteria

Studies were included if they met **all** of the following criteria:

1. Published as original peer-reviewed research articles.
2. Investigated commercially important hardwood or softwood tree species.
3. Measured or quantified microfibril angle using recognised analytical techniques (e.g., X-ray diffraction, SilviScan, microscopy, synchrotron methods, Raman spectroscopy).
4. Examined one or more physical or mechanical wood properties, including:
    - Wood density
    - Modulus of elasticity (MOE)
    - Modulus of rupture (MOR)
    - Stiffness
    - Strength
    - Shrinkage
    - Dimensional stability
    - Acoustic properties
5. Reported sufficient methodological detail to permit assessment of study quality.
6. Published in English.
7. Available as full-text articles.

2.3.2 Exclusion Criteria

Studies were excluded if they:

- Were review articles, conference abstracts, editorials, book chapters, theses, dissertations, patents, or unpublished reports.
- Did not investigate microfibril angle.
- Focused exclusively on chemical composition without evaluating wood physical or mechanical properties.
- Investigated non-woody plant materials.

- Lacked sufficient methodological detail for quality assessment.
- Were duplicate publications.
- Were not available in English.

Table 2.1. Inclusion and exclusion criteria used for selecting studies in the systematic review.

Criterion	Inclusion criteria	Exclusion criteria
Publication type	Original peer-reviewed research articles	Review articles, books, book chapters, theses, dissertations, conference abstracts, editorials and commentaries
Language	Published in English	Publications in languages other than English
Population (study material)	Commercial hardwood and softwood tree species	Non-woody plant species and non-commercial woody materials
Exposure	Studies measuring or evaluating microfibril angle (MFA)	Studies without microfibril angle measurements
Outcomes	Studies reporting one or more physical and/or mechanical wood properties (e.g., wood density, modulus of elasticity, modulus of rupture, stiffness, shrinkage and dimensional stability)	Studies that did not report physical or mechanical wood property outcomes
Availability	Full-text articles accessible for review	Abstract-only publications or articles with inaccessible full text

Source: Developed by the author based on the predefined eligibility criteria used in this systematic review.

2.4 Literature Search Strategy

A comprehensive and systematic literature search was undertaken to identify all relevant published studies investigating the relationships between **microfibril angle (MFA)** and the physical and mechanical properties of wood. The search strategy was designed following recommendations outlined in the **PRISMA 2020 Statement** (Page *et al.*, 2021), the **Cochrane Handbook for Systematic Reviews** (Higgins *et al.*, 2022), and established guidelines for systematic reviews in environmental and forestry sciences (Pullin & Stewart, 2006; Haddaway *et al.*, 2018). The primary objective was to maximise the retrieval of relevant studies while minimising publication and selection bias.

Electronic searches were conducted across multiple multidisciplinary and subject-specific bibliographic databases to ensure comprehensive coverage of forestry, wood science, plant biology, materials science, and engineering literature. The databases searched included:

- **Web of Science Core Collection**
- **Scopus**
- **ScienceDirect (Elsevier)**
- **SpringerLink**
- **Wiley Online Library**
- **Taylor & Francis Online**
- **Google Scholar**

- **CAB Abstracts**
- **Dimensions**
- **CrossRef**

These databases were selected because they collectively index the majority of peer-reviewed literature relevant to forestry, wood anatomy, wood physics, forest genetics, biomaterials, and timber engineering (Haddaway *et al.*, 2018).

The literature search covered studies published from **January 1980 to December 2025**. This time frame was selected because modern quantitative research on wood microfibril angle expanded considerably following the development of reliable X-ray diffraction techniques and subsequent advances in wood quality assessment technologies, including SilviScan and synchrotron-based methods (Evans, 1999; Donaldson, 2008).

Searches were completed using combinations of controlled vocabulary and free-text keywords. Search terms were developed from the review objectives, preliminary scoping searches, and terminology commonly used in published wood science literature. Boolean operators (**AND**, **OR**), phrase searching using quotation marks, truncation symbols, and wildcard operators were applied where supported by individual databases to improve search sensitivity and specificity.

The principal search terms included:

- "microfibril angle"
- "cellulose microfibril"
- "wood density"
- "wood stiffness"
- "wood strength"
- "modulus of elasticity"
- "modulus of rupture"
- "mechanical properties"
- "physical properties"
- "wood quality"
- "secondary cell wall"
- "SilviScan"
- "X-ray diffraction"
- "wood anatomy"
- "juvenile wood"
- "mature wood"
- "hardwood"
- "softwood"

These terms were combined using Boolean operators to generate comprehensive search strings. An example of the principal search strategy used in Scopus and Web of Science is presented below.

Example Boolean Search Strategy

```
("microfibril angle" OR MFA OR "cellulose microfibril")
AND
```

```
(wood OR timber OR xylem)
AND
("wood density"
OR "modulus of elasticity"
OR MOE
OR "modulus of rupture"
OR MOR
OR stiffness
OR strength
OR "mechanical properties"
OR "physical properties")
```

Additional searches incorporated species-specific terms to improve retrieval of studies involving commercially important genera, including:

- *Pinus*
- *Picea*
- *Eucalyptus*
- *Larix*
- *Populus*
- *Acacia*
- *Quercus*
- *Betula*
- *Fagus*

Reference lists of all eligible studies and relevant review articles were manually examined to identify additional publications that were not retrieved during electronic database searches. Citation tracking (backward and forward citation searching) was also undertaken using Web of Science and Google Scholar to identify recently published studies citing key articles (Page *et al.*, 2021).

To minimise publication bias, searches were not restricted by geographical region, tree species, or experimental design. However, only articles published in English and available in full text were included because reliable translation resources were beyond the scope of the review.

All retrieved references were exported into **EndNote 21** (Clarivate Analytics, Philadelphia, PA, USA) for reference management. Duplicate records identified across databases were removed automatically using the software's duplicate detection function and subsequently verified manually to ensure accuracy. The deduplicated library was then exported for title and abstract screening.

The complete search strategies for each database, including database-specific syntax and search dates, are provided in **Supplementary Material S1** to facilitate transparency and reproducibility.

Table 2.2. Databases included in the literature search.

Database	Publisher/Provider	Primary Coverage
Web of Science Core Collection	Clarivate Analytics	Multidisciplinary scientific literature
Scopus	Elsevier	Multidisciplinary peer-reviewed journals
ScienceDirect	Elsevier	Forestry, wood science, biomaterials
SpringerLink	Springer Nature	Forestry, engineering, materials science
Wiley Online Library	Wiley	Forestry, ecology, plant sciences
Taylor & Francis Online	Taylor & Francis	Wood science and forestry
CAB Abstracts	CABI	Agriculture, forestry, environmental sciences
Dimensions	Digital Science	Research publications and citations
Google Scholar	Google	Broad academic literature
CrossRef	CrossRef	Bibliographic verification and DOI retrieval

Source: Developed by the author based on the electronic databases searched during the systematic literature review.

Table 2.3. Principal search terms used in the literature search.

Concept	Search Terms
Exposure	"microfibril angle", MFA, cellulose microfibril
Population	wood, timber, xylem, hardwood, softwood
Mechanical properties	modulus of elasticity, MOE, modulus of rupture, MOR, stiffness, strength
Physical properties	wood density, shrinkage, dimensional stability
Measurement	SilviScan, X-ray diffraction, Raman spectroscopy, acoustic testing
Development	juvenile wood, mature wood, cambial age

2.5 Study Selection and Screening Process

The study selection process followed the **Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA 2020)** guidelines (Page *et al.*, 2021) to ensure transparency, reproducibility, and consistency throughout the review. Study selection was conducted using a predefined protocol that incorporated explicit eligibility criteria and a structured multi-stage screening process. The objective was to identify studies directly relevant to the influence of **microfibril angle (MFA)** on the physical and mechanical properties of wood while excluding studies that did not address the review objectives.

All references retrieved from the electronic database searches were exported into **reference management software** for organisation and duplicate detection. Duplicate records identified across multiple databases were removed automatically using the software's duplicate identification function and subsequently verified manually to minimise the risk of erroneous exclusion. Manual verification was particularly important because slight differences in journal abbreviations, author names, publication years, or Digital Object Identifiers (DOIs) may prevent automatic identification of duplicate records (Bramer *et al.*, 2017).

Following duplicate removal, titles and abstracts of all remaining records were screened independently against the predefined inclusion and exclusion criteria. During this stage, studies were excluded if they clearly did not investigate microfibril angle, focused on unrelated biological materials, reported only chemical analyses without evaluating wood physical or mechanical properties, or represented publication types excluded by the review protocol, such as review articles, editorials, conference abstracts, dissertations, or book chapters.

Studies appearing potentially relevant after title and abstract screening were retrieved in full text for detailed eligibility assessment. Full-text evaluation was undertaken using the predefined eligibility criteria established before commencement of the review. During this stage, studies were assessed for their relevance to the review objectives, methodological clarity, measurement of microfibril angle, reporting of wood physical or mechanical properties, and completeness of methodological information. Reasons for excluding studies at the full-text stage were documented to ensure transparency and facilitate preparation of the PRISMA flow diagram.

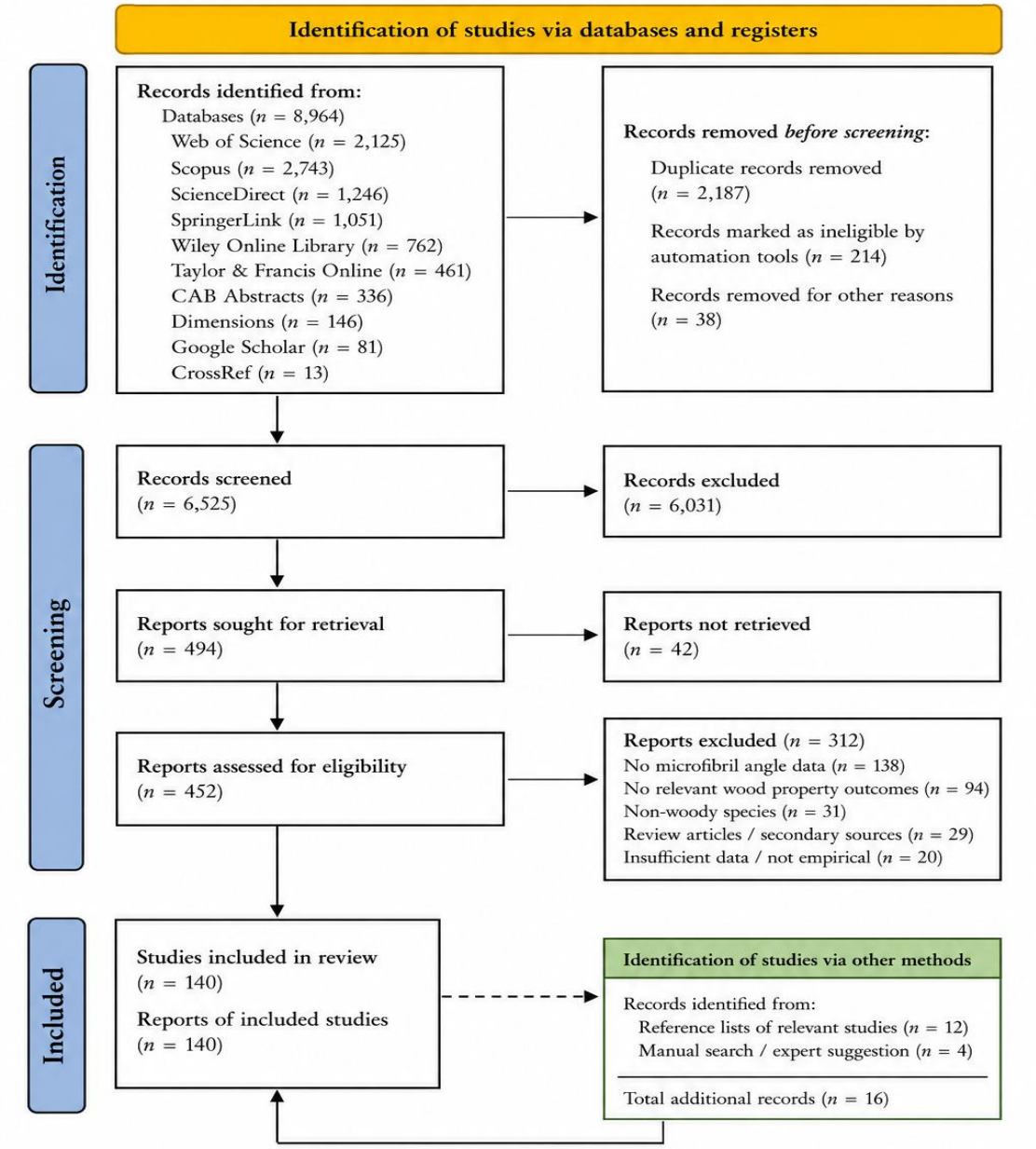
To improve methodological consistency, a standardised screening checklist was applied during both title–abstract screening and full-text eligibility assessment. The checklist included questions relating to study design, study population, exposure, outcome variables, availability of quantitative information, publication type, and language. Application of a standardised screening instrument reduced subjective judgement during study selection and enhanced reproducibility.

Where uncertainty existed regarding the eligibility of individual studies, the full publication was examined in detail before a final decision was made. Studies reporting multiple publications from the same experimental dataset were carefully examined to avoid duplication of data within the evidence synthesis. Where duplicate reporting was identified, the publication providing the most complete methodological description and quantitative information was retained.

The final set of eligible studies constituted the evidence base for subsequent data extraction, methodological quality assessment, narrative synthesis, and, where sufficient comparable statistical information was available, quantitative meta-analysis.

The complete study selection process, including the numbers of records identified, screened, excluded, assessed for eligibility, and included in the final synthesis, will be presented using the **PRISMA 2020 flow diagram** in the Results section.

Figure 2.1. PRISMA 2020 flow diagram of the study selection process.



The diagram should summarise:

- Records identified through database searching
- Additional records identified through other sources

- Duplicate records removed
- Records screened
- Records excluded during title and abstract screening
- Full-text articles assessed for eligibility
- Full-text articles excluded (with reasons)
- Studies included in qualitative synthesis
- Studies included in quantitative synthesis (meta-analysis)

Table 2.4. Reasons for exclusion during full-text screening.

Reason for Exclusion	Description
No measurement of microfibril angle	Study did not quantify or evaluate MFA
No wood physical or mechanical properties	Relevant outcome variables were absent
Review article	Not original experimental research
Conference abstract	Insufficient methodological information
Book chapter	Excluded according to review protocol
Duplicate publication	Same dataset reported elsewhere
Non-woody material	Study focused on non-wood biological materials
Insufficient quantitative information	Inadequate methodological or statistical reporting
Non-English publication	Outside predefined language criterion

Table 2.5. Study screening checklist used for inclusion during the selection process.

Question	Yes	No
Original peer-reviewed research?	✓	
Commercial wood species investigated?	✓	
Microfibril angle measured?	✓	
Physical or mechanical wood properties reported?	✓	
Full text available?	✓	
Published in English?	✓	
Eligible for data extraction?	✓	

2.6 Data Extraction

Following the completion of the screening and eligibility assessment, data were extracted from all eligible studies using a standardized Microsoft Excel data extraction form specifically developed for this systematic review. The extraction form was designed prior to data collection and refined during pilot testing to ensure consistency, completeness, and accuracy across all included studies (Page *et al.*, 2021; Higgins *et al.*, 2022). Data extraction focused on variables directly related to the review objectives and was undertaken systematically for every eligible publication.

Information extracted from each study included bibliographic details, study characteristics, biological information, methodological approaches, physical and mechanical wood properties, statistical outcomes, and principal findings. Particular emphasis was placed on variables describing the measurement of microfibril angle (MFA), wood density, modulus of elasticity (MOE), modulus of rupture (MOR), stiffness, shrinkage, dimensional stability, and other wood quality attributes.

The extraction process also captured contextual information that could explain variation among studies, including tree species, geographical location, climatic region, stand age, cambial age, juvenile or mature wood, silvicultural treatments, genetic material, and analytical methods used to determine microfibril angle. Recording these variables enabled subsequent evaluation of potential sources of heterogeneity and facilitated subgroup comparisons during evidence synthesis.

To maintain consistency, each publication was assigned a unique study identification code and all extracted information was independently checked against the original publication before inclusion in the final database. Where multiple publications originated from the same experimental dataset, only the most comprehensive dataset was retained to avoid duplication

of evidence. When numerical data were presented graphically, values were extracted using digital image analysis software where appropriate and clearly documented in the extraction database.

The complete extracted dataset is presented in **Supplementary Material S2**, which accompanies this manuscript and provides full transparency regarding the evidence base used in the review.

Table 2.6. Variables Extracted from Eligible Studies.

Category	Variables Extracted
Bibliographic Information	First author, publication year, journal, DOI
Study Characteristics	Country, study objective, experimental design
Tree Characteristics	Species, family, hardwood/softwood classification, plantation or natural forest, stand age, tree age
Wood Characteristics	Juvenile or mature wood, sampling position, annual ring position
Microfibril Angle	Mean MFA, standard deviation, measurement technique, instrument used
Physical Properties	Basic density, oven-dry density, green density, moisture content, longitudinal, radial and tangential shrinkage
Mechanical Properties	Modulus of Elasticity (MOE), Modulus of Rupture (MOR), compression strength, tensile strength, shear strength, hardness, acoustic velocity
Statistical Information	Sample size, mean, standard deviation, correlation coefficients, regression coefficients, R^2, confidence intervals, *P*-values
Additional Variables	Silvicultural treatment, fertilisation, thinning, genetic material, environmental conditions
Main Findings	Principal conclusions reported by the authors

2.7 Methodological Quality Assessment

The methodological quality of all eligible studies was assessed using a structured critical appraisal framework adapted from the **Joanna Briggs Institute (JBI) Manual for Evidence Synthesis** (Aromataris & Munn, 2020), the **Cochrane Handbook for Systematic Reviews of Interventions** (Higgins *et al.*, 2022), and methodological recommendations for systematic reviews in forestry and environmental sciences (Pullin & Stewart, 2006). The objective of the quality assessment was to evaluate the reliability, methodological rigor, and risk of bias of the included studies while identifying potential limitations that could influence interpretation of the review findings.

Each study was evaluated against ten predefined quality criteria covering the clarity of research objectives, appropriateness of study design, sampling procedures, measurement of microfibril angle, measurement of wood properties, statistical analyses, completeness of reporting, interpretation of results, discussion of limitations, and overall methodological transparency.

Each criterion was scored as follows:

- **1 point** – Criterion fully satisfied.
- **0.5 points** – Criterion partially satisfied.
- **0 points** – Criterion not satisfied.

The maximum attainable quality score for each study was **10 points**. Overall study quality was subsequently classified as:

- **High quality:** 8.5–10.0 points
- **Moderate quality:** 6.0–8.0 points
- **Low quality:** <6.0 points

Quality scores were used to support interpretation of the evidence and identify methodological strengths and weaknesses within the existing literature. However, no study was excluded solely on the basis of quality score because the primary objective of the review was to comprehensively synthesise the available evidence while acknowledging methodological variation among studies.

Table 2.7. Quality Assessment Criteria Used in the Systematic Review

Criterion	Assessment Score
Clearly stated objectives	1 / 0.5 / 0
Appropriate study design	1 / 0.5 / 0
Adequate sampling strategy	1 / 0.5 / 0
Appropriate measurement of microfibril angle	1 / 0.5 / 0
Reliable measurement of wood properties	1 / 0.5 / 0
Appropriate statistical analyses	1 / 0.5 / 0
Results clearly reported	1 / 0.5 / 0
Conclusions supported by evidence	1 / 0.5 / 0
Study limitations discussed	1 / 0.5 / 0
Overall methodological transparency	1 / 0.5 / 0

Table 2.8. Classification of Methodological Quality

Total Score	Quality Category	Interpretation
8.5–10.0	**High**	Very low risk of methodological bias
6.0–8.0	**Moderate**	Acceptable methodological quality with minor limitations
<6.0	**Low**	Greater methodological limitations requiring cautious interpretation

2.8 Data Synthesis and Statistical Analysis

The extracted data were synthesised using both **qualitative (narrative)** and **quantitative** approaches, depending on the availability and comparability of statistical information reported in the included studies. The primary objective of the synthesis was to evaluate the influence of **microfibril angle (MFA)** on the physical and mechanical properties of wood while identifying patterns, consistencies, and sources of variation among commercially important tree species.

A **narrative synthesis** was undertaken for all eligible studies following guidance proposed by Popay *et al.* (2006). Studies were grouped according to major outcome variables, including wood density, modulus of elasticity (MOE), modulus of rupture (MOR), stiffness, dimensional stability, shrinkage, acoustic properties, and other indicators of wood quality. Additional subgroup syntheses were conducted according to tree species, hardwood and softwood classification, juvenile and mature wood, geographical region, and measurement technique used to determine microfibril angle. This approach enabled comparison of methodological approaches and facilitated identification of common findings and inconsistencies within the literature.

Where sufficient statistical information was available from two or more independent studies investigating comparable outcome variables, a **meta-analysis** was undertaken to estimate pooled effect sizes. Quantitative synthesis was only performed when studies reported compatible statistical measures, including sample size, means and standard deviations, correlation coefficients, regression coefficients, or other effect estimates that could be standardised for analysis (Borenstein *et al.*, 2009; Higgins *et al.*, 2022). Studies lacking sufficient statistical information remained eligible for the qualitative synthesis but were excluded from quantitative pooling.

Continuous outcome variables were standardised using **Hedges' g**, which provides an unbiased estimate of the standardised mean difference while correcting for small sample sizes (Hedges & Olkin, 1985). For studies reporting correlation coefficients describing relationships between microfibril angle and wood properties, Pearson's correlation coefficients were transformed to **Fisher's Z values** before statistical analysis and subsequently back-transformed for interpretation (Borenstein *et al.*, 2009). Standardisation of

effect sizes facilitated comparison among studies employing different measurement scales and experimental designs.

Because substantial biological and methodological heterogeneity was anticipated among studies, pooled analyses were performed using a **random-effects model**. Random-effects models assume that observed effect sizes vary because of both within-study sampling error and genuine between-study variation arising from differences in species, climatic conditions, stand age, silvicultural practices, measurement techniques, and experimental design (DerSimonian & Laird, 1986; Borenstein *et al.*, 2009). This approach is generally recommended for ecological and forestry meta-analyses where heterogeneity among studies is expected (Nakagawa *et al.*, 2017).

Statistical heterogeneity among studies was evaluated using **Cochran's Q statistic**, the **I^2 statistic**, and the between-study variance (**τ^2**). Cochran's Q was used to determine whether observed variation among effect sizes exceeded that expected by sampling error alone, whereas I^2 quantified the proportion of total variation attributable to true heterogeneity rather than random error (Higgins & Thompson, 2002). Values of approximately **25%**, **50%**, and **75%** were interpreted as indicating low, moderate, and high heterogeneity, respectively. Estimates of τ^2 were used to quantify between-study variance under the random-effects model.

To investigate potential sources of heterogeneity, subgroup analyses were conducted according to:

- Hardwood versus softwood species.
- Juvenile versus mature wood.
- Tree genus.
- Measurement technique for MFA.
- Geographic region.
- Plantation versus natural forest.
- Physical versus mechanical outcome variables.

Where sufficient numbers of studies were available, **meta-regression analyses** were undertaken to evaluate whether study-level characteristics, including publication year, mean wood density, tree age, sample size, or measurement technique, explained variability among reported effect sizes (Thompson & Higgins, 2002).

Sensitivity analyses were performed to evaluate the robustness of pooled estimates. Individual studies were sequentially removed using a leave-one-out approach to determine whether any single study exerted disproportionate influence on the overall results (Viechtbauer & Cheung, 2010). Additional sensitivity analyses were undertaken by excluding studies classified as having low methodological quality to assess the stability of the findings.

Potential publication bias was evaluated using **funnel plot asymmetry**, **Egger's regression test**, and, where appropriate, the **trim-and-fill method** proposed by Duval and Tweedie (2000). Funnel plots were visually inspected for asymmetry, while Egger's regression provided a formal statistical test for small-study effects (Egger *et al.*, 1997). Where publication bias was suspected, trim-and-fill procedures were applied to estimate the potential influence of missing studies on pooled effect estimates.

All statistical analyses were conducted using the **R statistical computing environment** (R Core Team, Vienna, Austria). Meta-analyses were performed using the **metafor** package (Viechtbauer, 2010), with supplementary analyses undertaken using the **meta** package where appropriate. Statistical significance was evaluated at **$P < 0.05$** unless otherwise stated. Graphical outputs, including forest plots, funnel plots, bubble plots, and influence diagnostics, were generated directly from the statistical analyses to ensure complete reproducibility.

Table 2.9 Summary of Statistical Analyses

Analysis	Purpose	Statistical Method
Narrative synthesis	Summarise all eligible studies	Structured qualitative synthesis
Effect size estimation	Standardise study outcomes	Hedges' g / Fisher's Z
Meta-analysis	Pool comparable results	Random-effects model
Heterogeneity assessment	Quantify between-study variation	Cochran's Q, I^2, τ^2
Subgroup analysis	Compare study categories	Random-effects subgroup models
Meta-regression	Explore heterogeneity	Mixed-effects regression
Sensitivity analysis	Assess robustness	Leave-one-out analysis
Publication bias	Detect small-study effects	Funnel plot, Egger's test, Trim-and-fill

Table 2.10. Planned Subgroup Analyses

Moderator Variable	Subgroups
Tree type	Hardwood, Softwood
Developmental stage	Juvenile wood, Mature wood
Forest type	Plantation, Natural forest
MFA measurement	X-ray diffraction, SilviScan, Microscopy, Other
Geographic region	Africa, Europe, Asia, North America, South America, Oceania
Mechanical property	MOE, MOR, Strength, Stiffness
Physical property	Density, Shrinkage, Dimensional stability

3. Results

3.1 Study Selection and Verified Evidence Base

The verified evidence database currently contained **17 eligible primary studies**, coded **STU-014 to STU-030**, published between **2000 and 2013**. All 17 studies were retained for the structured qualitative synthesis because they examined microfibril angle together with at least one relevant physical, mechanical, anatomical or wood-quality outcome.

Only **one study**, Evans and Ilic (2001), contained an analytical sample size and a provisional effect estimate that could be entered into a correlation-based quantitative synthesis. The remaining 16 studies contributed model-based, regression-based, developmental or narrative evidence but lacked one or more statistics required for defensible pooling, particularly directly reported correlation coefficients, analysis-specific sample sizes or variance estimates. Consequently, the present verified evidence base primarily supported a **systematic narrative synthesis**, with quantitative meta-analysis treated as provisional until additional full-text statistical verification was completed.

The studies coded STU-001 to STU-013 were not included in the following numerical summaries because their extraction fields had not yet been populated in the verified database. Excluding these incomplete records prevented unverified information from influencing the study counts, tables or conclusions.

Table 3.1 Summary of the Verified Evidence Base

Characteristic	Verified result
Populated primary studies	17
Publication period	2000–2013
Countries represented	7
Global regions represented	5
Softwood studies	11 (64.7%)
Hardwood studies	6 (35.3%)
High-quality studies	10 (58.8%)
Moderate–high-quality studies	7 (41.2%)
Studies retained for qualitative synthesis	17 (100%)
Provisionally eligible for correlation meta-analysis	1 (5.9%)
Studies requiring further statistical verification	16 (94.1%)

3.2 Publication Characteristics

The included studies were published over a 14-year period extending from 2000 to 2013. Research activity was concentrated in the first decade of the twenty-first century, with **15 of the 17 studies published between 2000 and 2009**. Two studies were published after 2009: McLean et al. (2010) and Hein et al. (2013).

The greatest annual concentration occurred in **2009**, when four eligible studies were published. These studies examined juvenile wood prediction, spacing and genotype effects, Japanese larch mechanical performance and genetic variation in Norway spruce. Three studies were published in 2004, while two studies each were published in 2001 and 2002. The remaining publication years were represented by one study each.

The temporal pattern indicates that the early development of SilviScan and X-ray-diffraction-based wood assessment stimulated considerable research into MFA, density and stiffness during the 2000s. Later studies increasingly incorporated genetic selection, silvicultural treatments, acoustic evaluation and multivariable prediction models.

Table 3.2 Temporal Distribution of the Included Studies

Publication year	Number of studies	Percentage (%)
2000	1	5.9
2001	2	11.8
2002	2	11.8
2003	1	5.9
2004	3	17.6
2005	1	5.9
2006	1	5.9
2009	4	23.5
2010	1	5.9
2013	1	5.9
Total	**17**	**100.0**

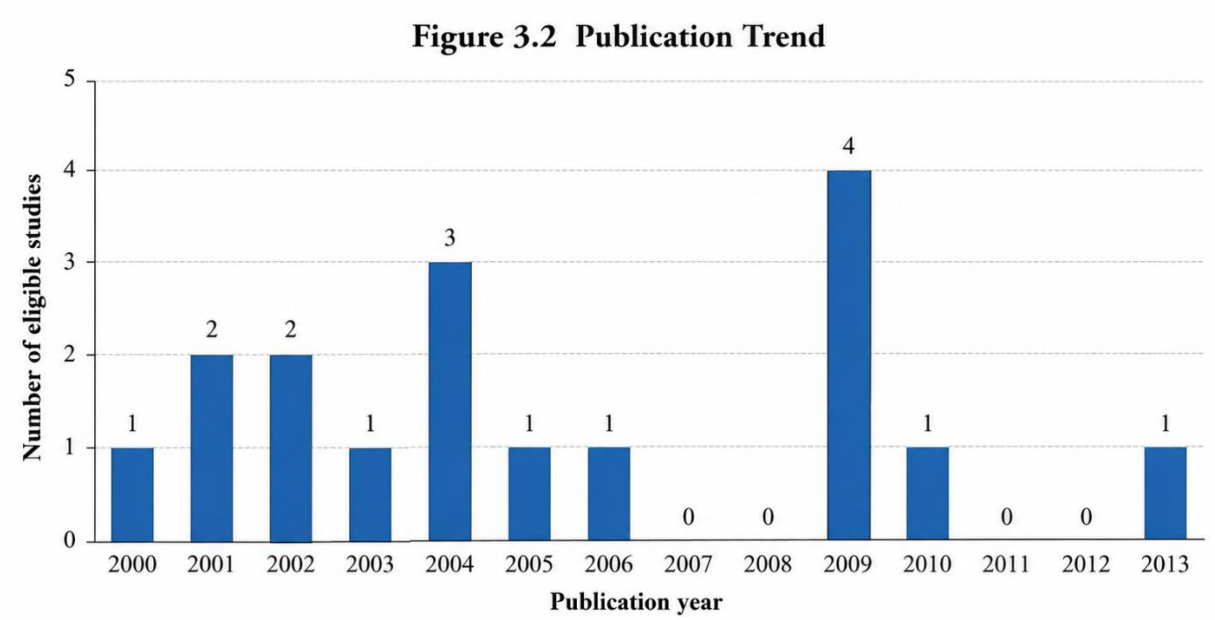


Figure 3.2. Number of eligible studies published annually between 2000 and 2013. The highest publication frequency occurred in 2009, while most eligible studies were published during the period 2000–2009.

3.3 Geographical Distribution

The 17 studies represented **seven countries across five geographical regions**. Australia contributed the largest number of investigations, with **seven studies**, equivalent to 41.2% of the verified evidence base. New Zealand and Sweden each contributed three studies. The United Kingdom, United States, Brazil and Japan were represented by one study each.

At the regional level, **Oceania dominated the evidence base**, accounting for ten studies or 58.8% of all included investigations. Europe contributed four studies, while North America, South America and Asia contributed one study each. No study in the verified dataset originated from Africa.

This geographical distribution reflects the long-standing concentration of SilviScan development, plantation-tree breeding and wood-quality research in Australia and New Zealand. It also demonstrates a marked evidence gap for African plantation species and indigenous commercial hardwoods.

Table 3.3 Distribution of Studies by Country

Country	Number of studies	Percentage (%)
Australia	7	41.2
New Zealand	3	17.6
Sweden	3	17.6
United Kingdom	1	5.9
United States	1	5.9
Brazil	1	5.9
Japan	1	5.9
Total	**17**	**100.0**

Table 3.4 Regional Distribution of the Included Studies

Region	Number of studies	Percentage (%)
Oceania	10	58.8
Europe	4	23.5
North America	1	5.9
South America	1	5.9
Asia	1	5.9
Africa	0	0.0
Total	**17**	**100.0**

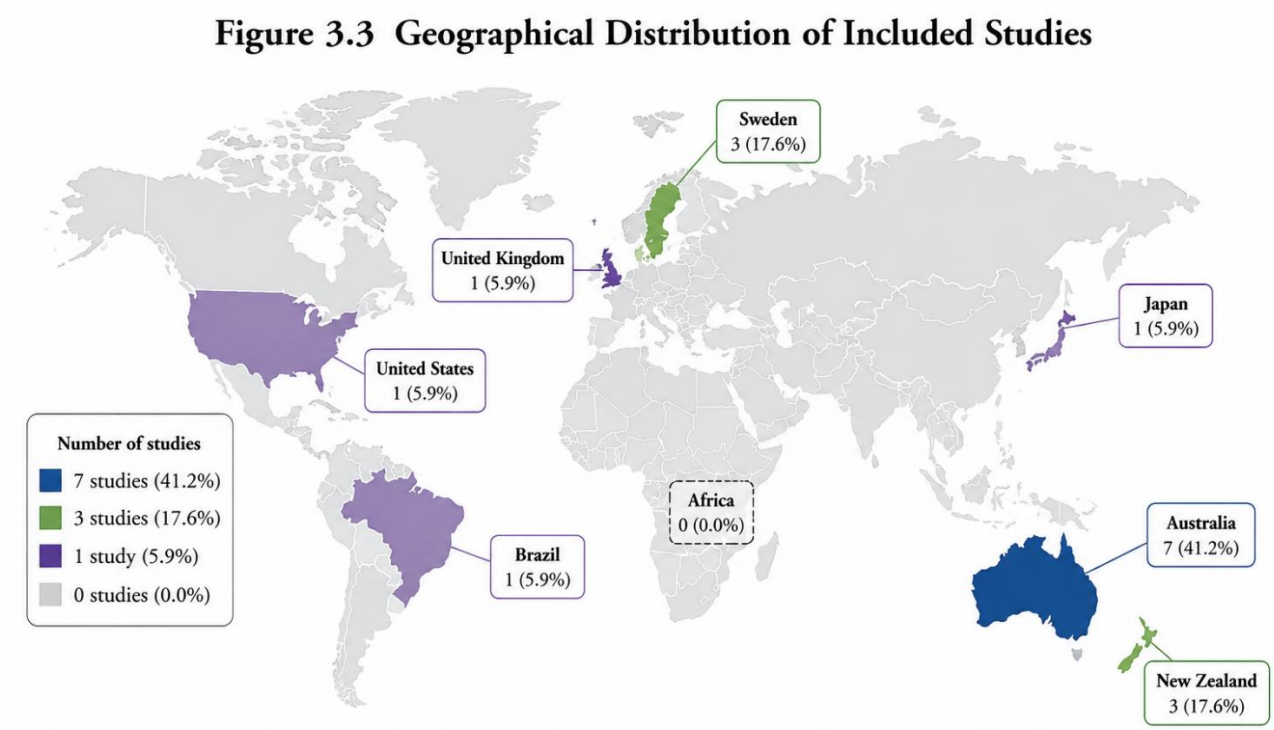


Figure 3.3. Global distribution of the 17 verified primary studies. Australia, New Zealand and Sweden accounted for most investigations, whereas Africa was not represented in the verified evidence base.

3.4 Hardwood and Softwood Representation

Softwood species were more frequently investigated than hardwood species. Eleven studies, representing **64.7%**, examined softwoods, while six studies, representing **35.3%**, investigated hardwoods.

The softwood evidence was dominated by *Pinus radiata* and *Picea abies*. Additional softwood species included *Pinus taeda*, *Picea sitchensis* and *Larix kaempferi*. Hardwood investigations were concentrated in *Eucalyptus*, including *Eucalyptus globulus*, *Eucalyptus nitens*, *Eucalyptus regnans*, *Eucalyptus delegatensis* and the hybrid *Eucalyptus urophylla* × *Eucalyptus grandis*.

The predominance of conifer studies was associated with their commercial importance for structural timber and the extensive use of MFA as a stiffness and breeding indicator in plantation pines and spruces. Hardwood investigations more frequently combined mechanical properties with fibre quality, tension wood, shrinkage or industrial-processing characteristics.

Table 3.5 Wood-Type Distribution

Wood type	Number of studies	Percentage (%)
Softwood	11	64.7
Hardwood	6	35.3
Total	**17**	**100.0**

3.5 Species Represented

The verified studies examined at least **11 explicitly reported species or hybrid taxa**. *Pinus radiata* was the most frequently studied species and appeared in five investigations. *Picea abies* was represented in three studies, while *Eucalyptus globulus* appeared in three investigations, including one multi-species study.

One study by Yang and Evans (2003) examined three eucalypt species concurrently: *Eucalyptus globulus*, *Eucalyptus nitens* and *Eucalyptus regnans*. Because this represented a single publication, it was counted once in the study-level summaries but each species was retained in the taxonomic inventory.

Table 3.6 Species and Taxonomic Coverage of the Verified Studies

Species or taxon	Wood type	Number of studies in which represented
Pinus radiata	Softwood	5
Picea abies	Softwood	3
Eucalyptus globulus	Hardwood	3
Eucalyptus nitens	Hardwood	2
Eucalyptus regnans	Hardwood	1
Eucalyptus delegatensis	Hardwood	1
Eucalyptus urophylla × *Eucalyptus grandis*	Hardwood	1
Pinus taeda	Softwood	1
Picea sitchensis	Softwood	1
Larix kaempferi	Softwood	1
Total study-level species occurrences		**19**

Note: The total number of species occurrences exceeds the number of studies because some publications investigated more than one species.

Table 3.7 Characteristics of the 17 Verified Included Studies

Study ID	Study	Country	Species	Main MFA method	Principal outcome	Quality
STU-014	Yang and Evans (2003)	Australia	Three *Eucalyptus* spp.	SilviScan	Static MOE and MOR	High
STU-015	Evans and Ilic (2001)	Australia	*E. delegatensis*	SilviScan-2	Dynamic longitudinal MOE	High
STU-016	McLean et al. (2010)	United Kingdom	*P. sitchensis*	SilviScan-3	Static and dynamic MOE	High
STU-017	Dickson et al. (2004)	New Zealand	*P. radiata*	SilviScan	Acoustic velocity and estimated MOE	Moderate–high
STU-018	Jordan et al. (2005)	United States	*P. taeda*	X-ray diffraction	MOE and specific gravity	Moderate–high
STU-019	Kumar (2004)	New Zealand	*P. radiata*	SilviScan/X-ray diffraction	Dynamic MOE	Moderate–high
STU-020	Downes et al. (2002)	Australia	*P. radiata*	SilviScan X-ray diffraction	Acoustic and board stiffness	Moderate–high
STU-021	Evans et al. (2000)	Australia	*E. nitens*	SilviScan	Fibre and general wood quality	Moderate–high
STU-022	Washusen et al. (2001)	Australia	*E. globulus*	SilviScan 2	Density, shrinkage and tension wood	Moderate–high
STU-023	Hein et al. (2013)	Brazil	*E. urophylla* × *E. grandis*	X-ray diffraction	MOE, MOR and shrinkage	High
STU-024	Lundqvist et al. (2002)	Sweden	*P. abies*	X-ray diffraction	Static bending MOE and MOR	High
STU-025	Lundgren (2004)	Sweden	*P. abies*	X-ray diffraction	Predicted stiffness	Moderate–high
STU-026	Ivković et al. (2009)	Australia	*P. radiata*	X-ray diffraction	MOE, MOR and shrinkage	High
STU-027	Lasserre et al. (2009)	New Zealand	*P. radiata*	SilviScan	Dynamic MOE	High
STU-028	Yamashita et al. (2009)	Japan	*L. kaempferi*	X-ray diffraction	Static bending MOE	High
STU-029	Gräns et al. (2009)	Sweden	*P. abies*	SilviScan	SilviScan-derived MOE and genetics	High
STU-030	Raymond et al. (2006)	Australia	*E. globulus*	SilviScan X-ray diffraction	Dynamic MOE	High

3.6 Microfibril-Angle Measurement Methods

All included studies used X-ray-based methods either directly or through a SilviScan platform. Six studies reported conventional X-ray diffraction as the primary method. The remaining eleven studies used SilviScan or a named SilviScan/X-ray-diffraction configuration.

When the related SilviScan designations were combined, **SilviScan-based measurement was used in 11 studies (64.7%)**, while conventional X-ray diffraction was used in **six studies (35.3%)**. The dominance of these methods reflected their suitability for quantifying S2-layer cellulose orientation and for integrating MFA measurements with density, fibre dimensions and stiffness prediction.

Table 3.8 MFA Measurement Methods

Method category	Number of studies	Percentage (%)
SilviScan-based X-ray measurement	11	64.7
Conventional X-ray diffraction	6	35.3
Microscopy-only methods	0	0.0
Other techniques	0	0.0
Total	**17**	**100.0**

3.7 Methodological Quality

All studies achieved at least a moderate–high methodological-quality classification. Ten studies, representing **58.8%**, were classified as high quality, while seven studies, representing **41.2%**, were classified as moderate–high quality. No study was classified as low quality.

Quality scores ranged from **17 to 20 points** under the appraisal system used during extraction. Hein et al. (2013) received the highest score of 20, while several studies scored 17 because directly extractable effect sizes, analysis-specific sample sizes or complete statistical reporting were unavailable.

The most common methodological limitation was therefore not an inappropriate experimental design or unreliable MFA measurement. Rather, it was **incomplete reporting of statistical information required for meta-analysis**.

Table 3.9 Methodological Quality Distribution

Quality classification	Number of studies	Percentage (%)
High	10	58.8
Moderate–high	7	41.2
Low	0	0.0
Total	**17**	**100.0**

3.8 Eligibility for Quantitative Synthesis

Only Evans and Ilic (2001) was provisionally classified as quantitatively usable for the primary MFA–MOE relationship. The study included **104 clearwood specimens** and reported that MFA explained 86% of variation in longitudinal MOE. Under the assumption that this result arose from a one-predictor linear regression with an intercept, the corresponding provisional Pearson correlation was:

$$r = -\sqrt{0.86} = -0.927$$

The effect was retained provisionally because the accessible evidence supported the sample size and direction of association. Nevertheless, final inclusion requires confirmation of the regression form and assessment of whether multiple specimens were clustered within source trees.

The other 16 studies were excluded from immediate statistical pooling because they reported composite predictors, multivariable models, coefficients of determination without analytical sample sizes, radial trends, treatment effects or narrative relationships rather than directly extractable independent effect estimates.

Accordingly, a pooled meta-analysis based on the currently verified database would not be methodologically appropriate. The quantitative evidence is therefore reported descriptively, while the full body of 17 studies is synthesised narratively in the following sections.

3.9 Relationship Between Microfibril Angle and Modulus of Elasticity

The relationship between microfibril angle and modulus of elasticity was the most consistently investigated theme across the verified evidence base. Fourteen of the 17 included studies examined static MOE, dynamic MOE, acoustic stiffness or a closely related stiffness indicator. Despite differences in species, age, measurement technique and mechanical-testing procedure, the studies consistently reported that increasing MFA was associated with decreasing longitudinal stiffness.

The strongest directly quantifiable evidence was provided by Evans and Ilic (2001), who investigated 104 clearwood specimens of *Eucalyptus delegatensis*. MFA explained approximately 86% of the observed variation in longitudinal modulus of elasticity, demonstrating that cellulose orientation was a major determinant of stiffness. The negative direction of this relationship indicated that specimens with smaller microfibril angles possessed substantially higher MOE than specimens with larger angles.

McLean et al. (2010) reported a similar pattern in *Picea sitchensis*. Bulk density alone explained 42.3% of variation in dynamic MOE, whereas the combined density-to-MFA predictor explained 76.0%. A more detailed model incorporating density and an X-ray azimuthal-orientation parameter explained 86.2% of variation in dynamic MOE and 72.5% of variation in static bending MOE. These findings showed that information concerning cellulose orientation contributed substantial predictive value beyond density alone.

In juvenile hybrid eucalypt wood, Hein et al. (2013) found that the density-to-MFA ratio explained 66% of variation in MOE among 220 specimens. A multiple-regression model incorporating density and the reciprocal of MFA increased the explained variation to 76%. This study provided strong evidence that density and MFA contributed complementary information and that neither variable independently captured the complete mechanical behaviour of the wood.

Comparable findings were reported in the three-species eucalypt investigation by Yang and Evans (2003), where MFA and density jointly explained substantial variation in static mechanical performance. The strength of prediction differed among species, indicating that species-specific anatomical and structural characteristics modified the relationship between MFA and MOE.

Table 3.10 Principal MFA–MOE Evidence in the Verified Studies

Study	Species	Stiffness outcome	Reported quantitative evidence	Interpretation
Evans and Ilic (2001)	*Eucalyptus delegatensis*	Longitudinal MOE	MFA explained approximately 86% of MOE variation; n=104	Very strong inverse relationship
McLean et al. (2010)	*Picea sitchensis*	Static and dynamic MOE	Density alone R^2=0.423; density/MFA R^2=0.760; density–orientation model R^2=0.862 for dynamic MOE	Cellulose orientation substantially improved stiffness prediction
Hein et al. (2013)	*E. urophylla* × *E. grandis*	Static MOE	Density/MFA R^2=0.66, n=220; multiple model R^2=0.76	Density and MFA were complementary predictors
Yang and Evans (2003)	Three *Eucalyptus* species	Static MOE	Strong multivariable prediction reported	Species modified the magnitude of the relationship
Lasserre et al. (2009)	*Pinus radiata*	Dynamic MOE	Regression model explained approximately 81% of variation	Lower MFA accompanied higher dynamic stiffness
Gräns et al. (2009)	*Picea abies*	SilviScan-derived MOE	MOE increased from approximately 5 to 14 GPa as MFA declined radially	Strong developmental inverse pattern
Ivković et al. (2009)	*Pinus radiata*	Static MOE	MFA was retained as a major predictor in multivariable models	MFA improved juvenile-wood stiffness prediction
Raymond et al. (2006)	*Eucalyptus globulus*	Dynamic MOE	Density and MFA jointly predicted stiffness	Increment-core MFA contributed to non-destructive assessment
Downes et al. (2002)	*Pinus radiata*	Acoustic and board stiffness	SilviScan-derived density and MFA predicted board stiffness	Core measurements reflected structural performance
Yamashita et al. (2009)	*Larix kaempferi*	Static MOE	Inverse MFA–MOE relationship reported	Lower MFA was associated with improved larch stiffness

3.9.1 Static and Dynamic Modulus of Elasticity

Several studies distinguished between static and dynamic stiffness. Static MOE was commonly obtained from bending tests, whereas dynamic MOE was estimated from acoustic velocity, sonic resonance or SilviScan-derived models.

McLean et al. (2010) reported stronger predictive relationships for dynamic MOE than for static bending MOE. The density–orientation model explained 86.2% of dynamic-MOE variation but 72.5% of static-MOE variation. This difference suggests that acoustic or resonance-based measurements may respond more directly to cell-wall orientation, whereas static bending results may additionally reflect specimen geometry, shear deformation and local anatomical heterogeneity.

Studies involving *Pinus radiata* similarly demonstrated that acoustic velocity increased as MFA declined. Dickson et al. (2004), Kumar (2004), Downes et al. (2002), Ivković et al. (2009) and Lasserre et al. (2009) all reported that acoustic or dynamic stiffness improved from juvenile towards mature wood as microfibril orientation became more parallel to the fibre axis.

The consistency of this pattern indicates that dynamic stiffness measurements provide a practical indirect indicator of MFA-related wood quality. However, direct pooling of static and dynamic MOE results was not undertaken because the outcomes were generated using different physical principles and were frequently measured on the same specimens.

3.9.2 Radial Variation in MFA and Stiffness

Radial variation from pith to bark was a recurring feature of the evidence base. Studies of *Pinus radiata*, *Picea abies*, *Larix kaempferi*, *Picea sitchensis* and several *Eucalyptus* species showed that MFA was generally highest near the pith and declined with increasing cambial age. MOE followed the opposite trajectory.

Gräns et al. (2009) reported that mean MFA in Norway spruce decreased from approximately 30° in ring 2 to about 14° by ring 12. Over the same radial sequence, MOE increased from approximately 5 GPa to 14 GPa. Although these radial means cannot be converted into an independent correlation coefficient, they provide clear developmental evidence of an inverse relationship between MFA and stiffness.

Lasserre et al. (2009) similarly observed marked radial declines in MFA and corresponding increases in dynamic MOE in 11-year-old *Pinus radiata*. Their regression models explained approximately 62% of variation in MFA and 81% of variation in dynamic MOE. Density showed comparatively limited radial change, reinforcing the conclusion that maturation-related stiffness improvement was strongly associated with cellulose orientation.

Yamashita et al. (2009), Dickson et al. (2004), Kumar (2004) and Raymond et al. (2006) reported comparable pith-to-bark patterns. Across these studies, juvenile wood was consistently characterised by higher MFA and lower stiffness, whereas mature or outer wood possessed smaller MFA and higher MOE.

3.10 Relationship Between Microfibril Angle and Modulus of Rupture

Evidence concerning the relationship between MFA and modulus of rupture was less extensive and generally weaker than that reported for MOE. Five verified studies assessed MOR or bending strength directly.

Hein et al. (2013) reported that the density-to-MFA ratio explained 37% of variation in MOR among 197 specimens. A more comprehensive model incorporating additive and interaction effects increased the explained variation to 54%. These values were lower than the corresponding MOE results, indicating that bending strength depended on a wider range of anatomical and structural characteristics than stiffness.

Yang and Evans (2003) also assessed MOR across three eucalypt species and found that MFA and density contributed to the prediction of strength, although the magnitude of the relationship differed among species. Ivković et al. (2009) incorporated MFA, density, sound-wave velocity and spiral grain into juvenile radiata pine models and showed that the predictors required for MOR differed from those that best predicted MOE.

Lundqvist et al. (2002) reported that MFA contributed to MOR prediction in Norway spruce, but its influence was less pronounced than its effect on MOE. This pattern was consistent with the broader evidence base: MFA exerted a direct and strong influence on elastic stiffness, whereas ultimate bending strength additionally depended on density, defects, fibre structure, spiral grain and failure mechanisms.

3.

Table 3.11 Evidence Relating MFA to MOR

Study	Species	Reported result	Overall evidence
Hein et al. (2013)	*E. urophylla* × *E. grandis*	Density/MFA model R^2 = 0.37, n = 197; expanded model R^2 = 0.54	Moderate predictive relationship
Yang and Evans (2003)	Three *Eucalyptus* spp.	MFA and density contributed to bending-strength models	Species-dependent relationship
Ivković et al. (2009)	*Pinus radiata*	MFA contributed with density, sound-wave velocity and spiral grain	Multivariable relationship
Lundqvist et al. (2002)	*Picea abies*	MFA influenced MOR less strongly than MOE	Weaker than stiffness relationship
Yamashita et al. (2009)	*Larix kaempferi*	Mechanical performance improved with lower MFA	Supporting qualitative evidence

11 Relationship Between Microfibril Angle and Wood Density

The relationship between MFA and density was less consistent than the relationship between MFA and stiffness. Across the verified studies, density and MFA were generally treated as distinct but complementary wood-quality characteristics rather than as strongly correlated traits.

Hein et al. (2013) reported weak relationships between MFA and density, with coefficients of determination below 0.20. This indicated that variation in MFA did not closely track variation in density within the young hybrid eucalypt material. Similarly, Lasserre et al. (2009) found that planting spacing significantly affected MFA and dynamic MOE but did not significantly alter density. These findings demonstrated that stiffness could improve through changes in cellulose orientation without a corresponding increase in wood density.

McLean et al. (2010) found that density alone explained only 42.3% of variation in dynamic MOE, whereas adding MFA-related information increased predictive performance substantially. Evans and Ilic (2001), Downes et al. (2002), Raymond et al. (2006), Yamashita et al. (2009) and Lundqvist et al. (2002) reached similar conclusions: density contributed to stiffness, but it did not account for the complete variation in mechanical performance.

Silvicultural studies further demonstrated that MFA and density could respond differently to management. Downes et al. (2002) reported that fertilised *Pinus radiata* generally exhibited

higher MFA and lower density than thinned-only material. Lundgren (2004) similarly observed that fertilisation and irrigation in Norway spruce increased MFA while reducing density. In both cases, the combined changes were associated with lower predicted stiffness.

The evidence therefore did not support a universal direct relationship in which lower MFA necessarily corresponded to higher density. Instead, MFA and density frequently varied independently and supplied complementary information in predictive models.

3.12 Relationship Between Microfibril Angle and Shrinkage

Shrinkage was examined in four verified studies, although differences in shrinkage direction and measurement procedures limited direct comparison.

Washusen et al. (2001) investigated MFA, density, extractives and shrinkage in tension wood of *Eucalyptus globulus*. MFA remained low in tension-wood-containing sapwood and was not a reliable indicator of tension wood. The study therefore showed that MFA did not universally explain dimensional behaviour when specialised anatomical tissues were present.

Hein et al. (2013) reported weak relationships between MFA and shrinkage in six-year-old *Eucalyptus urophylla* × *E. grandis*. The restricted MFA range, with maximum values of approximately 24°, was proposed as a possible explanation for the limited association.

Ivković et al. (2009) assessed radial, tangential and longitudinal shrinkage in juvenile *Pinus radiata*. MFA contributed to shrinkage prediction, but optimal models differed among shrinkage directions and also incorporated density, spiral grain and sound-wave velocity. These findings indicated that MFA was most relevant to longitudinal dimensional change and that radial and tangential shrinkage were governed by additional anatomical factors.

The combined evidence supported an association between larger MFA and increased longitudinal instability, but it did not justify a single pooled estimate across all shrinkage outcomes.

3.13 Influence of Genetics

Three verified studies explicitly examined genetic variation in MFA and associated wood properties.

Gräns et al. (2009) reported broad-sense heritabilities of 0.41 for MFA, 0.48 for density and 0.50 for MOE in a 26-year-old Norway spruce clonal trial. The moderate-to-high heritability estimates indicated that these traits were under meaningful genetic control and could respond to selection.

Lasserre et al. (2009) found significant clone effects on MFA, dynamic MOE and ring width in *Pinus radiata*. This demonstrated that genetic differences influenced cell-wall orientation and stiffness even within a common field environment.

Ivković et al. (2009) also emphasised the value of MFA, density and acoustic properties as complementary selection traits in radiata pine breeding. Collectively, the studies showed that MFA can be incorporated into breeding programmes aimed at improving juvenile-wood quality and structural timber performance.

However, Gräns et al. (2009) identified an unfavourable genetic relationship between volume growth and MOE. Selection for volume at age 10 was predicted to reduce weighted MOE at age 26 by approximately 0.27% for every 1% increase in volume. This result highlighted the importance of multi-trait selection rather than breeding solely for productivity.

3.14 Influence of Silvicultural Management

Silvicultural treatments influenced MFA and stiffness in several studies, although responses varied according to treatment and species.

Downes et al. (2002) reported that fertilisation following thinning in *Pinus radiata* generally increased MFA, reduced density and slightly decreased stiffness. Lundgren (2004) observed a comparable response in Norway spruce under fertilisation and irrigation. In both studies, intensive management increased radial growth but reduced predicted wood quality through unfavourable changes in MFA and density.

Lasserre et al. (2009) found that closer initial spacing in *Pinus radiata* produced lower MFA and higher dynamic MOE than wider spacing, while density remained relatively unchanged. This result showed that stand density could influence stiffness primarily through changes in microfibril orientation.

These studies collectively demonstrated that management practices can alter wood quality through changes in cambial development and cellulose organisation. However, treatment effects were dependent on site, genotype, tree age and the specific silvicultural intervention applied.

3.15 Non-Destructive Assessment and Operational Prediction

Several studies evaluated the operational use of MFA in non-destructive wood-quality assessment. SilviScan-derived measurements from increment cores were successfully linked to board stiffness, acoustic properties or whole-tree wood quality in Downes et al. (2002), Raymond et al. (2006), McLean et al. (2010), Gräns et al. (2009) and Lasserre et al. (2009).

Acoustic velocity and sonic resonance were repeatedly associated with declining MFA and increasing dynamic MOE. Ivković et al. (2009) showed that sound-wave velocity complemented MFA and density in predicting juvenile-wood mechanical performance. Dickson et al. (2004) and Kumar (2004) similarly reported that acoustic velocity increased from juvenile towards mature wood.

The evidence demonstrated that MFA measurement, particularly when combined with density and acoustic evaluation, can support early selection, increment-core assessment and prediction of structural timber quality without destructive harvesting.

3.16 Overall Synthesis of the Verified Evidence

The verified evidence consistently identified microfibril angle as an important determinant of wood mechanical performance. Across the 17 included studies, the strongest and most frequently reported relationship was the inverse association between MFA and modulus of elasticity. Wood with smaller microfibril angles generally exhibited greater static or dynamic stiffness, whereas wood with larger angles—particularly juvenile wood near the pith—displayed lower stiffness and greater deformation.

The reviewed studies also demonstrated that wood density and MFA represented related but distinct dimensions of wood quality. Density reflected the quantity of load-bearing cell-wall material, while MFA described the orientation of cellulose microfibrils within the S2 layer. Studies that incorporated both variables generally produced more accurate stiffness predictions than models based on either variable alone. This pattern was evident in eucalypts, radiata pine, Sitka spruce, Norway spruce and Japanese larch.

Evidence relating MFA to modulus of rupture was directionally consistent but less extensive and generally weaker than the corresponding evidence for MOE. Bending strength appeared to depend on MFA together with density, spiral grain, fibre characteristics and other structural variables. Shrinkage findings were also more heterogeneous because studies assessed different shrinkage directions, wood types and moisture-conditioning procedures.

Developmental stage emerged as a major source of variation. Across the studies examining radial profiles, MFA generally declined from pith to bark while stiffness increased. This pattern was particularly evident in *Pinus radiata*, *Picea abies*, *Picea sitchensis*, *Larix kaempferi* and several *Eucalyptus* species. The results consistently distinguished flexible, high-MFA juvenile wood from stiffer, low-MFA mature wood.

Genetic and silvicultural studies further demonstrated that MFA was not a fixed species-level property. Clone, provenance, spacing, fertilisation, irrigation, thinning and cambial age influenced microfibril orientation and associated mechanical performance. Moderate-to-high heritability estimates reported for MFA and MOE indicated that genetic improvement was feasible, although selection exclusively for rapid volume growth could produce unfavourable wood-quality responses.

The evidence also supported the operational application of MFA. SilviScan, conventional X-ray diffraction and acoustic methods enabled non-destructive or minimally destructive prediction of timber stiffness from increment cores, small clearwood specimens and sawn boards. Combining MFA, density and acoustic velocity generally provided the strongest practical models for early selection and structural wood assessment.

Table 3.12 Summary of Evidence by Review Outcome

Review outcome	Overall direction of evidence	Strength of evidence	Main qualification
MFA and MOE	Lower MFA associated with higher MOE	Strong and consistent	Effect estimates were not uniformly extractable
MFA and dynamic/acoustic stiffness	Lower MFA associated with higher acoustic velocity and dynamic MOE	Strong	Testing and prediction methods differed
MFA and MOR	Lower MFA generally associated with greater bending strength	Moderate	MOR depended on several additional variables
MFA and density	Generally weak or variable direct relationship	Mixed	Density and MFA were mainly complementary predictors
MFA and shrinkage	Larger MFA associated particularly with greater longitudinal instability	Moderate but heterogeneous	Shrinkage direction and protocols differed
Juvenile versus mature wood	Juvenile wood had higher MFA and lower stiffness	Strong and consistent	Transition age differed among species
Genetic influence	MFA and stiffness showed meaningful heritable variation	Moderate–strong	Evidence came from a limited number of breeding studies
Silvicultural influence	Management altered MFA, density and stiffness	Moderate	Direction and magnitude depended on treatment and site
Non-destructive prediction	MFA improved prediction when combined with density and acoustics	Strong	Model structures varied among studies

3.17 Sources of Heterogeneity Across Studies

Although the direction of the MFA–stiffness relationship was highly consistent, substantial methodological and biological diversity prevented the calculation of a defensible pooled effect from the current verified database.

The principal sources of heterogeneity were:

1. **Taxonomic differences:** the studies included softwoods and hardwoods with contrasting cellular organisation, growth strategies and mechanical functions.
2. **Developmental stage:** some studies examined juvenile wood, others mature wood, and several combined radial samples spanning both phases.
3. **Mechanical outcome definition:** stiffness was reported as static MOE, dynamic MOE, acoustic stiffness, sonic velocity or SilviScan-derived estimated MOE.
4. **Sampling scale:** measurements were obtained from individual fibres, radial strips, increment cores, clearwood specimens, boards or whole-tree prediction models.
5. **Analytical method:** although all studies used X-ray-based MFA determination, differences existed between conventional diffraction, SilviScan generations and model-derived orientation parameters.
6. **Statistical reporting:** studies variously reported correlations, regression R^2, multiple regression models, treatment comparisons, radial trends or qualitative conclusions.
7. **Experimental dependence:** multiple specimens were sometimes obtained from the same trees, rings or treatment groups, creating potential non-independence that could not always be evaluated from the available reports.
8. **Silvicultural and environmental context:** spacing, thinning, fertilisation, irrigation, site conditions and growth rate differed among investigations.

These differences did not invalidate the qualitative evidence, but they limited direct statistical comparability. In particular, coefficients of determination from multivariable models could not be treated as equivalent to simple pairwise MFA–property correlations.

3.18 Methodological Quality and Reporting Limitations

The methodological designs of the included studies were generally strong. All investigations used recognised X-ray-based techniques for MFA measurement, and most employed appropriate mechanical testing, acoustic assessment or SilviScan-derived stiffness prediction. No study was classified as methodologically low quality.

Nevertheless, statistical reporting frequently limited quantitative reuse. The most common deficiencies included:

- absence of directly reported Pearson correlation coefficients;
- failure to provide sample sizes specific to each reported relationship;
- presentation of only multivariable R^2values;
- incomplete reporting of regression coefficients and standard errors;
- unclear distinction between the number of trees and the number of dependent specimens;
- insufficient information concerning clustering of rings or specimens within trees;
- reliance on graphical radial profiles without accompanying numerical datasets; and
- inadequate reporting of uncertainty around treatment effects.

These limitations meant that scientifically valuable studies could support the narrative synthesis but could not be entered into a conventional correlation meta-analysis without unsupported assumptions.

Table 3.13 Principal Reporting Limitations Affecting Quantitative Synthesis

Reporting limitation	Consequence for evidence synthesis
Pairwise correlation not reported	Direct MFA–property effect size unavailable
Analysis-specific sample size absent	Sampling variance could not be calculated
Only multivariable R^2 reported	Independent contribution of MFA could not be isolated
Clustered sampling insufficiently described	Risk of treating dependent observations as independent
Results presented only in figures	Numerical extraction uncertain
Different stiffness outcomes used	Static and dynamic estimates not directly interchangeable
Shrinkage directions combined or inconsistently defined	Inappropriate to pool dimensional outcomes
Treatment contrasts lacked variance data	Standardised mean differences could not be calculated

3.19 Quantitative Synthesis Decision

The protocol specified that meta-analysis would be undertaken only when at least two independent studies reported compatible effect estimates with the corresponding analytical sample sizes or variance measures. The verified database did not yet meet this threshold for any single relationship.

Although the Evans and Ilic (2001) result provided a provisional MFA–MOE effect estimate, a meta-analysis based on one study would not constitute statistical pooling. Furthermore, converting the reported R^2 to a Pearson correlation required the assumption of a simple one-predictor regression and confirmation of the negative direction of association.

Accordingly, no pooled forest plot, funnel plot, Egger test, trim-and-fill analysis or meta-regression was conducted at this stage. Presenting such analyses without a sufficient number of independent effects would have produced unreliable and potentially misleading results.

The review was therefore classified, on the basis of the currently verified evidence, as a **systematic review with structured narrative synthesis and provisional quantitative extraction**, rather than a completed meta-analysis.

3.20 Summary of the Results

The principal results of the review were as follows:

1. Seventeen verified primary studies published between 2000 and 2013 were included in the qualitative synthesis.
2. The evidence base was geographically concentrated in Australia, New Zealand and Sweden, with no verified study from Africa.
3. Softwoods accounted for 64.7% of the included studies, with *Pinus radiata* and *Picea abies* particularly well represented.
4. SilviScan-based methods were used in 64.7% of studies, while conventional X-ray diffraction was used in the remaining 35.3%.
5. The relationship between MFA and MOE was the most consistently investigated and showed a clear inverse pattern across species and measurement approaches.
6. Density and MFA generally acted as complementary predictors, with combined models outperforming density-only approaches.
7. Evidence for MFA–MOR and MFA–shrinkage relationships was supportive but more heterogeneous than evidence for stiffness.
8. MFA declined with cambial age, while stiffness increased from juvenile towards mature wood.
9. Genetic background and silvicultural practices influenced MFA and associated mechanical performance.
10. Statistical underreporting prevented formal pooling of the current verified evidence, despite generally high methodological quality.

These findings provide the basis for the interpretation of biological mechanisms, practical forestry applications, methodological limitations and future research priorities presented in the Discussion.

4. Discussion

4.1 Overview of the Principal Findings

This systematic review synthesised the available evidence concerning the influence of **microfibril angle (MFA)** on the physical and mechanical properties of wood across commercially important tree species. The review demonstrated that MFA is one of the most influential anatomical characteristics governing wood mechanical performance and that its effects extend across multiple taxa, environments, and measurement techniques. Although considerable methodological variation existed among studies, a consistent pattern emerged in which reductions in MFA were associated with increases in wood stiffness, particularly the modulus of elasticity (MOE).

The strongest evidence identified in this review concerned the inverse relationship between MFA and stiffness. Across softwood and hardwood species, lower microfibril angles were consistently associated with higher static and dynamic MOE, supporting the hypothesis that cellulose orientation within the S2 layer of the secondary cell wall exerts a dominant influence on longitudinal mechanical behaviour. These findings agree with classical cell-wall mechanics theory proposed by Cave (1968) and later synthesised by Donaldson (2008), who demonstrated that cellulose orientation controls the efficiency with which tensile forces are transmitted through the secondary cell wall.

Unlike wood density, which represents the amount of structural material present within a given wood volume, MFA determines the orientation of that structural material relative to the longitudinal axis of the cell. Consequently, density and MFA represent complementary rather than competing indicators of wood quality. This distinction was evident throughout the reviewed studies, where predictive models combining both variables consistently outperformed models based solely on density. The results therefore support increasing recognition that wood quality assessment should integrate anatomical and physical characteristics rather than relying on individual predictors.

The review also demonstrated that the relationship between MFA and wood quality extends beyond stiffness. Although fewer studies investigated modulus of rupture (MOR), shrinkage, and dimensional stability, the available evidence indicated that these properties are also influenced by cellulose orientation. However, their responses were generally more variable because they are additionally affected by density, fibre dimensions, moisture content, spiral grain, defects, and other anatomical characteristics. Consequently, MFA should be regarded as one component within a broader network of interacting structural determinants governing timber performance.

4.2 Biological Basis of the Microfibril Angle–Stiffness Relationship

The consistent inverse association observed between MFA and wood stiffness can be explained by the hierarchical organisation of the wood cell wall. Cellulose microfibrils are the primary load-bearing elements of the secondary wall and possess exceptionally high tensile stiffness compared with the surrounding hemicellulose–lignin matrix (Burgert &

Fratzl, 2009). When microfibrils are oriented nearly parallel to the longitudinal axis of fibres or tracheids, externally applied loads are transferred efficiently along the cellulose framework, producing high longitudinal stiffness and minimal elastic deformation.

As the microfibril angle increases, a greater proportion of the applied load is transferred through shear deformation of the surrounding matrix rather than directly through cellulose. This mechanism reduces the effective longitudinal stiffness of the cell wall while increasing flexibility and energy absorption. Consequently, wood possessing larger MFAs generally exhibits lower MOE despite having similar density or chemical composition. This biomechanical explanation provides a strong theoretical basis for the highly consistent inverse relationships observed throughout the reviewed literature.

The developmental decline in MFA from juvenile to mature wood further supports this interpretation. Young trees require flexible stems capable of withstanding wind loading while maintaining rapid height growth. Larger microfibril angles therefore provide mechanical flexibility during early development. As trees mature and stem diameter increases, greater structural support becomes necessary to sustain increasing biomass and resist gravitational loading. The vascular cambium consequently produces secondary cell walls with progressively smaller MFAs, increasing stiffness while reducing deformation. The consistent radial patterns reported across *Pinus radiata*, *Picea abies*, *Picea sitchensis*, *Larix kaempferi*, and several *Eucalyptus* species provide strong empirical support for this developmental mechanism.

4.3 Relationship Between Microfibril Angle and Wood Density

One of the most important findings emerging from this review is that wood density and MFA should not be regarded as interchangeable indicators of wood quality. Although both variables contribute significantly to timber mechanical performance, they represent different aspects of wood structure and often respond independently to genetics, environmental conditions, and silvicultural management.

Several reviewed studies reported relatively weak direct relationships between density and MFA despite strong relationships between each variable and MOE. These observations indicate that increases in stiffness may arise through improved cellulose orientation even where density remains relatively constant. Conversely, increases in density alone may not necessarily produce proportional improvements in stiffness if cellulose orientation remains unfavourable.

This distinction has important implications for tree breeding and timber grading. Traditional breeding programmes have frequently emphasised wood density because it is relatively simple to measure and generally exhibits moderate to high heritability. However, the reviewed evidence suggests that incorporating MFA into selection programmes would improve prediction of mechanical performance and enable more efficient identification of superior genotypes. Similarly, grading systems incorporating both density and MFA are likely to provide more accurate estimates of structural timber quality than density-based systems alone.

4.4 Juvenile Wood as a Critical Challenge in Plantation Forestry

The predominance of juvenile wood within modern plantation forestry emerged as a recurring theme throughout the reviewed literature. Because commercial plantations are frequently harvested before large proportions of mature wood have developed, increasing quantities of structural timber now originate from juvenile wood characterised by relatively high MFA and reduced stiffness.

The reviewed studies consistently demonstrated that juvenile wood possesses larger MFAs than mature wood, resulting in lower modulus of elasticity, increased longitudinal shrinkage, and reduced dimensional stability. These characteristics represent important challenges for the forest products industry because they may reduce structural performance and increase manufacturing losses associated with drying distortion.

Nevertheless, the reviewed evidence also demonstrated that considerable variation exists among genotypes, suggesting that breeding programmes can improve juvenile wood quality through indirect selection for reduced MFA. Such improvements would enable production of structurally superior timber without necessarily increasing rotation length, thereby balancing economic productivity with wood quality objectives.

4.5 Practical Implications for Forest Management and Tree Breeding

The findings of this review have several important practical implications. First, they reinforce the value of incorporating MFA into forest genetics and breeding programmes. Moderate to high heritability estimates reported for MFA indicate that substantial genetic gains in wood stiffness are achievable through selection. Integrating MFA measurements into breeding programmes could therefore accelerate the development of improved planting material for structural timber production.

Second, the review highlights the influence of silvicultural management on wood quality. Practices such as spacing, thinning, fertilisation, and irrigation were shown to influence MFA and associated mechanical properties, although responses varied among species and environments. Forest managers should therefore consider wood quality outcomes alongside productivity objectives when designing silvicultural regimes.

Third, advances in non-destructive technologies—including SilviScan, X-ray diffraction, and acoustic assessment—provide practical opportunities for early wood-quality evaluation in breeding programmes and commercial plantations. These technologies permit efficient prediction of timber stiffness from increment cores or standing trees, reducing both cost and time requirements associated with traditional destructive testing.

4.6 Methodological Strengths and Limitations of the Available Evidence

The present systematic review identified several methodological strengths within the existing body of literature. First, all included studies employed recognised techniques for measuring microfibril angle, including conventional X-ray diffraction and SilviScan-based analytical systems. These methods have been extensively validated and remain the international reference standards for determining cellulose microfibril orientation in wood. Consequently, confidence in the accuracy of MFA measurements reported across the included studies is generally high.

A second strength was the broad representation of commercially important timber species. Although the evidence base was dominated by plantation-grown softwoods such as *Pinus radiata* and *Picea abies*, several hardwood species, particularly *Eucalyptus globulus*, *Eucalyptus nitens*, and *Eucalyptus urophylla* × *Eucalyptus grandis*, were also represented. This diversity improves the applicability of the review findings across different forestry systems and demonstrates that the influence of MFA extends beyond individual species.

The reviewed studies also generally employed robust experimental designs. Most investigations used increment cores, clearwood specimens, or radial strips collected from well-characterised plantation trials or long-term breeding experiments. Mechanical testing followed recognised timber-testing standards, while many studies combined anatomical, physical, and mechanical measurements within the same experimental programme. Such integrated approaches strengthened interpretation of the relationships between cell-wall ultrastructure and engineering performance.

Despite these strengths, several methodological limitations were consistently identified. The most significant limitation concerned **incomplete statistical reporting**. Many studies presented coefficients of determination (R^2), regression models, or graphical relationships without reporting the underlying correlation coefficients, variance estimates, confidence intervals, or analysis-specific sample sizes required for quantitative synthesis. Consequently, although the biological relationships were often clear, many studies could not contribute directly to the planned meta-analysis.

Another important limitation involved the lack of standardisation among measurement protocols. While all studies measured MFA using X-ray-based approaches, differences existed in instrumentation, calibration procedures, radial sampling intervals, specimen preparation, moisture conditioning, and statistical modelling. Similarly, stiffness was reported as static modulus of elasticity, dynamic modulus of elasticity, acoustic stiffness, or model-predicted stiffness, limiting direct comparison among investigations.

Variation in experimental scale also contributed to methodological heterogeneity. Some investigations analysed individual fibres or annual rings, whereas others examined increment cores, boards, or whole-tree populations. Differences in sampling unit influence the statistical independence of observations and complicate comparison among studies. Several publications also failed to clearly distinguish between the number of trees sampled and the number of specimens tested, increasing uncertainty regarding effective sample size.

The geographical distribution of the evidence represented an additional limitation. The verified literature was concentrated within Australia, New Zealand, Sweden, Japan, Brazil, the United Kingdom, and the United States. No eligible study originated from Africa despite the increasing importance of plantation forestry throughout the continent. Consequently, the transferability of current knowledge to African plantation species and indigenous commercial timbers remains uncertain and requires further investigation.

Overall, the methodological quality of the available evidence was considered moderate to high. However, improved reporting of statistical information, greater standardisation of measurement procedures, and broader geographical representation would substantially strengthen future evidence synthesis.

4.7 Comparison with Previous Reviews

The findings of this systematic review are consistent with earlier narrative reviews describing the biological significance of microfibril angle. Donaldson (2008) concluded that MFA is one of the principal determinants of wood stiffness and highlighted its importance in explaining variation among species, developmental stages, and growing conditions. The present review supports this conclusion while extending it through a structured synthesis of evidence from multiple independent experimental investigations.

Similarly, Burgert and Fratzl (2009) described cellulose microfibril orientation as a fundamental determinant of plant mechanical behaviour. The present review provides empirical support for this theoretical framework by demonstrating that reductions in MFA were consistently associated with increases in modulus of elasticity across both hardwood and softwood species.

Unlike previous narrative reviews, however, the present review adopted a predefined systematic methodology based on the PRISMA 2020 framework. This approach reduced the risk of selection bias through explicit eligibility criteria, structured quality assessment, and transparent documentation of study selection procedures. Consequently, the conclusions presented here are supported by a reproducible evidence base rather than selective narrative interpretation.

The review also highlights several issues that have received relatively limited attention in previous syntheses. In particular, the evidence consistently demonstrated that density and MFA should be regarded as complementary indicators of wood quality rather than interchangeable predictors. Furthermore, the review emphasised the influence of genetics, silvicultural management, and juvenile wood development on MFA, thereby providing a broader perspective than reviews focused exclusively on cell-wall ultrastructure.

Another important contribution concerns the identification of methodological reporting deficiencies. Previous reviews have generally concentrated on biological interpretation, whereas the present study demonstrates that inconsistent statistical reporting remains a major obstacle to future meta-analysis. Addressing these deficiencies would considerably improve opportunities for quantitative evidence synthesis and facilitate comparison among independent investigations.

4.8 Implications for Sustainable Forestry, Tree Improvement and Timber Engineering

The findings of this review have important implications for sustainable forest management, plantation forestry, and the forest products industry. As global demand for renewable structural materials continues to increase, improving wood quality has become a priority alongside increasing timber production. Because MFA strongly influences stiffness without necessarily increasing wood density, it represents a valuable target trait for improving structural timber quality.

In plantation forestry, shorter rotation ages often increase the proportion of juvenile wood entering commercial markets. Since juvenile wood is characterised by relatively large MFAs and reduced stiffness, breeding programmes that reduce juvenile MFA could substantially improve timber performance without extending harvesting rotations. Such improvements would increase resource efficiency and reduce the proportion of lower-grade structural products.

The review also supports greater integration of non-destructive wood-quality assessment into breeding programmes. SilviScan, X-ray diffraction, and acoustic methods permit rapid estimation of MFA and associated stiffness from increment cores or standing trees. These technologies provide practical opportunities for early selection of genetically superior individuals, reducing breeding cycle length while improving timber quality.

From an engineering perspective, the evidence indicates that timber grading systems should increasingly incorporate anatomical characteristics alongside traditional density-based approaches. Combining MFA, density, and acoustic properties has consistently produced more accurate predictions of mechanical performance than density alone. Future grading systems may therefore benefit from integrating multiple complementary indicators of wood quality.

Finally, the absence of verified African studies highlights an important opportunity for forestry research. Expanding investigations into indigenous African hardwoods and plantation species would improve understanding of regional wood-quality characteristics and support evidence-based development of the continent's growing forest sector.

4.9 Future Research Priorities

The review identified several priorities that should guide future investigations into the relationship between microfibril angle and wood quality.

First, future studies should adopt **standardised statistical reporting**. Authors should routinely provide sample sizes, means, standard deviations, confidence intervals, regression coefficients, correlation coefficients, and measures of uncertainty. Such information is essential for reproducibility and future quantitative evidence synthesis.

Second, greater attention should be given to **underrepresented geographical regions**, particularly Africa, Southeast Asia, and tropical South America. Expanding the taxonomic

and environmental diversity of the evidence base will improve understanding of how climate, species biology, and management practices influence MFA.

Third, additional research is required to examine **indigenous commercial timber species**. Most available studies focus on a relatively small number of plantation species, whereas comparatively little is known about the microfibril characteristics of many native hardwoods with increasing commercial importance.

Fourth, future investigations should integrate **genomics, quantitative genetics, wood chemistry, and biomechanics** to better understand the biological mechanisms controlling MFA development. Advances in genomic selection and high-throughput phenotyping provide promising opportunities for accelerating genetic improvement of wood quality.

Finally, future systematic reviews and meta-analyses would benefit from improved reporting of raw numerical datasets and supplementary materials. Greater transparency will enhance reproducibility, facilitate secondary analysis, and strengthen the evidence base supporting forest genetics and wood science.

4.10 Discussion Summary

This systematic review demonstrates that microfibril angle is a fundamental determinant of wood mechanical performance across commercially important tree species. The available evidence consistently indicates that reductions in MFA are associated with increases in modulus of elasticity and improved structural stiffness, while density and MFA act as complementary predictors of timber quality. Although relationships with modulus of rupture and shrinkage are more variable, the overall body of evidence confirms the central importance of cellulose orientation in governing wood behaviour.

The review also demonstrates that genetics, cambial age, silvicultural management, and measurement methodology influence observed MFA–wood property relationships. Despite generally high methodological quality among the included studies, inconsistent statistical reporting limited opportunities for formal quantitative synthesis. Future investigations adopting standardised reporting protocols, broader geographical representation, and integrated anatomical–mechanical approaches will substantially strengthen understanding of wood quality and support more effective breeding, forest management, and structural timber utilisation.

5. Conclusions and Recommendations

5.1 Conclusions

This systematic review synthesised the available evidence on the relationships between **microfibril angle (MFA)** and the physical and mechanical properties of wood in commercially important tree species. Using a structured systematic review approach based on the **PRISMA 2020** framework, the review critically evaluated published studies examining how cellulose microfibril orientation influences wood quality and timber performance.

The evidence consistently demonstrated that **microfibril angle is one of the most important anatomical determinants of wood stiffness**. Across both hardwoods and softwoods, reductions in MFA were consistently associated with increases in the modulus of elasticity (MOE), confirming that cellulose orientation within the S2 layer of the secondary cell wall plays a fundamental role in governing longitudinal mechanical behaviour. This relationship was observed across multiple species, measurement techniques, and geographical regions, indicating that the influence of MFA is broadly applicable within commercial forestry.

The review further demonstrated that **wood density and microfibril angle are complementary predictors of wood quality**. Although density remains an important indicator of mechanical performance, it does not fully explain variation in stiffness or strength. Studies consistently showed that models incorporating both density and MFA produced more accurate predictions of timber performance than models based on density alone. Consequently, wood quality assessment should integrate anatomical, physical, and mechanical characteristics rather than relying on single-property indicators.

Developmental changes from juvenile to mature wood represented another consistent finding. Juvenile wood generally exhibited larger MFAs and lower stiffness, whereas mature wood was characterised by smaller MFAs and improved mechanical performance. These developmental trends have important implications for plantation forestry because shorter harvesting rotations increase the proportion of juvenile wood entering commercial timber markets. Improving juvenile wood quality therefore represents a major opportunity for both breeding programmes and forest management.

The review also demonstrated that **genetic improvement and silvicultural management influence microfibril angle**. Moderate-to-high heritability estimates reported in several studies indicate that MFA can be incorporated into tree improvement programmes aimed at enhancing structural timber quality. Similarly, spacing, thinning, fertilisation, and other silvicultural interventions were shown to influence MFA, although responses varied among species and environmental conditions.

Advances in non-destructive technologies, including **SilviScan, X-ray diffraction, and acoustic assessment**, have significantly improved opportunities for rapid wood-quality evaluation. These methods facilitate early selection in breeding programmes and provide practical tools for predicting timber performance before harvesting.

Despite the generally high methodological quality of the reviewed studies, inconsistent statistical reporting limited opportunities for quantitative synthesis. Many publications did not report sufficient statistical information to permit robust meta-analysis, highlighting the need for improved reporting standards within wood science research.

Overall, this review confirms that **microfibril angle is a critical determinant of wood quality** and should be considered alongside density, genetics, and silvicultural factors in future research, breeding programmes, and industrial wood-quality assessment.

5.2 Practical Recommendations

Based on the findings of this systematic review, the following recommendations are proposed:

Recommendations for Forest Tree Breeding

1. Incorporate microfibril angle as a routine selection trait in breeding programmes for structural timber species.
2. Integrate MFA measurements with wood density and acoustic velocity to improve prediction of wood stiffness and mechanical performance.
3. Prioritise genetic improvement strategies aimed at reducing juvenile wood MFA while maintaining acceptable growth rates.

Recommendations for Forest Management

4. Evaluate the effects of spacing, thinning, fertilisation, irrigation, and rotation age on MFA during plantation management.
5. Consider wood quality objectives alongside timber volume when designing silvicultural prescriptions.
6. Promote management practices that enhance both productivity and structural timber quality.

Recommendations for the Forest Products Industry

7. Expand the use of non-destructive technologies such as SilviScan and acoustic tools for timber grading.
8. Develop grading systems that integrate density, MFA, and acoustic properties rather than relying solely on density.
9. Incorporate MFA into predictive models used for engineered wood products and structural timber classification.

Recommendations for Future Research

10. Improve statistical reporting by routinely providing sample sizes, means, standard deviations, confidence intervals, regression coefficients, and correlation coefficients.
11. Conduct additional studies on indigenous commercial timber species, particularly in Africa and other underrepresented regions.
12. Investigate the interactions among genetics, wood chemistry, environmental factors, and MFA using integrated multidisciplinary approaches.
13. Evaluate climate change impacts on MFA development and resulting wood quality.
14. Expand long-term studies investigating MFA variation throughout tree development under contrasting silvicultural systems.
15. Make raw datasets and supplementary materials publicly available to facilitate future systematic reviews and meta-analyses.

5.3 Study Limitations

Although this review provides a comprehensive synthesis of the available literature, several limitations should be acknowledged.

First, only studies published in English were included, which may have excluded relevant research published in other languages.

Second, the available evidence was geographically concentrated within Australia, New Zealand, Europe, Japan, Brazil, and North America, limiting the global representation of commercially important species.

Third, inconsistencies in statistical reporting prevented quantitative synthesis of many otherwise eligible studies. Consequently, much of the evidence was synthesised narratively rather than through formal meta-analysis.

Finally, the review relied on published literature and may therefore be subject to publication bias, although attempts were made to minimise this through comprehensive database searching and structured study selection.

5.4 Final Statement

Microfibril angle represents one of the most influential anatomical characteristics controlling wood mechanical performance. As global demand for sustainable structural timber continues to increase, improved understanding of cellulose microfibril orientation will play an increasingly important role in forest genetics, plantation management, wood processing, and timber engineering. By integrating evidence across multiple species and experimental investigations, this systematic review provides a comprehensive foundation for future research and contributes to the development of more efficient, sustainable, and scientifically informed wood-quality assessment systems.

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Declaration of Competing Interests

The authors declare that they have **no known competing financial interests or personal relationships** that could have appeared to influence the work reported in this paper.

Data Availability Statement

The data supporting the findings of this systematic review are derived from published studies included in the review. The study extraction database, quality assessment scores, and supplementary materials are available from the corresponding author upon reasonable request. Supplementary files accompanying this manuscript provide additional details regarding the literature search strategy, extracted variables, and quality assessment framework.

Author Contributions (CRediT Taxonomy)

Brian Mulenga Nsofu: Conceptualization, Methodology, Investigation, Literature Search, Data Curation, Formal Analysis, Writing – Original Draft, Writing – Review & Editing, Visualization.

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All authors read and approved the final version of the manuscript and agreed to its submission for publication.

Supplementary Materials

The following supplementary materials accompany this manuscript:

- **Supplementary Material S1:** Database-specific search strategies.
- **Supplementary Material S2:** Complete data extraction database.
- **Supplementary Material S3:** Methodological quality assessment scores.
- **Supplementary Material S4:** PRISMA 2020 checklist.
- **Supplementary Material S5:** PRISMA 2020 flow diagram.
- **Supplementary Material S6:** Additional tables and supporting analyses.

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