



Impact of Intensive Forest Management Practices on Wood Quality from Conifers: Literature Review and Reflection on Future Challenges

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Abstract

Purpose of Review Intensive forest management practices are being implemented worldwide to meet future global demand for wood and wood products while facilitating the protection of natural forest ecosystems. A potential decline in wood properties associated with rapid tree growth makes it essential to quantify the potential impact of intensive management on the process of wood formation and, in turn, on its suitability for various end-uses.

Recent Findings Wood produced over short rotations is generally of lower quality because wood properties tend to improve with cambial age (i.e. the number of annual growth rings from the pith). The intensification of silvicultural practices can thus have measurable consequences for the forest products value chain. The use of new planting material from tree improvement programs could offset such effects, but questions arise as to the effects of a changing climate on wood produced from these plantations and the best silvicultural approaches to manage them.

Summary Based on these recent findings, we provide reflections on the need for a modelling framework that uses the effects of cambial age, ring width and position along the stem to summarise the effects of tree growth scenarios on wood properties. We then present challenges related to our limited understanding of the effects of several drivers of wood properties, such as climate variation, genetic material, and forest disturbances, among others, and highlight the need for further data collection efforts to better anticipate the quality attributes of the future wood fibre resource. We conclude by providing examples of promising new tools and technologies that will help move wood quality research forward by allowing (1) fast, efficient characterisation of wood properties, and (2) up-scaling predictions at the landscape level to inform forest management decisions.

Keywords Wood quality · Intensive forest management · Silvicultural treatments · Plantation · Conifers · Future challenges

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Introduction

Commonly understood definitions of intensive forest management practices have been in use for over 70 years [1], with adjustments made over subsequent decades by specialists in various sub-disciplines. However, most definitions in use today [2–7] converge around the principle that silvicultural treatments can be used to maximise wood and timber production. These silvicultural treatments include plantations of hybrid or fast-growing tree species (e.g. [8]), respacing (e.g. [9]), thinning (e.g. [10]), pruning (e.g. [11]), fertilisation (e.g. [12]), and vegetation control (e.g. [13])—with or without herbicides, insecticides or biocontrol of pests (e.g. [14]).

Currently, the most commonly mentioned solution in the scientific literature to meet future global demand for wood while allowing the protection of natural forest ecosystems relates to increasing wood supply from plantations [2, 7].

Several jurisdictions around the world integrate the use of planted forests into their strategy for forest conservation [15–20]. As the adoption of intensive forest management practices increases, it is essential to consider their potential impact on the process of wood formation and, in turn, on wood quality. Indeed, silvicultural practices often result in important changes in growth patterns and tree form, which can lead to variability in wood properties, thereby influencing suitability for various end-uses [21, 22].

Pioneering work from Philip R. Larson in the 1960s [23] described the physiological processes underlying the deleterious effects of rapid growth on wood properties and emphasised that the concept of wood quality must consider specific end-uses. According to this principle—highlighted by many authors in recent years—the definition of wood quality may vary according to the desired end-product [24–28]. For the timber industry, for example, criteria such as wood density, relative proportions of heartwood and sapwood, proportion of juvenile wood (also referred to as corewood) and reaction wood, knots (size, status, frequency, etc.) and grain orientation are the most important to consider, while for the pulp and paper industries, fibre length, wood cell properties and chemical composition are the most relevant [29].

To better anticipate the consequences of silvicultural choices on future wood supplies, there is a need to understand the drivers of variation in wood properties [2, 25]. In turn, such knowledge can help increase supply chain productivity and improve economic performance.

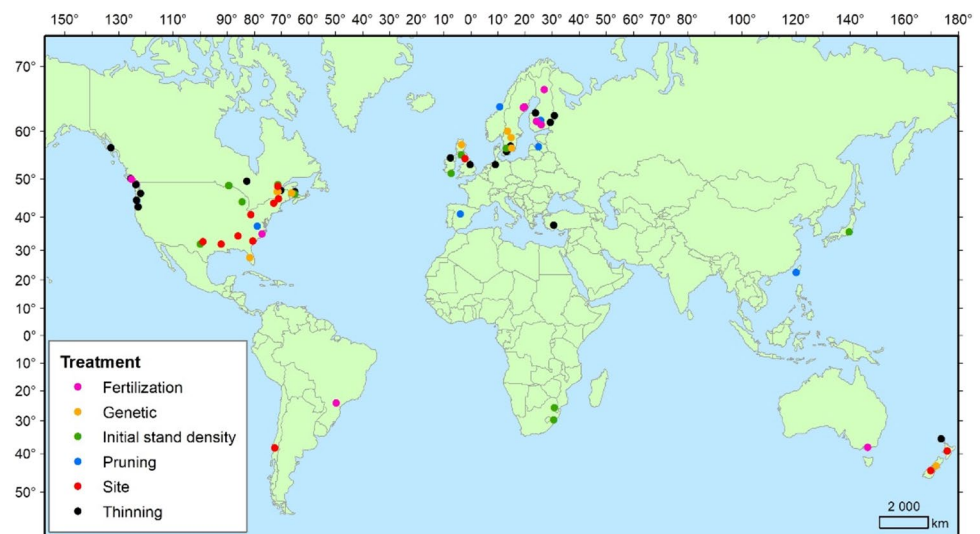
The intensification of silvicultural practices has measurable consequences for the forest products value chain. In the USA, for example, serious concerns were raised in 2010 regarding the bending design values for southern pine lumber from planted forests, which were found to be significantly lower than those obtained from natural forests. Consequently, the Southern Pine Inspection

Bureau issued new reduced design values for some grades of southern pine dimension lumber [30]. This allowed the construction industry to use lumber from planted forests under revised building codes [31]. Such adjustments further highlight the relative nature of the wood quality concept; not only does it vary according to different end-uses, but it can also evolve over time for a specific product.

With this reality in mind, we aimed to assemble current knowledge on the effects of intensive silvicultural practices on important wood properties. This way, readers can interpret the information provided based on their own understanding of wood quality. Our review builds upon previous review papers on the effect of silvicultural treatments on wood properties [25–29, 32–34]. Here, we focus more specifically on the effects of intensive silviculture on wood properties with an emphasis on coniferous species from around the world.

In line with current definitions of intensive forest management, papers considered in this review investigated the effects of ‘initial spacing’ thinning, respacing, pruning, fertilisation, site fertility, or genetics on wood properties. We used Google Scholar as our chosen search engine, as a preliminary comparison had shown it was the most inclusive among similar tools. The search terms included the following keywords: ‘the effect(s) of’, plus ‘initial spacing’, ‘thinning’, ‘respacing’, or ‘pruning’, ‘fertilization’ or ‘site fertility’ or ‘genetic(s)’ plus ‘wood properties’, ‘mechanical properties’, ‘wood density’, ‘lumber’, or ‘microfibril angle’, plus ‘plantation’. Once the search was completed, titles and abstracts of highlighted papers were sifted, and only relevant studies were included in the review. Main results from the retained papers were then summarised in the form of tables or graphs to facilitate the analysis. Figure 1 shows the location of each study included in this review.

Fig. 1 Geographic location of the research articles used in this review. If provided, the geographic coordinates of the study location were extracted; otherwise, we used the names of the location provided in the paper and extracted the coordinates for the studied area



The review is divided into four main sections. The first section summarises current knowledge on the effects of intensive forest management practices on wood properties. It is based on the main research findings extracted from the relevant empirical studies retained from our literature search. The subsequent sections provide reflections on (i) current knowledge gaps and future challenges, (ii) the need for a modelling framework to summarise the effects of intensive management practices on future wood properties under a changing climate and (iii) the emerging technologies in wood characterisation and utilisation that will help move wood quality research forward. We conclude by highlighting the detrimental effects of a decreasing age at harvest on wood quality and its implications for future production and processing.

Current Knowledge on the Effects of Intensive Forest Management Practices on Wood Properties

Initial Spacing

The choice of initial spacing at planting has an important effect on the secondary growth of trees, wood properties and volume production. Traditionally, the most common spacing used for conifer species was set at approximately 2 m in an orthogonal grid, which is equivalent to ~2500 seedlings per hectare [34–36]. However, in recent decades planting distances have tended to increase to encourage faster radial growth, leading to shorter rotations [34, 37–40] and reduction in establishment costs [41, 42]. In New Zealand, for example, typical stocking rates are now around 1,000 seedling per hectare, which represents an average square spacing of 3.2 m [43].

However, trees planted and grown at wider spacings generally have larger crowns that produce a larger juvenile core [32, 34, 39, 44, 45], which contains wood with lower density, higher MFA [46, 47] (Fig. 2, Table 1), larger knots [34, 37, 39, 48–50], greater stem taper [34, 51], increased stem curvature [52], and poor stem straightness in the bottom log [47, 52]. The greater presence of sweep and leaning stems in a stand have also been associated with increased production of compression wood [34], which is associated with high longitudinal shrinkage and a greater propensity to sudden failure under loads than normal wood [53]. These changes in tree morphology and wood properties may eventually alter sawing patterns and thus affect sawmill recovery and efficiency [47, 54–56].

Wider spacings are generally associated with lower modulus of elasticity (MOE) and modulus of rupture (MOR) in coniferous species [37, 46–48, 50, 55, 57] (Fig. 2, Table 1). The effect of wide spacing on wood density, however, is often

less severe and varies among species. For example, lower wood density was associated with wider spacings in jack pine (*Pinus banksiana* Lamb.) [58], Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* (L.) Karst.) [57] and patula pine (*Pinus patula* Schiede ex Schltdl. et Cham.) [47]. Other studies revealed only slight reductions in wood density at wide spacings in Norway spruce [59], black spruce (*Picea mariana* (Mill) B.S.P.) [50], and white spruce (*Picea glauca* (Moench) Voss) [37]. Finally, wood density did not vary significantly with spacing in Sitka spruce (*Picea sitchensis* (Bong.) Carr) [60], radiata pine (*Pinus radiata* D. Don) [46], Japanese cedar (*Cryptomeria japonica*) [48], young jack pine [39] and western hemlock (*Tsuga heterophylla* (Raf.) Sarg) [61] (Fig. 2, Table 1). As can be seen from the jack pine studies [39, 58], these effects also vary according to tree age.

Most research findings indicate a decrease in fibre length [44, 46, 58, 61] with increased spacing (Fig. 2, Table 1), with the exception of white spruce [45]. A reduction in cell wall thickness at wider spacings has also been reported in radiata pine [46].

While the adverse effects on wood quality attributes of planting at wider spacing are well documented, on some occasions this practice may also be beneficial. For example, on low fertility sites, or under serious drought conditions, wider spacing between trees can be advantageous, as more nutrients and water could be available to individual trees [62].

Thinning and Respacing

Thinning and respacing are intermediate treatments used to favour vigorous, healthy trees, which most likely will increase in size due to accelerated radial growth, thereby improving economic returns [34, 63]. Respacing (or pre-commercial thinning) is applied to young stands before canopy closure and generally before individual stems have reached merchantable size. The effects of respacing on wood properties are comparable to those of initial spacing [9, 64–67] (Table 2). Commercial thinning, in contrast, is usually applied to older stands after canopy closure, which corresponds, more or less, with the time of death of the lowest branches. Its effects on wood supplies are twofold. First, trees removed during thinning operations may include trees with low vigour and poor stem form, among other defects. Second, thinned trees are often of lower quality because they have not reached maturity and may thus contain a higher proportion of corewood [22]. However, little research has been dedicated to quantifying the specific properties of thinned stems. Instead, most work has focused on the effects of thinning on the properties of the crop at final harvest. Due to their older age and acceleration of radial growth at a later stage, commercial thinning may lead to a lower proportion of corewood in the remaining trees [68], while having little effect on knot size [34, 63].

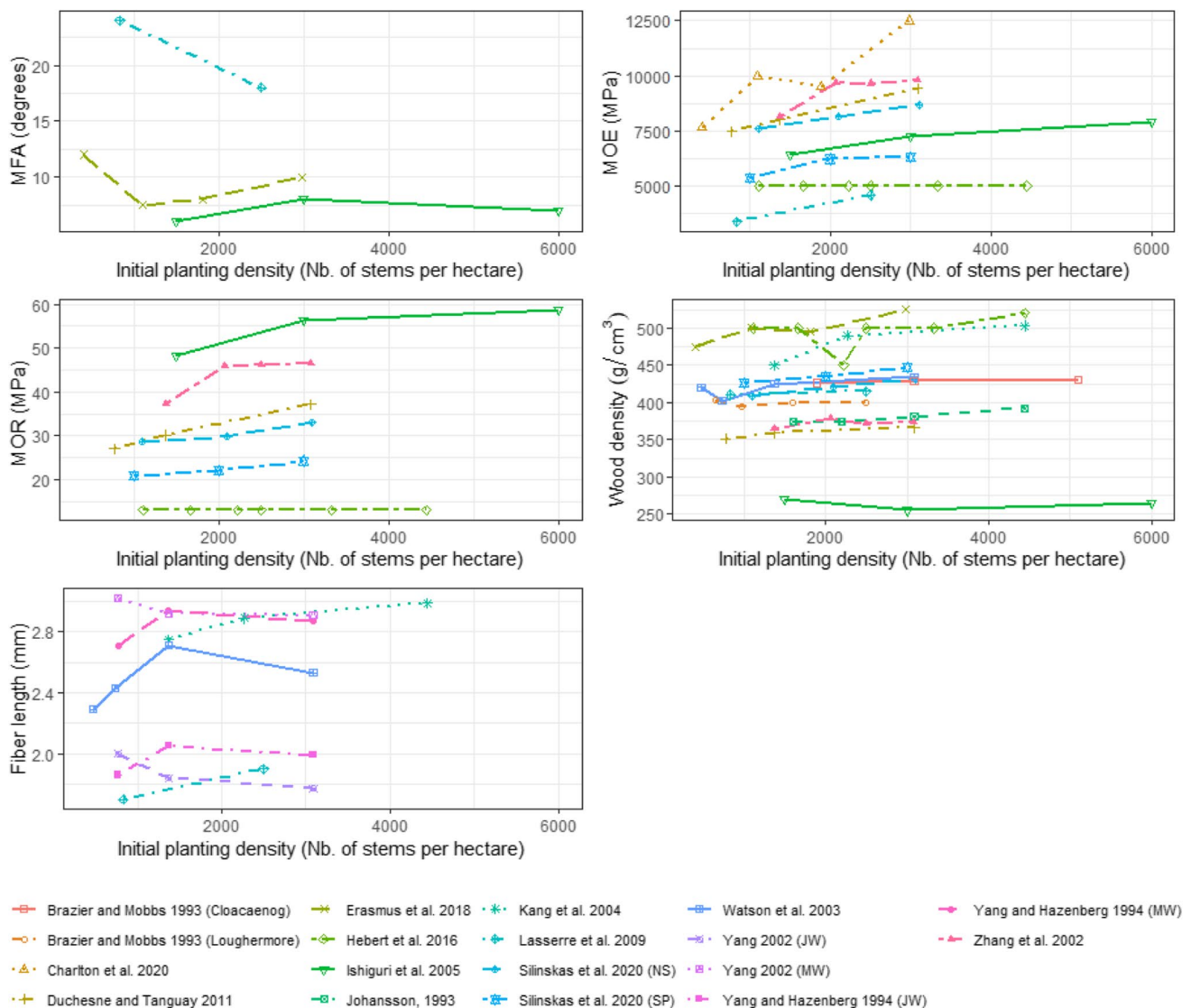


Fig. 2 Variation of MFA (degrees), MOE (MPa), MOR (MPa), wood density (g cm^{-3}) and fibre length (mm) along different initial planting densities for different published studies

The timing and intensity of thinning or respacing treatments are thus critical, as implementing them too early or too aggressively may result in lower wood density [9, 69, 70], larger knots [65, 67, 71], inferior mechanical properties [65, 72], shorter fibres [73] and lower grade lumber [10, 65], all of which have been reported in trees grown at excessively wide initial spacing (> 2.5 m, Fig. 2).

When thinning treatments are applied optimally, the impact on structural wood quality or chemical composition can either be negligible [74–78], minor [69, 79], or even beneficial [80]. Likewise, the production of compression wood has both been reported to increase [64, 81] or decrease [75] after thinning (Table 2). Results of the latter study were interpreted as a potential response to phototropic stimuli, which might favour the inclination of stems

as trees compete for space in unthinned stands. Compared with unthinned stands, trees in thinned stands may have the advantage to exhibit accelerated self-pruning of dead branches, because of the increased effects of wind, rain, snow, and solar radiation inside the stand [82, 83]. In contrast, thinning may contribute to a faster lateral expansion of the tree crown [84]. Thinning has also been reported to stimulate the formation of epicormic branches in Sitka spruce, especially when combined with a high lift pruning treatment [85].

Pruning

Artificial pruning is used to increase the length of the knot-free section of a log, which can increase both mechanical

Table 1 Additional information related to the references cited in Fig. 2

Figure	Reference	Species	Age	Supplementary information
MFA	[47]	Patula Pine	13	MFA for year 13 extracted from Fig. 4b, p. 252. MFA measured with Silviscan. Trees were pruned at 5, 7 and 9 years old
	[48]	Japanese cedar	30	MFA for year 30 extracted from Fig. 7, p. 383. MFA measured with iodine method
	[46]	Radiata pine	10	MFA for year 10 extracted from Fig. 1a, p. 1927. MFA measured with Silviscan
MOE and MOR	[55]	Patula pine	18	Data obtained from Fig. 4, p. 6. Static bending properties measured on boards. Results from board position 2 are reported
	[37]	White spruce	60	Data extracted from Table 22, p. 22. Static bending properties tested on board of different dimensions
	[39]	Jack pine	25	Data extracted from p.9 of the manuscript. Static bending properties tested on small clear specimens
	[48]	Japanese cedar	35	Data extracted from Table 4, p. 385. Static bending properties measured on boards
	[46]	Radiata pine	11	Data extracted from Table 2, p. 1926. Tested by resonance with HM-200
	[50]	Black spruce	48	Data extracted from Table 6, p. 466. Static bending properties tested on board of different dimensions
	[57] (NS)	Norway spruce	35	Data extracted from Table 4, p. 6. Static bending properties measured on smaller size boards
[57] (SP)	Scots pine	35	Data extracted from Table 4, p. 6. Static bending properties measured on smaller size boards	
Wood density	[60] (Cloacaenog)	Sitka spruce	45	Data extracted from Table 2, p. 338. Values obtained from board samples taken from battens
	[60] (Loughermore)	Sitka spruce	28	Data extracted from Table 2, p. 338. Values obtained from board samples taken from battens
	[37]	White spruce	60	Data extracted from Table 22, p. 22. Values reported at the DBH level
	[47]	Patula pine	13	Data extracted from Fig. 4b for year 13, p. 252. Trees were pruned at 5, 7 and 9 years old
	[39]	Jack pine	25	Data extracted from Fig. 5a for year 25, p. 9. Values reported at the stump level
	[48]	Japanese cedar	35	Data extracted from Fig. 5 for year 35, p. 381. Values reported at 1.2 m high
	[59]	Norway spruce	30	Data extracted from Fig. 1, p. 21. Values at the stump level. Two thinning treatments were applied
	[58]	Jack pine	60	Data averaged from Fig. 3, p. 458. Values reported at DBH level
	[46]	Radiata pine	10	Data extracted from Fig. 1c, p. 1927. Values reported at the DBH level
	[57] (NS)	Norway spruce	35	Data extracted from Table 2, p. 6. Values obtained from board samples coming from the bottom logs
	[57] (SP)	Scots pine	35	Data extracted from Table 2, p. 6. Values obtained from board samples coming from the bottom logs
	[61]	Western hemlock	38	Data extracted from Table 1, p.2463. Values reported at DBH level
	[50]	Black spruce	48	Data extracted from Table 12, p. 472. Values obtained from samples taken from lumber
	Fibre length	[58]	Jack pine	60
[46]		Radiata pine	11	Data extracted from Table 2, p. 1926. Fibre length was obtained by maceration
[61]		Western hemlock	38	Data extracted from Table 3, p. 2466

Table 1 (continued)

Figure	Reference	Species	Age	Supplementary information
	[45] (JW)	White spruce	38	Data extracted from Table 1, p. 16. Earlywood splint macerated by Franklin's method. Juvenile wood
	[45] (MW)	White spruce	38	Data extracted from Table 2, p. 17. Earlywood splint macerated by Franklin's method. Mature wood
	[44] (JW)	Black spruce	38	Data extracted from Table 1, p. 1000. Earlywood splint macerated by Franklin's method. Juvenile wood
	[44] (MW)	Black spruce	38	Data extracted from Table 1, p. 1000. Earlywood splint macerated by Franklin's method. Mature wood

properties [34, 86, 87] and lumber value [33], especially in the most valuable lowest log of elite trees [32, 88]. Knots cause local grain deviation in wood [89], which can cause reduced wood stiffness and strength [86, 87]. A key effect of artificial pruning is to considerably shorten the time required to complete branch occlusion. This leads to fewer loose knots (i.e. knots formed after branch death). For example, the occlusion time for Norway spruce branch stubs can reach 50 years or more under self-pruning conditions [90], while it can occur after 4 to 12 years in pruned trees (2-cm-thick branch wounds) [89].

Usually, artificial pruning of branches is implemented on the lowest branches at an early age, i.e. when they are small, healthy and covered by a thin layer of bark [91]. Early intervention is recommended to minimise the problems of infections and to facilitate rapid occlusion [32, 91]. However, pruned trees can be more susceptible to damage from browsing, or bark stripping and fraying, than unpruned trees [89]. Consequently, the density of ungulate populations should be considered before applying pruning treatments [89, 92].

Other than damage from wildlife, several other factors may influence the response of trees to pruning. These include timing (i.e. seasonality), site fertility, soil moisture availability, climate, tree age, species, the tools used and pruning height [93, 94]. According to Zobel [32], the optimum time for pruning is when the tree has reached about 12 cm in diameter at breast height. While Zobel [32] recommended removal of 33% of the live crown, more recent studies have shown it is possible to remove 50% of the live crown without a significant reduction in radial growth [11, 95, 96] or height growth [95]. However, lift pruning height has also been associated with the development of numerous epicormic sprouts, which can vary importantly according to species [85]. As highlighted in the same study, the relevance of using such a treatment should be considered carefully as pruning is a very expensive treatment that could end up costing two to three times the cost of thinning a stand. When applied, the frequency and severity of pruning treatments should be planned to allow for crown recovery and to limit the effects on growth, which can alter the dominance of pruned trees in the stand [93, 94]. In some cases, tree

pruning residues are considered as a useful feedstock for bioenergy, which can help mitigate dependence on fossil fuels [97, 98].

Since pruning artificially increases crown base height, it is generally assumed that wood within the pruned area will reach mature characteristics earlier than in unpruned trees [11, 32, 64]. This implies that microfibril angle (MFA) would decrease while fibre length and wood density would slightly increase after pruning [64]. However, recent studies from Chiu et al. [77] in Taiwan (*Taiwania Cryptomerioides* Hay) and in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) [28, 99] did not find any effects of pruning on MFA, tracheid length, or wood density. In addition, some authors have suggested that heartwood formation can be regulated by pruning [100, 101], although others disagree with this finding [102].

Pruning is often done in combination with thinning [71, 77, 89, 96] or fertilising treatments [95, 103]. Pruning can help limit the increase in stem taper generally caused by thinning [93], although whether this effect can be observed depends on stand density and age [94]. Pruning can also be applied to dead branches. Unlike pruning of live branches, pruning dead branches does not disrupt tree growth [94]. Its only effect would be to reduce the occurrence of loose knots.

Fertilisation

Fertilisation is often portrayed as a temporary increase in site fertility [104]. It can be used to help seedling establishment, especially on nutrient-poor sites. It can also accelerate growth and help tree development during the period of rapid juvenile growth (when nutrient demand is high), albeit to the detriment of wood quality. In the USA, mid-rotation fertilisation is a proven method for improving tree growth by counteracting nutrient limitations [12, 105]. Even late-rotation fertilisation 5 to 10 years before harvesting has been practiced to improve tree growth of Douglas fir in Canada [106]. The area of forest treated with fertilisation has thus increased substantially in recent years [105]. Most often, the applied macronutrients are nitrogen, phosphorus and potassium (NPK). Their effects on wood quality depend

Table 2 Impact of thinning or respacing treatment on wood properties according to different published studies

Authors	Plantation or natural regeneration	Country of study	Species	Age of trees	Time since treatment (years)	Type of thinning	Impact on wood properties after thinning treatment										
							CW	WD	Knots	FL	MFA	MOE and MOR	LW	WC	Lumber		
[67]	Plantation	UK, Northern Ireland	Sitka spruce	57	46	Respacing. Five respacing treatments were applied in 1960 giving 2858, 1452, 725, 477 and 320 trees per ha			+ Respacing over 2.6 m ²							- Respacing over 2.6 m ²	
[182]	Plantation	UK, Northern Ireland	Sitka spruce	57	46	Respacing. Five respacing treatments were applied in 1960 giving 2858, 1452, 725, 477 and 320 trees per ha		-		+							
[75]	Plantation	UK, England	Corsican pine	35	At ages 20, 25 and 30	Thinning: selective thinning. The thinning regime comprised a one row thinning at age 20 years followed by two intermediate selective thinnings at age 25 and 30 years at an approximate intensity of 70% of the yield class		-	/								
[77]	Plantation	Taiwan	Taiwania	20	9	Thinning and pruning: 3 thinning intensities: heavy (28 m ² ha ⁻¹), moderate (33 m ² ha ⁻¹), control (42 m ² ha ⁻¹). Pruning: heavy (4.5 m), moderate (3.6 m) and a control				/	/						
[76]	Plantation	Turkey	Turkish pine	33–35	18	Thinning: heavy, moderate; started at age 15 and then at every 5 years interval. In the heavily thinned plots, 34 – 40% of basal area was removed. In the moderately thinned plots, 15 – 20% of basal area was removed		/				/			/		

Table 2 (continued)

Authors	Plantation or natural regeneration	Country of study	Species	Age of trees	Time since treatment (years)	Type of thinning	Impact on wood properties after thinning treatment									
							CW	WD	Knots	FL	MFA	MOE and MOR	LW	WC	Lumber	
[70]	Plantation and natural regeneration	USA and Canada	Douglas fir	60 to 75	Several thinning were applied	Two different thinning treatments were chosen for this study: lightly thinned (70% basal area retention) and heavily thinned (30% basal area retention) with a control	-	-	-	-	-	-	-	-	-	-
[73]	Natural regeneration	Canada, Québec	Balsam fir	47	35	Pre-commercial thinning at 12 years old. One control and 2 precommercial thinning treatments. Heavy precommercial thinning (1500 stems ha ⁻¹), moderate (3000 stems ha ⁻¹), control (12,100 stems ha ⁻¹)	-	-	-	-	-	-	-	-	-	-
[74]	Plantation	Finland, Heinola and Punkaharju	Norway spruce	67 and 86	37 and 31	Thinning: 3 thinning intensities, where stand basal area after thinning were on average: 40, 27 and 24 m ² ha ⁻¹ in Heinola compared to 30, 28 and 17 m ² ha ⁻¹ in Punkaharju	-	-	-	-	-	-	-	-	-	-

Table 2 (continued)

Authors	Plantation or natural regeneration	Country of study	Species	Age of trees	Time since treatment (years)	Type of thinning	Impact on wood properties after thinning treatment									
							CW	WD	Knots	FL	MFA	MOE and MOR	LW	WC	Lumber	
[69]	Plantation	Sweden, Herrevad-skloster	Norway spruce	67	38	Thinning: 4 Thinning intensities varied from 0 to 60% and were based on basal area (BA) before thinning. (A) 5 = 20% (i.e. 20% of the BA removed five times) (B) 3 = 40% (i.e. 40% of the BA removed three times); (C) 1 = 60% (i.e. 60% of the BA removed once); and (D) 5 = 40% (i.e. 40% of the BA removed five times)	-	-	-	-	-	-	-	-	-	-
[10]	Plantation	Ireland, Galway city	Norway spruce, Sitka spruce and Douglas fir	50 to 54	Varies according to species	Thinning: Thinning from below combined with systematic thinning of trees in rows. Norway spruce plantations were thinned at 3 occasions in 1990, 2005 and 2011. Sitka spruce plantations were thinned 4 times in 1982, 2001, 2005 and 2011. Douglas fir plantations were thinned in 1986 and at turn of the century. The thinning stands were compared to unthinned stands	-	-	-	-	-	-	-	-	-	-

Table 2 (continued)

Authors	Plantation or natural regeneration	Country of study	Species	Age of trees	Time since treatment (years)	Type of thinning	Impact on wood properties after thinning treatment								
							CW	WD	Knots	FL	MFA	MOE and MOR	LW	WC	Lumber
[65]	Plantation	UK, Northern Ireland	Sitka spruce	57	46	Respacing at age 11. Four different respacing treatments (1.83 m × 3.66 m, 3.66 m × 3.66 m, 3.66 m × 5.49 m and 5.49 m × 5.49 m) were compared with those of timber from a control (1.83 m × 1.83 m)	/	/	+	-	-	-	-	-	-
[78]	Plantation	Sweden, Tonnersjöheden	Norway spruce	33	Varies according to the area	Thinning and spacing: 3 different spacing (2 m, 2.5 m and 3 m) treatments were thinned (from above or below). One area was pre-mercially thinned 8 and 13 years after planting, and another area thinned 9 and 14 years after planting. In winter 2004, the first thinning was undertaken, with two different thinning regimes: the stands with 2 and 2.5 m spacings were partly thinned from below and partly thinned from above, and stands with 3 m spacing were partly thinned from above and partly left unthinned	/	/	/	/	/	/	/	/	/

Table 2 (continued)

Authors	Plantation or natural regeneration	Country of study	Species	Age of trees	Time since treatment (years)	Type of thinning	Impact on wood properties after thinning treatment												
							CW	WD	Knots	FL	MFA	MOE and MOR	LW	WC	Lumber				
[80]	Plantation	Italy, Calabria	Calabrian pine	50	11	Thinning: 3 thinning treatments were applied with a control. Heavy thinning where 75% of the occurred trees were cut; moderate thinning where 50% of the occurred trees were cut and light thinning (LT) where 25% of the occurred trees were cut. MOE measured using acoustic tools											+LT		
[79]	Plantation	Canada, Ontario	Black spruce	49	6	Thinning: Commercial thinning at age 43 years old. Heavy (one row removed from every three rows) and light thinning (one row removed from every four rows) were compared		-							/				
[71]	Plantation	Taiwan	Taiwana	20	9	Thinning and pruning: Heavy thinning (HT) (27.5 m ² ha ⁻¹), moderate thinning (32.5 m ² ha ⁻¹) and no thinning (42 m ² ha ⁻¹). Heavy pruning (4.5 m), moderate pruning (3.6 m) and no pruning											+HT		+
[66]	Plantation	New Zealand	Radiata pine	24	19	Respacing from below at age 5, to 200, 350, 500 and 1100 stems ha ⁻¹ . LS=lower stocking											+LS	-LS	

CW = compression wood, WD = wood density, FL = fibre length, MFA = microfibril angle, MOE and MOR = modulus of elasticity and modulus of rupture, LW = latewood proportion, WC = wood chemistry, += increased, -= decreased, /= no change, HT = heavy thinning, LS = lower stocking, LT = light thinning

on several factors, including the combination of nutrients applied, their concentration, the preexisting site conditions [107] and the species being treated [108].

Most studies measuring the effects of fertilisation treatments on wood properties have focused on wood density, with variable responses reported (Table 3). Some studies indicated a reduction in wood density in conifers after fertilisation [105, 106, 109–111], while others found either no decrease in density or only a slight decrease [74, 112, 113]. The effect on wood density also tends to last for a limited period of time, i.e. around 5 years following treatment (e.g. [109, 111]). Generally, the reduction in wood density is more pronounced when fertilisation is applied at higher concentrations. For example, Antony et al. [105] showed a reduction in wood density of about 40 kg m^{-3} in a thinned loblolly pine (*Pinus taeda* L.) plantation after a mid-rotation application of heavy nitrogen fertiliser treatment (336 kg ha^{-1}), compared with the unfertilised control. The response of wood density to fertilisation treatments may also depend on the additional effects of stand density management operations.

Often, fertilisation is applied in combination with thinning treatments. For example, a recent study by Kantavichai et al. [114] reported that the decline in wood density following fertilisation was dependent on both initial stocking and the intensity of pre-commercial thinning treatments in Douglas-fir plantations in the US Pacific Northwest. According to their study, trees that produced the highest density and stiffest wood, came from stands that had been pre-commercially thinned to half their original stem density without further thinning and fertilisation treatments. Usually, when fertilisation and thinning are combined, the radial growth response is greater than when only fertilisation treatments are applied [112, 113].

Aside from wood density, few studies have examined the effects of fertilisation on other wood properties. As for wood density, the effects on wood fibre characteristics seem to be more pronounced when heavy fertilisation treatments are applied. For example, Antony et al. [105] found a significant decrease in cell wall thickness and a significant increase in tracheid radial diameter under a heavy fertilisation treatment (336 kg ha^{-1} of N). At lower concentrations (e.g. 112 kg ha^{-1} or 224 kg ha^{-1} of N), the effects on wood fibre characteristics were either not significant or negligible. Mäkinen and Hynynen [112] found only small differences between the fertilisation treatments (control vs fertilised with $150 \text{ kg N} + 75 \text{ kg P}_2\text{O}_5 + 75 \text{ kg K}_2\text{O ha}^{-1}$) in the earlywood: latewood ratio (3–9%), tracheid diameter (2–5%), tracheid length (4–5%) and cell wall thickness (0–10%) in Scots pine. Small increases in MFA after fertilisation have been reported, which led to a slight decrease in stiffness in loblolly pine and radiata pine [105, 110]. To reduce the negative impacts of fertilisation on wood mechanical properties, Downes et al. [110] suggested applying mild fertilisation

treatments more frequently. In terms of chemical properties, nitrogen fertilisation has been reported to increase lignin and extractive concentrations [107, 115], which could affect pulp bleaching processes in pulp and paper manufacturing.

Site

Silviculturists usually quantify site productivity using site index, which is typically defined as the average height of the dominant trees in even-aged stands at a given index age [116]. Higher values are therefore associated with higher overall site productivity. Since site conditions influence tree growth, it is generally assumed that wood properties will be affected too [24]. Studies looking at the link between site index and wood properties often show a decrease in wood properties with an increase in site index. For example, Antony et al. [117] observed that both MOE and MOR values decrease in loblolly pine with an increase in site index. Their observations were consistent with earlier ones made by Brazier and Mobbs [60] in Sitka spruce. Watson and Bradley [118] also reported a decrease in wood density with an increase in site index in several commercial conifer species, while fibre length showed the opposite trend.

Silviculturists can also use the concept of site quality to characterise a site. In this case, site quality is assessed using physical and biological variables—such as water and nutrient availability, temperature and precipitation, latitude or soil type—or using a classification system that stratifies the landscape into ecologically meaningful units [116]. Generally, most studies on the effects of site quality on wood properties have focused on wood density; however, recent efforts have been made to predict site level or regional variation in MOE and MOR for some coniferous species (e.g. [117, 119]). For example, it has been reported that the MOE and MOR values of loblolly pine and radiata pine increased on warmer sites [117, 119]. It is believed that air temperature measured in the autumn is the most important and consistent variable influencing MOE values as it influences the production of latewood [120]. As such, sites benefiting from an extending growing season were also found to result in lower MFA [121].

Temperature, rainfall and site fertility have also been recognised as environmental drivers of wood density (e.g. [122]). For example, in radiata pine growing in New Zealand, higher wood density was observed in warmer sites at lower elevations [122]. Moore et al. and Rossi et al. [65, 123] also demonstrated that wood density decreased with increasing elevation and latitude in Sitka spruce and black spruce, respectively, while Giroud et al. [124] showed no effect of a latitudinal gradient on wood density in black spruce, jack pine and balsam fir. In black spruce, wood density was also found to be higher on either very dry (e.g. [125]) or wet sites (e.g. [126]).

Our review of literature has shown that studies based on site index tend to report contrasting results to those including site quality and climatic variables. It is thus difficult to summarise the effect of site productivity or site quality on wood properties. To better understand the variation in wood properties along a gradient of site conditions or site productivity, many different variables or combinations of variables should be considered and tested. Often, the influence of site productivity is studied in combination with climatic conditions and genetic factors (e.g. [127]). To meet the challenge of adapting forest management practices to climate change impacts, it will also be important for future studies to disentangle the effects of site from those of genotype on key determinants of wood quality [125].

Genetics

Genetic improvement of forest trees, or tree breeding programs, have long been considered important for increasing growth rates and wood quality with respect to certain traits of interest, such as wood density. However, as plantation rotations were reduced over time, foresters and tree breeders realised that fast-grown trees contained a large proportion of corewood with unfavourable wood properties. This motivated forest geneticists to include more wood quality traits in tree improvement programs [128–131]. Traits such as wood density, microfibril angle, fibre properties, stiffness and dimensional stability are now commonly included in tree breeding programs. Among the traits tested, wood density, acoustic velocity (used to estimate wood stiffness), and microfibril angle appear to be the most heritable (Table 4). High narrow-sense heritability (i.e. the proportion of phenotypic variance due to additive genetic variation) values and their low standard errors suggest high genetic control for these traits [129]. However, estimates of individual narrow-sense heritability often vary with cambial age (i.e. the number of annual growth rings from the pith) and among species, which complicates the task of genetic selection [132–134].

Depending on the wood quality traits evaluated, heritability was found to increase with cambial age [133–135], while in some cases, it reached maximum values at a specific cambial age [133, 136]. In addition, some traits of interest, such as wood stiffness, are highly correlated with other traits like microfibril angle and wood density, which themselves are not always well correlated (Table 5). Correlations between wood quality traits may also be complicated by environmental factors (genotype-by-environment interactions) [136–138]. To better control the often negative correlations between tree growth and wood quality characteristics, tree breeders stress the need for improving their understanding of the molecular genetics of wood traits [8, 139].

Current Knowledge Gaps and Future Challenges

Over the past 40 years, the Earth's temperature has risen by 0.18 °C per decade [140], which has resulted in an average increase in tree growing seasons of approximately 3.6 days per decade in Europe [141]. There are geographical variations in such effects, and in some regions, an extended growing season has already caused measurable phenological changes in trees [142–145], which could lead to changes in wood properties. Despite recent efforts, few studies have conducted in-depth investigations of the effects of climate warming on wood properties. According to a review on the wood anatomy of boreal species under a changing climate by Zhang et al. [26], the proportion of latewood in coniferous species appears to be negatively correlated with climate warming, while the proportion of earlywood and fibre length would likely increase with warming temperatures.

It is anticipated that water availability will be the most important limiting factor to tree growth in the twenty-first century, thus exceeding temperature across large portions of the boreal zone [146•]. In areas, where acute drought stress is expected to increase, such as in Central Europe and western North America, changes in wood cell formation might be more pronounced [62, 147]. This may affect conifers, as tracheid length is largely driven by the water availability during cell formation [148, 149]. For example, Jyske et al. [69] observed an increase in the cell wall thickness of both earlywood and latewood tracheids of Norway spruce following induced drought. Despite MFA being considered to be under strong genetic control, a decrease in MFA has been observed under drought conditions [26]. Earlywood cell adaptations are believed to support hydraulic functional responses to climate, while latewood cells are believed to support mechanical functional responses to climate [150].

Drought-induced changes such as thicker cell walls and lower MFA may prove beneficial in terms of wood mechanical properties. However, drought can also cause significant reductions in annual radial growth and height increment [147], as well as drastically increasing the risk of tree mortality [151]. Such effects could largely overcome potential benefits in terms of wood properties. In comparison to broadleaved species, conifers have the tendency to maintain larger margins of safety from hydraulic failure, which may favour their chances of survival during drought periods [152]. However, this margin of safety varies between species according to their water potential regulation strategies (i.e. isohydric vs anisohydric) [151].

With the observed and predicted increases in global temperatures and changes in precipitation and radiation budgets, forests will also become more susceptible to a wider range

of natural disturbances. While many uncertainties remain regarding changes in disturbance dynamics under climate change [153–155], warmer and drier conditions are expected to increase the frequency and severity of wildfire, drought and insect disturbances, while warmer and wetter conditions are likely to increase disturbances arising from wind and pathogens [154].

It remains uncertain how forest management practices should be adapted in response to climate change and new forest disturbance regimes [156]. Intensive forest management scenarios with short rotation lengths may bear the key advantage of reducing exposure time, thereby increasing the likelihood of a given crop reaching the final harvest prior to being disturbed. From a wood supply perspective, shorter rotations can confer an additional advantage of reduced risk of loss from catastrophic disturbances because younger stands tend to be less vulnerable to various hazards such as wind damage (e.g. [157]), insect attacks (e.g. [158]), drought stress (e.g. [159]) and, to some extent, wildfire (e.g. [160]). Following drought events, Bennett et al. [159] found that larger trees tend to suffer from higher mortality rates, which also suggests that shorter rotations can lead to a reduced risk. However, Büntgen et al. [161] reported that fast-grown trees may be more vulnerable to biotic stressors.

To reduce risk at the landscape level, one suggestion is to reduce stand density through more intensive thinning to limit growth restrictions caused by drought (e.g. [62]) or to increase resistance to insect attacks (e.g. [162–164]). In their systematic review of the effects of thinning, Moreau et al. [165•] revealed a generally positive influence of thinning on forest resistance and resilience to stressors such as fire, drought, insects and pathogens. However, multiple factors may influence these processes, and the review, as well as other studies [157, 166], also highlighted a tendency for windthrow resistance to decrease temporarily after thinning.

Despite uncertainties about future wind regimes, increases in wind exposure may also alter wood cell development. Under high wind exposure, conifers are more likely to develop compression wood [167], which is characterised by higher wood density, higher microfibril angle, shorter fibre or tracheid length, higher proportion of lignin, and thicker cell walls [22] than normal mature wood. The high exposure time needed to induce a compression wood response [167] suggests a significant increase in sustained wind speeds would be required to directly affect wood quality. However, if the occurrence of extreme wind events causes root systems to tilt rather than fully overturning (e.g. [168]), this will inevitably lead to the production of compression wood in conifers. This is a concern because the presence of this type of wood in solid wood products can lead to sudden failure under load stresses [34, 53, 169].

Genetic improvement programs have started to investigate the impact of different biotic and abiotic agents on wood quality traits, but several questions remain. For example, Nabais et al. [125] recently questioned the assumed link between wood density and drought tolerance and highlighted that, for some species, other variables, such as tree competition, soil fertility or resistance to pathogens, are important drivers of wood density variation that may undermine the assumed density-drought relationship. Therefore, they suggested that selection for drought tolerance should not systematically be based on wood density as a proxy. Other studies testing the relationships between tree resistance to insects and diseases on the one hand, and tree growth or wood quality traits on the other, are providing new knowledge that could guide tree improvement strategies. For example, Lenz et al. [170] recently showed that weevil resistance in Norway spruce is genetically positively correlated with other traits such as tree height, height-to-diameter ratio, and wood acoustic velocity. It is still unclear, however, how these relationships will vary among species and which wood quality traits might serve as reliable proxies of tree resistance to insects and diseases [171]. An important challenge to this work is the time required to confirm the efficacy and durability of the resistance of various genotypes to diseases or insects in different environments. A proposed way to overcome this challenge is to combine breeding with genetic engineering [172].

In summary, a key challenge of future wood quality research will be to predict the impact of intensive management practices under changing climatic conditions and a higher frequency and intensity of disturbances from biotic or abiotic stressors. Recent literature provides clear evidence that trees adapt their wood cell development in response to variations in temperature, water availability and CO₂ atmospheric concentration. However, linking environmental conditions to wood properties remains an emerging field of research. Further studies will be required before we can fully predict the effects of climate change—and its interactions with silvicultural treatments—on future wood quality attributes. An important limitation of the empirical approach generally used in wood quality studies is that the applicability of results is generally restricted to the range of tested conditions. It is practically impossible to test each potential combination of species, site, genetic material, silvicultural scenarios, and climatic conditions under which trees are managed. Also, the need to sample mature stands to evaluate the full impacts of silvicultural decisions implies that timely questions can only be answered several decades later (at least in temperate and boreal forests). In the meantime, the genetic material, silvicultural approach, species of interest, and even the wood properties of interest will have likely changed.

Table 3 Impact of fertilisation treatment on wood properties according to different published studies

Authors	Plantation/ natural regen- eration	Country of study	Species	Age of trees	Time since treatment (years)	Type of fertiliser	Impact on wood properties after fertiliser application						
							WD	Fibres	MFA	MOE	LW/EW	WC	
[105]	Plantation	USA, North Carolina	Loblolly pine	33	19	Tree level of N (from nothing to 336 kg ha ⁻¹) and a small amount of P (28 kg ha ⁻¹). The fertiliser was applied the year after the thinning treatment TWT = tracheid wall thickness TWR = tracheid wall diameter	-	-	TWT + TWR	~	-	-	
[115]	Plantation	Sweden, Flaka- liden	Norway spruce	39	11	Control and irrigated-ferti- lised treatment with N. The initial annual dose of N added was 100 kg N ha ⁻¹ . Then, the amount was adjusted each year according to foliar nutrient analysis for a 10-year period	-	-	-	+	-	-	+ Lignin and extractive con- centrations
[110]	Plantation	Australia	Radiata pine	21 to 32	7	Four fertiliser treatments were applied after thinning (control, N, P and NP)	-	-	-	-	-	-	-
[106]	Plantation	Canada, Van- couver island	Douglas fir	53 to 61 at DBH	5	Late fertilisation treatment. Aerial fertilisation at the equivalent of 200 kg ha ⁻¹ of N was applied	-	-	-	~	-	-	-

Table 3 (continued)

Authors	Plantation/ natural regen- eration	Country of study	Species	Age of trees	Time since treatment (years)	Type of fertiliser	Impact on wood properties after fertiliser application			
							WD	Fibres	MFA	MOE LW/EW WC
[74]	plantation	Finland, Parik- kala and Suonenjoki	Norway spruce	63 and 76	23 and 25	Thinned from below and fertilised the following year after the thin- ning. 3 levels of thinning and 3 levels of fertilisation. Fertilisation treatments were unfertilised; 150 kg nitrogen (N), 75 kg phosphorus oxide (P ₂ O ₅) and 75 kg potassium oxide (K ₂ O) per ha; and 300 kg (N), 150 kg (P ₂ O ₅) and 150 kg (K ₂ O) per ha. Fertiliser was applied at 5-year intervals	/			
[109]	Plantation	Canada, BC	Douglas fir	24	12 to 13	3 levels of thinning and 3 levels of fertilisation of N (0, 224 and 448 kg ha ⁻¹). Half of the treated plots were referti- lised 10 years after the first treatment of fertilisation	- For 3 to 4 years after treatment			- In LW

Table 3 (continued)

Authors	Plantation/ natural regen- eration	Country of study	Species	Age of trees	Time since treatment (years)	Type of fertiliser	Impact on wood properties after fertiliser application				
							WD	Fibres	MFA	MOE	LW/EW
[107]	Plantation	Finland	Norway spruce	N site: 64; S site: 48	Northern site: 37; southern site: 41	Control plots and 15 different Ca, N, P, K fertilised plots. Fertiliser were applied every 5 years. At the northern site, 92 to 150 kg ha ⁻¹ of N was given at each occasion compared to 82–180 kg ha ⁻¹ at the southern site					+N concentra- tion in the northern site + extrac- tive concen- tration in the southern site
[112]	Plantation	Finland, Juva and Iitti	Scots pine	60 and 78	About 30	Two fertilisation (con- trol and one fer- tilised) of NPK applied every 5 years and two thinning levels (delayed and intensive com- mercial thin- ning). Fertilisa- tion treatments were applied as follows: (F0) – unfertilised and (F1) – 150 kg nitrogen (N), 75 kg phos- phorus oxide (P ₂ O ₅) and 75 kg potassium oxide (K ₂ O) ha	~	~	~	~	

Table 3 (continued)

Authors	Plantation/ natural regen- eration	Country of study	Species	Age of trees	Time since treatment (years)	Type of fertiliser	Impact on wood properties after fertiliser application				
							WD	Fibres	MFA	MOE	LW/EW
[113]	Natural regen- eration	Sweden, Vin- deln	Scots pine	56	12	The treatments were control, thinning with 40% basal area removal, fertilisation with 150 kg N ha ⁻¹ , and thinning × fertilisation. The fertilisation treatment was applied once, the year after the thinning	/				
[111]	Plantation	Brazil	Loblolly pine	17	17	Trees were fertilised at an early age according to six different doses of composted pulp-mill sludge (CPMS), control, 20, 40, 60, 80 and 100 t ha ⁻¹ . A selective thinning was applied at 9 years old	-	Up to the 6th year			

WD = wood density, MFA = microfibril angle, MOE = modulus of elasticity, LW/EW = latewood/earlywood, WC = wood chemistry, — = decreased, + = increased, / = no change, ≈ = little change, TWR = tracheid wall diameter, TWT = tracheid wall thickness

The Need for a Modelling Framework

Wood quality models can be used to anticipate wood properties in various conditions that may not have been empirically tested. A review by Drew et al. [173••] summarised recent progress in wood quality modelling and proposed a simple classification in two general groups, i.e. fully empirical and process-based. Here, we focus on the former and highlight how empirical knowledge such as that included in this review can be assembled into a statistical modelling framework that facilitates the extrapolation of results to untested conditions. This approach is based on the work of Larson [23], who proposed that the distinctive radial patterns of wood physico-mechanical properties were largely the result of crown processes, such that the type of xylem formed depends on both the proximity to the live crown and the age of the cambial initials, due to the differential distribution of growth regulators (i.e. auxin gradient) along the stem. Further understanding of the process of xylem formation in trees and of developmental constraints on cambial maturation led to the formulation of competing, but overlapping, hypotheses that the distinctive radial patterns of wood properties is driven by the need for optimising both mechanical stability and hydraulic efficiency in tree stems [174]. These concepts led to the development of a stem quality modelling approach whereby the systematic within-stem variation in wood properties is described as functions of cambial age, height in the stem and annual ring width, the latter being used as a proxy for crown vigour [175–179]. This modelling strategy allowed early assessments and comparisons of the impacts of any silvicultural scenarios on wood properties provided that their effects on tree growth could be simulated, i.e. predictions from growth models were used as input to the wood properties models [180].

Because this statistical modelling approach has the capacity to address the effects of multiple, potentially confounding factors [181], it has been widely used to detect and quantify the impact of drivers of wood properties variation, including site characteristics [126], silviculture [182] and genetics [183]. However, the use of annual ring width (or ring area) as a proxy for the effects of environmental conditions has important limitations, as both silvicultural treatments [47, 182] and climatic conditions [184, 185] have been shown to influence wood properties beyond the effects that could be anticipated from their effects on tree growth.

To improve model predictions, climatic variables are increasingly included as predictors of wood properties variation in such models (e.g. [70, 186–188]). One approach is to develop correlations or response functions between seasonal or monthly climatic variables on the one hand, and annual ring-level wood properties on the other [186], but this may hinder the possibility of detecting the effects of

acute climatic events such as frost and droughts that can alter wood properties [189, 190]. Dendroclimatological approaches have been developed to quantify the effects of acute climatic events on tree growth [191, 192], which could be applied to studies of wood properties. Babst et al. [193] provide a comprehensive synthesis of models developed to simulate radial growth as a function to climatic variables from dendrochronological measurements. Models driven by temperature, water balance and day length could offer a promising approach for simulating wood properties, which could be used in the described framework.

Key to informing silvicultural decision-making is the integration of wood properties models into growth modelling platforms. Ideally, these platforms should include risk assessment modules and allow simulations of changes in forest disturbance regimes under different climate projections [2, 25, 194, 195]. Not only should platforms be user-friendly, but they should also follow the free and open source (FOSS) philosophy, so that the information is widely accessible, and the workflow is transparent and fully reproducible. CAPSIS is one notable example of such a platform that has been used extensively and has fostered international collaborations [196]. In addition to informing silvicultural decision-making before empirical tests can yield results, the developed platforms provide an identifiable locus for the integration of the most up-to-date knowledge on the links between growth conditions and wood properties. Such integration is key to meeting the challenges associated with ensuring that both wood supply and wood quality from intensively managed forests continues to meet demands associated with new product development.

Emerging Technologies in Wood Characterisation and Utilisation

New technologies offer fresh opportunities for fast and efficient characterisation of wood properties. For example, recent efforts have led to new algorithms or models for assessment of wood density and mechanical properties through high-resolution scanning technologies such as computed tomography (CT) (e.g. [197, 198], micro-CT [199], and other methods using a combination of X-ray densitometry and ultrasonic measurements [200]. As they offer the possibility to characterise wood properties rapidly and at a fine scale, such technologies will facilitate greater knowledge acquisition on the effects of intensive forest management practices on wood quality.

A concomitant challenge is the need to expand wood properties assessments to scales that are relevant to the strategic decisions that must be made in forest management. Airborne laser scanning (ALS) data has been used to link statistical descriptors of forest inventory metrics

Table 4 Heritability values of some quality traits from (a) spruce species and (b) pine species of some published studies

Species	Black spruce [137], 24 years old, Canada	White spruce [128], 15 years old, Canada	[135], 19 years old, Canada	[134], 20 years old, Canada	Sitka spruce [13], 20 years old, UK	Norway spruce Hamrup et al. [30], 40 years old, Sweden
References						
Wood quality trait						
Velocity	Mixed: 0.53 (0.12) Boreal: 0.48 (0.11)	0.38 (0.07)			0.63 (0.19)	
MOE	Mixed: 0.36 (0.11) Boreal: 0.37 (0.09)	0.22 (0.05)		EW: 0.27 (0.15) LW: 0.41 (0.19)	0.52 (0.18)	
MFA				EW: 0.28 (0.15) LW: 0.34 (0.17)	0.52 (0.27)	EW: 0.20 (0.18) LW: 0.01 (0.11)
Wood density	Mixed: 0.28 (0.08) Boreal: 0.32 (0.09)	0.32 (0.06)	0.46 (0.13)	EW: 0.69 (0.26) LW: 0.13 (0.11)	0.71 (0.22)	0.53 (0.21)
Cell wall thickness				EW: 0.52 (0.22) LW: 0.06 (0.06)		
Specific fibre surface				EW: 0.48 (0.20)		0.64 (0.23)
Latewood proportion			0.32 (0.11)			
Ring width						
DBH		0.23 (0.05)		EW: 0.20 (0.13) LW: 0.20 (0.13)	0.29 (0.14)	0.13 (0.14)
Height		0.33 (0.07)				0.17 (0.16)
Spiral grain					0.56 (0.18)	0.04 (0.12)
Grain angle						
(b) Individual heritability (with error)						
Species	Slash pine	Jack pine	Radiata pine		Scots pine	
References	[132], 8 years old, USA	[133], 20 years old, Canada	[138], 6 years old, New Zealand and New South Wales		[130], 11 years old but 18 years old for DBH and grain angle, Sweden, 2 sites	
Wood quality trait				[8], A review with average values, New Zealand and Australia		
Velocity	0.42 (0.07)					
MOE						
MFA						
Wood density						
DBH	0.28 (0.06)		0.11 (0.05)		Site 1: 0.12 (0.07) Site 2: 0.23 (0.12)	
Height	0.36 (0.07)	0.18 (0.05)	0.13 (0.05)			
Stem straightness		0.18 (0.05)	0.19 (0.06)			
Stem forking		0.08 (0.07)				
Spiral grain						
Grain angle			0.26 (0.11)			
						Site 1: 0.40 (0.14) Site 2: 0.49 (0.18)

Table 4 (continued)

Branch angle	Site 1: 0.38 (0.13) Site 2: 0.38 (0.15)
Branchiness	Site 1: 0.27 (0.10) Site 2: 0.32 (0.14)
Fibre length	0.54
MOE = modulus of elasticity, MFA = microfibril angle, DBH = diameter measured at breast height, EW = earlywood, LW = latewood	

to wood properties measured on sample plots, to produce wall-to-wall, landscape-level assessments of wood properties [201–203]. As they have yet to include explicit links between ALS metrics, stand structure and wood properties, such models require local parameterisation and validation. The fusion of terrestrial laser scanning (TLS) and ALS data may help include such explicit links between canopy structure, tree crown characteristics and wood properties, and thus improve model precision transferability across multiple scales [204]. Further development could include the use of spectral information from satellite imagery, which can complement the characterisation of forest structure given by ALS data by providing longitudinal estimates of photosynthetic activity or vegetation stress [205, 206].

At the other end of the forest value chain, it will also be crucial to work closely with the engineered wood products industry to understand which wood quality traits most closely determine the suitability of wood for use in specific products [129, 207]. The detrimental effects of intensive forest management practices on wood traits may be at least partially offset by innovations in wood processing technology. For example, corewood of fast-grown conifers can be used for the central portion of laminated beams or its fibre added to concrete or plastic composites [2]. Other examples include the production of oriented strand board (OSB), particleboard, and medium density fibreboard [208••]. Moore and Cown [208••] argued that corewood panels would have similar mechanical properties and internal bond strength to those from outerwood panels, although their dimensional stability could be compromised. Different processing options should be explored to develop wood products that provide the best possible alignment between market demand and the properties of the resource [209].

Conclusion

All things considered, the most important effects of intensive silvicultural practices on wood properties are related to the trend of decreasing age at harvest (i.e. rotation age) [25, 32, 34, 174, 208••, 210]. With advances in genetic improvement, trees can more rapidly reach a merchantable size, which leads to shorter rotations. This, in turn, leads to higher proportions of corewood, which is characterised by lower mechanical properties, poorer dimensional stability and overall lower quality of lumber for most end-uses [33, 34].

As highlighted in this review, cambial age is a prime determinant of the within-stem variation in wood properties [174]. Many physico-mechanical properties, such as wood density, and strength and stiffness, are low near the pith, increase rapidly in the first few growth rings of the juvenile wood period and then attain more stable values at

Table 5 Genetic and phenotypic correlations for (a) spruce species and (b) pine species of some published studies

(a) Genetic correlations (GC) and phenotypic correlation (PC)	
Species	References
Black spruce	Despont et al. 2017, 24 years old, Canada
White spruce	[128], 15 years old, Canada
Norway spruce	[136], 16 years old, Sweden
Sitka spruce	[131], 20 years old, UK
Hamnrip et al. [130], 40 years old, Sweden	
Correlation	GC: -0.84 and PC: -0.38
Velocity and MFA	GC: -0.84 and PC: -0.38
Velocity and wood density	GC: 0.32 (0.22) and PC: 0.27
Velocity and grain angle	GC: -0.13 (0.24) and PC: -0.12
Velocity and DBH	GC: -0.36 (0.27) and PC: -0.18
Velocity and height	
Velocity and volume	
Velocity and ring width	
Wood density and ring width	GC: 0.01 and PC: -0.05
Wood density and DBH	GC: 0.17 and PC: 0.12
Wood density and diameter to height ratio	GC: 0.03 and PC: -0.11
Wood density and MFA	GC: -0.39 and PC: -0.50
Wood density and MOE	GC: -0.63 and PC: -0.39
Grain angle and DBH	GC: -0.41 and PC: -0.40
Spiral grain angle and MFA	
Specific fibre surface and MOE	
Specific fibre surface and MFA	
Specific fibre surface and wood density	
Specific fibre surface and height	
MFA and LW width	
White spruce	[134], 20 years old, Canada
Norway spruce	[136], 16 years old, Sweden
Sitka spruce	[131], 20 years old, UK
Hamnrip et al. [130], 40 years old, Sweden	
Correlation	GC: -0.61 (0.09) and PC: -0.58 (0.01)
Velocity and MFA	GC: -0.61 (0.09) and PC: -0.58 (0.01)
Velocity and wood density	GC: -0.38 (0.12) and PC: -0.15 (0.01)
Velocity and grain angle	GC: 0.07 (0.30) and PC: -0.04
Velocity and DBH	GC: 0.88 (0.08) and PC: 0.66
Velocity and height	GC: -0.79 (0.16) and PC: -0.49
Velocity and volume	
Velocity and ring width	
Wood density and ring width	
Wood density and DBH	
Wood density and diameter to height ratio	
Wood density and MFA	
Wood density and MOE	
Grain angle and DBH	
Spiral grain angle and MFA	
Specific fibre surface and MOE	
Specific fibre surface and MFA	
Specific fibre surface and wood density	
Specific fibre surface and height	
MFA and LW width	
White spruce	[128], 15 years old, Canada
Norway spruce	[136], 16 years old, Sweden
Sitka spruce	[131], 20 years old, UK
Hamnrip et al. [130], 40 years old, Sweden	
Correlation	GC: 0.23 and PC: 0.04
Velocity and MFA	GC: 0.23 and PC: 0.04
Velocity and wood density	EW, GC: 0.28 (0.29) and PC: -0.11; LW, GC: -0.05 (0.46) and PC: -0.19
Velocity and grain angle	EW, GC: 0.69 (0.17) and PC: 0.50; LW, GC: 0.78 (0.17) and PC: 0.36
Velocity and DBH	EW, GC: 0.07 (0.30) and PC: -0.04
Velocity and height	EW, GC: 0.88 (0.08) and PC: 0.66
Velocity and volume	EW, GC: -0.35 (0.28) and PC: -0.04
Velocity and ring width	EW, GC: 0.06 and LW, GC: 0.73
Wood density and ring width	EW, GC: -0.79 (0.13) and PC: -0.48; LW, PC: -0.26
Wood density and DBH	EW, GC: 0.12 (0.34) and PC: 0.22; LW, PC: 0.15
Wood density and diameter to height ratio	EW, GC: -0.91 (0.05) and PC: -0.80; LW, PC: -0.92
Wood density and MFA	EW, GC: 0.69 (0.20) and PC: -0.11; LW, PC: -0.14
Wood density and MOE	GC: 0.38 and PC: 0.07
Grain angle and DBH	
Spiral grain angle and MFA	
Specific fibre surface and MOE	
Specific fibre surface and MFA	
Specific fibre surface and wood density	
Specific fibre surface and height	
MFA and LW width	

Table 5 (continued)

Species	Slash pine [132], 8 years old, USA	Jack pine [133], 20 years old, Canada	Scots pine [130], 11 years old but 18 years old for DBH and grain angle, Sweden, 2 sites	Radiata pine [138], 6 years old, New Zealand and New South Wales
References				
Correlation				
Velocity and DBH	GC: -0.12 and PC: -0.10			
Velocity and height	GC: 0.19 and PC: 0.06			
Velocity and volume	GC: -0.08 and PC: -0.10	GC: 0.48		
Height and stem straightness		GC: -0.02		
Height and stem forking			Site 1, GC: 0.10 and PC: 0.13 and Site 2, GC: -0.19 and PC: 0.03	
Grain angle and DBH			Site 1, GC: 0.04 and PC: 0.12 and Site 2, GC: -0.25 and PC: -0.03	
Grain angle and height			Site 1, GC: -0.04 and PC: -0.05 and Site 2, GC: 0.42 and PC: 0.04	
Grain angle and straightness			Site 1, GC: 0.23 and PC: 0.03 and Site 2, GC: 0.59 and PC: 0.09	
Grain angle and branch angle				
Spiral grain angle and stem straightness				GC: -0.38 (0.61)
Spiral grain angle and DBH				GC: 0.34 (0.53)

MFA = microfibrial angle, MOE = modulus of elasticity, DBH = diameter at breast height, EW = earlywood, LW = latewood, GC = genetic correlation, PC = phenotypic correlation

higher cambial ages [175–177, 211]. Some properties, such as longitudinal shrinkage and microfibril angle (MFA), follow a decreasing trend with cambial age [211–213], and in these cases, lower values are generally more desirable. Some coniferous species have high density near the pith, but this is generally associated with a high microfibril angle, and thus has properties analogous to that of compression wood (also referred to as ‘flexure’ wood) [22, 214].

Overall, the increasing demand for wood fibre combined with the needs to manage the risk of disturbance and protect natural forest ecosystems will imply that an increasing proportion of timber will come from intensively managed plantations at the global scale. Our review has highlighted that genetic selection can help mitigate the impact of a shift towards intensive forest management on future wood quality. However, the importance of cambial age as a driver of the variation of wood properties implies that for most species, sites, genetic material and end-uses, shorter rotations will come at the expense of overall wood quality.

In intensive silvicultural scenarios, the magnitude of this detrimental effect will obviously depend on the chosen rotation length, among other factors; however, it will also depend on the distribution of annual rings within the stem, which can be modified by the application of thinning, fertilising or pruning treatments. Delayed thinning, pruning and delayed harvesting can all help increase the proportion of mature wood in timber. Precise recommendations of silvicultural scenarios that can strike a balance between the needs to produce timber rapidly and maintain adequate wood properties will need to be devised for each species, genetic material and site of interest. Key to achieving this is the development of wood properties models and their integration into growth modelling simulators. Such simulation platforms exist but are only available for a limited number of species and sites. Although they offer an ideal framework to consider the effects of future climate on wood properties, this knowledge has rarely been included in wood quality simulators.

As several jurisdictions make the transition from visual grading of solid wood products to non-destructive mechanical grading [215], there is a growing concern that the lumber produced from intensively managed stands may not always meet the requirements and the grading specifications of the end-users. As highlighted in this review, the wood processing industry can adapt to some extent to the supply of wood of lesser quality, but some thresholds should not be exceeded. The minimum requirement of the C16 mechanical grade for timber frame construction in Europe provides an example of such threshold [65, 216]. A better understanding of the links between silvicultural practices, visual grading, wood properties, and non-destructive mechanical grading is thus required [2, 217]. This highlights the importance for silviculturists, wood scientists and tree breeders to work collaboratively

to ensure that future wood quality will not deteriorate under rapidly changing conditions. A desired outcome of such collaborative efforts is that practitioners are given access to the knowledge and material that will allow them to select species and provenances with the best resistance and resilience to stressors without sacrificing either wood volume or quality.

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Data Availability No new data were generated or analysed in support of this research.

Declarations

Conflict of Interest The authors declare that they have no conflict of interest.

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