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Doctoral dissertation

Potential of silvicultural practices focusing on wood properties of
hardwood species in Hokkaido

北海道における広葉樹の材質特性に着目した育林の可能性

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Chapter 1

General introduction

1.1 Research background

In recent years, global demand for hardwood timber has been increasing, driven by growing interest in interior materials and high value-added wood products (Savidge 2003; Woxblom and Nylinder 2010; Acker 2021). Consequently, the sustainable production of hardwood timber has become a critical issue for forestry sectors worldwide. However, in 2006, several factors including environmental policies (e.g. North America), resource policies (e.g. Southeast Asian countries), and increases in export tariffs (e.g. Russia) triggered the “wood shocks” (Hata and Inoue 2023). Growing global concern over environmental issues and shifts in these international political conditions have thus had a profound impact on the global wood market as a whole (Figure A1). In particular, in northern hemisphere, because hardwoods—unlike softwoods—have limited plantation resources and rely heavily on natural forests, they experienced pronounced supply instability and price surges. These circumstances highlighted the renewed importance of producing and supplying domestic hardwoods on a stable basis (Bruck et al. 2023). Against this backdrop, the sustainable use of hardwood resources and the development of silvicultural techniques in natural forests to ensure stable supply have emerged as urgent challenges (Asada et al. 2017).

In Japan, overall wood self-sufficiency rate recovered to approximately 42.5% by 2024, following a long period of decline and renewed policy efforts to promote domestic timber use (Forestry Agency of Japan 2024; Hayafune and Higuma 2025). This

increase has been driven primarily by the expanded utilization of domestically produced softwood, reflecting the large area of post-war softwood planted forests and their increasing harvestability (Forestry Agency of Japan 2024; FAO 2020). In contrast, the domestic share of hardwood supply remains low, at around 15% for certain hardwood product categories (Forestry Agency of Japan 2023). Consequently, hardwood utilization in Japan continues to depend largely on imports and on naturally regenerated hardwood species, including those that establish naturally within softwood planted forests. This reliance reflects the fact that hardwood planted forests occupy only a small fraction of planted forests in Japan, and that intensively managed hardwood planted forests remain rare (Yamaura et al. 2018).

Historically, hardwood forests in Japan were managed primarily under coppicing systems in satoyama landscapes to provide fuelwood and materials for agricultural tools. However, as a result of the energy revolution and rural depopulation since 1960s, demand for fuelwood and tool materials declined, leading to the abandonment of satoyama management and subsequent degradation of forest resources (Terada et al. 2010; Itô et al. 2012). Meanwhile, large-diameter, high-quality hardwood timber had traditionally been harvested mainly from secluded natural forests, but excessive logging from the prewar through wartime periods, combined with stagnation of hardwood management in the postwar era, caused both quantitative and qualitative degradation of hardwood resources, making the procurement of high-quality logs extremely difficult. However, since the third “wood shock” triggered by the spread of COVID-19 in 2021, the structure of domestic timber demand has undergone a major shift, with a particularly sharp increase in demand for hardwoods (Hata and Inoue 2023). In addition, changes in consumer awareness favoring domestically produced timber have

driven the overall timber market toward domestic or local products, further accelerating this trend and making the establishment of a production system for domestic hardwoods an urgent necessity. Along with these shifts in demand, large-diameter, high-quality logs with fewer defects have been traded at prices far exceeding previous levels in timber markets and specialized transactions throughout Japan (ITTO 2023; Refer to appendices).

Hokkaido is home to diverse hardwood species in both primary, semi-primary and secondary forests and has played an important role as one of the major production areas of high-quality hardwood timber. Since the late Meiji era, logs produced in Hokkaido have been exported overseas, and their quality has been highly valued internationally (Hirano 2023). However, in contrast to the postwar policy of expanding softwood plantations (Masaki et al. 2017), silviculture of hardwood species in Hokkaido has lacked systematic development of planned cultivation techniques. As a result, many hardwood resources have been replaced by softwood plantations, and the methods for regeneration and harvesting are unclear (Hirata et al. 2011). Furthermore, in Hokkaido, where selection cutting has been widely practiced since land development, excessive harvesting rates have significantly deteriorated forest stands (Watanabe 2003). In addition, the proliferation of dwarf bamboo on the forest floor has deteriorated light conditions (Akashi et al. 2021; Refer to appendices) (Figure A2), while the rapid increase in deer populations has caused browsing damage (Akashi et al. 2022), both of which severely hinder forest regeneration. Consequently, insufficient management after regeneration has led to the reduction of stem diameter growth and timber quality, resulting in a noticeable decline in the availability of high-quality logs that were once highly esteemed. This situation highlights the urgent need to establish a well-designed management framework for resource regeneration and forest development to ensure the sustainable production of

hardwood timber. In particular, in forests that have already undergone degradation in stand quality, it is crucial to define appropriate species selection and silvicultural objectives, and to implement management strategies that harmonize economic profitability with environmental conservation (Nakajima et al. 2017).

However, hardwoods, especially those species that have traditionally been traded at high value, generally exhibit greater variability in tree form and require longer periods to attain harvestable size compared to softwoods. As a result, simply applying the silvicultural systems established for softwood plantations—such as thinning and final felling cycles—often leads to higher costs and poses challenges for sustainable forest management (e.g., FFPRI cost assessments). Therefore, hardwood management requires alternative approaches that can enhance profitability while reducing costs, distinct from those used for softwoods. Specifically, actively utilizing natural regeneration can help reduce planting costs (Yamazaki and Yoshida 2020; Yoshida et al. 2023). In addition, promoting the formation of multilayered or uneven-aged stands can prevent the concentration of large-scale harvesting and planting operations, thereby distributing management costs more evenly over time and ensuring more regular income (Barrette et al. 2023). On the other hand, depending on tree species, there are inherent limits to cost reductions achievable through such silvicultural practices (Yamazaki and Yoshida 2018), and enhancing profitability remains essential. Therefore, enhancing sustainability requires not only minimizing costs but also taking more proactive steps to improve profitability. In this context, proposed strategies include expanding the utilization of underused hardwood species for general timber use and cultivating trees with wood properties suited to specific applications (Bragg. 1999). Incorporating such approaches can be effective in uncovering opportunities for improving profitability that are often

overlooked in conventional forest management, and further consideration is needed to realize these possibilities (Gradel et al. 2017).

Based on this background, the use of hardwood species that have not previously been actively utilized for general timber purposes has been gaining momentum, and growing interest in the use of high value-added wood products. In recent years in Japan, some tree species have been reassessed due to alleviated concerns over strength performance and advances in wood processing technologies (Matsumura et al. 2006; Ohsaki et al. 2019). For instance, in warm temperate regions, fast-growing species such as *Melia azedarach* are expected to serve as new sources of timber supply (Kasuya et al. 2025), while in cool-temperate regions, species with abundant resources, such as *Betula ermanii* and *Betula platyphylla* (Tomita et al. 2020), have become representative examples of active utilization. Although these are hardwood species, management practices—such as regeneration methods (planting or natural regeneration) and the timing of cleaning cutting and thinning operations to promote growth—are increasingly established (Sano and Shibuya 2015; Yoshida et al. 2023). Therefore, ensuring a stable timber supply through planned management while increasing the proportion of wood suitable for general use is considered a key strategy for improving profitability. To promote broader utilization of these hardwoods, it is, of course, indispensable to suppress wood defects—such as stem curvature, knots, and decay—defined by the Japanese Agricultural Standards (JAS: <https://www.maff.go.jp/j/jas/index.html>). Generally, such defects can be controlled through silvicultural operations including stand density regulation to maintain tree form or vigor and pruning to reduce knot formation, and considerable knowledge has already been accumulated in this regard (Macdonald and Hubert 2002; Hart 2010). Consequently, future research should focus on how to deal with

species-specific defects that are inherent to each hardwood species. In cases where defects can be mitigated through processing technologies—as with *Melia azedarach*—traditional silvicultural methods focusing on growth enhancement can still be effectively applied (Duong and Matsumura 2018; Utsumi et al. 2019). However, for defects that must be suppressed during the growth stage—such as those found in birch species—it is necessary to first identify their occurrence patterns and develop appropriate management practices to mitigate them (Nakaya et al. 2024). Nevertheless, for species that have not been actively utilized as general-purpose timber, knowledge of their specific wood defects remains limited, and few findings can yet be applied to forest management. Therefore, it is crucial to clarify the relationships between species-specific wood defects and the growth conditions of individual trees as a first step toward overcoming these challenges.

On the other hand, several studies have proposed improving the profitability of hardwood forestry by utilizing wood properties that are particularly valued in the market (Bragg et al. 1997; Bragg 2006; Quambusch et al. 2021). For example, trees exhibiting aesthetically appealing grain patterns (figured wood) or coloration, as well as those with superior durability or workability, which can command prices several to dozens of times higher than ordinary wood. Although such trees may account for only a few percent of the total harvest, they have the potential to substantially increase overall revenue (Bragg 2006). Therefore, the deliberate production of high-value timber can be an effective strategy for enhancing profitability. In tropical regions, species such as mahogany (*Swietenia* spp.), ebony (*Diospyros* spp.), and teak (*Tectona grandis*) are highly valued worldwide for their distinctive coloration, durability, and workability, and thus serve as major sources of revenue in tropical forestry (Brown et al. 2004; Palanisamy et al. 2009; Deblauwe 2021). In temperate regions, *Acer saccharum* (sugar maple) is well known for

occasionally producing “birdseye” figure—a decorative grain pattern highly prized for use in fine furniture, musical instruments, and gunstocks. According to forestry records from the late 19th century in the United States, individual logs of sugar maple exhibiting outstanding birdseye figure were sold for as much as USD 1,000 per log at that time, equivalent to approximately USD 46,000 in 2002 (Hough 1884; Bragg 2006). In tropical regions, insufficient forest management has led to the depletion of valuable species such as mahogany, ebony, and teak, resulting in their production being confined to limited areas today. Similarly, in the case of sugar maple, studies have reported that inadequate management practices have suppressed the formation of trees exhibiting the birdseye figure (Pillow 1955; Bragg 2006). These examples highlight the necessity of implementing appropriate forest management that addresses both the quantitative and qualitative aspects of timber production. Conversely, advances in technologies that enable the evaluation and selection of trees or logs based on wood quality are expected to play a key role in recovering overlooked revenue sources. Combined with the development of appropriate silvicultural practices to promote desired wood traits, these advances can contribute substantially to the realization of sustainable and profitable hardwood forestry.

However, studies that quantitatively evaluate defects and desirable wood properties across most hardwood species and across a wide range of wood traits, and that further examine the relationships of these properties with individual characteristics or site conditions, remain very limited (Quambusch et al., 2021). As a result, silvicultural practices based on such body of knowledge are not yet widely established. In particular, these wood properties are thought to be influenced not only by genetic factors but also by growth patterns, by the external characteristics of individual trees, and by their growth environment (Bragg et al., 2006; Quambusch et al., 2021). Therefore, it is critically

important to verify growth promotion under conventional forest management aligns with desirable wood properties. Detailed investigation of these relationships plays a determinative role in identifying concrete management for recovering potential profitability.

1.2 Major hardwood species in Hokkaido

The major hardwood species composing Hokkaido's forests are dominated by *Betula* spp., which account for 22.8% of the total volume (including softwood species), followed by *Quercus* spp. (14.9%), *Tilia* spp. (10.9%), and *Acer* spp. (8.0%) (Table 1, Hokkaido Forestry Statistics: <https://www.pref.hokkaido.lg.jp/sr/sum/kcs/rin-toukei/05rtk.html>). The *Betula* spp. includes *Betula maximowicziana* (monarch birch), *B. ermanii* (erman's birch), and *B. platyphylla* (Japanese white birch). All of these species are early-successional trees capable of natural regeneration and represent the most dominant hardwood species regenerating after disturbance or site preparation in Hokkaido. Although small-scale plantations exist, they are predominantly distributed as naturally regenerated secondary forests, often forming nearly pure stands (Osumi 2005; Suzuki et al. 2025). In contrast, their distributions and life spans differ markedly among *Betula* spp., and their wood properties and end uses are diverse (Shimase 2021). *B. maximowicziana* has relatively high strength and is used for interior woodwork, furniture, flooring, and musical instruments. On the other hand, *B. ermanii* is sometimes used for flooring and other purposes, but commercially it has often been referred to as “zatsukaba” (low-grade birch), and most of it has historically been processed into pulp chips (Ohsaki et al. 2019). Similarly, *B. platyphylla* has had little circulation as general timber, being primarily used as low-quality material for chopsticks, ice cream sticks, and pulp chips. Even though these

species are all classified as *Betula* spp., *B. ermanii* and *B. platyphylla* have so far not been recognized as valuable timber species, and their wood defects have not been studied, nor have their wood properties such as wood density and strength been measured (Tomita et al. 2020).

Quercus spp. in Japan mainly includes *Quercus crispula* (Japanese oak), *Q. serrata*, and *Q. dentata*, with *Q. crispula* being the dominant oak species in Hokkaido. *Q. crispula* produces robust and durable wood and has long been used for high-value products such as furniture and flooring. In recent years, its evaluation as barrel timber has increased markedly, leading to a rapid rise in demand (Asada et al., 2017; Hasegawa et al., 2018). The suitability of oak for barrel production depends on specific wood properties, including straightness of grain and the formation of tyloses (Alamo-Sanza and Nevares, 2018; Kim et al., 2024). These properties are essential for producing leak-free barrels, directly determining whether the wood can function as barrel timber. In Hokkaido, *Q. crispula* is a common species in well-developed secondary forests, where natural regeneration is generally difficult and requires a long time. As a result, stand structure and competitive environments are largely shaped by past and ongoing management practices, allowing their effects to accumulate over long periods. Under such conditions, forest management strongly influences individual growth patterns and stem characteristics. However, it remains largely unclear to what extent key wood properties relevant to barrel suitability can be controlled through forest management practices.

Acer pictum (painted maple) is one of the major maple species in Hokkaido. Although its natural and artificial regeneration are limited, it is typically associated with late-successional forests and often forms a major component of mature stands (Suzuki et al., 2025). This species has dense and beautifully grained wood that is used for interior

materials, furniture, and utensils. It is also highly valued for its decorative appeal resulting from the occurrence of complex and beautiful grain patterns known as figure. However, scientific knowledge about the mechanisms and frequency of figure formation remains very limited, and it is not yet clear whether such features can be controlled through forest management.

1.3 Objectives and Structure of the Doctoral Dissertation

The aim of this study is to clarify how wood properties—which are key factors in improving the profitability of hardwood forest management—relate to the growth and site conditions of individual trees in Hokkaido, the region with the highest hardwood production in Japan. In doing so, this study focuses on four major species (Figure 1): *B. platyphylla* and *B. ermanii*, for which demand has recently increased due to emerging uses, and *A. pictum* and *Q. crispula*, which are expected to produce high-value timber.

As mentioned above, research on wood properties of hardwood species is less advanced than that of softwood species. Therefore, to link wood properties with growth conditions, it is necessary to adopt a novel research approach that integrates silviculture and forest products science. In this study, I conducted species-specific investigations using the following approach. First, I examined growth conditions of individual trees—including tree size, age, mean ring width, visible features, and environmental factors such as surrounding tree density and site moisture conditions—and quantified the key wood properties for each species. Next, the relationships between key wood properties and growth conditions were analyzed using structural equation modeling, revealing the relative importance of each growth parameter and the strength of its direct and indirect effects on key wood properties. Based on these results, I then discussed silvicultural

practices that take the key wood properties into account for each species.

Using this common research approach, Chapter 2 examines the relationship between the size of false heartwood, considered a major defect in *B. platyphilla* timber, and individual tree characteristics (tree size, growth rate, crown ratio, number of branch scars) as well as site conditions (number of neighboring trees, topographic wetness of the growth site). Vertical variations of false heartwood within individual trees are also investigated. In Chapter 3, the study investigates the relationship between wood density of *B. ermanii*, which is expected to be a promising material for baseball-bats, and its growth conditions (tree size, annual ring width) as well as site condition (local propensity for site moisture). In this analysis, the outermost mature wood in the stem cross-section is treated as the representative value for each individual, while radial variations in wood density within individuals are also examined. Chapter 4 clarifies the occurrence of figure (figured wood) in individual *A. pictum* trees and its relationships with tree characteristics. *A. pictum* is particularly valued for its decorative appearance and high market price among the species that produce figured wood in Hokkaido. This chapter examines the frequency and size of figure in relation to tree characteristics, including tree size, annual ring width, stem crookedness, and positional relationships with forks. Finally, Chapter 5 examines the growth conditions of individual trees in secondary *Q. crispula* stands that are suitable for barrel timber. In particular, it focuses on two key indicators of barrel timber quality: grain angle and the tyloses filling ratio in early vessels. The study investigates how these two wood properties relate to individual tree characteristics and growth conditions, including tree size, annual ring width, stem crookedness, wood eccentricity, and site moisture conditions. Furthermore, it scientifically evaluates traditional empirical rules for predicting grain angles based on observations of standing

trees and logs, specifically analyzing the relationship between measured grain angle and bark crack angle to clarify the reliability of using bark observations to predict internal stem twist.

Based on the results presented in the previous chapters, Chapter 6 provides a comprehensive discussion on whether the key wood properties identified for each species can be managed through silvicultural practices, such as thinning, tree selection and site selection. Furthermore, the future outlook for hardwood forest management in Hokkaido is described.

1.4 Table

Table 1. Major tree species composing natural forests in Hokkaido and their timber volume, growth conditions, and wood utilization.

Species	Volume (1000 m ³)	Volume (%)	Growth status	Wood use
<i>Betula</i> spp.	95270.79	22.78	All of these species are early - successional trees capable of natural regeneration, and plantations of these species also exist; secondary forests forming nearly pure stands are common.	<i>B. maximowicziana</i> is valued for high-end furniture, interior woodwork, and decorative boards. <i>B. Ermanii</i> is used for flooring, baseball-bat and low-quality material. <i>B. platyphilla</i> is used for furniture, wood items and low-quality materials.
<i>Quercus crispula</i>	62235.53	14.88	Oak also planted, but natural regeneration is generally difficult and takes time. Secondary forests are common, and some of them form nearly pure stands.	<i>Q. crispula</i> is used for high-value applications such as furniture, flooring, and even whiskey barrel.
<i>Tilia japonica</i>	45847.35	10.96	This is widely distributed in Hokkaido and often found in secondary forests near urban areas, its regeneration and utilization have not been sufficiently implemented.	<i>T. japonica</i> is used for carvings, woodcrafts, furniture components, surface material for plywood and lumber core boards.
<i>Acer pictum</i>	33480.49	8.01	Painted maple does not regenerate either naturally or artificially, yet they constitute a major component of secondary forests.	<i>A. pictum</i> is used for interior materials, furniture, utensils, decorative veneer and musical instrument material.
Other	181370.31	43.37		

1.5 Figure

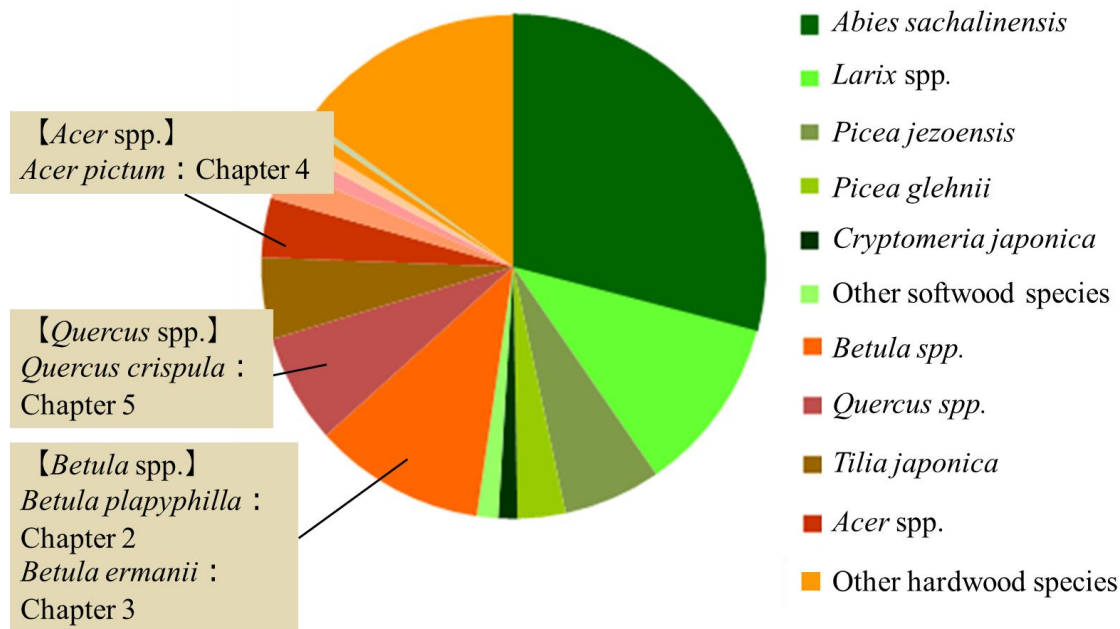


Figure 1. Growing stock volume by species (including plantations and natural forests).

Softwood and hardwood species each account for approximately half of the forest composition, and among the hardwood species, *Betula plapyphilla*, *B. ermanii*, *Quercus crispula*, and *Acer pictum*, which have large standing volumes, were selected as the subjects of this study.

1.6 Appendices



Figure A1. Scenes from the Asahikawa premium log market:

In recent years, auction prices for domestically produced hardwoods have risen sharply.



Figure A2. A dense layer of dwarf bamboo covers the understory:

In many forests in Hokkaido, regeneration is inhibited by dense dwarf bamboo cover, which is considered one of the major management problems.

Chapter 2

Tree and stand characteristics associated with the occurrence of false heartwood in individual Japanese white birch trees

2.1 Introduction

False heartwood (also called red heartwood) is defined as the central part of wood, with a different nuance of color than surrounding normal wood, in tree species that normally do not have any heartwood (Venet, 1986; Hörnfeldt et al., 2010). The conditions for its occurrence and formation process have been studied in beech (*Fagus*), maple (*Acer*), and birch (*Betula*) species (Campbell and Davidson, 1941; Shigo, 1984; Hallaksela and Niemistö, 1998; Wernsdörfer et al., 2005; Giroud et al., 2008; Havreljuk et al., 2013). The first step in the formation process is the penetration of oxygen and microorganisms into wood from damaged areas of the stem, such as fallen branches (Trendelenburg, 1939; Shigo, 1986; Kohler, 2006; Belleville et al., 2011). In subsequent stages, especially when tree vigor is weak, under dry conditions (Shigo, 1986; Kohler, 2006), the oxidation of phenolic substances (Koch, 2004; Hofmann et al., 2022) and enzymes released by fungi (Trendelenburg, 1939; Pape, 2002) may expand discoloration in the stem.

In general, the commercial value of wood containing false heartwood is significantly reduced since irregular coloring is not attractive to many consumers. Therefore, previous studies have attempted to predict the presence or absence of false heartwood and its proportion to stem cross-sectional area based on tree appearance characteristics (Knoke and Wenderoth, 2001; Račko and Čunderlík, 2002, 2010; Wernsdörfer et al., 2005; Belleville et al., 2011; Baral et al., 2013). Several studies have

stated that the development of false heartwood is related to age, suggesting that it may be possible to produce wood with less false heartwood by accelerating growth to shorten the time to harvest (Hallaksela and Niemistö, 1998, Knoke, 2003; Giroud et al., 2008; Drouin et al., 2009; Baral et al., 2013). Kohler (2006), on the other hand, emphasized that a combination of factors leads to the formation of false heartwood and that the most important factor influencing its formation is the growth environment of the stand, including stand density. Furthermore, Giroud et al. (2021) demonstrated the importance of topography and site moisture conditions; dryness conditions contributed to increasing the proportion of false heartwood in white birch (*Betula papyrifera* Marsh.). However, although one study examined multiple factors in an integrated manner (Belleville et al., 2011), the relative importance of each factor is not clear. Furthermore, the decline in commercial value is also due to the difficulty in distinguishing between false heartwood and decayed wood (Kohler, 2006). False heartwood without decay has been reported to have higher moisture content and more abundant fungi than normal wood (Campbell and Davidson, 1941), but the difference in the mechanical properties (strength and hardness) was unclear. Nevertheless, false heartwood and decay are thought to be related (Trendelenburg, 1939; Campbell and Davidson, 1941; Siegle, 1967; Shigo and Hillis, 1973; Basham, 1991; Arač et al., 2021). Stem damage, which is considered to be the starting point of false heartwood formation can also be an entry point for heart rot fungi (Trendelenburg, 1939).

Japanese white birch (*Betula platyphylla* var. *japonica* (Miq.) H. Hara) trees grow quickly with a potential life span of approximately 100 years (Osumi, 2005), and their high reliability of natural regeneration (Aoyama et al., 2009; Yamazaki and Yoshida, 2018) makes planning for sustainable wood use easy. The wood of this species has been

used only for low-quality applications, such as pulpwood, but the development of processing technology has made it possible to efficiently use logs even with small diameters for high value-added wood products, such as furniture and interior materials (Shimase, 2021). To promote the use of *B. platyphylla* for a wider variety of applications, it is necessary to understand the basic characteristics of false heartwood, such as its frequency of occurrence, requirement for formation, and relationship to decay incidence. This study aims to verify the following hypotheses about the proportion of false heartwood (PFH), and its relationship with decay, in individual *B. platyphylla* grown in a relatively old (approximately 70 years old) secondary stand; higher PFH is associated with (1) a lower crown ratio, (2) a greater number of branch scars, (3) a greater individual tree basal area, (4) a lower growth rate, (5) lower site moisture conditions (wetness) surrounding the tree, and (6) occurrence of decay.

This study also addresses the vertical distribution of false heartwood within the tree stem. Several studies have shown that the size of false heartwood varies with vertical tree stem position (Hallaksela and Niinistö, 1998; Wernsdörfer et al., 2006; Giroud et al., 2008; Baral et al., 2013) and that false heartwood is mostly located under the lowest live branch (Basham, 1991; Belleville et al., 2011; Giroud et al., 2008). According to Wernsdörfer et al. (2006), there are three stages of false heartwood development, which are thought to proceed in the following order: false heartwood initiation, a transition stage in which false heartwood develops especially at the middle stem height, thus showing a vertically spindle shape, and a late stage in which false heartwood becomes vertically conical along the stem. Therefore, the following hypotheses are also tested in this study; false heartwood (7) occurred only under the lowest live branch, and (8) shows a vertically conical shape, considering that the age of the study stand is close to maturity.

2.2 Materials and methods

2.2.1 Study site and sampling

Field surveys were conducted in the Uryu Experimental Forest, Field Science Center for Northern Biosphere, Hokkaido University, Japan. The mean annual temperature and precipitation in the forest are 6.0 °C and 1,500 mm, respectively, according to the Japan Meteorological Agency (<https://www.jma.go.jp/jma/index.html>). The maximum snow depth reaches more than 200 cm. The dominant vegetation is natural mixed forest consisting of cool temperate hardwood and subboreal softwood species. In addition, there are natural secondary forests dominated by *Betula* spp.

From January to April 2020 and 2021, experimental cutting was conducted in a ca. 70-year-old natural secondary forest, which was located on the upper slope (prone to dryness) from the lower slope (44°22' N, 142°12' E, 280 m above sea level). This forest was crowded in terms of tree density (546 stems·ha⁻¹), as it was established without human interference (such as thinning) after field burning in approximately 1950. Three clear-cut plots (two plots of 1.09 and 0.99 ha cut in 2020, one plot of 1.09 ha cut in 2021) were set as the study area. *B. platyphylla* overwhelmingly dominated the study area (69% in volume, 69% in basal area, 65% in stem density), with *Quercus crispula* Blume, *Betula ermanii* Cham, *Abies sachalinensis* (F. Schmidt.) Mast., as occasional associates (Table 1). The understory was densely covered with *Sasa senanensis* (Franch. et Sav.) Rehder.

2.2.2 Methods

Tree measurements were conducted one year before each cutting (April 2019 and 2020).

All living trees with a diameter at breast height (DBH; 1.3 m above ground) greater than 12 cm were numbered with tags for individual identification. Their DBH was measured in 2 cm intervals with a caliper, and location (x - y coordinates) was recorded by GPS (Mobile Mapper 100, Ashtech). In addition, photographs of each standing tree were taken (Camera; D 750, Nikon Co., Lens; AF-S NIKKOR 18-35 mm f/3.5-4.5 G ED, Nikon Co.) at the time of complete defoliation (December-February) from two points facing each other at approximately more than 10 m away from the stem so that the breast height to the crown top was captured with small lens distortion.

The trees were felled with a chainsaw at an average height of 0.67 (SD = 0.16) m above ground. After transporting the log to the stock yard using a heavy machine while retaining the individual identification number, disks with 5 cm thickness were collected from the butt end of the log (951 disks). The existence of decay on the butt end of the log (cross section) was also recorded mainly by visual inspection. If it was difficult to judge by visual inspection alone, it was determined to be decaying when the material easily crumbled by scratching with a tool.

The disks were brought back to the lab, and the cross sections were photographed along with a scale (Camera; D 750, Nikon Co., Lens; AF-S NIKKOR 18-35 mm f/3.5-4.5 G ED, Nikon Co.). The periphery of the surface area (excluding the bark) and false heartwood were manually delineated in ImageJ (Schneider et al., 2012), and the respective areas were measured. Here, false heartwood is defined as “wood with a different nuance of color from surrounding wood” (Venet, 1986), and the proportion of false heartwood (PFH) was calculated as the proportion to the disk surface area. Ring widths for the most recent 10 years were measured along a single radial direction from the cambium toward the pith, which was assumed to represent average radial growth. The

cross-sectional area growth rate for the last 10 years (GR) was calculated from the increase in stem cross-sectional area, estimated using the cumulative radial increment and the current radius from the pith. In addition, I randomly selected 100 disk photographs and counted the number of these annual rings. The possibility of counting false annual rings was minimized by enlarging the image data.

The photographs of individual standing trees taken during the complete defoliation season (see above) enabled us to record tree form and stem characteristics. First, the crown ratio (CR; the ratio of crown length to tree height) was recorded. In this study, the ratio of crown length to tree height was read directly on standing tree photographs at a resolution of 10%. Here, the crown refers to the area where the live branches are continuous up to the shoot ends from the lowest live branch. Next, branch scars (Figure 1) located from breast height to the bottom of the lowest living branch were counted by using the two images taken from opposite positions; those with a width greater than 1/3 of the stem diameter at the height were targeted. The number of branch scars (NBS) was measured with accuracy by enlarging the photographs and paying attention to the position and characteristics of individual branch scars to avoid omissions and duplicates in the count. In these steps, the trees (469/951 individuals) that were difficult to discriminate due to overlapping stems or branches of other trees were excluded from the analysis.

As an indicator of local tree crowding, I calculated the total basal area of living trees with a diameter at breast height (DBH) of 12 cm or more within a 5-meter radius from the study tree (i.e., amounts of neighboring trees; BAS). This radius corresponds to the maximum crown radius of trees in the study site. I used GIS software (QGIS; QGIS Development Team, 2021) and the location information (x - y coordinates) of individual

trees for the analysis. A digital elevation model (DEM) provided by the Geospatial Information Authority of Japan (10-m resolution) was overlaid in QGIS. Slope inclination was calculated at a 400 m² resolution, and the topographic wetness index (TWI) was derived as a relative indicator of site wetness for each individual tree (Beven and Kirkby, 1979).

In addition, 32 randomly selected birch trees (DBH = 23.8 (SD = 2.0) cm) in the study area were felled to investigate the vertical distribution of false heartwood. Their stump height, whole tree height and lowest live branch height (defined as the branching height of the lowest foliage layer forming a contiguous living canopy) were measured. Subsequently, disks of 5 cm thickness were collected from these trees at the stump height, 1 m, 1.3 m, 2 m, and then every 1 m to the treetop. All disks were brought back to the lab, and PFH was measured on each disk photograph as described above. The false heartwood volume of the entire tree was then calculated as follows:

$$[1] \quad \text{FHVlog} = \left(\frac{\text{FHT} + \text{FHB}}{2} \right) \times \log \text{ length}$$

$$[2] \quad \text{FHV} = \sum^n \text{FHVlog}$$

where FHVlog is the false heartwood volume per log (m³), FHV is the false heartwood volume of the entire tree (m³), FHT is the surface area of false heartwood for the top end (m²), and FHB is the surface area of false heartwood for the butt end (m²) (Giroud et al. 2008). FHV was converted to PFHV, which is the proportion of false heartwood volume to entire stem volume.

2.2.3 Analysis

I performed structural equation modeling (SEM) to determine the strength of the direct and indirect effects of each factor on the proportion of false heartwood (PFH). A hypothetical model (Figure 2) was developed that accounted for previous studies. Based on the mechanism of false heartwood formation, I hypothesized that basal area (BA) and number of branch scars (NBS) would have a positive direct effect. Similarly, I hypothesized that the growth rate (GR), crown ratio (CR), and TWI had a negative direct effect on PFH. For indirect effects, the paths were assumed to indicate that BA affects PFH indirectly by affecting GR, CR, and NBS. Since CR could affect NBS and GR, TWI could affect PFH via GR, and indirect paths from these two variables were also assumed. Regarding the amounts of neighboring trees (BAS), only indirect paths through BA, NBS, CR, and GR were assumed. SEM analyzes the relationship between hypothesized variables in the form of a linear combination (Lam and Maguire, 2012). Hence, I examined the bivariate relationships using simple linear regression analysis according to the hypothesis in Figure 2, and the assumption of linearities was satisfied for the variables between which I assumed a causal relationship. Normality for each variable was confirmed at $P > 0.05$ based on the Shapiro–Wilk test (Razali and Wah, 2011). For all unstandardized path coefficients, the significance level was set at a risk rate of less than 5%. However, SEM is a statistical method used to test a theoretical hypothesis. Therefore, nonsignificant paths were retained in the model if prior studies showed a significant relationship or if they were conceivable theoretically valid (Laughlin and Fulé, 2008; Lam and Maguire, 2012).

The model fit was evaluated by the goodness-of-fit index (GFI), adjusted goodness-of-fit index (AGFI), comparative fit index (CFI) and root mean square error of approximation (RMSEA). The values of GFI, AGFI and CFI range between 0 and 1, and

the better the model is, the closer the value is to 1. RMSEA values between 0.05 and 0.08 indicate an adequate fit. The SEM was analyzed using the “lavaan” (Rosseel, 2012) package in R version 4.1.3 (R Development Core Team, 2022).

The relationship between false heartwood and decay was tested using the chi-square test for differences in the proportion of false heartwood occurrence in all study trees and trees with decay. In addition, to determine if there were differences in the proportion of decay depending on PFH, all trees were classified into the following PFH classes: PFH = 0, 1-10, 11-20, or PFH $\geq$ 21%. Then, a chi-square test was performed, and an adjustment for multiple comparisons was made using Tukey’s method when overall differences were found.

This study also investigated the vertical distribution of false heartwood (i.e., shape and relationship with the lowest live branch height) in individual trees. The relationship of the proportion of false heartwood volume to entire tree stem volume (PFHV) with PFH at relatively low tree height positions (stump, 1 m, 1.3 m, 2 m, and 3 m) was analyzed using Pearson's correlation coefficient.

2.3 Results

Among the 482 trees investigated in this study, false heartwood was found in 387 trees (80.3%). The proportion of individuals with PFH $\geq$ 11% reached 45.9% (Figure 3). The average PFH was 16.4 (SD = 14.0) %, with a maximum of 63.6% (Table 2). The number of annual rings varied greatly (average 67.9 (SD = 8.5) with a range of 43 to 88 years) among individuals and showed a positive correlation ($r = 0.65$, $p < 0.01$, Figure 4) with BA based on the measurement of the randomly 100 disk photographs.

In the SEM analysis, the path from TWI to GR was not significant, and the

model without this path was adopted as the final model. The values of the model fit metrics were 0.98, 0.94, 0.94 and 0.07 for GFI, AGFI, CFI and RMSEA, respectively; they generally indicated statistically acceptable solutions. The model explained approximately 17% of the variance in the PFH ($R^2 = 0.17$, Figure 5) when all estimated direct and indirect effects were considered.

The most important among all direct effects on the PFH was the crown ratio (CR) (standardized coefficient -0.32 ; $p < 0.01$, Table 3 and Figure 5). Furthermore, the direct effect of the number of branch scars (NBS) on PFH was significantly positive (0.13 , $p < 0.01$, Table 3 and Figure 5). The indirect effect of CR on PFH via NBS was significantly negative (-0.04 , $p < 0.01$, Table 4). The total effect of CR was -0.36 ($p < 0.001$, Table 5 and Figure 5). The effects of individual size (BA) and the amounts of neighboring trees (BAS) on CR and NBS were both significant (BAS to CR was negative).

For the effect of BA on PFH, the direct effect was 0.19 ($p < 0.01$, Table 3 and Figure 5), and the indirect effect including all significant paths was -0.06 ($p < 0.05$, Table 4), with the direct effect exceeding the indirect effect. The total effect of BA was significantly positive (0.13 , $p < 0.01$, Table 5). The effect of BAS on PFH was expressed as an indirect effect of paths through CR or NBS and through both factors, with the total effect being significantly positive (0.06 , $p < 0.01$). The direct effect of growth rate (GR) on PFH was not significant (-0.06 , $p = 0.17$, Table 3 and Figure 5). The direct effect of TWI on PFH was significantly negative (-0.14 , $p < 0.001$, Table 3 and Figure 5).

The percentage of trees with decay was 12.0% (58/482 trees), and 87.9% (51 trees) of them had false heartwood. The percentage was not significantly different ($p > 0.1$) from the percentage of false heartwood in all trees (80.3%). In contrast, the percentage of decay occurrence in each PFH class was significantly greater for $\text{PFH} \geq$

21% than for PFH = 0% and 1-10% ($p < 0.05$, Figure 6).

Regarding the vertical distribution, PFHV was 12.4 (SD = 11.9) % on average (range 0-41.3%). The highest frequency was observed in the 11-20% class (Figure 7). The PFHV was strongly correlated with the PFH at the lower tree heights, with correlation coefficients between 0.98 to 0.99 for each tree height (i.e., stump, 1, 1.3, 2 and 3 m height). The relative tree height at which the mean PFH reached its maximum was 9.7%, which corresponded to 1.82 (SD = 1.52) m in terms of actual height (Figure 8). The mean PFH above this height decreased gradually toward the lowest live branch, where false heartwood disappeared in almost all trees (31/32 trees), resulting in an overall vertical conical shape (Figure 8).

2.4 Discussion

In this study, I conducted an integrated analysis of the factors that cause false heartwood, which is considered a defect when using *B. platyphylla* wood for commercial purposes. Additionally, I was able to clarify the relative importance of the various causal factors to PFH.

SEM analysis revealed that CR was the most influential factor on PFH (Table 3 to 5, and Figure 5). The direct effect of CR on PFH was negative, suggesting that trees with more developed crowns had smaller false heartwood. This result supported hypothesis 1 that PFH is negatively correlated with CR. It is generally believed that trees with higher CR have high vigor due to the presence of abundant canopy leaves (Waring et al., 1981). Previous studies have often assumed that the vigor of trees is important for false heartwood (Basham, 1991; Kohler, 2006; Wernsdörfer et al., 2006; Giroud et al., 2008; Drouin et al., 2009). Individuals with high vigor were regarded as less likely to

form false heartwood because they can quickly recover from external damage that triggers false heartwood (Baral et al., 2013). CR also had a negative indirect effect on PFH through NBS (Table 4 and Figure 5). NBS had a positive direct effect on PFH (Table 3; supporting hypothesis 2 that PFH is positively correlated with NBS), which may be due to increased oxygen penetration into the wood enhanced by more fallen branches (Solomon and Shigo, 1976; Belleville et al., 2011; Havreljuk et al., 2013). As a result, the total effect of CR was the strongest among all variables.

The significant direct effect of BA on PFH supported hypothesis 3 that PFH is positively correlated with BA (Table 3 and Figure 2). This may be explained by the fact that large trees are reaching an age (> 70 years old; Figure 4) close to the life span of this species (c.a. 100 years; Osumi, 2005). In addition, the positive influence in the path $BA \rightarrow NBS \rightarrow PFH$ implied that larger-sized individuals (mostly older trees) tend to develop false heartwood as they experience more events, such as stem damage, that lead to false heartwood formation. The close relationship of PFH expansion with tree age was consistent in previous studies (Cambell and Davidson, 1941; Knoke, 2003; Giroud et al., 2008; Belleville et al., 2011; Havreljuk et al., 2013), although they did not support the claim that it is solely determined by age. On the other hand, the indirect effects of BA through CR had a negative impact on PFH, reflecting the fact that trees with larger BA occupied canopy space earlier and maintained higher CR. Although the positive influence of $BA \rightarrow NBS \rightarrow PFH$ was hidden by the negative influence of $BA \rightarrow CR \rightarrow PFH$ (i.e., the indirect effect of BA was negative: Table 4), the presence of the direct effect ($BA \rightarrow PFH$) overcomes it, resulting in a positive total effect (Table 5).

In contrast, the effect of GR on PFH was negative but not significant, which did not support hypothesis 4 that PFH was negatively correlated with GR (Table 3 and

Figure 5). As expected, GR had a significant positive effect on CR. In contrast, the effect on GR from BA was negative, contrary to the expectation that trees with larger BA would exhibit higher growth rates. In a crowded even-aged stand, especially on a slope, similar to this study site, there is likely to be constant and intense belowground competition (Takahashi et al., 2003; Ohno, 2011), in which larger trees are known to occasionally show reduced growth affected by a lack of water resources. Because the growth rate fluctuated due to such size-dependent incidents, it may not be representative of the tree vigor at this study site.

Most studies have reached a consensus that drying stress is one of the most important factors in the formation of false heartwood (Trendelenburg, 1939; Shigo, 1986; Kohler, 2006; Giroud et al., 2021). This study also found that the value of TWI, which indicates the topographic wetness of the site, had a significant negative effect on PFH, supporting hypothesis 5 (Table 3 and Figure 5). This result suggests that PFH was generally higher in trees growing on the upper slope, which tended to have a greater water deficit than those growing on the lower slope. The relative importance of the effect of the TWI follows that of the CR.

2.4.2 Relationship with decay

Although decay can occur in all trees, a possible link between decay and false heartwood has widely been suggested (Trendelenburg, 1939; Campbell and Davidson, 1941; Siegle, 1967; Shigo and Hillis, 1973; Basham, 1991; Arač et al., 2021). The results of this study also indicated that the decay incidence was significantly higher in trees with larger PFH ($\text{PFH} \geq 21\%$) than in individuals with no false heartwood ($\text{PFH} = 0\%$) or with relatively small PFH ($\text{PFH} = 1\text{-}10\%$). In contrast, there was no significant difference between the

frequency of false heartwood in all study trees (80.3%) and in decayed trees (87.2%). These contrasting results make it difficult to answer hypothesis 6 that false heartwood is a direct cause of decay. According to Shigo and Hillis (1973), the formation of false heartwood progresses more rapidly than decay, and decay triggered by false heartwood is expected to occur with a time delay. Decay is considered to be formed by temporally and spatially complex processes that intricately involve wound conditions (position, frequency, and severity) (Wiedenbeck and Smith, 2019) and compartmentalization (Shigo and Hillis, 1973). Further investigations are needed to determine their causal relationship.

2.4.3 Vertical distribution of false heartwood

On average, PFH within the entire tree stem reached a maximum at 9.7% relative tree height, close to the value (9%) reported for paper birch (Giroud et al., 2008). In most trees (31/32 trees), false heartwood was no longer observed above the lowest live branch, suggesting that a crown strongly limits the vertical formation of false heartwood. This result supports hypothesis 7, consistent with many other studies (Basham, 1991; Wernsdörfer et al., 2006; Giroud et al., 2008; Belleville et al., 2011). Some studies conducted on several tree species have reported that false heartwood often exhibits a vertical spindle shape (in which the PFH is smaller at both relatively low and high tree height positions), and the shape changes with time (Hallaksela and Niemistö, 1998; Wernsdörfer et al., 2005; Giroud et al., 2008). In this study, the vertical false heartwood shape was conical on average (Figure 8), supporting hypothesis 8. The current study site, which was at the older stage (approximately 70 years old) for *B. platyphylla*, may already be in a more advanced stage of development of false heartwood (Wernsdörfer et al., 2006). In addition, PFHV was strongly correlated with PFH measured at relatively low tree

height positions (height of stump, 1 m, 1.3 m, 2 m, and 3 m). In this type of old birch secondary stand, it may be possible to estimate the PFHV by observing the PFH at the lower height position, including the stump height.

2.4.4 Implication for silvicultural management

This chapter clarified the relationship between the false heartwood of individual *B. platyphylla* trees and growth and stand characteristics. In this study, false heartwood at stump height was found in 80.3% of 482 study trees (Figure 3). I suppose that this high occurrence of false heartwood would result from the condition of this study site, a crowded stand established after field burning without any subsequent human interference, in a drought-prone location. Many of the secondary birch stands in Hokkaido are often abandoned and dense, similar to this study site. Therefore, when using wood from these secondary stands, it is necessary to keep in mind the possibility of a high occurrence of false heartwood.

BAS was negatively correlated with CR and positively correlated with NBS. This implied that reducing local crowding could lead to a more developed crown and fewer branch scars, both of which can reduce false heartwood. This strongly suggests that thinning, as standard management for an even-aged stand, also contributes to the reduction of false heartwood; the silvicultural measure for growth promotion would be compatible with defect control in birch forestry. When developing secondary birch forests, it will be possible to increase the proportion of high-value timber in the future by leaving trees with high CR at the time of thinning (Baral et al., 2013). Furthermore, when considering the development of young secondary birch stands, a previous study recommended intense thinning (90% of the number of trees in the stand) to enhance

individual growth (Sano and Shibuya, 2015). This could also lead to a reduction in false heartwood by reducing individual crowding to continuously maintain a high CR, although this may also result in the development of live knots. In addition, the contribution of a higher TWI to a lower PFH suggested that lower-slope sites are more favorable than upper-slope sites for reducing false heartwood. In upper-slope sites, it may be effective to increase thinning intensity to compensate for the negative effect of TWI (Kohler, 2006).

2.5 Tables

Table 1. Tree species composition of the study stand in a secondary forest.

Species	Density (stems · h ⁻¹)	Volume (m ³ · ha ⁻¹)	Basal area (m ² · ha ⁻¹)	Mean DBH and standard deviation (cm)
<i>Betula platyphylla</i> var. <i>japonica</i>	352	116.0	15.7	23.0 ± 6.3
<i>Quercus crispula</i>	54	20.6	2.5	23.4 ± 7.4
<i>Betula ermanii</i>	26	6.1	0.9	19.6 ± 5.5
<i>Abies sachalinensis</i>	17	5.5	0.7	21.1 ± 7.9
Others	96	21.0	2.9	19.0 ± 5.7
Total	546	169.1	22.7	22.1 ± 6.5

Others include *Acer pictum* Thunb., *Phellodendron amurense* var. *amurense*, *Alnus hirsute* Turcz. Var. *hirsute*., etc.

Table 2. Mean, standard deviation and range of the observed variables for *B. platyphylla* var. *japonica* tree individuals.

Observed variable	Description	Mean and standard deviation	Range
PFH (%)	The proportion of false heartwood area to the disk surface area (excluding the bark)	16.4 ± 14.0	0.0-63.6
BA (m ²)	Individual basal area calculated from DBH	0.04 ± 0.02	0.01-0.15
GR (%)	Individual growth rate for the last 10 years	14.1 ± 4.6	5.1-32.4
CR (%)	Ratio of crown length to tree height	24.9 ± 10.1	10.0-50.0
NBS	Number of branch scars with width more than 1/3 of the stem diameter at the height	23.7 ± 9.8	0.0-64.0
BAS (m ²)	Basal area sum of neighboring (within 5 m radius) trees	0.23 ± 0.10	0.02-0.54
TWI	Topographic wetness index at the scale of 400 m ²	7.2 ± 0.6	5.2-8.7

Table 3. Estimated direct effects of the structural equation modeling, along with corresponding standard errors, *Z* values and *p* values (see Figure 5). (PFH: The proportion of false heartwood, BA: Basal area, GR: Growth rate, CR: Crown ratio, NBS: Number of branch scars, BAS: Basal area sum of neighboring trees, TWI: Topographic wetness index)

Path model	Direct effect	Standard error	Standardized coefficients	<i>Z</i> value	<i>p</i> value
PFH =					
BA	110.947	28.067	0.19	3.953	0.000
GR	-0.173	0.127	-0.06	-1.362	0.173
CR	-0.435	0.063	-0.32	-6.875	0.000
NBS	0.194	0.064	0.13	3.023	0.003
TWI	-3.222	0.974	-0.14	-3.307	0.001
GR =					
BA	-34.517	9.375	-0.18	-3.682	0.000
CR	0.054	0.022	0.12	2.474	0.013
BAS	0.371	2.182	0.01	0.170	0.865
CR =					
BA	138.477	18.550	0.32	7.465	0.000
BAS	-12.131	4.526	-0.12	-2.680	0.007
NBS =					
BA	149.974	18.428	0.36	8.139	0.000
CR	-0.274	0.043	-0.28	-6.398	0.000
BAS	9.947	4.289	0.10	2.319	0.020

Table 4. Estimated combined indirect effects of the structural equation modeling, along with corresponding standard errors, *Z* values and *p* values (see Figure 5). (PFH: The proportion of false heartwood, BA: Basal area, CR: Crown ratio, BAS: Basal area sum of neighboring trees)

Path model	Indirect effect	Standard error	Standardized coefficients	<i>Z</i> value	<i>p</i> value
PFH =					
BA	−33.860	16.790	−0.06	−2.017	0.044
CR	−0.062	0.021	−0.04	−2.980	0.003
BAS	7.897	2.611	−0.02	3.024	0.002

Table 5. Estimated total effects (i.e., direct path and all possible indirect paths) of the structural equation modeling, along with corresponding standard errors, *Z* values and *p* values (see Figure 5). (PFH: proportion of false heartwood, BA: basal area, CR: crown ratio)

Path model	Total effect	Standard error	Standardized coefficients	<i>Z</i> value	<i>p</i> value
PFH =					
BA	77.088	26.699	0.13	2.887	0.004
CR	−0.497	0.061	−0.36	−8.172	0.000

2.6 Figures

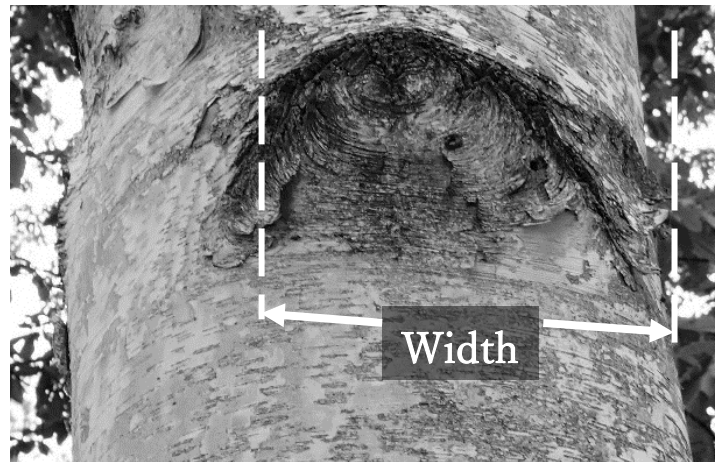


Figure 1. The mustache-patterned branch scar that characterizes birch. Scars with a width greater than $\frac{1}{3}$ of the stem diameter at height were targeted in this study.

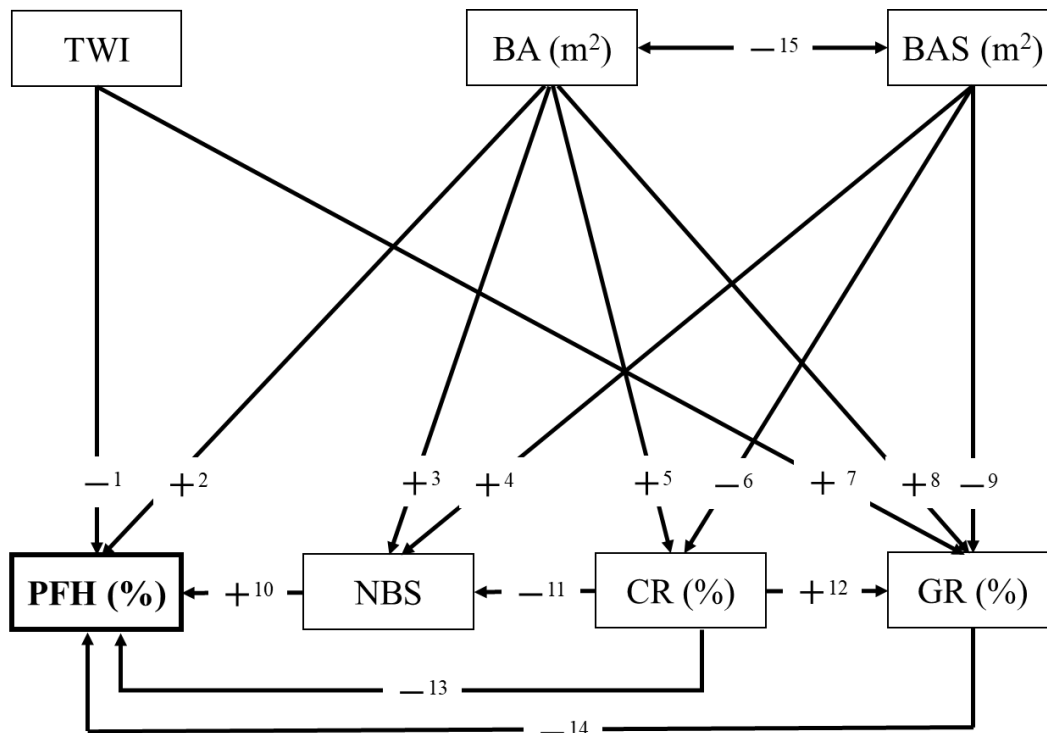


Figure 2. Hypothetical model to explain the proportion of false heartwood (PFH). The direct or indirect pathways for each factor on PFH are shown. Signs (+ or -) indicate expected directions of relationships. BA: basal area, GR: growth rate, CR: crown ratio, NBS: number of branch scars, BAS: basal area sum of neighboring trees, TWI: topographic wetness index.

The numbers assigned to each path correspond to the literature on which they are based.

¹ Trendelenburg, 1939; Shigo, 1986; Kohler, 2006; Giroud et al., 2021.

² Hallaksela and Niemistö, 1998; Knoke, 2003; Giroud et al., 2008; Belleville et al., 2011.

³ Knoke, 2003; Wernsdörfer et al., 2005.

⁴ Knoke, 2003.

⁵ Hemery et al., 2005.

⁶ Knoke, 2003.

⁷ Pastur et al., 2007.

⁸ Chi et al., 2015.

⁹ Knoke, 2003; Chi et al., 2015.

¹⁰ Knoke, 2003; Wernsdörfer et al., 2005; Giroud et al., 2008; Belleville et al., 2011.

¹¹ Knoke, 2003.

¹² Hasenauer and Monserud, 1996.

¹³ Basham, 1991; Giroud et al., 2008; Drouin et al., 2009.

¹⁴ Wernsdörfer et al., 2006; Baral et al., 2013.

¹⁵ Jönsson et al., 2007.

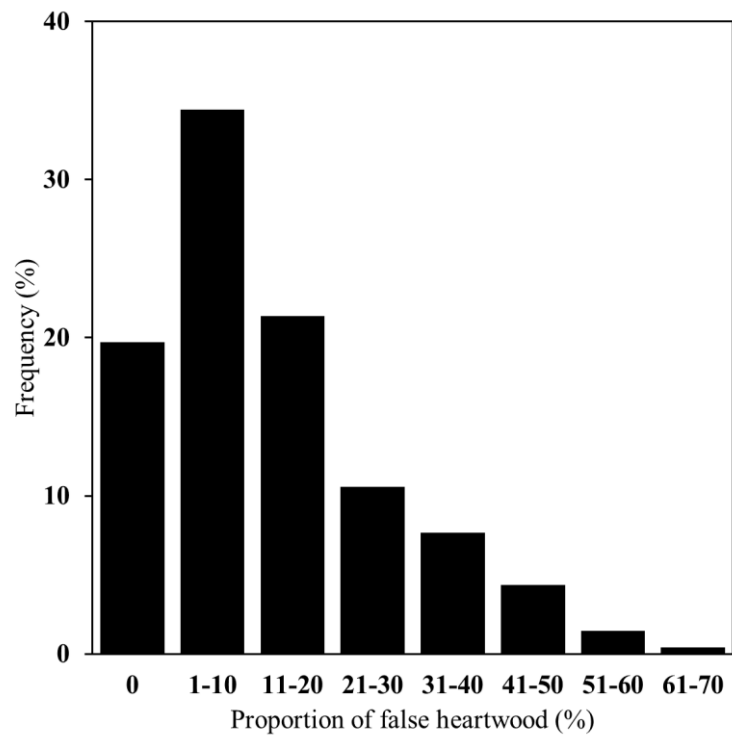


Figure 3. Frequency distribution of the proportion of false heartwood for *Betula platyphylla* var. *japonica* ($n = 482$) in the study stand.

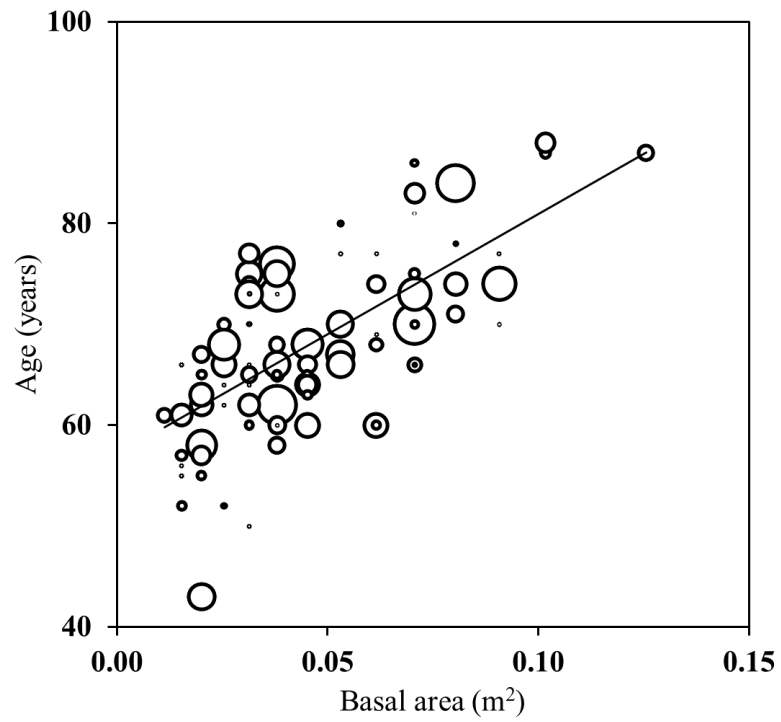


Figure 4. Relationship between tree basal area (m^2) and tree age (years) in 100 randomly selected trees. The regression line represents the relationship between basal area and age. The circle size corresponds to the proportion of false heartwood (max = 50.5%, min = 0%).

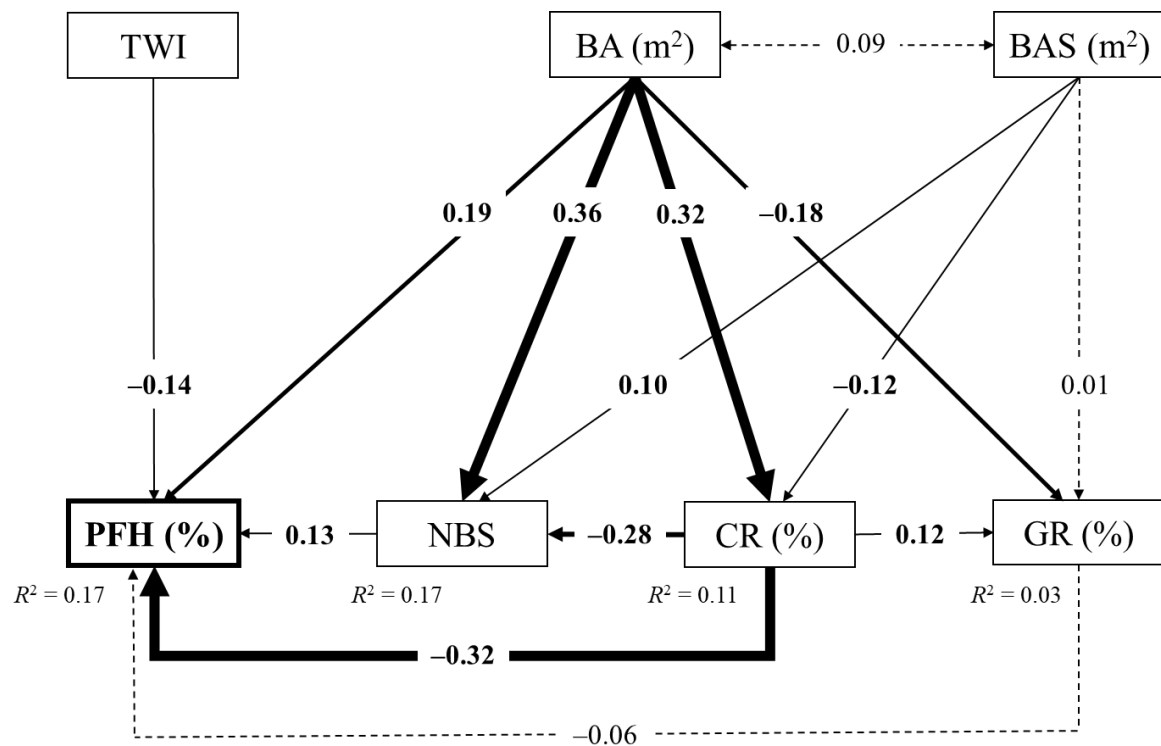


Figure 5. Structural equation modeling (Goodness-of-fit index: GFI = 0.985, AGFI = 0.942, CFI = 0.943, RMEA = 0.066) with standardized parameter estimates. The error arrows of the observed variables are omitted to simplify the diagram. Estimated standardized path coefficients (direct effects) are placed on each path. The squared multiple correlations (R^2) are included for each endogenous latent variable. The thickness of a single arrowhead corresponds to the magnitude of its estimates. The dashed single arrowheads depict nonsignificant paths. The double arrowheads depict the error covariance between the errors of BA (basal area) and BAS (basal area sum of neighboring trees) latent variables. PFH: proportion of false heartwood, GR: growth rate, CR: crown ratio, NBS: number of branch scars, TWI: topographic wetness index.

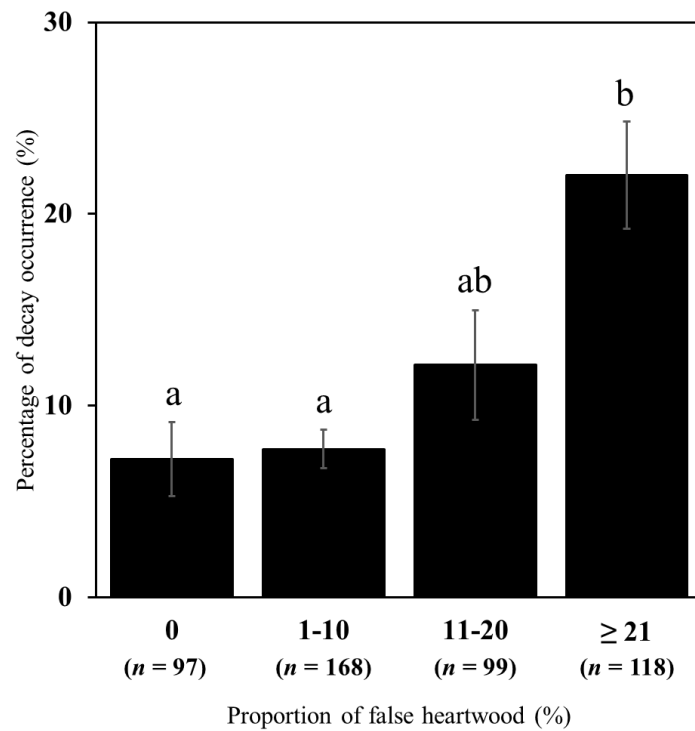


Figure 6. Percentage with decay by the proportion of false heartwood ($n = 482$). The legend indicates the percentage of decay rate included in each PFH. The different letters indicate significant differences at $p < 0.05$ in the Tukey test.

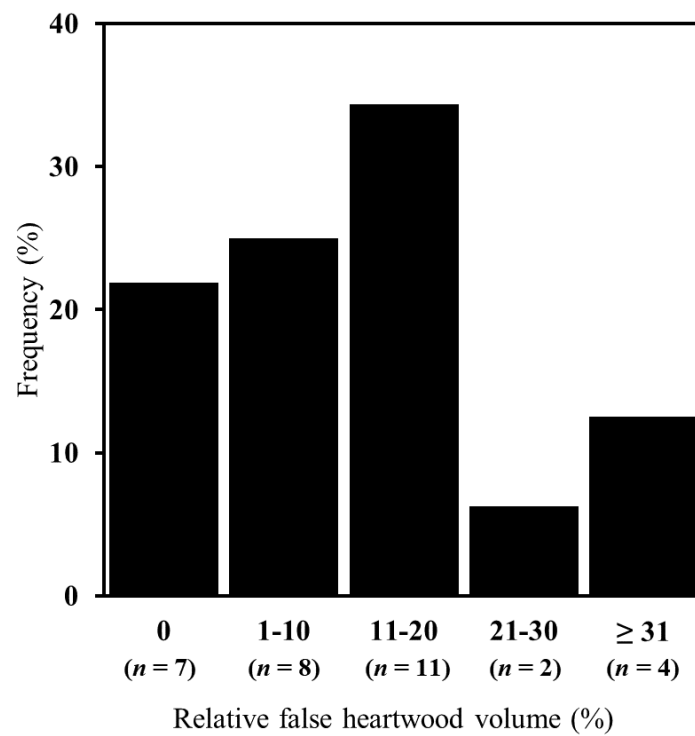


Figure 7. Frequency distribution of the proportion of false heartwood volume to the entire stem volume for *Betula platyphylla* var. *japonica* ($n = 32$) in the study stand.

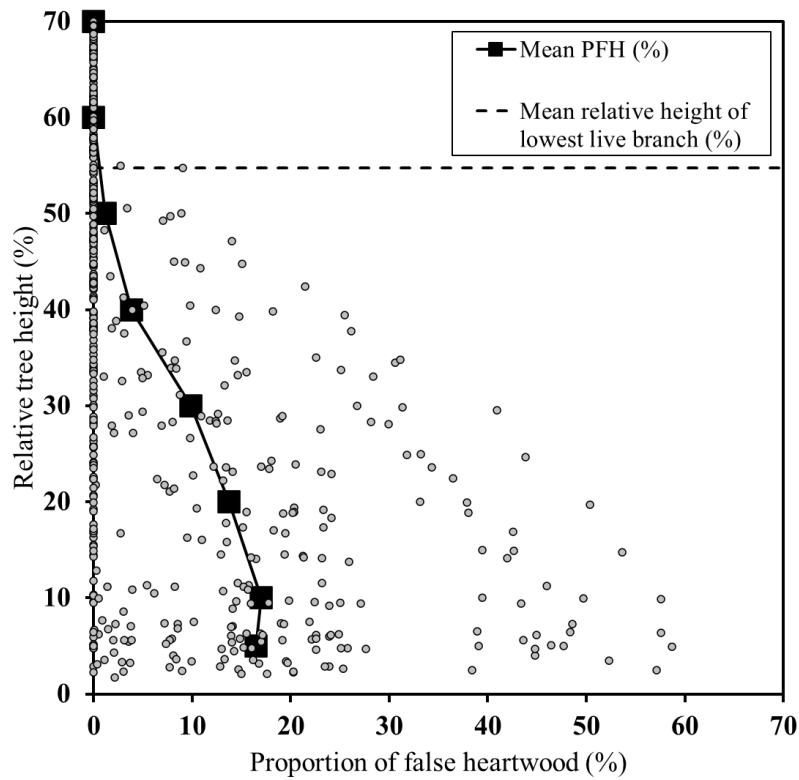


Figure 8. Distribution of the proportion of false heartwood (PFH) along relative tree height. The PFH at each height of 32 trees are pooled and shown. The dashed line indicates the mean relative height of the lowest live branch. The squares indicate the mean PFH of relative height classes approximately 5, 10, 20, 30, 40, 50, 60, and 70%.



Chapter 3

Relationship between wood density and growth conditions in Erman's birch (*Betula ermanii*) for potential use as baseball-bat material: does growth promotion affect wood density?

3.1 Introduction

Erman's birch (*Betula ermanii* Cham.) is one of the representative pioneer tree species in Hokkaido and tends to become dominant following disturbances such as windthrow, landslides, or forest fires (Fischer et al., 2002; Aoyama et al., 2011; Hynynen et al., 2024). Although it is abundant and grows rapidly, in the timber market it has been considered a low-value species, used mainly for pulp and low-quality lumber under the name “zatsukaba,” and its utilization value has historically been estimated as low (Shimase 2014; Ito et al., 2018). However, in recent years, the expansion of furniture and interior wood applications has been observed, driven by advances in processing technology, reassessment of wood properties, and increased interest in sustainable timber use (Ohsaki et al., 2019; Tomita et al., 2020; Yoshida et al., 2022). In addition, the depletion of ash (*Fraxinus* spp.) resources and the decrease in maple (*Acer* spp.) imports have raised attention to the potential use of Erman's birch for baseball-bat material (Tomita et al., 2020).

To support this expanded use, techniques for assisting natural regeneration of birch species have made significant progress in recent years. Conventional regeneration methods, such as soil scarification, have been shown to increase the establishment rate of

pioneer seedlings (Gastaldello et al., 2007). Furthermore, replacing the topsoil to improve site moisture and nutrient conditions has been reported to promote subsequent growth after establishment (Yoshida et al., 2022). Regarding later growth, individual growth is expected to be promoted through competition reduction achieved by thinning and selective removal of surrounding trees (Sano and Shibuya 2015).

However, Erman's birch has not been actively utilized until now, and therefore basic information on its wood properties is lacking. As a diffuse-porous species, the average air-dry wood density of Erman's birch is around 700 kg/m³, which falls within the suitability range for baseball bats (550–750 kg/m³; Tomita et al., 2020). However, in professional baseball, where ball speed is higher and greater performance is required, the usable air-dry wood density is limited to around 700 kg/m³ (Tomita et al., 2020). To be used as baseball bat material, these conditions must be met; however, most Erman's birch is harvested from naturally regenerated forests without intensive silvicultural management, so significant variation in air-dry wood density among individuals is expected even within the same stand. Moreover, in naturally regenerated forests, neighboring trees often share similar site conditions and disturbance histories, suggesting that individual wood density may exhibit spatial autocorrelation rather than being independently distributed within a stand.

On the other hand, it remains unclear whether such individual variation is due to the growth characteristics of each tree (e.g., diameter, ring width) or to site conditions (e.g., site moisture). Wood density is a fundamental and important indicator that influences mechanical strength, drying properties, and workability (Zamudio et al., 2002), and in softwoods it is generally known to be closely related to ring width. For example, in Norway spruce (*Picea abies* L.) and black spruce (*Picea mariana* Mill.), wood density

increases as ring width decreases (Bergqvist 1998, Bouriaud et al., 2015), because the proportion of relatively dense latewood increases (Franceschini et al., 2013). In contrast, in hardwoods, the relationship varies depending on the type of vessel arrangement. In ring-porous species, slower-growing individuals tend to have a higher proportion of earlywood vessels in the ring, resulting in lower wood density (Guilley et al., 1999; Bergès et al., 2008; Humar et al., 2008), whereas in diffuse-porous species, the relationship between ring width and wood density is not clear, and previous studies have shown inconsistent results (Cameron et al., 1995; Erdene-Ochir et al., 2021; Heräjärvi 2004; Diaconu et al., 2016; Giagli et al., 2019; Jones et al., 2024).

In existing studies on softwoods, several other factors affecting wood density have been identified. First, wood density is known to vary depending on site moisture conditions at the growth site. This is generally because site moisture availability from late summer to early autumn promotes the formation of latewood-like tissues—through enhanced cell-wall thickening associated with intra-annual density fluctuations (IADFs)—thereby influencing the density profile within the annual ring (Camarero 2022, 2024). On the other hand, significant variation in wood density among individuals growing under the same environmental conditions suggests that genetic factors may also be involved (Louzada & Fonseca, 2002; Wimmer and Downes, 2003).

In addition, in the process of making baseball bats, free-of-heart-center (FOHC) wood is often used to avoid juvenile wood, which tends to exhibit processing or performance defects due to its heterogeneous physical properties. However, little is known about the transition from juvenile wood to mature wood within the stems of Erman's birch.

Therefore, this study investigates variation in air-dry wood density among

individual Erman's birch trees within naturally regenerated mixed forests in Hokkaido, with particular attention to its spatial association with growth characteristics and site conditions. Within-stem (radial) variation in wood density is also examined to support the interpretation of inter-individual patterns.

The study tests the following two hypotheses regarding Erman's birch wood density:

- (1) There is no relationship with ring width or tree size.
- (2) It shows a negative correlation with site wetness.

Based on these, I discuss the implications for management practices, such as selective removal and thinning, aimed at promoting growth.

3.2 Materials and Methods

3.2.1 Survey and Sampling

The survey was conducted at the Uryu Experimental Forest, Field Science Center for Northern Biosphere, Hokkaido University. The mean annual temperature is 5.0°C, the mean annual precipitation is 1706.7 mm, and the maximum snow depth exceeds 200 cm (10-year averages from 2014 to 2023; <https://www.jma.go.jp/jma/index.html>).

A study plot of approximately 12 ha was established on gentle slopes extending from a ridge to a stream (44°40'N, 142°25'E; elevation 450 m). This stand is a naturally regenerated mixed forest of cool-temperate hardwood and sub-boreal softwood species. Due to past intensive selective logging, sparse openings are observed throughout the stand. Erman's birch (*Betula ermanii*), one of the dominant species, had an average diameter at breast height (DBH: at 1.3 m above ground) of 29.5 (SD = 12.6) cm and a basal area per hectare of 2.8 m², accounting for 18.1% of the total (Table 1). Other dominant species included Japanese oak (*Quercus crispula* Blume; 32.3%) and Sakhalin fir (*Abies*

sachalinensis [F. Schmidt]; 25.2%).

In December 2023, all trees with DBH ≥ 20 cm (including species other than Erman's birch) within the study plot were surveyed. Each tree was assigned an individual identification number (ID), and DBH was measured to the nearest 2 cm using a diameter tape. The x - y coordinates of each tree were recorded using a GPS (Mobile Mapper 100, Ashtech).

From January to April 2024, felling was conducted within the plot (accounting for 40.4% of stand volume). A total of 140 Erman's birch trees were felled at approximately 0.5 m above ground using chainsaws and transported as whole stems with IDs intact using machinery. At the logging landing, discs approximately 5 cm thick were cut from a point 2.5 m from the base (corresponding to 3 m in tree height).

The collected discs were first processed into strip-shaped pieces approximately 5 cm wide, including the pith. After one side of the cross-sectional surface was planed, the cross-sectional surface was scanned at 1200 dpi. Next, each strip was split into two pieces with the pith as the dividing line, and from the pith outward in the radial direction, $30 \times 30 \times 30$ mm specimens were continuously cut (a total of 1,130 specimens) and conditioned at 20°C and 65% relative humidity.

All specimens were weighed, and their volumes were calculated from their length, width, and height to determine air-dry density. The mean ring width of each specimen was calculated by dividing the width of its cross-sectional surface by the number of growth rings present on that surface.

3.2.2 Analysis

To evaluate the variation of wood density within the stem (changes with distance from

the pith), the wood density of the specimens ($n = 1,130$) sampled continuously in the radial direction from the pith for each tree was analyzed. Differences among distance classes at 30 mm intervals from the pith were tested using one-way analysis of variance (ANOVA). When significant differences were detected, Tukey's multiple comparison test was applied to identify which classes differed (significance level: $p < 0.05$). Measurements beyond 270 mm from the pith were excluded from the analysis due to extremely small sample sizes.

To clarify the relative importance of ring width, tree size, and site conditions on wood density and to assess the strength of their direct and indirect effects, structural equation modeling (SEM) was used. For each of the 140 trees, the average wood density obtained from the two specimens closest to the bark was used as the individual representative value. The mean ring width of each specimen was assumed to have a negative direct effect on wood density, whereas DBH was assumed to have a positive direct effect. A covariance between ring width and tree size was also specified, as a relationship between these variables was possible.

Local site moisture conditions were assumed to have a negative effect on wood density. Using the x - y coordinates of each tree, the topographic wetness index (TWI) was calculated in GIS (QGIS) based on a digital elevation model, following the procedure described in Chapter 2, and incorporated into the model. Because site moisture conditions may also influence growth, a path from TWI to ring width was included. Significance was set at $\alpha = 0.05$ for all unstandardized path coefficients.

Model fit was evaluated using χ^2 , the Goodness of Fit Index (GFI), and the Standardized Root Mean Square Residual (SRMR). A non-significant χ^2 value is desirable. GFI ranges from 0 to 1, with values closer to 1 indicating a better-fitting model. SRMR

has a lower bound of 0, with values closer to 0 indicating better fit. Analyses were conducted using R version 4.3.2 (R Development Core Team 2023) with the “lavaan” package (Rosseel 2012).

Additionally, to investigate spatial clustering and patterns of wood density within the stand, Moran’s I was calculated to evaluate spatial autocorrelation (Moran 1950; Duncan and Stewart 1991). Moran’s I was computed in R using the spatial coordinates (x – y) of individual trees. Spatial autocorrelation was evaluated across multiple neighborhood scales by calculating Moran’s I using k -nearest neighbor spatial weights matrices for k ranging from 1 to $n - 1$. Moran’s I ranges from -1 to 1 , where values near 1 indicate strong positive autocorrelation, values near -1 indicate strong negative autocorrelation, and values near 0 indicate no spatial autocorrelation (Moran 1950). Significant positive spatial autocorrelation in wood density may indicate the influence of spatially structured site conditions or, assuming genetic similarity among geographically proximate trees (Viherä-Aarnio and Velling 2017), potential genetic effects on wood density.

3.3 Results

First, regarding changes in wood density within the stem, wood density was lowest in the specimens closest to the pith (distance from the pith = 0–30 mm) and increased significantly up to the 60–90 mm distance class. Beyond this, variation was small and no significant differences were observed (Figure 1).

The mean representative wood density for each tree (closest to the bark) was 666.2 kg/m^3 (SD = 67.8), and the mode was 650 kg/m^3 . The maximum and minimum values were 810.6 and 491.0 kg/m^3 , respectively (Figure 2).

In the structural equation modeling (SEM) explaining the relationships between wood density and each factor, the χ^2 test was not significant ($p > 0.05$), indicating good agreement between the model and the observed data ($n = 140$). Model fit indices were GFI = 0.995 and SRMR = 0.027, indicating an acceptable fit.

SEM results showed that the direct effect of ring width on wood density was not significant, with a standardized coefficient of -0.08 ($p = 0.36$) (Table 2, Figure 3). Similarly, the direct effect of DBH on wood density was not significant (standardized coefficient = 0.11 , $p = 0.18$). In contrast, the direct effect of TWI on wood density had a standardized coefficient of -0.16 ($p = 0.05$), statistical nearly significance.

Spatial autocorrelation of wood density was significant and positive for distance classes $k = 1-86$ (corresponding to average distances of $9.13-375.01$ m), whereas all distance classes beyond $k = 86$ showed no significant autocorrelation (Figure 4). Moran's I generally decreased with increasing distance class.

3.4 Discussion

In this study, the wood density of Erman's birch did not show a significant relationship with ring width or tree size (supporting Hypothesis 1), while it was negatively affected directly by topographic wetness (TWI) (supporting Hypothesis 2). This indicates that wood density is not constrained by growth rate but is directly influenced by the site moisture conditions of the site. Generally, in softwoods and ring-porous hardwoods, growth rate has been reported as a major determinant of wood density (Bergqvist 1998; Bergès 2008; Humar et al., 2008; Bouriaud et al., 2015; Rathgeber 2017). However, in the diffuse-porous Erman's birch, mechanisms determining wood density appear to operate independently of stem growth conditions.

In Japanese birch species (*B. ermanii*, *B. platyphylla*, *B. maximowicziana*), it has been reported that mechanical properties including wood density increase from the pith toward the bark, with the increasing trend slowing beyond approximately 50 mm from the pith (Ohsaki et al., 2019). In this study, wood density increased significantly up to the 60–90 mm distance class from the pith, with little variation beyond this, suggesting the transition from juvenile to mature wood occurred around this distance. The total variation in wood density from pith to bark was less than 100 kg/m³, smaller than that reported for other species (Kimberley et al. 2015), consistent with the finding that wood density was not influenced by tree size. Thus, Erman's birch forms relatively homogeneous wood radially, making it easier to handle compared with species exhibiting large wood property variations.

Approximately 90% of Erman's birch trees examined in this study had wood densities suitable for general baseball bats (550–750 kg/m³), with about 30% within the range suitable for professional bats (around 700 kg/m³) (Tomita et al., 2020). This suggests that many trees in the studied stand may be suitable for use as baseball bats. However, representative wood densities showed considerable individual variation. The difference between the maximum and minimum values exceeded 300 kg/m³, indicating substantial within-stand variability. Although previous studies on other birch species reported similarly large ranges in wood density (differences of approximately 200–300 kg/m³ between minimum and maximum values) (Lachowicz et al., 2019; Dobrowolska and Krzosek 2025), their results were based on multiple stands across broader geographic areas and are not directly comparable. Nevertheless, these studies suggest that the occurrence of high-quality trees is largely random and not associated with geographic distribution or large-scale environmental gradients (Lachowicz et al., 2019).

The negative direct effect of TWI on wood density indicates that local site moisture conditions associated with microtopography directly influence wood-density formation. Previous studies have shown that seasonal moisture availability, particularly from summer to autumn, affects latewood production and therefore wood density in softwoods (Zalloni et al., 2016; Camarero et al., 2022). However, comparable evidence for diffuse-porous hardwoods remains limited. In the study area, TWI values ranged from 7.0 (lower slope) to 2.5 (ridge), corresponding to an estimated wood density difference of approximately 45 kg/m³ based on the unstandardized coefficient (−10.0). This corresponds to roughly two-thirds of the observed stand-level variation (SD $\approx$ 68 kg/m³), indicating that microtopography-driven differences in site moisture conditions have a substantial effect on wood formation.

Furthermore, wood density showed significant positive spatial autocorrelation across a broad range of distance classes ($k = 1\text{--}86$; corresponding to average distances of 9.13–375.01 m), indicating that nearby trees tend to have similar wood density. This pattern, with strong similarity at short distances that gradually weakens with increasing distance, is consistent with the SEM results showing the influence of local site moisture conditions. Genetic relatedness among spatially proximate trees may also contribute to the observed autocorrelation, although previous trials with birch from multiple geographically distant provenances suggest that genetic effects on wood density are likely small (Viherä-Aarnio and Velling 2017).

At a finer scale, soft X-ray densitometry of *Betula platyphylla* wood has indicated higher density at annual ring boundaries (Ohsaki, personal communication), suggesting a potential negative correlation between ring width and wood density. However, individual variation in wood density is influenced by multiple wood structural

traits, including cell wall thickness, vessel diameter, and vessel fraction. Future work clarifying the relationships between these fine structures and wood density will help elucidate how site moisture conditions affect wood formation.

3.4.2 Implication for silvicultural management

This study revealed that local-scale environmental factors, such as site moisture conditions determined by microtopography, play a more important role in influencing the wood density of Erman's birch than individual growth rate or tree size. The fact that wood density is not constrained by growth rate suggest. On the other hand, the observation that wood density is higher in drier sites than in wetter sites suggests that such site-related differences in wood properties could be considered in silvicultural planning. For example, drier sites such as ridges may be more suitable for producing higher-density wood, which is generally preferred for certain high-value applications, whereas wetter lower slope positions may be better suited for volume-oriented timber production.

Furthermore, for use as baseball bat material, fine structures such as grain angles and microfibril angles are also important factors (Tomita et al., 2020) and are known to be related to catastrophic multi-piece failures (MPF) of bats (Drane et al. 2012). This study focused on the basic property of wood density, but clarifying the relationships between these wood properties and growth environment or site conditions is expected to facilitate wood selection and silvicultural planning for specific applications.

3.5 Tables

Table 1. Stand composition and density of tree species in the study plot (12 ha), showing the number of stems per hectare, mean basal area per hectare, and mean diameter at breast height (DBH) with standard deviations.

Species	Number of stems per hectare	Basal area per hectare (m ² /ha)	mean diameter at breast height (cm) ± standard deviation
<i>Quercus crispula</i>	19.9	5.0	48.2 ± 29.9
<i>Abies sachalinensis</i>	31.8	3.9	37.0 ± 13.4
<i>Betula ermanii</i>	34.9	2.8	29.5 ± 12.6
<i>Tilia japonica</i>	10.8	1.1	33.3 ± 12.8
<i>Acer pictum</i>	14.0	1.0	28.1 ± 9.6
others	27.8	1.7	26.2 ± 9.0
sum	139.2	15.4	33.4 ± 17.2

Table 2. Estimated effects of each factor on wood density, standardized coefficients, and *p*-values from structural equation modeling (SEM).

Path	Estimate	Standardized coefficients	<i>p</i>-values
Wood density ←			
Annual ring width	−11.348	−0.077	0.362
TWI	−10.043	−0.162	0.051
DBH	0.838	0.112	0.180

3.6 Figure

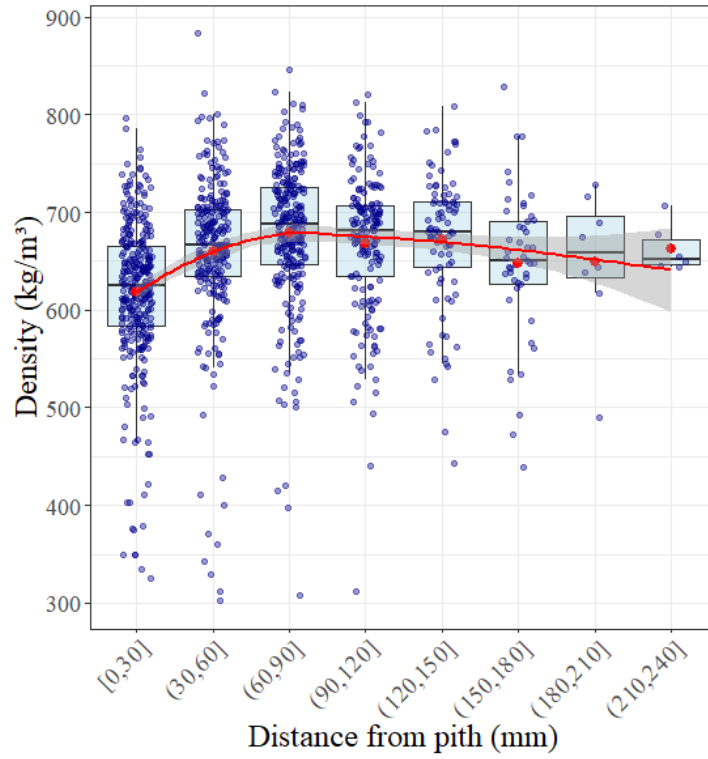


Figure 1. Changes in wood density with distance from the pith in individual *Betula ermanii* trees. Hollow points represent wood density for each tree at each distance class; red points and horizontal bars within the boxes indicate the mean and median, respectively, for each distance class. The red line shows the fitted curve of wood density against distance from the pith.

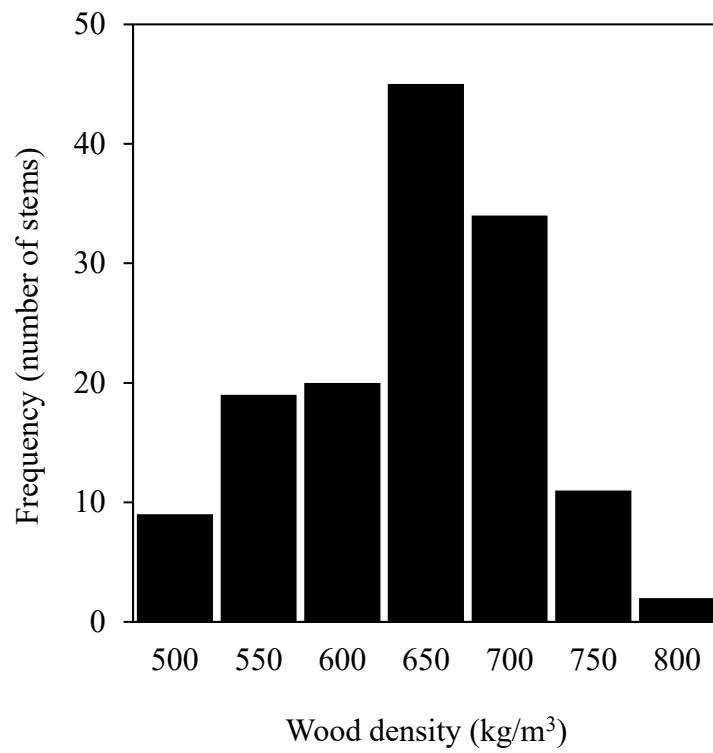


Figure 2. Frequency distribution of wood density near the bark (representative values for individual *Betula ermanii* trees).

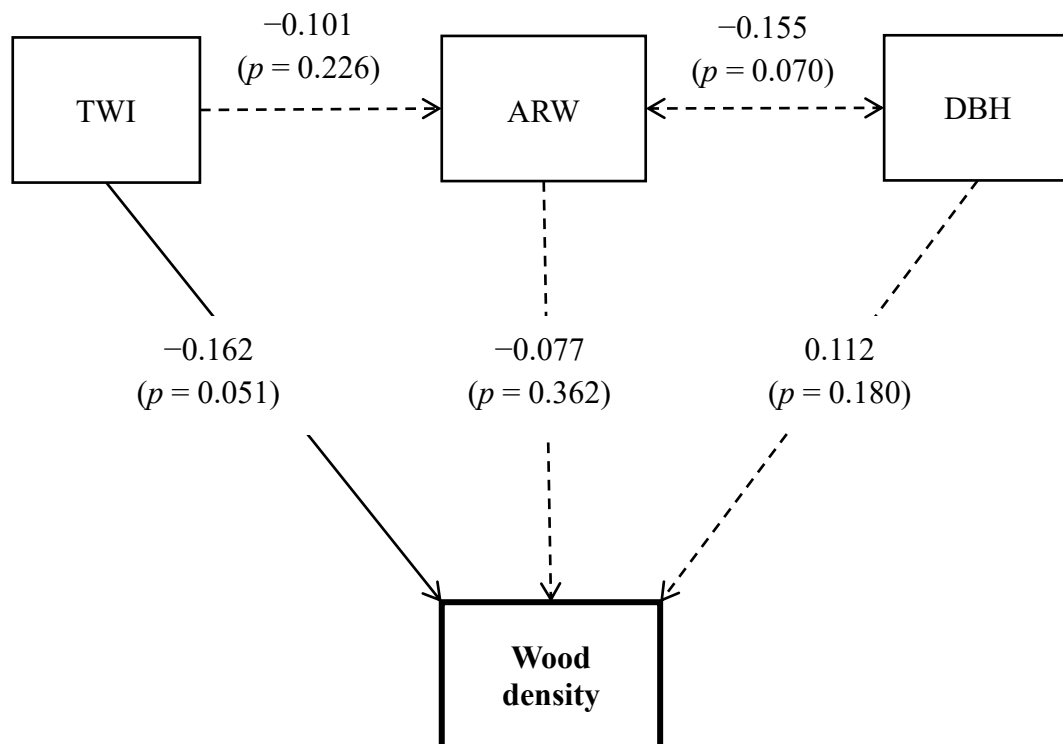


Figure 3. Relationships between wood density (representative values) and ring width, tree size, and site characteristics in individual *Betula ermanii* trees. Solid arrows indicate significant effects; dashed arrows indicate non-significant effects. Numbers on the arrows represent standardized coefficients and p -values. TWI: topographic wetness index, ARW: annual ring width, DBH: diameter breast height (tree size)

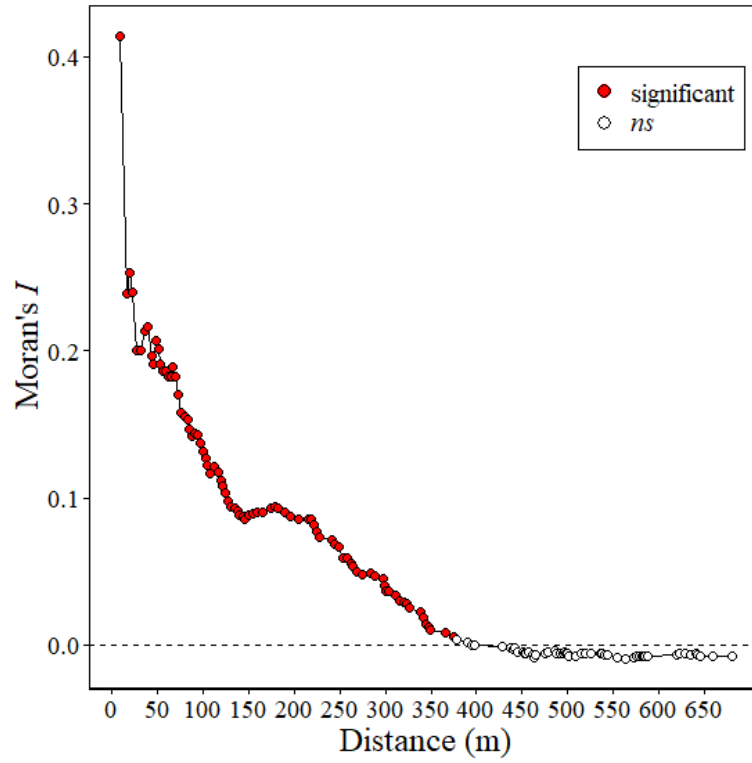


Figure 4. Correlogram of Moran's I for wood density. Moran's I values are plotted against the actual mean distance corresponding to k , showing the spatial autocorrelation of wood density. The dots indicate the values of Moran's I at each distance. The dashed horizontal line represents Moran's $I = 0$, which serves as the baseline for no spatial autocorrelation. Moran's I was significant at distance class from $k = 1$ to 86.



Chapter 4

Figured wood occurrence in *Acer pictum* is related to tree form

4.1 Introduction

Many hardwood species are produced from natural forests, yet appropriate silvicultural methods for their management are often underdeveloped (Puettmann et al., 2015; Schütz et al., 2016). Recently, demand for hardwood logs is increasing on a global scale (Acker 2021), highlighting the urgent need for effective silvicultural practices to ensure a consistent and sustainable supply. However, many variable hardwood species are generally more difficult to control in terms of tree form and take longer to grow than softwood species, making it challenging to achieve profitability that offsets high silvicultural costs. Therefore, several studies have proposed taking advantage of certain wood characteristics that significantly increase the unit price of hardwood logs (Bragg et al., 1997; Bragg 2006; Quambusch et al., 2021). One such feature is “figured wood”—a valued aesthetic trait long utilized in high-end furniture, fine crafts, and musical instruments. Figured wood refers to a decorative pattern in which the wood grain is irregularly arranged (Bäucker and Liesebach 2018; Sarvašová et al. 2021) and can be classified into several types, such as wavy, curly, and birdseye (Figure A1). In this study, the term “figured wood” refers specifically to wavy and birdseye figures, which are caused by local variations in fiber grain orientation (Bragg et al., 1997; Bäucker and Liesebach 2018; Quambusch et al., 2021). The larger the proportion of figured area on a board, the higher its decorative value, and when figure appears throughout an entire log,

its value can reach several to dozens of times the normal market price (Bragg 2006; Krajnc et al. 2015; Quambusch et al. 2021). Bragg et al. (1997) reported that in northern North America, sugar maple (*Acer saccharum* Marsh.) can nearly double overall revenue if less than 1% of the harvested logs contain high-quality birdseye figure. Consequently, identifying and retaining more trees with these characteristics, combined with silvicultural practices such as thinning, may help enhance the profitability of hardwood forest management.

Figured wood such as wavy and birdseye in maple species (*Acer* spp.) is generally attributed to abnormal growth or complex grain patterns (Bragg et al., 1997; Bäucker and Liesebach 2018; Quambusch et al., 2021). Several studies have reported that its development is associated with factors such as reduced vigor and distortion in tree form, which in turn lead to irregular growth and grain anomalies (Bragg et al. 1997; Bragg 2006; McKenna et al., 2015). Although the detailed anatomical mechanisms differ among types of figures, they may share common underlying physiological or morphological conditions that disturb cambial activity and fiber orientation. Tree form distortion, an observable external characteristic, is believed to promote the formation of reaction wood along the stem, contributing to the development of various types of figured wood (Panshin et al., 1980; McKenna et al., 2015). It has also been suggested that larger trees are more likely to develop figured wood because they are thought to have been exposed to competition and stress from the surrounding trees for a relatively long period of time (Bragg et al., 1997). In other words, denser stands experience stronger competition, which promotes the formation of figure (Pillow 1955; Bragg 2006). Environmental and genetic factors are also thought to play important role in its expression (McKenna et al., 2015; Kärkkäinen et al., 2017; Quambusch et al., 2021). However, it is not easy to accurately

evaluate the factors causing the occurrence of figured wood, and previous studies have each considered only a single factor. Therefore, there is not enough evidence to explain whether figured wood can be controlled through forest management and how silviculture affects the appearance characteristics that are important in determining which tree is harvested or retained. It is essential to quantitatively link the amount of figured wood to multiple characteristics of individual standing trees (Quambusch et al., 2021).

In recent years, the Japanese wood market has reached a major turning point by breaking away from an import dependency and seeing an increasing demand for domestic hardwood (Shimase 2024). Despite the increasing momentum to enhance domestic hardwood production, a sustainable silvicultural system has yet to be established to support this transition. Painted maple (*Acer pictum* Thunb. (Wesm.) H.Ohashi,) is one of the dominant tree species comprising the natural mixed forests of northern Japan (Takahashi 2017), and its wood is used for furniture, flooring, and musical instruments. Similar to other maple species in the Northern Hemisphere (Krajnc et al., 2015), it attracts considerable interest from both producers and users due to the potential for high-value wood. The frequency of standing trees with figured characteristics is unknown, and the causes of figured wood formation in *Acer pictum* have not yet been studied. The aim of this study was to examine how tree characteristics of individual *Acer pictum* trees—such as stem crookedness, fork height, mean annual ring width, and individual size—affect the occurrence of wavy and birdseye figured wood, and to evaluate the relative strength of these factors. Specifically, this study investigated whether stem crookedness promotes figured wood occurrence (hypothesis 1), whether fork increases its occurrence (hypothesis 2), whether wider annual rings reduce it (hypothesis 3), and whether larger trees tend to develop more figured wood (hypothesis 4). I also analyzed whether the

occurrence of figured wood forms spatial clusters.

4.2 Materials and methods

4.2.1 *Study site*

The trees were harvested in the Uryu Experimental Forest, Field Science Center for Northern Biosphere, Hokkaido University, Japan. The forest experiences a mean annual temperature of 5.0 °C and annual precipitation of 1,707 mm (Japan Meteorological Agency, 10-year average from 2014–2023; <https://www.jma.go.jp/jma/index.html>), with maximum snow depth exceeding 200 cm at the peak of winter each year.

The dominant vegetation is an uneven aged natural mixed forest composed of cool-temperate hardwood and sub-boreal softwood species. In January 2021, a 16.8-ha study site was established on a gentle slope extending from a ridge to a small stream (44°40'N, 142°25'E, 450 m above sea level). The stand was relatively open because it had been partially and heavily harvested approximately 70 years ago.

4.2.2 *Tree measurements and sampling*

In April 2021, all standing trees with DBH $\geq$ 20 cm within the study site were measured, including non-maple species. Each living tree was tagged for individual identification. DBH was measured in 2-cm intervals using a caliper, and each tree's location (x - y coordinates) was recorded using a GPS device (Mobile Mapper 100, Ashtech). *Acer pictum*, the target species of this study, had a mean diameter at breast height (DBH, 1.3 m above ground) of 30.3 (SD = 10.4) cm. The mean basal area per tree was 0.09 m² (SD = 0.07), and this species accounted for 9.8% of the total stand basal area. Other dominant species included *Quercus crispula* Blume (29.1%), *Abies sachalinensis* (24.6%), and

Betula ermanii Cham. (19.0%) (Table 1).

Tree form characteristics of *Acer pictum* were documented as follows: stem crookedness (SC) was assessed using a straight 2 m pole placed along the stem surface between 1 and 3 m above ground. The lower end of the pole was positioned at 1 m height on the stem. Because the stem deviates from a straight line, a gap appears between the pole and the stem surface. The maximum width of this gap within the 1-3 m section was measured to the nearest 5 cm and used as an index of stem crookedness (Figure 1). Fork height (FH) was measured using photographs of the entire tree, including a red-and-white pole marked in 20 cm increments, taken from the side that allowed the fork to be most clearly visible while avoiding obstruction by neighboring trees. On the photographs, the lowest branch exceeding half the diameter of the main stem was defined as the fork, and its height was recorded in 20-cm increments, taking into account the snow depth around each tree.

Tree felling was conducted from January to April 2022, removing 66% of the stand volume. Trees were cut using a chainsaw at 0.5 m above ground. Logs were transported to the log yard with a bulldozer while maintaining their individual identification numbers. From each tree, 60 logs of 0.3 m length were collected at a height of 2.7-3.0 m above ground (corresponding to the upper part of the 1-3 m stem section), and figured wood was evaluated in these logs.

4.2.3 Identification of figured wood

Sawing was performed using a basic sawmill setup, consisting of a chainsaw (STHIL MS500i) mounted on a frame made of clamped pipes. Logs were first split longitudinally through the pith to produce two half-logs. From each half-log, a single 5-cm-thick board

was sawn parallel to the radial plane. This resulted in two boards per log, yielding a total of 120 boards. The surfaces of the boards were planed using an automatic planer (P100RL, HiKOKI) to achieve smoothness. The boards were then sanded with an electric sander until wood grain was clearly visible (electric sander: BDS-1000, RYOBI), and the surface of each board was photographed under consistent lighting conditions (camera: D750, Nikon Co.; Lens: AF-S NIKKOR 18-35 mm f/3.5-4.5 GED).

The photographs of the boards were first binarized to monochrome after adjusting the white balance to a constant (using NX Studio; https://www.nikon-image.com/products/software_app/lineup/nx_studio/), allowing the surface shading of the boards to be represented as gray value (GV). Lower GV values indicate lighter (whiter) areas, while higher values indicate darker (blackier) areas (Figure 2). Because the absolute brightness of the images depended on relative lighting and camera conditions, GV represents relative rather than absolute shading differences. However, the entire image processing procedure can be replicated following the same workflow and software settings, ensuring methodological reproducibility. Figured wood areas were identified by relatively large, fine-scale fluctuations in GV (Figure 2). In this study, any 2 cm grid showing a GV variation (difference between the maximum and minimum GV values within the grid) of 10 or more was classified as containing figured wood. The proportion of the surface area exhibiting wavy and birdseye figured wood, relative to the total board surface area, was used as the index for the proportion of figured wood (PFW). All boards were 30 cm in length, with widths ranging from 24.1 to 48.2 cm. The surface area ranged from 396 to 1968 cm², respectively, with an average of 997.3 (SD = 328.0) cm². However, if a grid showed GV variation ≥ 10 but was clearly identified by visual inspection as discoloration, decay, or other non-figured features, it was excluded from the figured wood

area. The threshold of 10 GV was determined using three randomly selected boards (see appendices for details; Figure A2).

PFW of wavy and birdseye for each individual tree was calculated as the average of the two boards prepared. Additionally, the number of annual rings from pith to bark was counted on the boards where figured wood was measured (average number of rings was 63.9, SD = 16.3), and the average annual ring width (ARW) was calculated. As previously noted, various types of figured wood exist.

4.2.4 Statistical analysis

The relationship between PFW and distance from the pith was evaluated using simple linear regression, with distance measured in 2-cm intervals. Here, “distance from the pith” refers to the distance from the former pith position, corresponding to the inner edge of each board. This is because the analyzed tangential surfaces did not contain anatomical pith, as each board was sawn through it. Statistical significance was assessed at a significance level of $\alpha = 0.05$.

I performed structural equation modeling (SEM) to determine the strength of direct and indirect effects of each factor (stem crookedness, fork height, basal area at breast height, annual ring width) on PFW (proportion of figured wood). SEM was used because it allows simultaneous estimation of direct and indirect effects among multiple variables, accounts for measurement error, and enables testing of theoretical causal hypotheses regarding figured wood formation. SEM can be generally expressed as:

$$\eta = B\eta + \Gamma\xi + \zeta$$

where η represents endogenous variables, ξ exogenous variables, B and Γ are path coefficient matrices, and ζ residuals (Bollen and Noble 2011). A hypothetical model was developed, incorporating insights from previous studies (Figure 3). As tree form distortion is thought to influence grain orientation, I assumed that SC (stem crookedness) would have a positive, and FH (fork height) a negative, direct effect on PFW. A negative effect from FH to ARW was also assumed, because trees with high FH can be considered to have smaller, elevated crowns due to competitive interactions with surrounding trees. Since individual size was assumed to have a positive effect on figured wood occurrence, a direct positive path from basal area at breast height (BA) was set. Because BA and ARW are biologically related traits, I incorporated their relationship into the SEM by specifying a covariance between them. Given that figured wood is believed to result from low vigor, I hypothesized that ARW would have a negative direct effect on PFW. I applied different transformation functions depending on the distribution characteristics of each variable. PFW values, being proportions bounded between 0 and 1, were transformed using the arcsine square root function to stabilize variance. Other variables (SC, FH, BA, ARW) exhibited positively skewed distributions, so natural logarithm transformations were applied to reduce skewness and improve linearity for SEM. These transformations were chosen to meet the assumptions of SEM and to obtain reliable parameter estimates. Furthermore, I applied robust estimation methods that provide reliable corrections for deviations from normality (Rossel 2012; Ibrahim and Mohammed 2020). These methods yield dependable estimates even in the presence of outliers or non-normal distributions that could impact estimation techniques (e.g., maximum likelihood and least squares methods). For all unstandardized path coefficients, the significance level was set at a risk rate below 5%. Since SEM is a statistical tool used to test theoretical hypotheses,

nonsignificant paths were retained in the model (Laughlin and Fulé 2007; Lam and Mguire 2012).

The evaluation of SEM was based on fit indices, including p -values and standard errors, for individual path coefficient tests. In contrast, overall model fit was assessed using the Chi-square test (χ^2), the goodness-of-fit index (GFI), and the standardized root mean square residual (SRMR). A nonsignificant χ^2 result is preferred, indicating a better fit between the model and observed data. GFI values range from 0 to 1, with values closer to 1 indicating a better model fit. An SRMR value below 0.09 is considered indicative of a good model fit (Hu and Bentler 1999; Fan et al. 2016). The SEM analysis was conducted using the “lavaan” package (Rosseel 2012) in R version 4.3.2 (R Development Core Team 2023).

To evaluate the spatial structure of figured wood (PFW) within the stand, I calculated Moran's I to quantify the degree of spatial autocorrelation among individual trees. Moran's I measures whether observations at closer geographic distances are more similar (positive autocorrelation) or more dissimilar (negative autocorrelation) than expected by chance (Moran 1950; Duncan & Stewart 1991; Šilhán 2021; Zevgolis 2022). The statistic ranges from -1 to 1 , with values near 1 indicating strong positive autocorrelation, values near -1 indicating strong negative autocorrelation, and values around 0 indicating no autocorrelation. Spatial weights were defined based on k -nearest neighbors, where k ranged from 1 to 57 (58 individuals, excluding outliers). For each value of k , the average Euclidean distance between a focal tree and its k nearest neighbors was calculated to define distance classes. Moran's I was then computed for each k -distance class to assess whether PFW values were spatially clustered, dispersed, or randomly distributed at different neighborhood scales.

4.3 Results

Figured wood was present in 87% of the study trees (52 out of 60 individuals; Figure 4). The wavy type was the most common, observed in 70.8% of individuals with figured wood, while the birdseye type was also noted (10.4%), including cases where both types co-occurred (18.8%). The area of the figures on the board ranged from 4 to 196 cm², with an average of 42.3 (SD = 51.1) cm². The mean PFW was 7.0% (SD = 9.8%), with a maximum value of 46.2% (Table 2). The most frequent PFW class was 1% to 10%, accounting for 65% of all study trees, while only 5% of the trees had a PFW of 31% or more (Figure 4).

Considerable intra-individual variations were observed within each distance class (Figure 5), indicating that even at the same radial distance, the proportion of figured wood varied substantially among individual trees. Nevertheless, in total, a weak negative relationship was found between the distance from the former pith line and PFW ($R^2 = 0.031$, $p < 0.001$), showing that the proportion of figured wood tends to decrease from the pith outward.

SEM analysis explaining the relationship between PFW and each factor showed that χ^2 value was rejected with $p = 0.270$, indicating that the model was in good agreement with the observed data ($n = 60$). The value of the model fit metrics was 0.965 and 0.079 for GFI and SRMR, respectively; they generally indicated statistically acceptable solutions. The model also explained approximately 38% of the variance in the PFW ($R^2 = 0.381$).

The SEM results indicated that the direct effect of stem crookedness (SC) on PFW was 0.668 (standardized coefficient = 0.375, $p = 0.002$), which was the largest

among all standardized direct effects (Table 3, Figure 6). Fork height (FH) had a significant negative effect on PFW, with a direct effect of -0.088 (standardized coefficient = -0.308 , $p = 0.013$), representing the second largest standardized direct effect. Additionally, FH had a significant negative effect on ARW (estimate = -0.278 , standardized coefficient = -0.308 , $p = 0.005$), indicating that taller forks were associated with slightly narrower annual rings. However, the effect of FH on PFW via ARW was very small and non-significant (estimate = -0.006 , standardized coefficient = -0.022 , $p = 0.887$). The direct effects of average annual ring width (ARW) and basal area (BA) on PFW were not significant (ARW: estimate = 0.022 , standardized coefficient = 0.071 , $p = 0.548$; BA: estimate = -0.004 , standardized coefficient = -0.020 , $p = 0.856$). A strong positive covariate relationship was found between BA and ARW (estimate = 0.069 , standardized coefficient = 0.436 , $p = 0.002$).

Moran's I value for PFW was non-significant at all distance class ($k = 1-57$; $28.6-567.8$ m, $p > 0.05$, Figure 7), suggesting that there is no spatial autocorrelation in PFW.

4.4 Discussion

Many of the trees (87%) exhibited some type of figured wood—wavy, birdseye and mixed with both—yet the mean PFW (proportion of figured wood) in the sample boards was relatively low, at just 7.0% (SD = 9.8%) (Figure 4). In addition, a previously unreported pattern was found through radial analysis of PFW, showing a decrease in PFW with increasing distance from the pith (Figure 5). In this study, I conducted an integrated analysis of the factors influencing PFW in individual standing *Acer pictum* trees. Our results revealed that tree form, specifically SC and FH are more important than other

factors. (Figure 6; Table 3).

Although the demand for figured wood of *Acer pictum*, particularly for furniture and musical instruments, is high, its frequency of occurrence in natural stands has remained unclear. In this study, 87% of the sampled trees exhibited some degree of figure. However, the extent of figured wood within individual stems was generally limited: most trees had PFW values below 10%, and the maximum observed value was 46.2%. While a higher proportion of figured wood is expected to enhance commercial value, only a small fraction of trees exhibited extensively figured surfaces. For example, only 5% of the trees showed PFW values exceeding 30% (Figure 4). Previous studies on sycamore maple (*Acer pseudoplatanus* L.) reported that the frequency of trees producing commercially valuable wavy-figured wood is relatively low (approximately 1–7%) (Krajnc et al. 2015; Bäucker and Liesebach 2017; Quambusch et al. 2021). Although these studies relied on visual and market-based criteria rather than quantitative measures such as PFW, the low proportion of extensively figured individuals observed in the present study suggests a similarly limited availability of high-value figured wood in *A. pictum*.

SEM analysis results supported hypothesis 1, showing a significant positive direct effect of SC on PFW (Figure 6; Table 3). FH also had a significant negative effect (supported hypothesis 2), reinforcing its importance. Our model explained 38% of the variation in PFW, and I found that most of this explained variation was attributable to these aspects of stem form. Interpreting the SEM estimates in the original scale, an increase of 1 cm in SC was associated with an approximate 0.610% increase in PFW. An increase of 100 cm in FH, on the other hand, corresponded to an approximate 1.874% decrease in PFW. These findings suggest that portions of the tree with greater deviations in stem form are more likely to develop figured wood due to irregular grain orientation

(Beals and Davis 1977). Since both SC and FH are associated with the formation of reaction wood (Shimaji 1983; Du and Yamamoto 2007; Jiangtao and Jian 2015), it is likely that observed figured wood resulted from this physiological response (Panshin et al. 1980; McKenna et al. 2015).

These changes quantify the effects of SC and FH on the occurrence of figure wood within the range of this study tree in actual units and realistic values. These results suggest that variation in stem form and local stem deformations may be related to figure wood formation in *Acer pictum* and are broadly consistent with previous observations regarding the influence of stem deviation and crook formation on grain orientation (Beals and Davis, 1977; Panshin et al. 1980; McKenna et al. 2015).

In the present study, the effect of ARW on PFW was minimal and not statistically significant and therefore did not support hypothesis 3 (Figure 6; Table 3). This result indicates that the occurrence of figured wood is more closely related to local variations in stem geometry and associated mechanical stress, rather than to the long-term radial growth rate. In other words, irregularities in cambial activity and grain orientation may develop independently of growth vigor, suggesting that physiological responses to mechanical stimuli, rather than slow growth itself, play a dominant role in figure formation (Beals and Davis 1977).

Larger individuals are often subject to prolonged competition and environmental stress, which may result in abnormal growth patterns and irregular grain orientation (Bragg et al. 2015). Based on this premise, we hypothesized that basal area (BA) would positively influence the proportion of figured wood (PFW). However, the effect of BA on PFW was not statistically significant, and hypothesis 4 was therefore not supported (Figure 6; Table 3). In contrast, a significant decrease in PFW with increasing

distance from the pith was observed within individual trees (Figure 5), indicating that figured wood is more frequently formed in the inner, younger portions of the stem. Similar radial trends have been reported in several tree species, including maple, beech, oak, and various tropical species, where wood density is generally higher during early growth stages and decreases toward the outer stem (Plourde et al. 2015; Purba et al. 2021; Sedlar et al. 2021). In addition, regions exhibiting figured wood have been reported to possess higher wood density than non-figured areas (Stanciu et al. 2015), and wood properties such as grain orientation are often unstable during early growth stages (Purba et al. 2021). Taken together, these findings suggest that figured wood formation may be favored in the juvenile wood zone, where higher density and unstable grain orientation are more prevalent. Although our data set is subject to potential survivorship bias, as it consists only of trees that survived to the sampled size ($\text{DBH} \geq 20 \text{ cm}$), the present results nonetheless suggest that, as trees increase in girth, areas devoid of figured wood become more prevalent, thereby reducing the overall proportion of figured wood within the stem.

The absence of significant spatial autocorrelation in PFW indicates that figured wood does not exhibit clear spatial structuring at the stand level. This suggests that neighboring trees are not more similar in PFW than expected under a random spatial distribution. In natural forest stands, geographically proximate individuals may experience similar microenvironmental conditions or exhibit elevated genetic relatedness due to limited seed and pollen dispersal (Manel et al. 2003; Vekemans and Hardy 2004; Seidler and Plotkin 2006). If such environmental or genetic factors strongly governed the proportion of figured wood, spatial clustering would be expected. The lack of a detectable spatial signal in our analysis suggests that these factors either exert only weak or highly localized effects on PFW, or that the spatial resolution and sample size of this study were

insufficient to detect such patterns.

Nevertheless, previous studies have shown that both environmental and genetic factors can influence figured wood occurrence (McKenna et al. 2015; Bäucker and Liesebach 2018; Quambusch et al. 2021). The discrepancy between these findings and our results may be due to the relative environmental uniformity of our study site, as well as the fact that prior research involved genetically distinct individuals, whereas our study focused on a single stand with likely limited genetic variation. Future studies using sites with greater environmental variability and population genetic approaches are needed to clarify the relative importance of genetic and environmental factors in the development of figured wood.

4.4.2 Implication for silvicultural management

This chapter clarified the relationship between the occurrence of figured wood in *A. pictum* and the growth characteristics of individual trees. Our finding that tree form characteristics—such as stem crookedness (SC) and fork height (FH)—significantly affect the proportion of figured wood (PFW) suggests that silvicultural practices, particularly those that regulate stand density, may influence figured wood formation in a long term. Moreover, since growth promotion does not adversely impact PFW, thinning is unlikely to hinder the development of figured wood. However, this does not entirely rule out the possibility that rapid growth induced by intensive thinning could affect figured wood formation, as such growth may cause irregular fiber orientation or changes in stem form that differ from long-term growth patterns (Pape 1999; Tavankar et al. 2021). Generally, when surrounding tree density is low, SC tends to increase, while FH tends to decrease in a long-term (Itô et al. 1997; Li et al. 2016). Therefore, intensive thinning that

supports the development of a wide canopy may be effective for producing high-PFW timber. Additionally, trees with pronounced stem crookedness or low fork height are often viewed as inferior and typically removed during thinning. However, selectively retaining some of these trees may help cultivate a higher-value stand in the long term. This finding implies that revising conventional silvicultural practices—particularly the selection criteria used in thinning—could expand options for improving stand profitability. Importantly, thinning is not categorically beneficial for figured wood occurrence; its effectiveness depends on which trees are selected and which thinning strategies are applied. Finally, when processing harvested trees, incorporating curved sections in logs may create opportunities to produce high-value timber. Forked sections could also potentially yield high-value timber; however, due to increased transportation costs and processing difficulties, they are unlikely to be practical as a main harvesting target and may be best considered as a special, optional source.

4.5 Tables

Table 1. Tree species composition in the study stand of a secondary forest. All trees with a diameter at breast height (DBH) of 20 cm or larger were surveyed.

Species	Density (stems/ha)	Basal area (percentage of total stand basal area: m ² /ha)	Mean DBH (standard deviation: cm)
<i>Acer pictum</i>	11.0	0.9 (9.8%)	30.3 (10.4)
<i>Quercus crispula</i>	7.4	2.6 (29.1%)	56.4 (36.3)
<i>Abies sachalinensis</i>	15.6	2.2 (24.6%)	40.2 (10.4)
<i>Betula ermanii</i>	19.0	1.7 (19.0%)	31.0 (10.4)
Others	22.2	1.6 (17.5%)	28.5 (9.6)
Total	75.2	9.0 (100%)	34.6 (18.2)

Table 2. Mean, standard deviation, and range of observed variables for *Acer pictum* Thunb. individuals.

Observed variable	Description	Mean and (standard deviation)	Range
PFW (%)	The figure wood area to the board surface area	7.0 (9.8)	0.0–46.2
BA (m ²)	Basal area calculated from DBH for individual	0.09 (0.07)	0.03–0.45
FH (cm)	Fork height for individual	398.0 (116.0)	100–660
ARW (mm)	Average annual ring width for individual	4.6 (1.4)	1.8–7.8
SC (cm)	Tree stem crookedness at 1–3 m for individual	4.6 (6.1)	0–25

Table 3. Estimated effects of structural equation modeling, along with corresponding standard errors. *Z* values and *P* values (see Figure 6). The direct effects are indicated with “→”, and the covariance is indicated with “~~”.

Path	Estimate	Standard error	<i>Z</i> value	<i>P</i> value	Standardized coefficients
BA → PFW	−0.004	0.021	−0.181	0.856	−0.020
FH → PFW	−0.088	0.035	−2.490	0.013	−0.308
SC → PFW	0.668	0.211	3.170	0.002	0.375
ARW → PFW	0.022	0.037	0.600	0.548	0.071
FH → ARW	−0.278	0.100	−2.788	0.005	−0.308
BA ~~ ARW	0.069	0.022	3.093	0.002	0.436

4.6 Figures

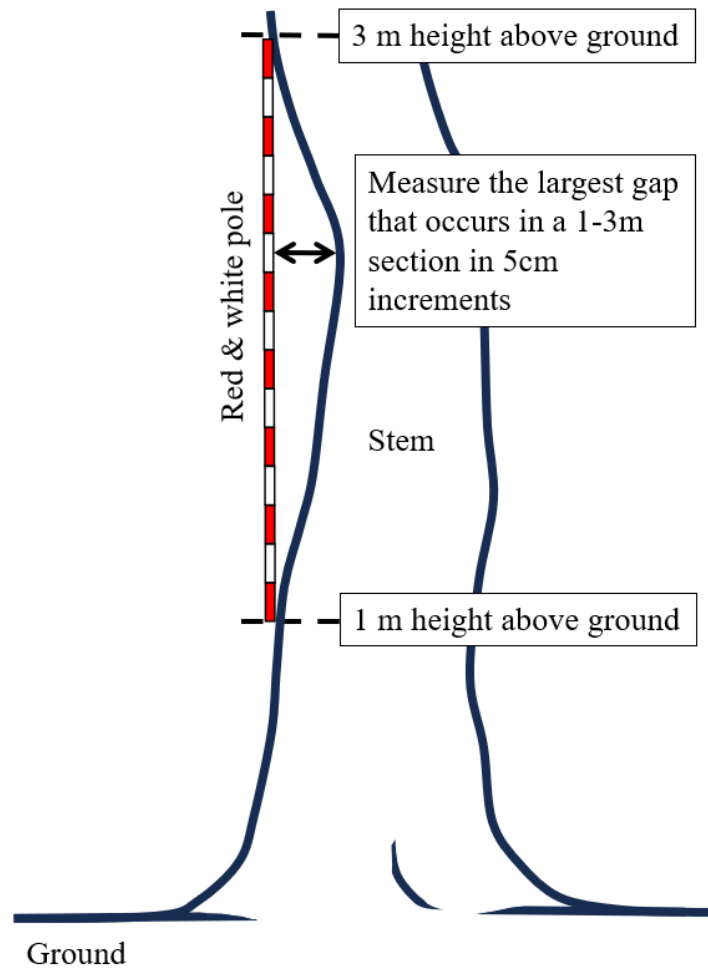


Figure 1. Illustration of how to measure stem crookedness (SC).

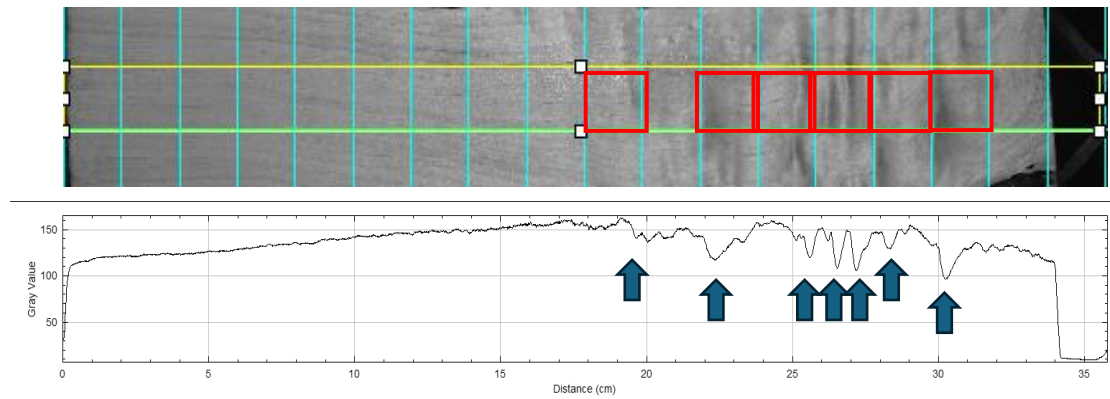


Figure 2. Example of the measuring the proportion of figured wood (PFW) in individual trees using Image J. One 2×2 cm grid showing a change in gray value (GV) of 10 or more was classified as containing figured wood (red squares). The proportion of these areas relative to the total target area was calculated as PFW. Arrows indicate regions identified as figured wood.

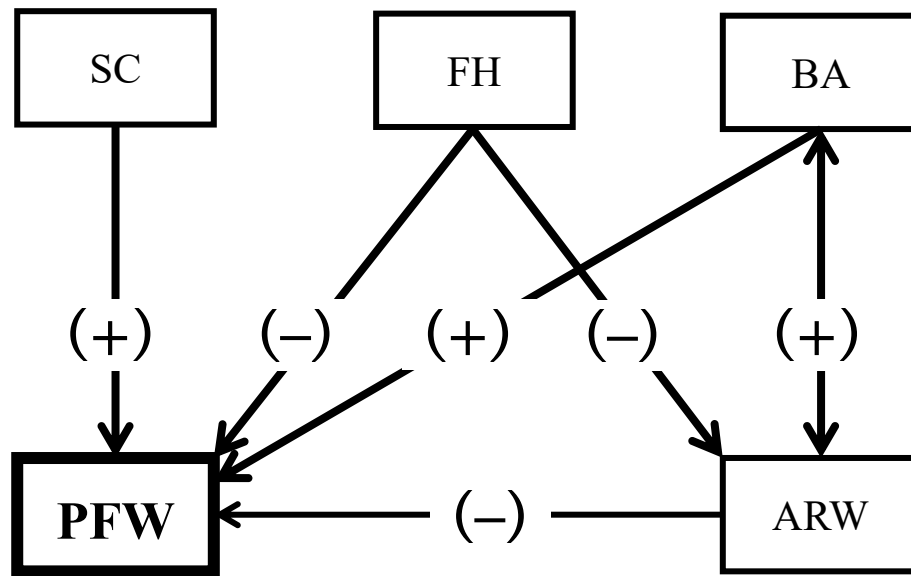


Figure 3. Hypothetical model explaining the proportion of figured wood (PFW). Direct and indirect pathways of each factor influencing PFW are shown. The signs (+ or -) indicate the expected direction of each relationship. SC: stem crookedness, FH: fork height, BA: basal area, ARW: annual ring width.

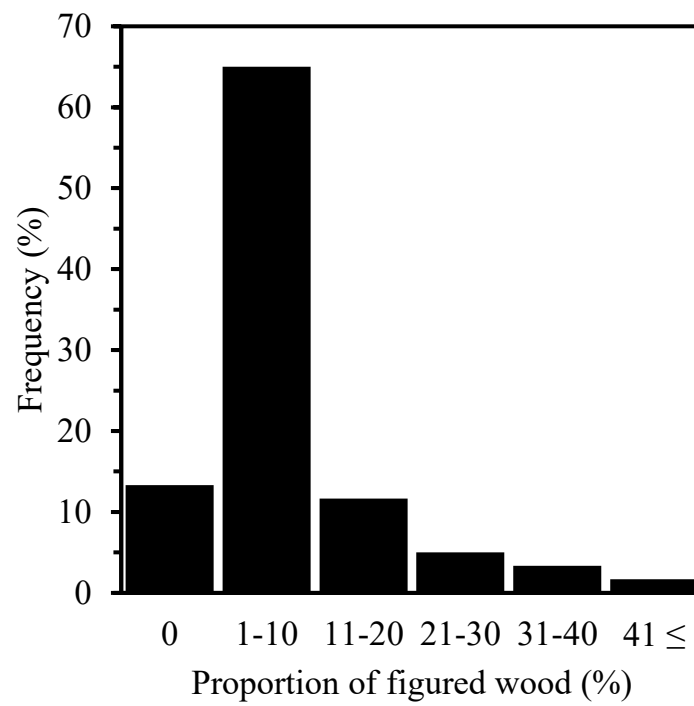


Figure 4. Frequency distribution of the proportion of figure wood (PFW) for *Acer pictum* ($n = 60$) in the study stand.

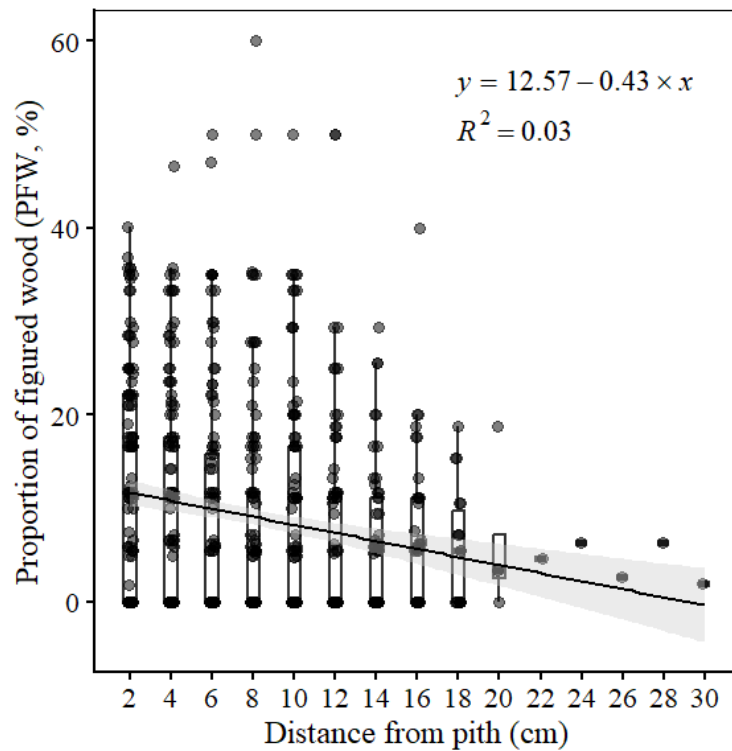


Figure 5. Proportion of figured wood (PFW) at each radial distance from the former pith line. Each box represents the distribution of PFW at a specific radial distance, with the central line indicating the median, the box edges representing the first and third quartiles (25th and 75th percentiles), and the whiskers extending to values within 1.5 times the interquartile range. Individual PFW values for each distance per tree are overlaid as jittered points to illustrate the variation. A weak negative correlation was observed between PFW and radial distance, and a simple linear regression was fitted to evaluate this relationship, with the regression line, 95% confidence interval, regression equation, R^2 , and p-value shown in the plot.

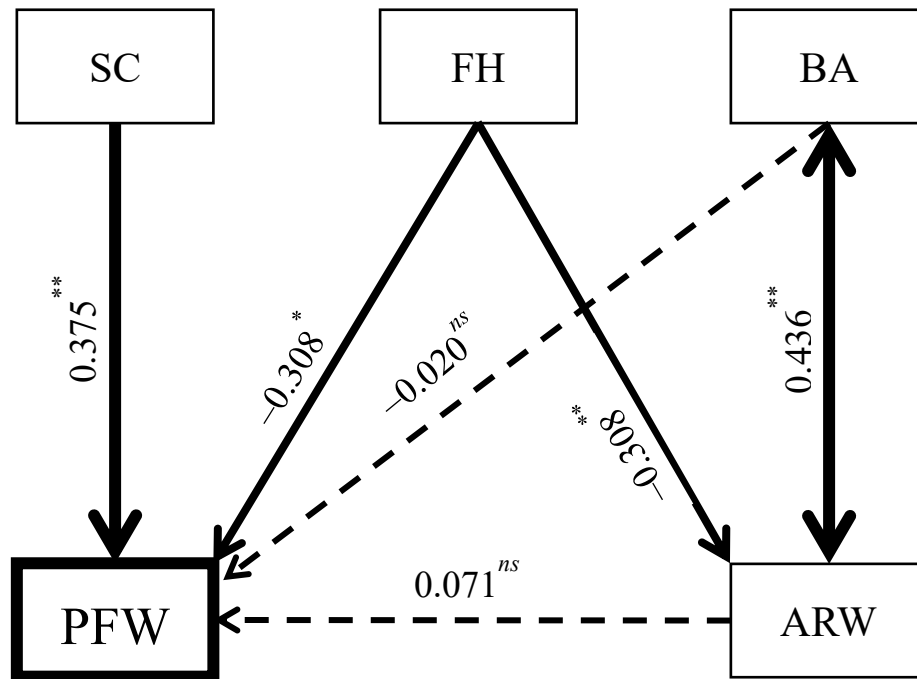


Figure 6. Structural equation modeling with standardized parameter estimates (Goodness-of-fit index: $\chi^2 = 0.270$, GFI = 0.965, SRMR = 0.079). Error arrows of the observed variables are omitted for clarity. Standardized path coefficients (direct effects) are indicated along each path. Arrow thickness reflects the magnitude of the estimates. Dashed arrows represent nonsignificant paths. *: < 0.05, **: < 0.01, ns: nonsignificant. PFW: proportion of figured wood, SC: stem crookedness, FH: fork height, BA: basal area, ARW: annual ring width.

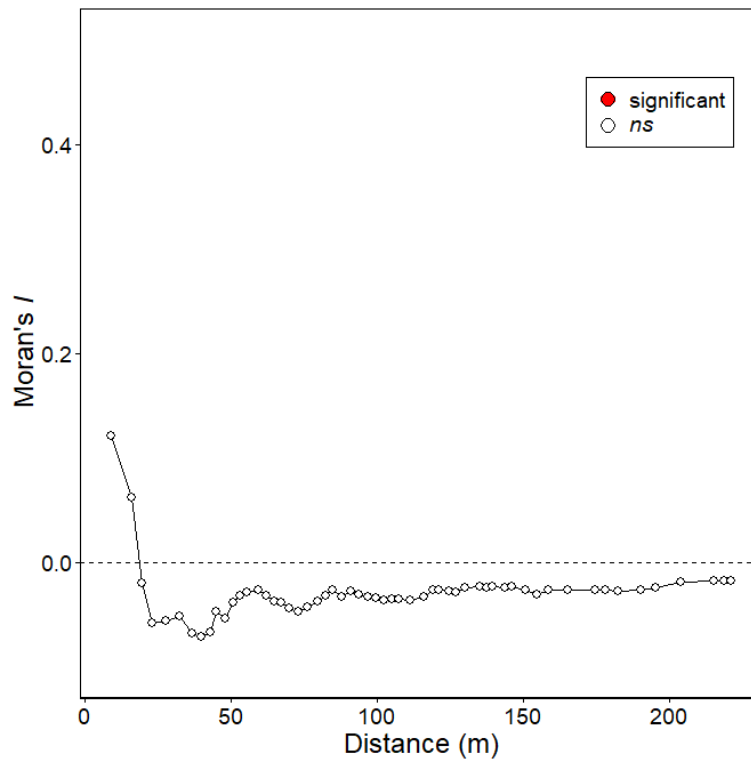


Figure 7. Correlogram of Moran's I for the proportion of figured wood (PFW). Moran's I values are plotted against the actual mean distance corresponding to k , showing the spatial autocorrelation of PFW. The open dots indicate the values of Moran's I at each distance. The dashed horizontal line represents Moran's $I = 0$, which serves as the baseline for no spatial autocorrelation. Moran's I was not significant at any distance class.

4.7 Appendices

Figure A1. There are several types of figured wood, such as wavy, curly, and birdseye.



1. Wavy type: This type is the most common type of figured wood, characterized by a wavy pattern.

(photo by the author)



2. Curly type: This type is a common figured pattern, similar to the wavy type, but distinguished by a finer wave structure.

(photo by Hu 2024)



3. Birdseye type: This type of figure is relatively common, though not as frequent as the wavy or curly types. It is characterized by a bird's-eye-like pattern.



Sometimes, the appearance of this figure can be foreshadowed by features on the bark, but in most cases these signs are subtle and easily overlooked.

(Top photograph: adapted from

<https://www.curlymaplewood.com/birdseye-maple>. Bottom photograph: by the

author.)

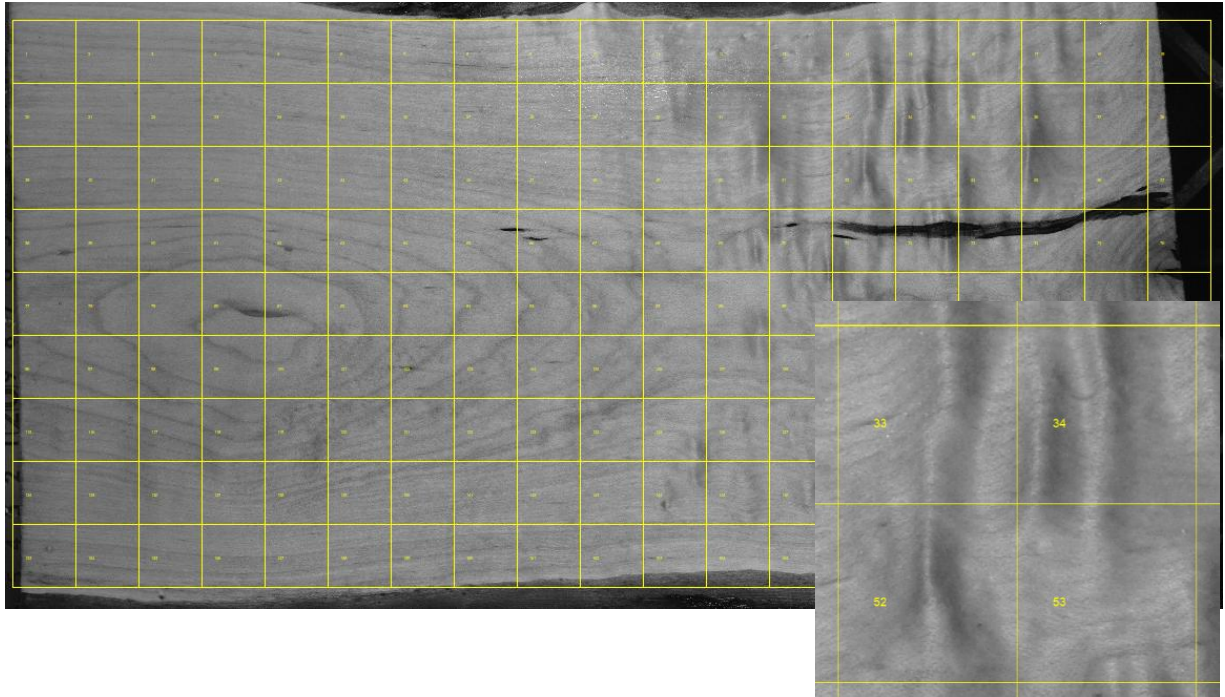
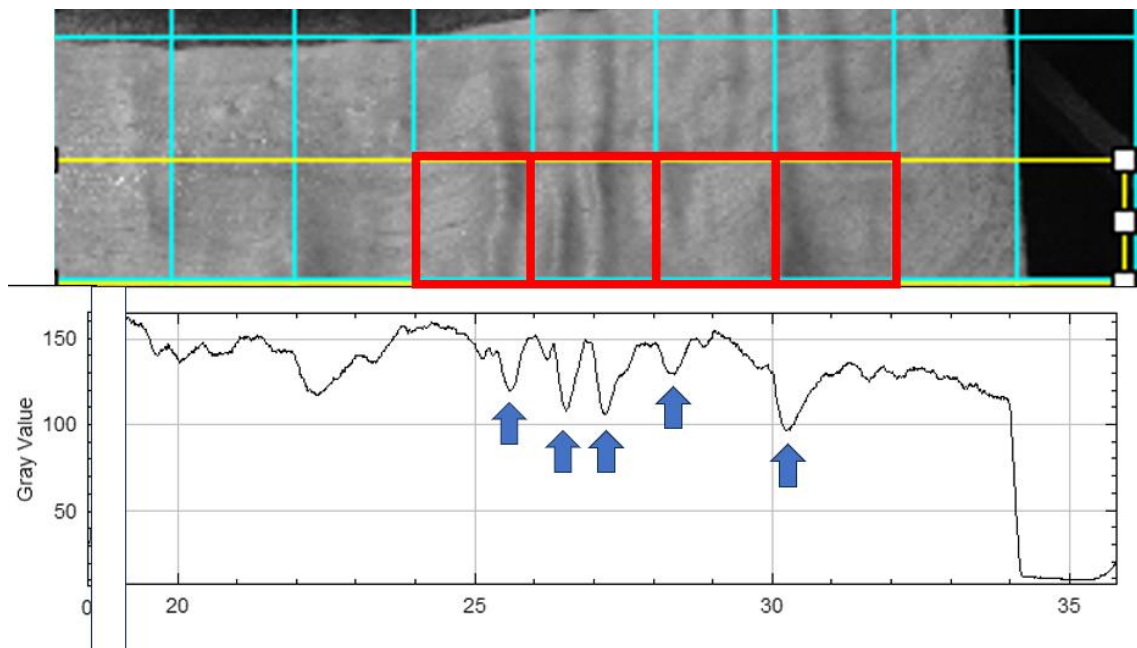


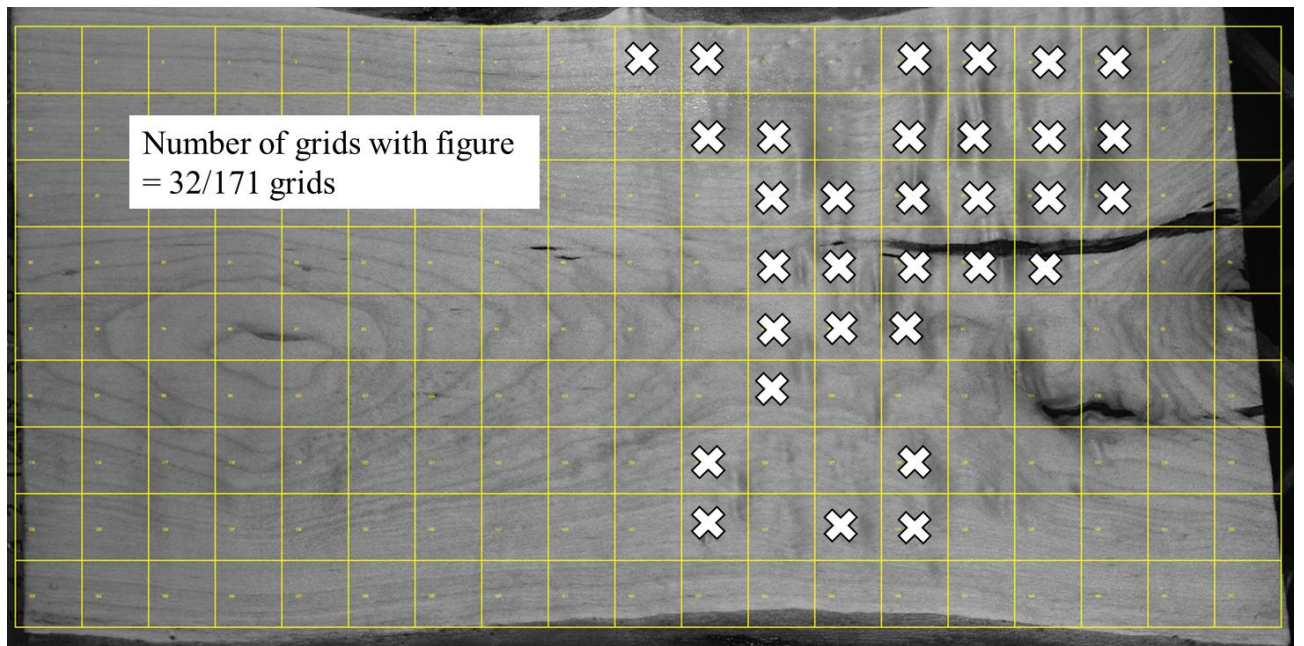
Figure A2. Detailed method for measuring grey value (GV)

How to determine the threshold of the GV

The threshold of the GV fluctuation within the grid with figured wood was determined using three randomly selected boards in the following steps. First, the board surface was visually checked to see if figured wood appeared within the 2 cm grid, and the coordinates of each grid were recorded.



Next, sub grids measuring 2 cm by 0.1 cm were created within each grid, and the average GV of each sub grid was calculated using Image J. Then, the difference between the maximum and minimum GV of the sub grids within the 2 cm grid was calculated. Furthermore, the difference between the maximum and minimum GV of the grids that were visually judged to have figured wood was confirmed. As a result, the difference was 10 or more in all grids that were visually judged to have figured wood. Based on this result, in this study, if there was a variation of 10 GV or more within a 2 cm grid, the grid was judged to have figured wood. However, even if there was a variation of 10 GV or more, if it was clearly judged not to be figured wood by visual inspection (discoloration, decay, etc.), the grid was excluded from the figured wood area.



The number of grids in which figuring was observed was used to determine the area of figured wood. The proportion of this area to the total board surface area was then calculated, serving as an index of the proportion of figured wood (PFW).



Chapter 5

Growth characteristics of standing individual Japanese oak (*Quercus crispula*) qualifying for barrel timber in a secondary forest

5.1 Introduction

Oak species are generally found in temperate forests and play important cultural, economic, and ecological roles (Johnson et al. 2019). Oak timber is hard and relatively resistant to decay, so it has traditionally been used for furniture and interior materials. In addition, oaks play a major role in flavor formation during the aging process of whiskey and wine, so their heartwood is used as a barrel material (Alamo-Sanza and Nevares 2018; Gollihue et al. 2021). However, to use oak as a barrel material, several strict conditions necessary for retaining liquid need to be clarified. The supply of suitable wood is limited, and the price of oaks used for barrel material is often significantly higher than usual (Alamo-Sanza and Nevares 2018; Ruppitsch et al. 2021; Kim et al. 2024). Therefore, understanding the factors that influence oak wood quality is crucial for both sustainable forest management and a stable supply of barrel material. Studying wood properties and their environmental determinants can help optimize resource utilization and meet the growing demand for high-quality oak timber (Moore et al. 2015). To hold liquids, barrel wood is required to have a small grain angle and abundant tyloses formation in vessels (Mosedale 1995; Kim et al. 2024). The grain angle refers to the arrangement angle of wood fibers with respect to the stem (Kubler 1991; Aebischer and Denne 1996). Although

studies on the grain angle in hardwood species are limited (Aebischer and Denne 1996; Rauchfuss and Speer 2006), most studies on its causal factors focusing on softwood species (Kubler 1991; Pape 1999; Gapare et al. 2007; Hallingbäck et al. 2010; Wing et al. 2014; Moore et al. 2015; Nakada et al. 2024). Previous studies have shown that the grain angle in softwood species exhibits directional patterns and is influenced by genetic factors (Harris 1989; Pape 1999; Rauchfuss and Speer 2006; Thomas et al. 2023). In hardwood species—especially oaks—the grain angle reportedly increases in a single direction within each individual tree (Aebischer and Denne 1996). Nevertheless, the expression of the grain angle also depends on growth conditions, tree shape, and environmental factors specific to each individual (Harris 1989; Pape 1999). For example, it has been suggested that the grain angle may be correlated with eccentricity on the cross-section of wood caused by the growth conditions of an individual tree (Misra 1943). It has also been reported that slow-growing individuals tend to have larger grain angles than fast-growing individuals do (Danborg 1994; Pape 1999). In addition, softwood species show that the grain angles within individual trees may gradually decrease from the pith to the cambium (Moore et al. 2015), meaning that larger individual trees tend to have a smaller average grain angle. Furthermore, trees with strongly curved stems may develop larger grain angles as a result of corrective growth during stem reorientation toward the vertical direction in response to gravity (Warensjö, 2003). On the other hand, grain angle in standing trees is thought to contribute to a more even distribution of water absorbed by the roots across the crown by allowing water to spread laterally and circumferentially during axial transport within the stem (Kubler, 1991). Therefore, it is thought that grain angles increase when the available water at the growing site for individual trees is insufficient. However, despite these considerable findings, there is no consensus, and

even basic information on grain angles has not been obtained for most hardwood species, including oaks (Aebischer and Denne 1996; Rauchfuss and Speer 2006).

From a practical standpoint, the crack angle of the outer bark has been empirically considered an indicator for judging the suitability of standing trees or logs for barrel timber. This has been supported by the fact that the grain angle is formed simultaneously with the bark fibers and the cambium (Kubler 1991). However, as mentioned above, the grain angle from the pith to the cambium can change during the growth process (Aebischer and Denne 1996; Pape 1999; Nakada et al. 2024). The extent to which the outer bark crack angle reflects the grain angle across the entire radial direction of the stem (from the pith to the cambium) is scientifically unclear. Tyloses are substances formed when radial or axial parenchyma cells adjacent to the xylem expand, partially or completely blocking the interior of the xylem (Kishima 1966; De Micco et al. 2016). When earlywood vessels are blocked by tyloses, the xylem loses its water permeability function, which can contribute greatly to its use as barrel wood (Ruppitsch et al. 2021). In certain tree species, such as white oak (*Quercus alba* L.) and French oak (*Quercus petraea* L.), tyloses are considered endogenous and form during the transition from sapwood to heartwood (Kim et al. 2024). In many tree species, tyloses are formed as a result of cavitation caused by water shortage or are induced by a response to damage to the stem or by the invasion of pathogens (Yadeta and Thomma 2013; De Micco et al. 2016; Pérez-de-Lis et al. 2018; Ruppitsch et al. 2021). According to Dufraisie et al. (2018), the proportion of early wood vessels in sapwood with tyloses is related to the supply of water within the standing tree, so tyloses formation in sapwood is not active in trees with high vigor. Therefore, it is possible that factors that are thought to reflect vigor, such as tree age and the growth rate of individual standing trees, are related to the

formation of tyloses. However, no studies have explicitly investigated these causal factors.

Japanese oak (*Quercus crispula* Blume) is a typical tree species found in cool temperate forests and is known as the largest and longest-lived hardwood in Japan (Sano 1997). Barrels made from Japanese oak are highly regarded internationally because of their unique aroma and flavor, particularly for whiskey (Noguchi 2017), resulting in increased demand in recent years. However, few individual trees meet the necessary conditions for use as barrel material. However, as with many hardwood species, there is no basic knowledge about the grain angle in Japanese oak. In addition, although physiological studies on tyloses have been conducted (Sano et al. 1995), most studies have focused on limited scopes with small sample numbers, and little is known about the variation between and within individual trees. In this study, I measured the grain angle and tyloses filling ratio at the small end of the first log, which generally has the highest timber value, of individual Japanese oak trees growing in a single stand (7.1 ha area). I aimed to clarify basic characteristics such as the variation and spatial distribution within the stand, as well as to verify the following hypotheses.

The grain angle is

Hypothesis 1. correlated with the outer bark crack angle.

Hypothesis 2. positively affected by wood eccentricity.

Hypothesis 3. negatively affected by stem growth.

Hypothesis 4. negatively affected by individual size.

Hypothesis 5. negatively affected by wet local growing site moisture conditions.

Hypothesis 6. positively affected by stem curvature.

The tyloses filling ratio is

Hypothesis 7. negatively affected by the amount of growth.

Hypothesis 8. negatively affected by wet local growing site moisture conditions.

Hypothesis 9. positively affected by tree age.

In softwood species, although genetic factors have also been considered causal factors in previous studies, they are limited to cases that have compared them at a regional scale (Hallingbäck et al. 2010; Thomas et al. 2023; Nakada et al. 2024). I presume that genetic variation within a single oak stand is expected to be considerably small. Nevertheless, I also performed spatial analysis of individual standing oak trees to investigate the possible contributions of genetic factors.

5.2 Materials and methods

5.2.1 Study site and sampling

A field survey was conducted in the Uryu Experimental Forest, Field Science Center for the Northern Biosphere, Hokkaido University, Japan (44°7'N, 142°10'E, 252 m above sea level). The average annual temperature and precipitation are 5.0°C and 1707 mm, respectively. The maximum snow depth exceeds 200 cm (average for the 10 years from 1994 to 2023: Japan Meteorological Agency <https://www.jma.go.jp/jma/index.html>).

A study site of 7.1-ha was established in a natural mixed secondary stand on a gentle slope. This stand had been disturbed by humans in the past (with field burning) and was dominated by *Q. crispula* (38.7% and 39.1% for tree density and basal area, respectively; Table 1). Most of the oaks were not primarily of coppice origin (Figure S1), with an average diameter at breast height (DBH, measured at 1.3 m above the ground) of

27.4 cm, a standard deviation of 9.9 cm, and a maximum DBH of 94 cm. The mean tree age was 77.4 (SD = 11.5) years. The other dominant species in the stand were *Abies sachalinensis* (F. Schmidt.) (30.7% in terms of basal area), *Acer pictum* Thunb. (Wesm.) H. Ohashi (10.0%), and *Betula ermanii* Cham (9.3%) (Table 1).

Tree measurements were conducted on all standing trees (including trees other than *Q. crispula*) with a DBH of 10 cm or greater at the study site in April 2020. Each tree was assigned an individual identification number, and the DBH was measured at 2 cm intervals using a caliper. Location information (*x*-*y* coordinates) for each tree was obtained using a GPS (Mobile Mapper 100, Ashtech), and a numerical topographic map was overlaid using GIS software (QGIS Development Team, 2021). The topographic wetness index (TWI: Beven and Kirkby 1979), which is a relative indicator of topical wettability, and the slope inclination were calculated at a resolution of 400 m² for all individual trees.

Next, the stem curvature and the outer bark crack angle of an individual oak were measured in the area corresponding to the first log (1-3 m above ground), which is generally the most valuable part of a standing tree. As an index of stem curvature, a 2 m pole was alongside the part of the stem between 1 and 3 m above ground, and the maximum distance between the stem and the pole was recorded in 5 cm increments. To evaluate the outer bark crack angle over the stem surface, photographs of the stem in the range of 1-3 m were taken from two directions, one at a random position and the other at a position opposite it. In the photographs, the stem was divided into four vertical sections, considering that the length of a single bark crack (in the 1-3 m range) was approximately 0.5 m at most (Figure S2). The angle of one representative outer bark crack (relative to the angle of the stem) within each section was subsequently measured, and the average

of the eight measures was used as an index for each individual tree.

Between December 2021 and March 2022, timber harvesting took place at the study site (74.3% of the stand volume). The trees were felled at a height of 0.5 m above ground using a chainsaw. Felled trees were collected in their entirety while retaining their ID. Then, in the stock yard, 5 cm thick disks were collected from a position at 2.5 m (corresponding to a tree height of 3 m). The disks were brought back to the laboratory, and the cross-sections were photographed along a scale (Camera; D 750, Nikon Co., Lens; AF-S NIKKOR 18-35 mm f/3.5-4.5 G ED, Nikon Co.). The disks were then stored in a freezer to prevent changes in the site moisture content of the wood. Subsequent treatments were carried out under frozen conditions so that the tyloses filling ratio could be maintained similar to that in a standing tree (Murmanis 1975).

The wood eccentricity on the cross-section of each individual tree was measured on the photograph of the disk. First, the mean radius was calculated from the cross-sectional area of the disk via Image J, and the x - y coordinates of the center of mass and the pith were determined. The distance (deviation) from the center of mass to the pith was subsequently expressed as a ratio to the disk radius, which was used as an index of wood eccentricity.

To measure the grain angle and the tyloses filling ratio, strips 30 mm in height and width were cut from each disk through the pith to the bark. In this process, knots and reaction woods were avoided, and the strips were carefully cut so that the grain was perpendicular to the axis of the tree to record the purest possible grain angle (Ohkura 1958). The cross section of the strip was planed, and a high-pressure air compressor was used to remove fine debris from inside the earlywood vessels to allow for a clear view (Figure S3). The images of each strip were then scanned at a resolution of 1200 dpi

(EPSON, GT-X830), all annual rings were recorded, and the average ring width was calculated.

5.2.2 Measurement of grain angles

In this study, the grain angles of individual trees (237 trees) with DBHs of 20 cm or greater were measured via the splitting method to evaluate the usability of barrel timber (Ohkura 1958). The splitting method can provide more information about the grain angle because it can observe not only the surface of the wood but also the change in the grain angle from the pith to the cambium. First, reference lines were drawn through the pith to the cambium on both cross-sections of the strip so that the two lines were parallel. The strip was then split longitudinally in two by hitting a hatchet placed along the reference line with a plastic hammer, ideally following the grain.

The split strips were scanned at a resolution of 1200 dpi (EPSON, GT-X830), and the grain angle of each annual ring was recorded via MATLAB R2019b and the Image Processing Toolbox (Math Works, Inc.). Here, the *split line* refers to the trace of the naturally developed split that appears on the surface opposite the hatchet insertion side, reflecting the local orientation of wood fibers. The grain angle (GA: %) (Figure S4) was calculated by dividing the distance between the split line and the reference line for each annual ring by the height of the strip (30 mm). In this study, the direction of the GA was represented by the S system and the Z system, which indicate that the split line is above or below the reference line (when the pith is placed on the left side when the split surface is down), respectively (Nakada et al. 2024). Normally, the split line and the reference line coincide. However, due to disturbances in the grains caused by knots or figured grains, there were cases in which the split line did not align with the reference line at the pith. In

this study, out of the 237 trees measured, 87 individuals were selected for analysis, excluding those in which the split line and reference line did not closely match at the pith or those with a maximum grain angle exceeding 50%.

5.2.3 Measurement of the tyloses filling ratio

The tyloses filling ratio (TFR) was measured on the scanned image. All earlywood vessels and those earlywood vessels filled with tyloses were visually counted within each of the continuous 2 cm square sections from the pith to the bark (Figure S3). The ratio of the number of earlywood vessels filled with tyloses to the total number of earlywood vessels in each section was used as an index of the TFR. The presence or absence of tyloses in the vessels was easily discernible by enlarging the images, but individuals in which more than 10% of the vessels could not be counted owing to debris remaining in the vessels or the vessels being crushed were not included in the analysis (119 individual trees).

5.2.4 Analysis

The relationships between the arithmetic average grain angle from the pith to the cambium (AGA) and the outer bark crack angle (OBCA) in each individual tree were evaluated via Pearson's correlation analysis. Next, to confirm the presence or absence of directionality (right or left twist) in the GA, the bias in the occurrence was evaluated via a chi-square test. Statistical significance was assessed at the 0.05 level.

To investigate spatial variation in grain angle and tyloses filling ratio (TFR) among individual Japanese oak trees within the stand, spatial autocorrelation analysis using Moran's *I* was conducted (Moran, 1950). The analysis was based on spatially explicit tree-level data obtained within the study area. Moran's *I* was used to evaluate

whether AGA and TFR values of neighboring trees were more similar or dissimilar than expected by chance. Moran's I ranges from -1 to 1 , with values near 1 indicating strong positive spatial autocorrelation, values near -1 indicating strong negative spatial autocorrelation, and values around 0 indicating no spatial autocorrelation (Moran 1950; Duncan and Stewart 1991). Spatial autocorrelation was evaluated across multiple neighborhood scales using k -nearest neighbor spatial weights matrices, following the same procedure described in Chapters 3 and 4. Moran's I was calculated for each value of k to assess scale-dependent spatial patterns in AGA and TFR. All analyses were conducted in R version 4.3.2 (R Development Core Team 2023) using the *spdep* package (Bivand and Wong 2018).

I then used structural equation modeling (SEM) to analyze the relative importance of each factor on GA and to clarify their direct and indirect effects. Two representative metrics are commonly used to characterize the grain angle of individual trees: the average and the maximum grain angle. Although these metrics were strongly correlated ($r = 0.87$, $p < 0.01$), AGA was used in the SEM analysis because it better represents the overall tendency of grain angle within an individual tree. Because the direction of grain angle (S or Z system) is not relevant to the usability of barrel timber, grain angle values were converted to absolute values at the annual-ring level prior to averaging. Accordingly, the AGA used in the SEM represents the mean of the absolute grain angle values from the pith to the cambium (AGAab).

Since there is limited research on GA in hardwood species, I built a hypothetical model (Figure S5a) on the basis of previous studies, which focused mainly on softwood species (Kubler 1991; Aebischer and Denne 1996; Pape 1999; Moore et al. 2015). First, because AGAab increases as wood eccentricity (Misra 1943; Kubler 1991), individual

stem size (basal area) and stem curvature increase (Harris 1989; Warensjö 2003; Moore et al. 2015), a positive direct effect was set for each trait. Next, because stem growth and a high tendency toward site wetness are thought to have a negative effect on GA (Kubler, 1991), I hypothesized that the average annual ring width (ARW) and the topographic wetness index (TWI) each have a negative direct effect. In addition, because stem growth is expected to have a positive effect on individual stem size, an indirect path via the basal area was also set for ARW. Furthermore, because local site moisture conditions are also thought to affect stem growth, a path from TWI to ARW was set. ARW, TWI, individual size, and stem curvature were each converted to natural logarithms, and eccentricity and AGA were converted to arcsine values.

Similarly, the TFR was analyzed via SEM to clarify the relative importance of each factor and the direct and indirect effects (Figure S5b). For evaluation, tyloses are likely to form in the transition zone, where sapwood changes to heartwood (De Micco et al. 2016; Dufraisie et al. 2018). Therefore, the TFR in the 2 cm square area in the transition zone (located 4 cm away from the cambium) was used as an index of individual tree tyloses formation ability (TFR_{tr}). Since stem growth and a high tendency toward site wetness are thought to have a negative effect on the TFR (De Micco et al., 2016; Dufraisie et al., 2018), I hypothesized that the ARW and TWI have a negative direct effect on the TFR. Here, ARW was taken as the value for 10 years before and after the transition zone (a total of 20 years), where the TFR was measured. Next, since tree age is thought to have a positive effect on the TFR (Dufraisie et al. 2018), a positive direct effect was set. Furthermore, since the site moisture conditions of the growing site are thought to affect stem growth, an indirect effect via TWI and ARW was also set. As with the analysis of the GA, the values of ARW, TWI, and tree age were transformed to natural logarithms,

and TFR was transformed to an arcsine value.

The significance level for all unstandardized path coefficients was set at a risk level of less than 5%. Model fit was evaluated by the chi-square value, goodness-of-fit index (GFI), root mean square error of approximation (RMSEA), and standardized root mean square residual (SRMR). It is considered desirable for the chi-square value not to reject the hypothesis. The GFI is generally interpreted as ranging from 0 to 1, with values closer to 1 indicating better model fit. The lower limit of RMSEA and SRMR is 0, and the closer the value is to 0, the better the fit. The analysis was performed via the package “lavaan” (Rosseel 2012) of the statistical analysis software R version 4.3.2 (R Development Core Team 2023).

5.3 Results

5.3.1 *Grain angle*

Among the oak individuals examined in this study ($n = 87$), those with AGA (average grain angle) -1.5% to 1.5% were the most common, followed by those with AGA of -4.5% to -1.5% (Figure 1a). The average value was -0.7% ($SD = 3.8\%$), with a range of -10.9% to 9.6% (Table A1). The proportions of individuals with AGA exhibiting S and Z systems were 42.3% and 57.7%, respectively, and no significant bias in their occurrence was observed ($\chi^2 = 1.39$, $p = 0.24$). The radial grain angle direction within an individual was not necessarily consistent, and no clear trend was observed in terms of its increase or decrease in the radial direction (Figure A6). In some trees, the grain angle increased from pith to bark, whereas in others, it peaked during the juvenile growth phase and subsequently declined toward 0%. In approximately half of the cases, the grain angle direction even reversed during radial growth, with 52.9% (including those that

temporarily reversed) of individuals showing a shift from S to Z orientation, or vice versa. On the other hand, among individuals with AGAab (average grain angle of absolute value), those with a value of 7.5% or greater were the most common, followed by those with a value of 4.5% to 6%. The average value was 5.9% (SD = 3.3%), with a range of 0.9% to 19.4% (Figure 1b, Table A1). Even in absolute values, the grain angles of individual trees did not show any particular pattern across the radial direction of the stem (Figure 2).

The proportions of the S and Z systems in OBCA (outer bark crack angle) were similar (41.2% and 58.8%, respectively) to those in AGA, but there were also cases where OBCA rotated in opposite directions to AGA (44.8%). As a result, the correlation of OBCA with AGA was only weak ($r = 0.19$, $p = 0.08$, Figure 3).

The Moran's I values for AGAab at all distances were $p > 0.1$ (Figure 4), indicating no significant spatial clustering.

SEM analysis revealed that the chi-square value of the model was $p = 0.520$, indicating that the model fit the observed data well. The GFI, RMSEA, and SRMR were 0.969, 0.000, and 0.053, respectively, and converged to statistically acceptable values. The direct effect of eccentricity on AGAab was 0.33 (values are standardized coefficients, $p < 0.01$), which was the most important of all the effects (Table 2 and Figure 5). This was followed by the direct effect of ARW, with a coefficient of 0.29 ($p < 0.05$). Conversely, ARW had a significant positive effect on individual size (0.58, $p < 0.01$), but the effect of the latter on AGAab was not significant (there was no indirect effect of ARW through individual size). The direct effect of stem curvature on AGAab was also not significant. With respect to the topographic factor (TWI), both the direct and indirect effects (through the ARW) were not significant.

5.3.2 Tyloses filling ratio

The TFRtr ($n = 119$) was 26.8% (SD = 25.7%), with high variability among individual trees (range of 0-91.1%; Figure 6). The most frequent group of the TFRtr was those with 1 to 10%.

Within an individual tree, the TFR was highest near the transition zone from sapwood to heartwood (4-6 cm from the cambium) and tended to decrease toward the pith (Figure 7).

The Moran's I value for TFRtr was significant at only a limited number of distance classes (distances of 12.2 and 14.5 m; $p < 0.05$; Figure 8).

SEM analysis revealed that the chi-square value was $p = 0.164$, indicating that the model fit well with the observed data. The GFI, RMSEA, and SRMR were 0.984, 0.089, and 0.041, respectively, converging to statistically acceptable values. The direct effect of ARW on the TFR was -0.21 (standardized value, $p < 0.05$), which was the most important of all the factors (Table 3 and Figure 9). The direct effect of TWI on the TFR was marginally significant ($p < 0.08$), indicating a weak tendency to have a negative influence. Conversely, the indirect effect of TWI on the TFR through ARW was not significant. The direct effect of tree age on the TFR was also not significant.

5.4 Discussion

I demonstrated the relative importance and direct/indirect effects of multiple factors on the grain angle and tyloses filling ratio, which are key characteristics when Japanese oak is used as barrel timber. The direct effect of wood eccentricity had the most important effect on AGAab (average grain angle of absolute value), suggesting that homogeneous

stem growth contributes to the formation of stems with fewer small grain angles. Furthermore, the direct effect of ARW (average annual ring width) had a significant effect on both characteristics (positive and negative effects on AGAab and TFRtr (tyloses filling ratio into the transition zone), respectively), suggesting that relatively little growth contributes to the high suitability of Japanese oaks for barrel wood.

5.4.2 Grain angle

The average for AGAab was 5.9% (SD = 3.3%), with the most frequent value being 7.5% or more. When wood is used for barrels, assuming a standard wood length of 100 cm and a thickness of 3 cm, liquid leakage may occur if the grain angle exceeds 3.0% (angle of 1.7°). The proportion of individual trees with an AGAab smaller than this value was 13.4%. To use oak as barrel wood, in addition to having a small grain angle and an abundance of tyloses (Alamo-Sanza and Nevares 2018), as described in this study, other conditions, such as a large diameter and limited bending of the stem, are needed. Therefore, the fact that there were few trees with small grain angles supports the rarity of oaks that qualify for barrel wood.

Although the grain angle of softwood species is clearly directional (Mikami and Nagasaka 1975), only a limited number of hardwood species have been reported to exhibit similar directional properties, and these reports are largely descriptive rather than quantitative (Ohkura 1963; Aebischer and Denne 1996; Rauchfuss and Speer 2006). In this study, the average grain angle (AGA) of the target individuals included both S and Z systems, and no significant bias was observed in their occurrence, making it clear that the grain angle of Japanese oak is not directional. On the other hand, within the stem, the grain angle patterns from the pith outward showed considerable variation among

individual trees. These diverse patterns contrast with the consistent trend reported by Aebischer and Denne (1996), in which the grain inclination in *Quercus* species increased uniformly from the pith to the outer stem.

Traditionally, the OBCA (outer bark crack angle) that appears on the stem surface is empirically believed to be related to the internal grain angle. Therefore, the selection of standing trees (or logs) to be used for barrel timber has been determined through observations, although no scientific verification has been carried out. In this study, this empirical rule was examined, and the correlation was only marginally significant ($p = 0.08$), providing weak support for hypothesis 1. This weak relationship is thought to be due to OBCA only presenting recent internal trends (Kubler 1991; Li et al. 2024). In fact, when the relationship of OBCA with the grain angle over the last 10 years was examined, there was still a weak but significant positive correlation ($r = 0.44$, $p < 0.01$). Especially in the case of large-diameter Japanese oaks, such as those used for barrel timber, OBCA is therefore not necessarily suitable as an indicator across the entire radial direction of the stem.

Previous studies in softwood species have investigated the relationship between wood eccentricity and grain angle, but no significant consensus has been reached (Misra 1943; Kubler 1991). This study demonstrated that the positive effect of wood eccentricity was the most important of all the examined factors (supporting Hypothesis 2), indicating that heterogeneous growth of the stem can cause a large grain angle in oak, a hardwood species. Wood eccentricity occurs when the stem grows unevenly; the main causes include the high steepness of the growing site, as well as the relative spatial position and its changes with neighboring trees (Kubler 1988). Intensive thinning generally increases light availability across the entire crown of residual trees; however, the resulting rapid

crown expansion and reorganization may induce eccentric growth and increase grain angle (Kubler 1991; Pape 1999).

In *Q. petraea* and *Q. robur*, a positive trend in which the grain angle increased with annual ring width was observed in several stands (Aebischer and Denne 1996). Similarly, in our study, the direct effect of ARW on AGAab was also positive (contrary to hypothesis 3). Although the coefficient was small, trees with high stem growth tended to have relatively large grain angles, possibly because they are relatively sensitive to changes in the surrounding environment (such as water and light supplies) during the growth process. On the other hand, the direct effect of individual size on AGAab was not significant (did not support hypothesis 4). Consequently, the indirect effect of ARW on AGAab through individual size was also not significant, suggesting that the effect of stem growth is independent of individual size.

The site moisture condition and its heterogeneity within the growing site can be a mechanism for the grain angle, as has been observed in cases of deficit or excess site moisture (Harris 1989; Kubler 1991). Recent research further supports this finding, showing that variations in soil water availability can affect cambial dynamics, thereby altering the grain angle (Balducci et al. 2016). However, in this study, the effect of the TWI (topographic wetness index) on AGAab was small and not significant (did not support hypothesis 5). Japanese oak stands, including those at this study site, are located mainly on upper slopes, and the lack of moisture variation within the site may be related to this result. In addition, the effect of stem curvature on AGAab was also not significant (did not support hypothesis 6), suggesting that the grain angle is not controlled directly by physical bending of the stem.

The spatial autocorrelation of AGAab was negative or close to zero and was not

significant at any distance, showing that AGAab is distributed randomly in space and does not tend to have similar values in proximity. The random distribution at small spatial scales suggests that AGAab is not dependent on microtopography. Indeed, this result was consistent with the fact that microtopical site factors (TWI) had no significant effect on AGAab. This finding also suggests that genetic influences may not be important factors. Previously, it was shown for softwood species that the grain angle is genetically influenced when the regional spatial scale is considered (Wu et al. 2008; Hallingbäck et al. 2010). However, it was not clear whether such a trend could be observed at the stand scale (7.1-ha) examined in this study. Several studies have reported that oaks form genetic patch structures within populations (Bacilieri et al. 1994; Geburek and Tripp-Knowles 1994; Berg and Hamrick 1995; Carabaña et al. 2007; Sandurska et al. 2024), with widths of approximately 40-50 m in the case of Japanese oak (Ubukata et al. 1999). Such structures, which are caused by the limited dispersal ability of pollen and seeds of oak species, may lead to the spatial clustering of genetically related individuals, especially at short distances (Jose-Maldia et al. 2024; Sandurska et al. 2024). If genetic factors play a significant role in the grain angle, spatial autocorrelation should be observed across a wider range of distance classes. Further investigations are needed to evaluate the effects of genetic factors.

5.4.3 *Tyloses filling ratio*

When there is even a slight grain angle, a low TFR can cause considerable liquid leakage (Rubio-Bretón et al. 2013). The average TFRtr of Japanese oak was 26.8% (standard deviation 25.7%), with some individual trees not forming any tyloses and others with a maximum TFRtr of over 90%. This suggests that, while Japanese oak is used for barrel

production despite its lower average tyloses filling rate, only a subset of individuals may possess wood properties comparable to those of white oak, resulting in more limited suitability at the population level. In terms of the radial variation in the TFR (tyloses filling ratio) within a cross-section, the ratio was highest near the transition zone from sapwood to heartwood and decreased toward the pith. According to Sano et al. (1995), formed tyloses can collapse due to wetwood, which is triggered by bacteria entering through dead branches or wounds in the stem (Nakada 2014). Therefore, it is reasonable to assume that tyloses decrease over time because of more frequent collapses near the pith.

For TFRtr, I found that the ARW in the corresponding zone was the most important factor. The direct negative coefficient suggests that tyloses formation tends to be more prevalent in individual trees with low growth (supporting Hypothesis 7). Similar results have been reported for *Q. petraea* and *Q. robur* (Dufraisie et al. 2018). It is thought that in individuals with low growth, resources are allocated to maintain and protect existing structures rather than growing new cells, which promotes tyloses formation. In general, older trees are at greater risk of pathogen invasion in the stem, so it is thought that defense through sealing vessels becomes more important than investment in growth (Dufraisie et al. 2018). However, no effect of tree age on TFRtr was found, leading to the rejection of Hypothesis 9.

The effect of TWI on TFRtr was marginally significant, with a negative coefficient (hypothesis 8 was slightly supported). It is thought that at sites with high TWI values (locations prone to wetting), a stable water supply suppresses bubble formation in the xylem (De Micco et al. 2016; Ruppitsch et al. 2021), thereby reducing the need for tyloses formation. This effect may be more pronounced given the limited topographic

variation at the study site.

When spatial autocorrelation of TFRtr was examined in the 7.1-ha study area, the only significant values were 12.2 and 14.5 m. This suggests that TFRtr tends to be similar within a short distance range, beyond which the correlation becomes weaker or negligible. One of the reasons for this may be the effect of microtopography. This is consistent with the SEM analysis of this study, which revealed a tendency for TWI to be marginally significant. In addition, if genetic distance among individual trees correlates with physical distance, genetic influences may partly explain the observed spatial structure. However, to date, no studies have directly demonstrated the involvement of genetic factors in tyloses formation.

5.4.4 Implication for silvicultural management

In Chapter 5, the study examined the growth characteristics and site conditions of Japanese oak (*Quercus crispula*) individuals with barrel-timber qualified, defined by low grain angle and high tyloses filling ratio. Combining the results for the grain angle and TFR, individual trees with minimal wood eccentricity and moderate growth are highly qualified for use as barrel timber. This finding indicates that forest management aimed at rapidly promoting growth may not be compatible with producing high-quality oak timber. To grow Japanese oaks suitable for barrel timber, maintaining steady growth under moderately competitive conditions, which requires a long period until harvest, is important.

Clearly, predicting the GA by observing only the stem surface (bark) is insufficient. While the cross-section of a tree would provide a more accurate assessment, this requires cutting the tree. Nevertheless, observing the shape of the crown of standing

trees may provide a potential indicator for predicting GA, because trees with imbalanced crowns may also have greater cross-sectional eccentricity. Structural equation modeling suggests that trees with higher growth rates may exhibit larger GA and lower TFR. Therefore, in the management of Japanese oak stands, low-intensity, frequent thinning that maintains relatively modest growth and avoids drastic changes to the surrounding environment is recommended, as this approach can help balance growth, wood quality, and tyloses formation.

Currently, it is difficult to obtain high-quality oak trees, and other tree species can be used as alternatives to the species that have been used traditionally (Tao et al. 2013; Alamo-Sanza and Nevares 2018). However, there are no substitutes for tree species with unique roles that give whiskey its distinctive flavor, such as Japanese oak, so it is necessary to maintain resources even at a high cost. In addition, like many oak species, Japanese oak is regarded as a keystone species in its ecosystem in its distribution area. For this reason, resource management through silviculture requires long-term consideration while keeping in mind the balance between growth and timber quality, as well as utilization and conservation.

5.5 Tables

Table 1. Tree species composition of the study stand in a secondary forest.

Species	Stem density (%)	Basal area m ² /ha (%)	Mean DBH and standard deviation (cm)
<i>Quercus crispula</i>	174.2 (38.7)	11.6 (39.1)	27.4 ± 9.9
<i>Abies sachalinensis</i>	118.7 (26.3)	9.1 (30.7)	28.1 ± 13.9
<i>Acer pictum</i>	62.2 (13.8)	3.0 (10.0)	23.0 ± 9.0
<i>Betula ermanii</i>	41.7 (9.3)	2.8 (9.3)	26.6 ± 11.6
Others *	5.37 (6.4)	3.2 (10.9)	25.2 ± 10.7
Total	450.3 (100)	29.7 (100)	26.7± 11.4

*Trees with DBH $\geq$ 10 cm were examined. Others include *Betula platyphylla*, *Tilia japonica*, and *Magnolia obovata*.

Table 2. Estimated direct effects on the average grain angle of absolute value (AGAab) of the structural equation modeling, along with corresponding standard errors, *Z* values and *P* values (see Figure 5).

Path model	Direct effect	Standard error	Standardized coefficients	<i>Z</i> value	<i>P</i> value
AGAab =					
Eccentricity	0.001	0.000	0.330	3.449	0.001
ARW	0.051	0.021	0.294	2.474	0.013
Basal area	−0.005	0.010	−0.063	−0.537	0.591
Stem curvature	−0.005	0.004	−0.145	−1.497	0.134
TWI	0.078	0.059	−0.132	1.335	0.182
Basal area =					
ARW	1.163	0.175	0.583	6.646	0.000
ARW =					
TWI	0.655	0.364	0.190	1.799	0.072

Table 3. Estimated direct effects of the structural equation modeling on the tyloses filling ratio in the transition zone (TFR_{tr}), along with corresponding standard errors, *Z* values, and *P* values, are shown in Figure 9.

Path model	Direct effect	Standard error	Standardized coefficients	<i>Z</i> value	<i>P</i> value
TFR _{tr} =					
ARW	−0.240	0.104	−0.208	−2.306	0.021
Tree age	0.071	0.168	0.038	0.423	0.672
TWI	−0.842	0.462	−0.164	−1.822	0.068
ARW =					
TWI	−0.701	0.401	−0.158	−1.746	0.081

5.6 Figures

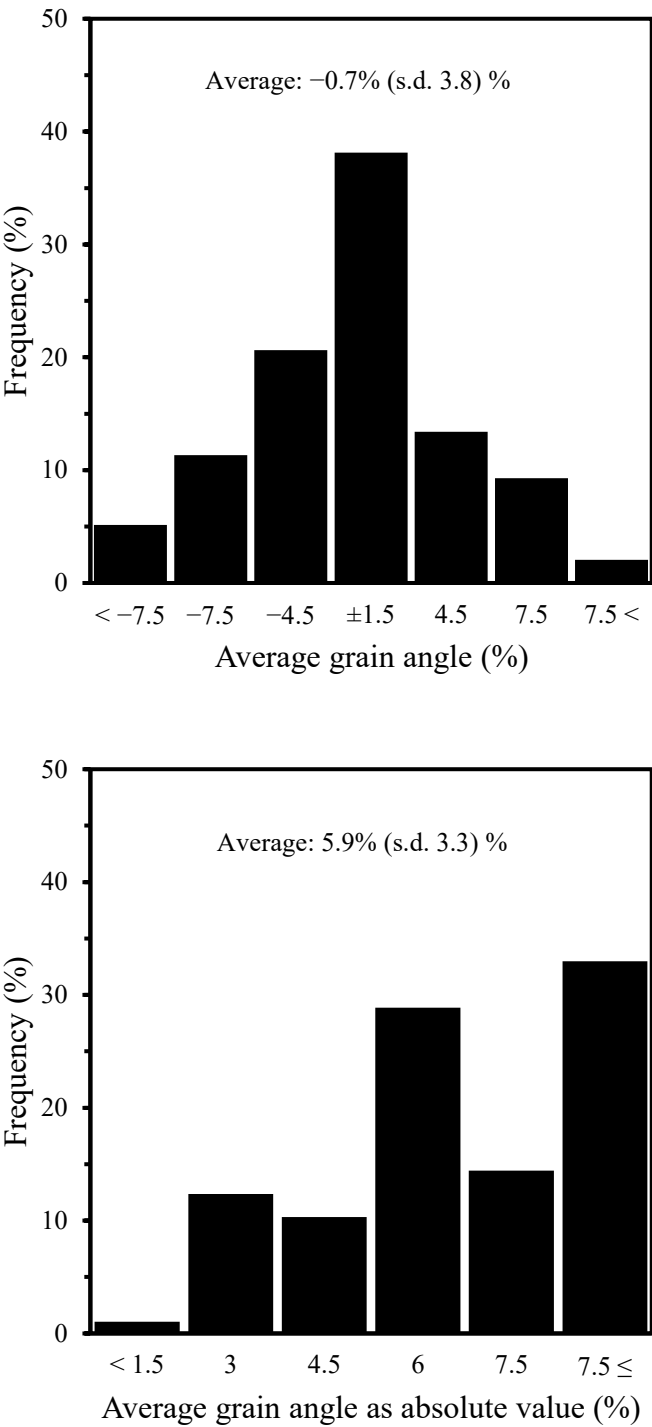


Figure 1a and 1b. Frequency of the average grain angle and the average absolute values of the grain angle. The average grain range was -10.9% to 9.6% .

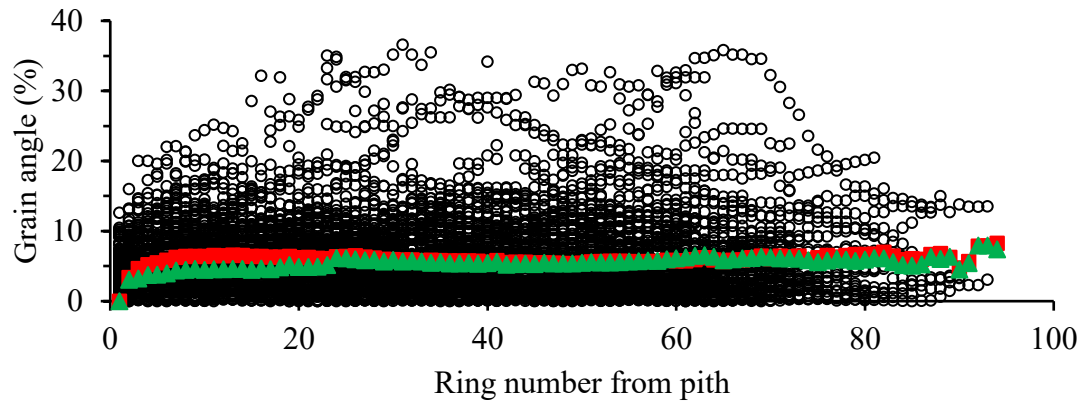


Figure 2. The grain angle for each annual ring in all the study trees (based on the absolute values). Red squares and green triangles represent the average and standard deviation, respectively.

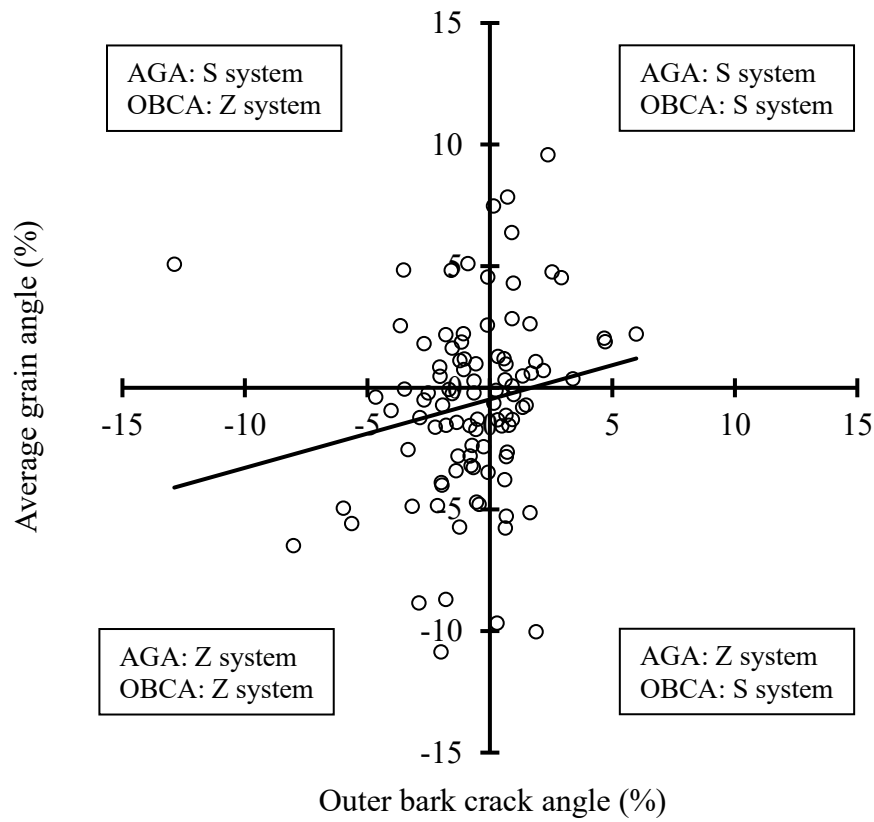


Figure 3. Relationship between the outer bark crack angle (OBCA) and the average grain angle (AGA) in all the study trees. The regression line represents the relationship between OBCA and AGA ($r = 0.19$, $p = 0.08$).

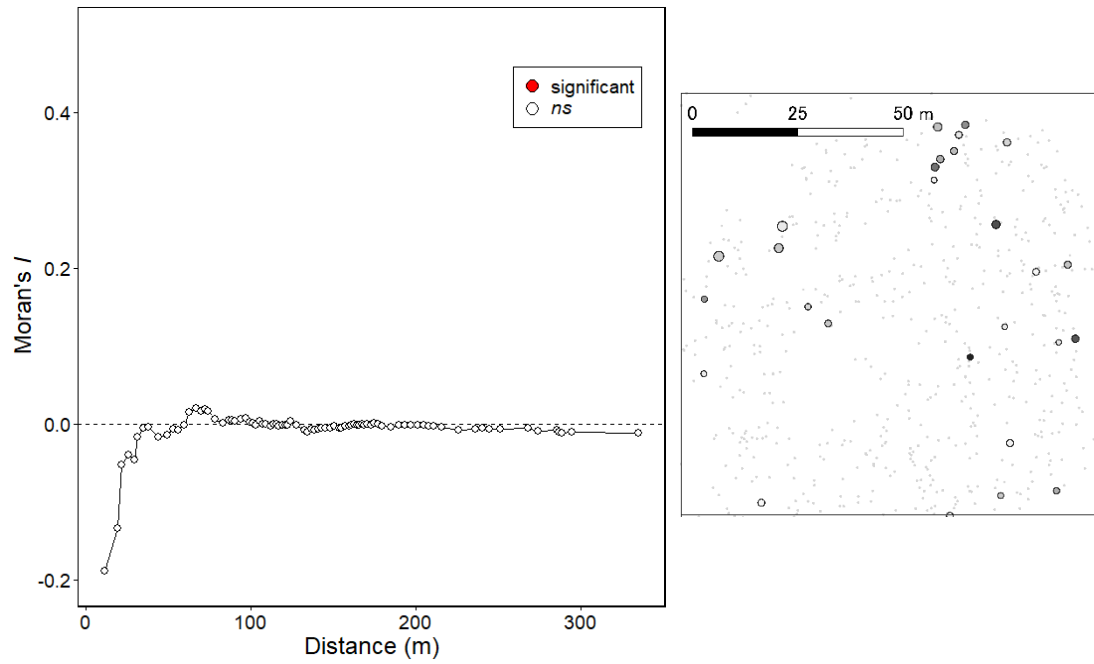


Figure 4. Correlogram of Moran's I for the average grain angle of absolute value (AGAab), along with the distribution of trees within a 1-ha area of the study stand. The circle size represents the tree size (DBH), while darker colors indicate larger AGAab values. The small gray dots indicate the locations of the other tree species.

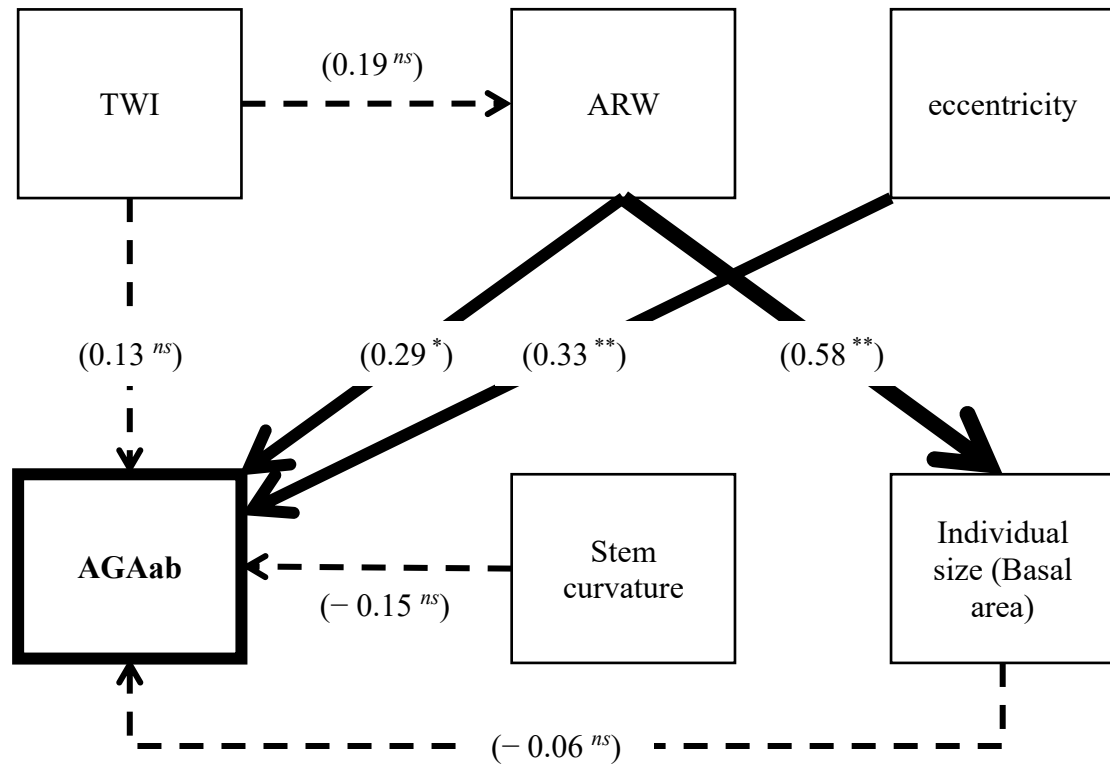


Figure 5. Structural equation modeling with standardized parameter estimates. The error arrows of the observed variables are omitted to simplify the diagram. The estimated standardized path coefficients (direct effects) are placed on each path. The thickness of a single arrowhead corresponds to the magnitude of its estimates. The dashed single arrowheads depict nonsignificant paths. *: < 0.05 , **: < 0.01 , *ns*: nonsignificant.

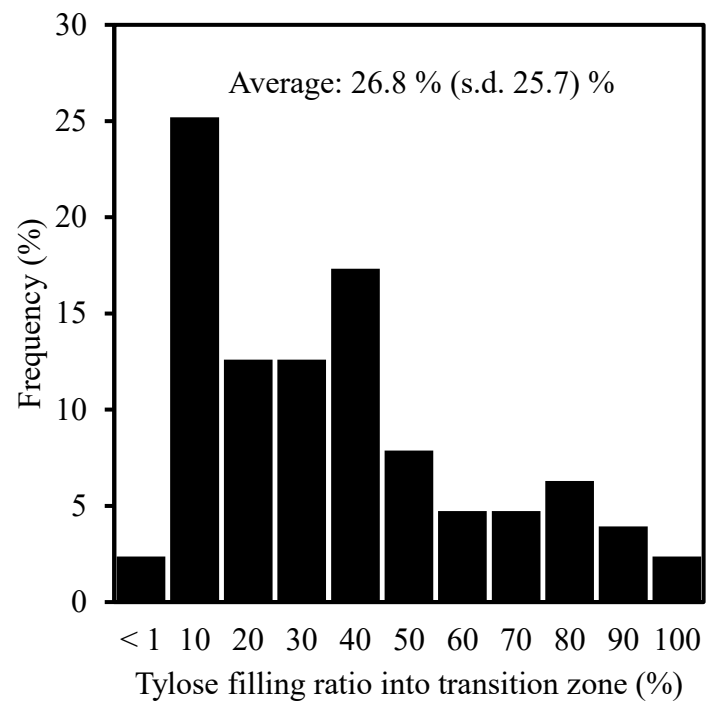


Figure 6. Frequency of the tyloses filling ratio in the transition zone.

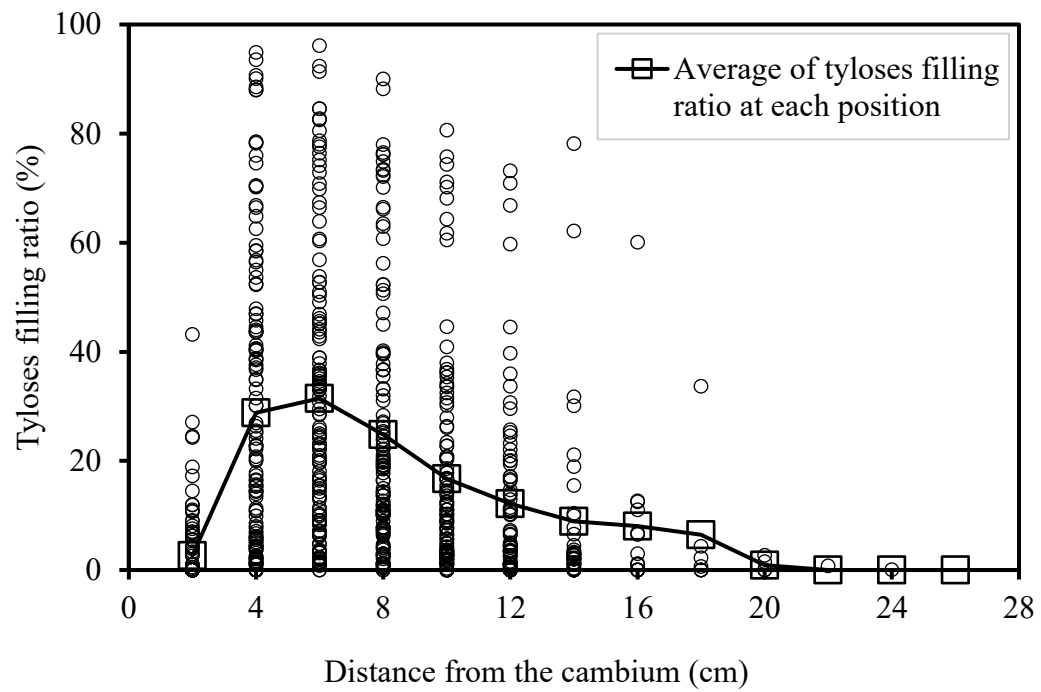


Figure 7. The tyloses filling ratio (TFR) with distance from the cambium. The line in the figure shows the average TFR for all trees.

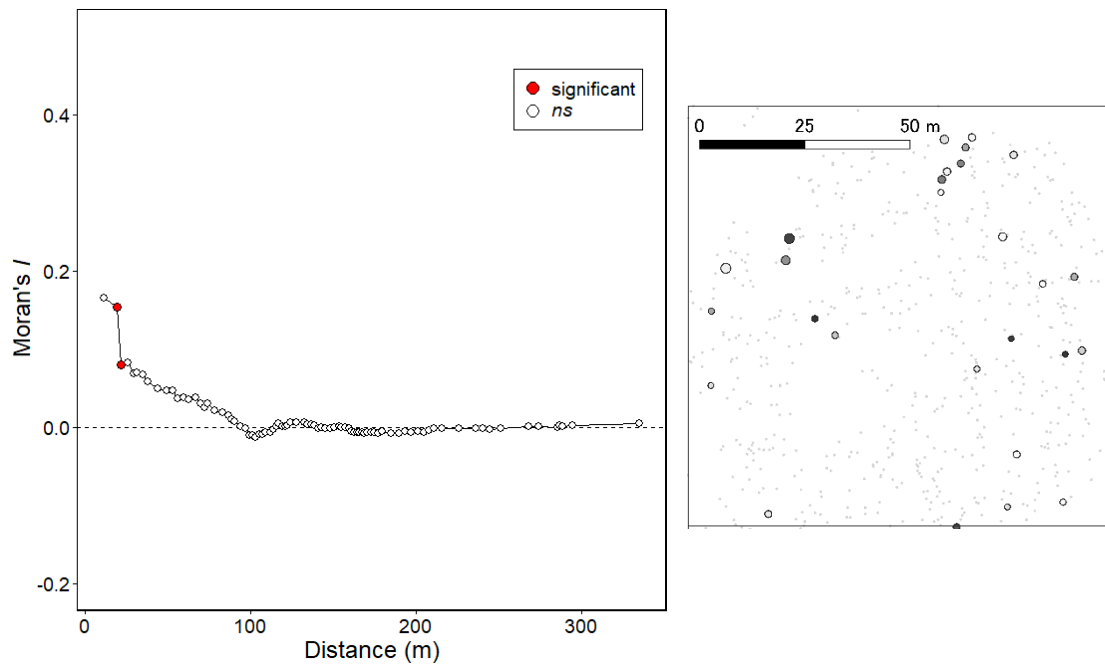


Figure 8. Correlogram of Moran's I for the tyloses filling ratio in transition zone (TFRtr), along with the distribution of trees within a 1-ha area of the study stand. The circle size represents the tree size (DBH), and darker colors indicate higher TFRtr values. The small gray dots indicate the locations of the other tree species.

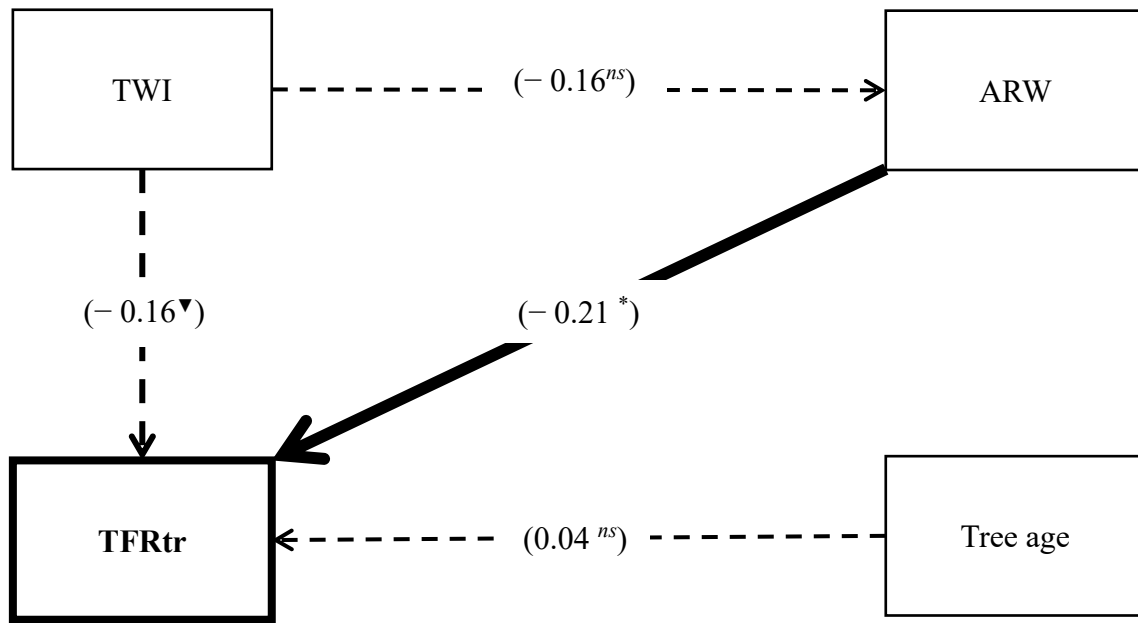


Figure 9. Structural equation modeling with standardized parameter estimates. The error arrows of the observed variables are omitted to simplify the diagram. The estimated standardized path coefficients (direct effects) are placed on each path. The thickness of a single arrowhead corresponds to the magnitude of its estimates. The dashed single arrowheads depict nonsignificant paths. ∇ : marginally significant, $*$: < 0.05 , ns : nonsignificant.

5.7 Appendices

Table A1. Means, standard deviations, and ranges of the grain angle, outer bark crack angle and tyloses filling ratio for *Quercus crispula*.

Observed variable (unit)	Description	Mean and standard deviation	Range
AGA (%)	The average grain angles from pith to cambium for individual trees.	-0.7 ± 3.8	-10.9-9.6
AGAab (%)	The absolute value of AGA for individual trees.	5.9 ± 3.3	0.2-15.8
OBCA (%)	The outer bark crack angle for individual trees.	1.9 ± 1.6	-6.0-8.0
TFR (%)	The average tyloses filling ratio from pith to cambium for individual trees.	28.1 ± 27.3	0-91.1
TFRtr (%)	The TFR in transition zone.	26.8 ± 25.7	0-96.1



Figure A1. The study site is dominated by *Q. crispula*, and most of the oaks have independent stems, suggesting that the stand is not of coppice origin.

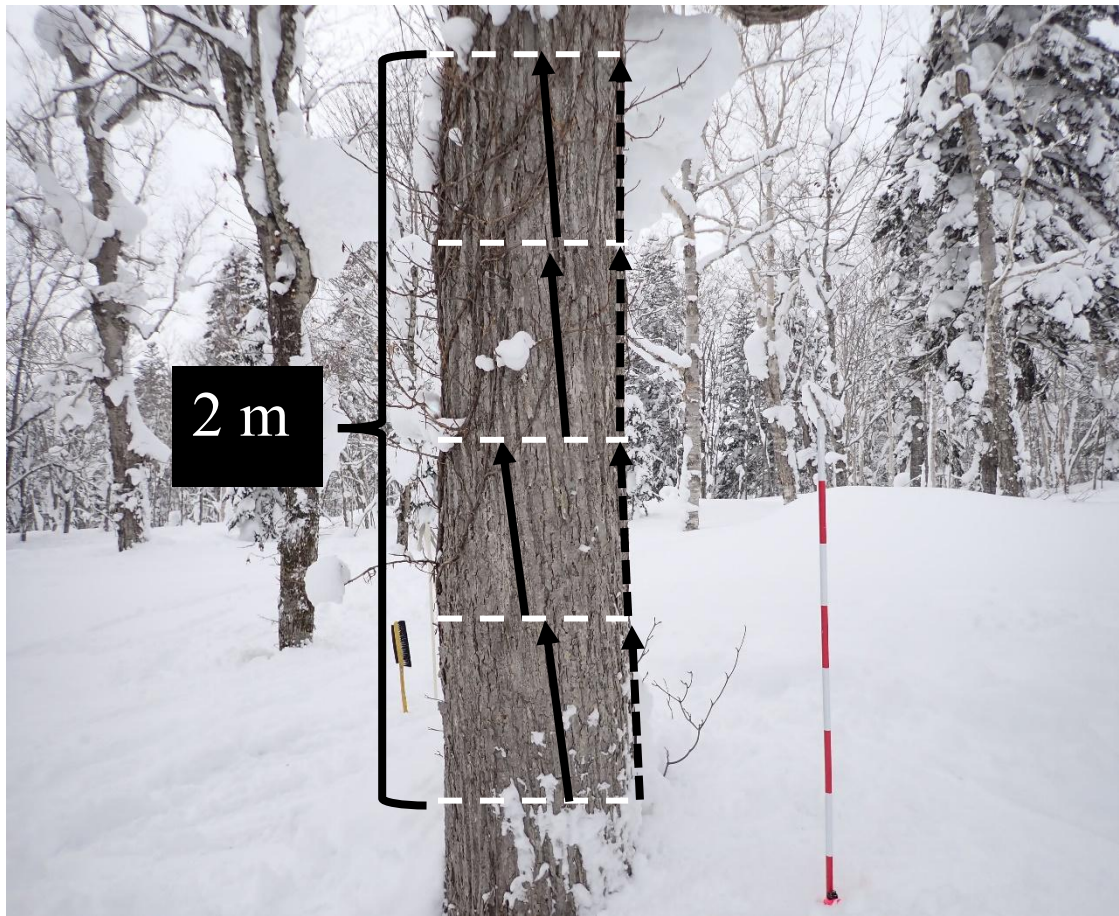


Figure A2. Measurement of the outer bark crack angle (OBCA). The stem equivalent to the first log (height 0.5-2.5 m) was divided into four vertical sections (white dashed lines), and the angle of the most representative bark crack within each section was determined (the difference between the dashed and the solid arrows). The average of these four values was then used as the OBCA for individual trees.

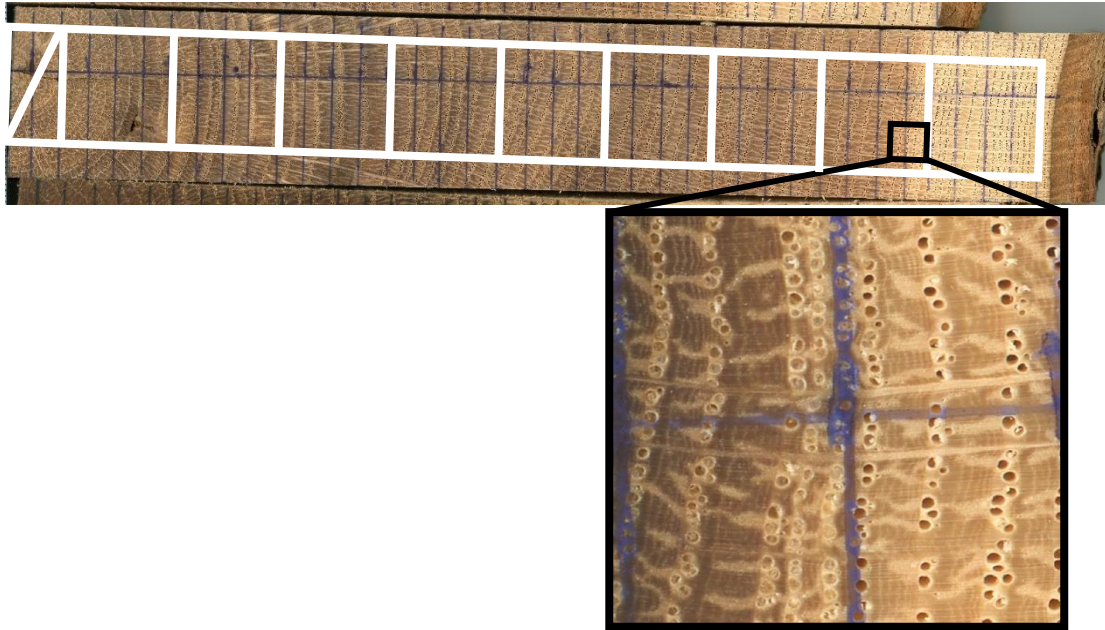


Figure A3. An example of the measurement of the tyloses filling ratio (TFR). The ratio of earlywood vessels filled with tyloses to the total number of vessels was calculated for each 4 cm² (white square) from the cambium.

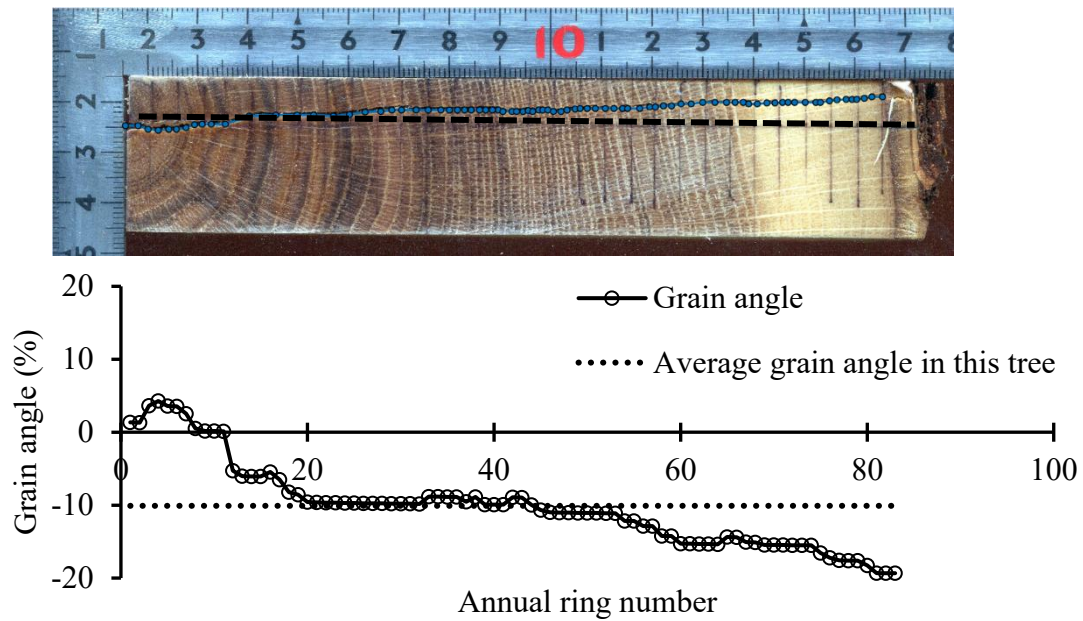


Figure A4. An example of the measurement of the grain angle (GA) of each individual tree via the splitting method. The dashed line is the reference line that passes through the pith to the cambium. The dots indicate the positions of the splitting lines for each annual ring boundary. The deviation from the reference line is recorded for each annual ring, as shown in the figure below.

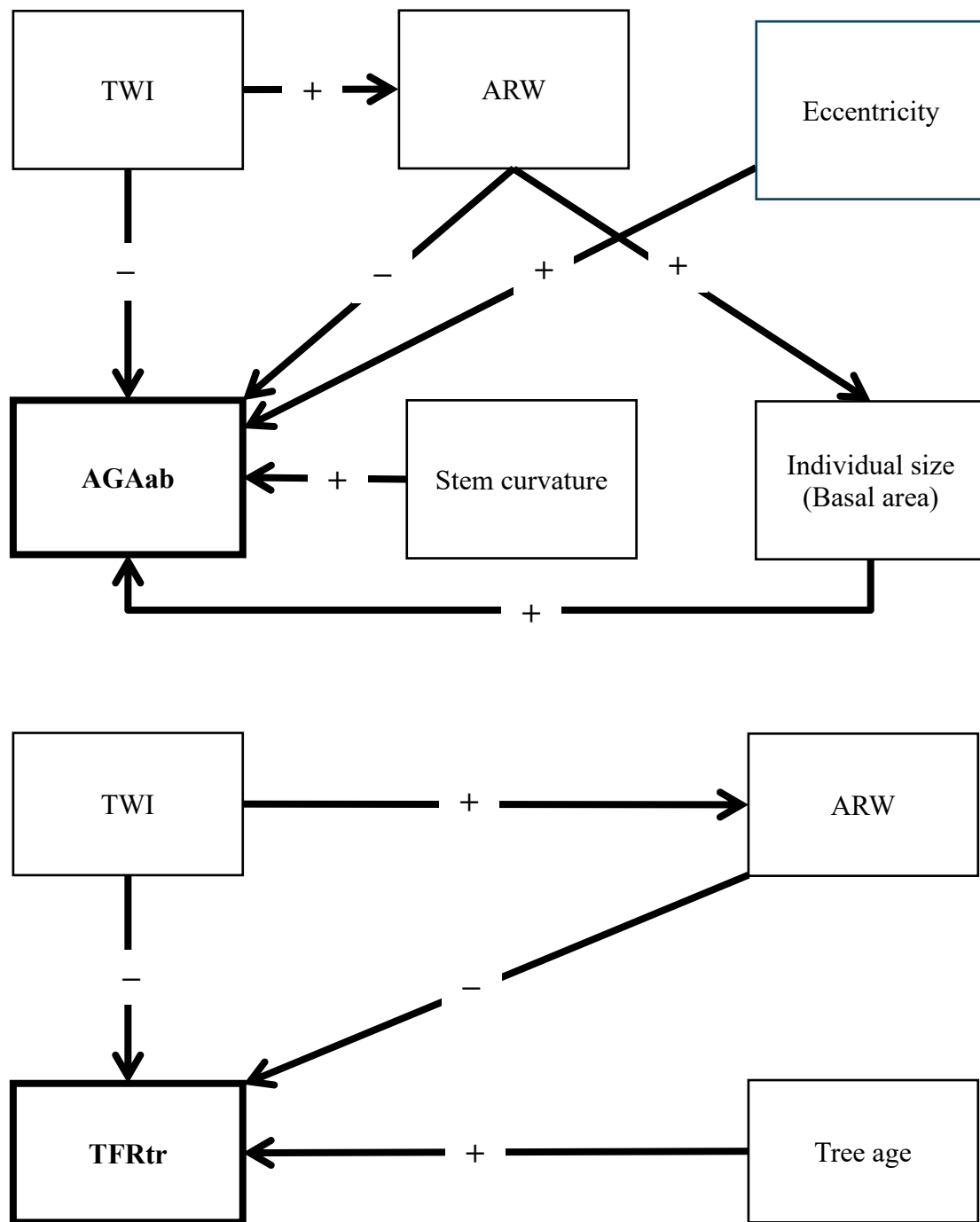


Figure A5. Hypothetical models to explain the average grain angle of absolute value (AGAab) and the tyloses filling ratio in transition zone (TFRtr). The direct or indirect pathways for each factor on AGAab and TFRtr are shown. The signs (+ or -) indicate the expected directions or relationships.

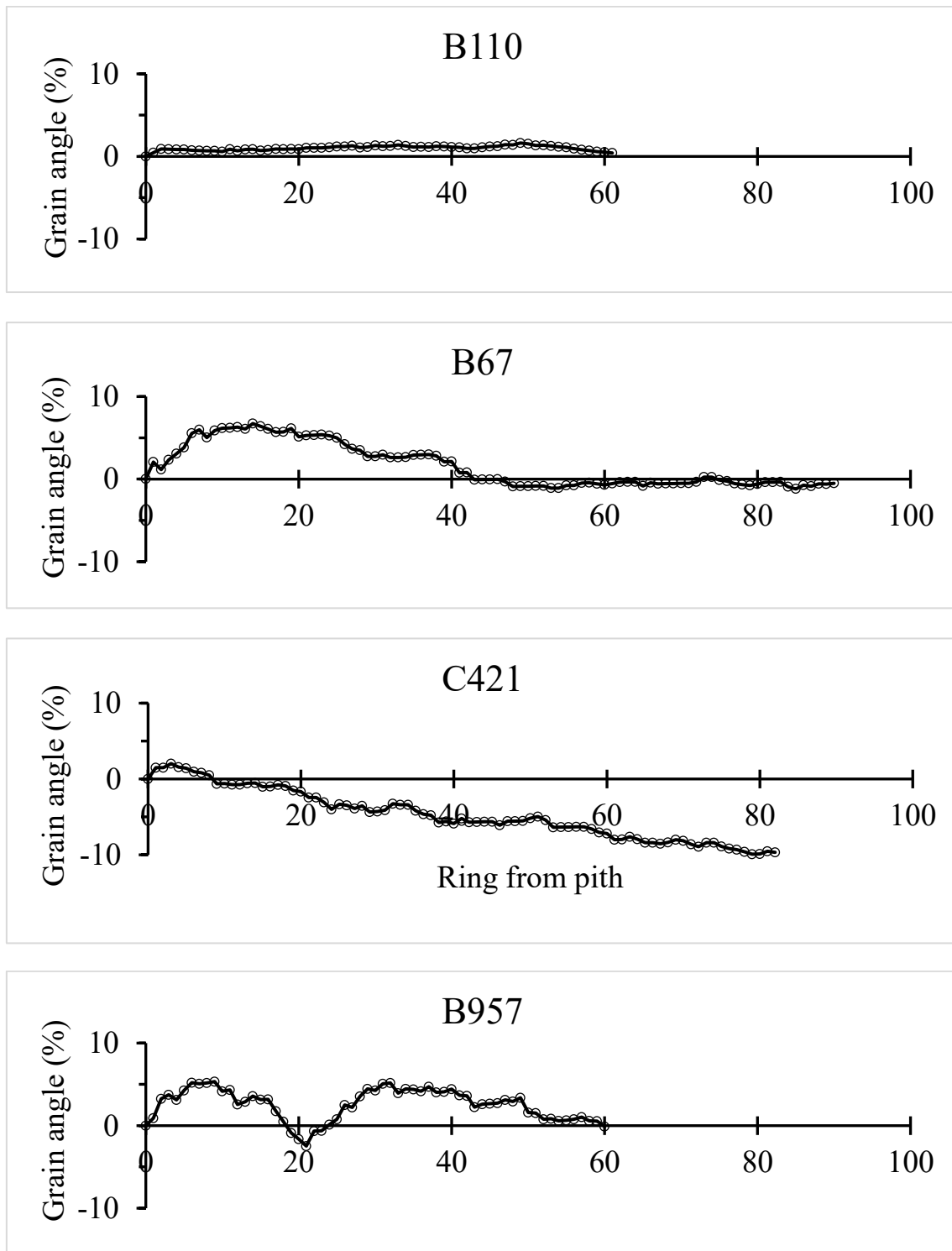


Figure A6. Examples of the grain angle for each annual ring in individual trees.



Chapter 6

General Discussion

6.1 Toward species-specific hardwood silvicultural management to improve profitability

This doctoral dissertation represents the first study to elucidate the relationships between key wood properties essential for improving the profitability of hardwood forest management and the growth conditions including site condition of individual trees, by integrating silvicultural approaches—analyzing tree growth and site factors—with wood science techniques. In particular, by analyzing wood properties that affect the profitability of major hardwood species in Hokkaido—such as *B. platyphylla*, *B. ermanii*, *A. pictum*, and *Q. crispula*—and their potential responses to silvicultural practices, this study provides practical insights for managing hardwood forests to improve economic returns while preserving the long-term value of natural hardwood resources.

Overall, the results indicate that the optimal management objective (e.g., promoting diameter growth vs. maintaining slow, steady growth) differs among species, and even local site factors. For example, growth enhancing interventions—such as thinning—appear broadly compatible with defect control and wood quality in species like *B. platyphylla*, *B. ermanii* and *A. pictum*, where accelerated growth did not increase key defects or reduce mechanical properties (Chapter 2, 3, 4). However, the implications of thinning are more complex in hardwood stands than in softwood plantations. Whereas softwood silviculture often emphasizes thinning to enhance growth rates (Rio et al., 2017), hardwood species such as *Quercus* spp. require careful consideration of issues like

epicormic branching (Attocchi 2013); thus, lower intensity but more frequent thinning is generally recommended (Kerr 1996). Indeed, for *Q. crispula*, slow and stable growth proved essential for developing traits desirable for barrel timber (low grain angle and high tyloses filling), and excessive growth stimulation may degrade target wood quality (Chapter 5).

Local site conditions significantly influenced several wood properties, highlighting the importance of appropriate site selection in management planning. Site moisture availability, in particular, is understood to affect both tree growth and wood formation (Gruber et al., 2010; Eilmann et al., 2011; Pandey 2021). Although the sites examined in this dissertation were located on gentle terrain with limited topographic variation, the results still showed that even small differences in local site conditions frequently affected wood properties. Thus, even when identical silvicultural treatments are applied, their effects may be weakened or altered depending on the site condition. Therefore, in natural hardwood forests containing multiple species, management methods must be optimized according to the target species and desired wood properties.

This chapter first discusses the silvicultural implications for each species based on the results presented in the preceding chapters. It then synthesizes these findings to consider their broader implications for hardwood forestry, followed by a discussion of the limitations of the present research and directions for future studies. Finally, as the conclusion of this dissertation, the chapter emphasizes the importance of research that bridges the boundary between silviculture and wood science.

6.2 General implications for silvicultural management

6.2.1 *Thinning methods and tree selection criteria for improving key wood properties*

The four hardwood species examined in this study—*B. platyphilla*, *B. ermanii*, *A. pictum* and *Q. crispula*—showed both shared and species-specific relationships between wood properties, growth characteristics, and site conditions. In this section, I will discuss thinning for each tree species, primarily in relation to growth characteristics.

Both *B. platyphilla* and *B. ermanii* are typical pioneer species, and their rapid growth and abundant resources make them suitable for management aimed at mass timber production (Osumi 2005; Aoyama et al., 2009; Aoyama et al., 2011; Yamazaki and Yoshida 2018). Although there has been no clear management guideline for these species due to their historical lack of active silvicultural intervention (Shimase 2014; Ito et al., 2018), they can be considered species for which heavy-rotation management, taking advantage of their fast growth, is required to produce large quantities of logs. For *Betula* spp., it is generally recommended to conduct intensive cleaning cutting (removing over 90% of stem density) at relatively early stages of stand development (Sano and Shibuya 2015). In this context, conventional thinning methods typically select dominant trees based on indicators such as tree form and crown development to achieve both rapid growth and high-quality timber in the future (Cameron, 1996; Skovsgaard et al., 2021).

Results from this study suggest that, in *B. platyphilla*, forest management aimed at promoting growth, such as thinning, is effective in suppressing defects like false heartwood (Chapter 2). The underlying mechanism is likely that reduced competition within the stand improves crown development and tree vigor, thereby lowering the risk of false heartwood formation (Table 1).

Similarly, in *B. ermanii*, wood density, which is closely related to timber strength, showed no significant dependence on diameter or ring width, suggesting that growth promotion does not negatively affect wood density (Chapter 3; Table 1). This

indicates that silvicultural interventions, such as thinning, could enhance growth rates and improve productivity without compromising wood quality.

In the natural forests of Hokkaido, *A. pictum* and *Q. crispula* are major species that dominate the middle to late stages of stand development (Ishikawa and Ito 1988). Compared with early-successional pioneers such as *Betula* spp., both species grow more slowly and exhibit higher shade tolerance, and they are therefore commonly found in more advanced secondary forests (Anzai et al., 2023). As with other hardwood species, timber from *Acer* spp. and *Quercus* spp. is generally harvested from natural forests (Puettmann et al., 2015; Schütz et al., 2016); however, given their ecological importance and the high value of their wood, research aimed at developing plantation-based management has been expanding (Naji et al., 2015; Nicolescu et al., 2025). These studies have shown that, in general, lower planting densities result in significantly wider ring widths and larger stem diameters than higher planting densities (Naji et al., 2015; Nicolescu et al., 2025), and that retaining high-vigor trees during thinning is a rational strategy due to their lower mortality risk (Río et al., 2025). Nevertheless, although thinning effectively promotes growth by reducing competition, producing high-quality timber still requires a long rotation—sometimes more than 120 years—and intensive interventions to control stem form and suppress epicormic branching (Nicolescu et al. 2025). Such intensive management inevitably increases costs. Therefore, a wider range of management options will be needed in the future to ensure that the value of the final products justifies these costs.

The figured wood of maples, and the oaks wood suitable for barrel, both examined in this study, possess exceptionally high added value and are traded at premium prices (Bragg 2006; Krajnc et al. 2015; Alamo-Sanza and Nevares, 2018; Quambusch et

al. 2021; Ruppitsch et al. 2021; Kim et al. 2024). In *A. pictum*, the proportion of figured wood (PFW) was positively related to indicators of stem distortion such as stem curvature and fork height, while it showed little dependence on growth rate (Chapter 4; Table 1). This suggests that figured wood formation is primarily driven by local mechanical stress or irregular cambial activity rather than by growth itself. Importantly, growth-promoting management such as thinning is unlikely to reduce the occurrence of figured wood, implying that both productivity and high-value timber yield can be achieved concurrently. In practical silviculture, however, it is not feasible to manage stands exclusively for the retention of trees with figured wood (Bragg 2006). Within the broader objective of producing high-quality saw logs—trees that are large in diameter and straight—an optional strategy would be to retain individuals that would normally be removed, such as those with crooked stems or low fork heights, thereby increasing the likelihood of future figured logs without compromising overall stand quality.

In contrast, the case of *Q. crispula* was markedly different. This species requires stable, slow growth to achieve the characteristics suitable for barrel timber, such as low grain angle and a high tyloses filling ratio (Chapter 5). Both characteristics were associated with trees that exhibited minimal wood eccentricity and gradual, steady growth, implying that rapid diameter expansion may interfere with the formation of desirable anatomical properties (Table 1). Consequently, heavy thinning or other interventions that drastically accelerate growth are likely to reduce wood quality for barrel timber. This finding is consistent with conventional silvicultural practices that recommend frequent, low intensity thinning to control stem form and suppress epicormic branching.

6.2.2 Site selection for improving key wood properties

This section discusses suitable site conditions for improving key wood properties in each species, with site conditions primarily represented by the degree of site moisture. Although the primary approach should be to manage stands in a way that promotes steady diameter increment, growing trees in locations identified as suitable based on ecological conditions and the findings of the present study have significance in increasing the probability of producing high-value timber.

First, even within the same *Betula* spp., suitable sites are differentiated by ecological niches and thus differ between *B. platyphilla* and *B. ermanii*. For *B. platyphilla*, the ecologically suitable growth range extends from mesic to slightly dry conditions, whereas for *B. ermanii* it ranges from mesic to dry conditions (Forest agency research and extension division 1981; Tanimoto 1990). The results of this study showed that false heartwood, a major defect in *B. platyphilla*, was smaller under wetter site conditions. This suggests that, when selecting sites as a silvicultural strategy to suppress false heartwood formation in *B. platyphilla*, mesic environments close to its ecological optimum—such as areas nearer to valley bottoms rather than ridges—are recommended.

In contrast, for *B. ermanii*, this study revealed that wood density was higher at relatively dry sites. This finding suggests that, if the objective is to cultivate *B. ermanii* with high wood density suitable for professional baseball bats, selecting relatively dry sites, particularly ridge positions, would be advantageous.

For *A. pictum*, although the direct relationship between figured wood and site moisture was not explicitly examined, the observed strong positive relationship between figure occurrence and stem form allows an indirect interpretation. Trees with crooked stems, which are often associated with sloping sites (Matsuzaki et al. 2006), showed a higher proportion of figured wood, particularly when stem curvature was strong or forks

occurred near the sampling position. This suggests that selecting sites with slopes within a practicable range may be an effective approach to increasing the occurrence of figured stems.

For *Q. crispula*, the results showed that site moisture did not affect grain angle, whereas it had a negative effect on the tyloses filling ratio. In other words, drier sites are more favorable in terms of suitability for barrel timber. Accordingly, *Q. crispula* intended for barrel production is recommended to be cultivated on relatively dry ridge sites rather than in valley bottoms. The ecologically suitable growth range of *Q. crispula* is reported to extend from slightly dry to dry conditions (Mizutani et al., 2022). Therefore, the present result—that cultivation on relatively dry ridge sites is preferable—is consistent with the species-specific ecological growth optimum.

Overall, the results of this study indicate that the key wood properties of the four hardwood species were related to individual growth or site conditions but were not necessarily compatible with existing management methods. These findings suggest that, although traditional silvicultural practices often leave the outcomes to chance, adjusting management according to the growth characteristics of each species may increase the likelihood of achieving the desired wood properties.

6.3 Future studies

6.3.1 *Issues for future research*

Building on the findings of this study, several issues remain to be addressed and should be prioritized in future research. First, although this study focused on environmental and growth-related factors, genetic variation among individuals may also contribute to wood property differences (McKenna et al., 2015; Nakada et al., 2024). Natural regeneration in

hardwood forests often results in high genetic diversity, influencing growth vigor, stem form, and other wood traits (Gerwein 2006). For example, wind-pollinated, small-seeded species such as *B. platyphylla*—and similarly *B. ermanii*—are expected to show relatively high within-stand genetic diversity (Chen et al., 2021; Inatsu et al., 2021). While false heartwood occurrence is unlikely to be directly controlled by genetics, traits like vigor or branch shedding may be affected. While previous studies have shown that wood density of *Betula* spp. does not differ among seed sources at broad geographic scales (Viherä-Aarnio and Velling 2017), it remains unclear whether genetic effects exist at finer spatial scales—for instance, within a single stand. Indeed, in Chapter 3 of this study, wood density exhibited spatial autocorrelation within a limited range. Whether this pattern reflects localized topographic factors or spatial structure arising from the relationship genetic relatedness cannot be determined without direct genetic assessment. In *A. pictum*, no relationship was found between spatial proximity and the occurrence of figured wood. Given that physical proximity often reflects genetic relatedness (Vekemans and Hardy 2004; Seidler and Plotkin 2006; Manel et al., 2003), this suggests that genetic effects may be weak. Nevertheless, previous studies on maples have shown that figure formation can be inherited through clonal or parent–offspring relationships, implying that genetic factors may still play a role (McKenna et al., 2015; Bäucker and Liesebach, 2018; Quambusch et al., 2021). Thus, the relative importance of stem-form–related mechanical influences versus genetic inheritance remains unresolved. In oak species, limited dispersal distances of acorns (Carabaña et al., 2007; Sandurska et al., 2024), results in patch structures (approximately 40–50 m within stands in case of *Q. crispula*; Ubukata et al., 1999). Even so, both traits related to cooperage suitability—grain angle and tyloses filling ratio—showed very limited or no spatial autocorrelation in this study. This

indicates that local relatedness does not strongly determine these wood properties. However, because spatial pattern analysis provides only an indirect indication of genetic structure, more direct methods are required in future studies to detect potential genetic influences. If genetic effects are identified, understanding how such genetic variation interacts with wood property variation will be essential for refining predictive models for silvicultural management. In this context, future genetic analyses would serve as a complementary layer to the present findings rather than an alternative explanation. By combining genetic information with the current findings (patterns between growth, stem form, and wood properties), it will be possible to develop a more integrated and mechanistic framework for understanding and managing wood quality variation in natural hardwood forests.

Next, one limitation of this study is that the analysis for each species was conducted within a single stand, and thus the range of environmental conditions examined—such as topography—was relatively limited. From a practical forestry perspective, however, the stands examined in this study encompasses site conditions commonly targeted in operational management, as areas with extreme site heterogeneity are typically excluded. To generalize the findings and evaluate the robustness of the observed relationships, future research should nonetheless incorporate multiple stands differing in climatic and edaphic conditions, management history, and competitive environments, thereby enabling a broader assessment of how large-scale environmental heterogeneity shapes wood property variation, particularly at the species level. In addition, to translate the present findings into practical forest management, it will be important to develop pilot silvicultural treatments grounded in the relationships detected here—for example, site selection involving moderate slopes, thinning regimes that adjust growth

rates, or targeted retention of trees with favorable stem form. Implementing such trial treatments across contrasting environments and conducting long-term monitoring of growth and wood-property development would help verify whether the patterns observed in this single stand hold under operational conditions, ultimately providing a more robust foundation for applying these insights to management and value-enhancement strategies.

Another limitation lies in the scope of the stem sampling, which was restricted to a limited portion of each tree in this study. Wood properties may vary considerably along the vertical and radial axes of the stem (Giroud et al. 2008; Belleville et al. 2011). For example, in *B. platyphylla*, the proportion of false heartwood reaches its maximum at approximately 9.7% of relative tree height from the stem base and then gradually decreases toward the upper stem (Chapter 2), whereas vertical variation in wood density remains unknown for *B. ermanii*. In European birch (*Betula pendula*), it has been reported that wood density is highest in both the lower and upper parts of the stem, with differences of nearly 50 kg/m³ compared with intermediate sections (Dobrowolska et al., 2020). This has important implications for determining where logs should be cut in harvesting operations. Likewise, for *A. pictum*, understanding how figure appears along the entire log is essential for establishing criteria for selecting and cutting high-value logs in the field. For *Q. crispula*, grain angle and the tyloses filling ratio are directly linked to cooperage performance, where leakage leads to substantial losses; therefore, assessing cooperage suitability across a certain vertical range of the stem is necessary. Nevertheless, sampling positions in this study were deliberately selected from stem sections most relevant for evaluating wood properties of the first log, which generally represents the highest-value portion of the stem. Despite its limited sampling extent, the present study provides a meaningful and targeted foundation for guiding more detailed assessments of

intra-tree variability. Building on this foundation, subsequent studies should incorporate vertical and radial variations within stems using more detailed sampling to obtain a more complete picture of intra-tree variability.

6.3.2 Perspectives for future study

Although the wood properties examined in this study represent major factors that can enhance the market value of these species (Bragg 2006; Baral et al., 2013; Krajnc et al. 2015; Alamo-Sanza and Nevares, 2018; Tomita et al., 2020; Quambusch et al. 2021; Ruppitsch et al., 2021; Kim et al., 2024), incorporating other traits—such as wood color, heartwood size, and grain characteristics—into silvicultural planning would further expand their potential uses (Damayanti et al., 2020; Makoto et al., 2021). Moreover, while the species investigated here include representative pioneers and late-successional hardwood that are in high demand in Hokkaido, many other valuable hardwood species also exist, such as *Kalopanax septemlobus* and *Fraxinus mandshurica*., which are popular for furniture, as well as *Tilia japonica*, which is widely used for plywood. To advance sustainable hardwood forest management, it will be essential to consider wood-property variation in these highly valued species—those that tend to be harvested preferentially—in order to ensure a sustained and reliable supply of timber resources and to maintain diverse forest structure (Barrette et al., 2023; Nocetti and Brunetti 2024). Long-term field experiments that integrate genetic, physiological, and silvicultural perspectives—conducted across diverse tree species and their varied wood properties—would provide the basis for establishing management systems that harmonize timber quality, productivity, ecosystem diversity, and long-term sustainable use.

6.3.3 Silviculture focusing on wood properties of hardwoods

In softwood plantations, management methods aimed at efficiency and profitability have often followed an “agricultural model,” emphasizing clear-cutting and even-aged stands (Kuuluvainen et al., 2012; Puettmann et al., 2015). Such approaches create single-layered forests with uniform species and age classes, allowing management, harvesting, and cultivation operations to be standardized and simplified. While these methods have enabled mass production and cost reduction in plantation forestry, they are increasingly misaligned with contemporary societal values. Simplified and uniform forest management has been shown to reduce biodiversity, diminish landscape value, and increase the risks of natural disasters (Potterf et al., 2024; Forzieri et al., 2024). Moreover, with ongoing climate change, maintaining species and structural diversity in managed forests will be essential to ensure a stable and resilient timber supply in the future (Hurtado et al., 2025; Pickering et al., 2025).

Sustainable forestry aims to maximize the economic value of harvestable timber while minimizing the long-term negative impacts of forest management on the forest environment (Bragg 2006). As the demand for domestic hardwoods in Japan is expected to increase in the future, integrating silvicultural and wood science perspectives will become increasingly essential for their sustainable use. However, management approaches that have been established primarily for softwood plantations are not recommended for direct application to hardwood species, which exhibit greater diversity in growth form, anatomy, and responses to environmental conditions. Direct application of such methods would not only increase silvicultural costs but could also result in reduced wood quality. Instead, silvicultural practices must be developed based on a deep understanding of the specific growth and wood property relationships of each species.

Bridging these two research domains will enable a more comprehensive understanding of how forest management influences the formation of valuable wood properties, supporting both resource utilization and conservation.

This study contributed to enhancing the feasibility of forest management aimed not only at the traditional goal of “faster and larger” production, but also at producing timber of higher value, by employing a novel approach that integrates silviculture and wood science. In particular, the wood properties examined in this study are expected to support economic stability and diversification of silvicultural practices, thereby contributing to maintaining the ecological and social values of forests.

Future modeling efforts should aim to integrate multiple objectives—timber quality, productivity, and ecosystem function—into unified silvicultural frameworks. Such interdisciplinary approaches will be essential for designing adaptive management systems that sustain both forest value and resilience under changing environmental conditions.

6.4 General conclusion

Hardwood forest management has long tended to regard “growth promotion” as the primary means of improving profitability (Rytter, 2013; Draper et al. 2021). In this study, growth promotion was found to be compatible with desirable wood properties in many cases; however, it was also shown that accelerated growth does not necessarily lead to improved wood quality across all species or all wood traits. Future management should therefore consider not only how to increase growth but also how to cultivate trees of higher value. Maximizing the value of individual trees, rather than focusing on growth alone, may contribute to more stable long-term profitability (Bragg, 2006).

In addition, enhancing the added value of hardwood timber in order to improve the overall profitability of hardwood forest management represents an effective way to make hardwood-oriented management economically viable. Such economic viability can be regarded as an important prerequisite for implementing nature-positive forestry, including initiatives related to the Taskforce on Nature-related Financial Disclosures (TNFD) and biodiversity credit schemes.

This dissertation represents an initial step toward such practice, demonstrating how quantitative relationships revealed through field data among growth characteristics, site conditions, and wood properties provide a scientific basis for future discussions on adaptive and value-oriented management of natural hardwood forests.

6.5 Table

Table 1. Growth and site conditions influencing key wood properties that contribute to improved profitability of each tree species.

Species Factors	<i>B. platyphilla</i> False heartwood	<i>B. ermanii</i> Wood density	<i>A. pictum</i> Figured wood	<i>Q. crispula</i> Barrel suitability
	■ Crown ratio : + ■ Number of branch scars : — ■ Tree size : — ■ Number of neighboring trees : —	nothing	■ Stem crookedness : + ■ Fork height : —	【Grain angle】 ■ Wood eccentricity : — ■ Annual ring width : — 【Tyloses filling ratio】 ■ Annual ring width : —
Site condition	■ Site moisture : +	■ Site moisture : —	nothing	nothing

The plus (+) and minus (–) symbols following each factor indicate the direction in which the factor acts to suppress wood defects or to enhance advantageous wood properties. For example, in *B. platyphilla*, a plus (+) sign for crown ratio indicates that a larger crown ratio contributes to the suppression of false heartwood, which is a wood defect, whereas a minus (–) sign for the number of branch scars indicates that fewer branch scars contribute to the suppression of false heartwood. In contrast, in *A. pictum*, a plus (+) sign for stem crookedness indicates that greater stem crookedness enhances the development of figured wood, which is considered an advantageous wood property.

Abstract

The use of hardwoods in Japan has generally been increasing. In particular, for species that have traditionally been used for high-value general purposes such as furniture, the demand for specialty products such as musical instruments and whiskey barrels has rapidly increased in recent years. In addition, species that had previously been limited to low-quality uses have seen an expansion in demand due to reassessment of wood quality, advances in processing technologies, and dramatic improvements in natural regeneration techniques that can greatly reduce silvicultural costs.

Despite this high demand, appropriate silvicultural systems and management practices for hardwood cultivation have not been fully established. One reason is that many hardwoods exhibit greater variability in tree form and require longer periods to reach harvestable size compared to softwoods. Simply applying plantation systems developed for softwood species often results in yields that do not justify the cost of cultivation, making sustainable forest management difficult. Therefore, hardwood silviculture requires an approach different from that used for softwoods, one that allows both efficient production and high profitability.

One possible solution is to cultivate the wood properties that are key to price increases during the silvicultural process, and to match them with demand for specific uses so that the cost of cultivation can be recovered. However, compared with softwoods, fundamental information on hardwood wood properties is limited, and little is known about their relationship with individual growth characteristics, site conditions, or whether these properties can be enhanced through forest management such as thinning.

This study focused on four representative hardwood species distributed in Hokkaido, Japan's largest hardwood-producing region: Japanese white birch (*Betula platyphylla*), Erman's birch (*Betula ermanii*), painted maple (*Acer pictum*), and Japanese oak (*Quercus crispula*). The objective was to clarify the relationships between key wood properties that determine the profitability of each species and their growth conditions and site characteristics. The specific wood properties addressed were: (Chapter 2) false heartwood, which is a defect in white birch; (Chapter 3) wood density, which is important for expanding new uses of Erman's birch; (Chapter 4) figured grain in painted maple, contributing to high-value products; and (Chapter 5) grain angle and tyloses formation in Japanese oak, which are important indicators of suitability for barrel production. Individual studies were conducted for each species, and based on these results, Chapter 6 presents implications for hardwood forest management.

The study was conducted at the Uryu Experimental Forest of Hokkaido University (44°21'N, 142°15'E). A common approach was applied: first, a tree-by-tree survey was conducted to record individual tree size and visible characteristics, after which the trees were harvested, and wood samples were collected linked to the individual tree information. From these samples, growth indicators such as ring number and ring width were recorded, and the samples were processed to a manageable size and shape. Key wood properties for each species were then measured, evaluated, and quantified. Direct and indirect relationships between individual growth conditions and wood properties were comprehensively analyzed using structural equation modeling.

Chapter 2 investigated false heartwood, a defect (irregular discoloration in the center of the wood) of white birch, which is increasingly used for furniture and flooring. False heartwood occurred in 80.3% (387/482) of the sampled trees. The proportion of false heartwood to cross-sectional area (false heartwood rate) was negatively affected by crown ratio and the topographic wetness index (TWI, representing local site moisture), and positively affected by branch scars and the density of surrounding trees. Among these factors, crown ratio had the strongest effect on false heartwood rate and was negatively correlated with the density of surrounding trees. These results indicate that suppressing false heartwood in white birch is compatible with growth promotion

through thinning and density management.

Chapter 3 examined wood density in Erman's birch, which has attracted attention as a potential material for baseball bats. Wood density ranged from 491.0 to 810.6 kg/m³, with a mean of 666.2 kg/m³ (SD = 67.8). There was no clear relationship with ring width or tree size, but a negative association with TWI was observed. Significant positive spatial autocorrelation was detected, indicating that neighboring trees tended to have similar wood density, consistent with a strong influence of local site conditions. The lack of constraint of wood density by growth promotion through thinning suggests that active growth promotion can be compatible with maintaining wood quality.

Chapter 4 investigated figured wood in painted maple, which is highly valued for furniture and musical instruments, and the proportion of figured area to board surface area. Figured wood occurred in 87% of trees, ranging from 0 to 46.2% with a mean of 7.0% (SD = 9.8). The proportion of figured wood was strongly positively or negatively associated with tree form characteristics, such as stem crookedness and fork height, while its relationship with ring width or tree size was weak. Since tree form is generally related to surrounding tree density, thinning may promote figured wood formation via its effect on tree form. Selectively retaining trees with strong crookedness or low fork height, which are often removed as inferior during thinning, may help cultivate higher value stands in the long term.

Chapter 5 examined fiber inclination (deviation between the tree axis and grain direction) and tyloses filling ratio (proportion of large vessels per unit area filled with tyloses) in Japanese oak, which has become increasingly demanded as whiskey barrel material. High suitability for barrel production depends on small grain angle and high tyloses filling ratio. Grain angle ranged from -10.9% to 9.6%, with a mean of -0.7% (SD = 3.8), and was most positively influenced by stem eccentricity, followed by ring width. Tyloses filling ratio ranged from 0 to 91.1%, with a mean of 26.8% (SD = 25.7), and was most negatively affected by ring width. Stem eccentricity is associated with crown asymmetry, and thinning generally opens the canopy, promoting growth and crown asymmetry. Therefore, intensive thinning may increase grain angle and reduce tyloses filling ratio. These results suggest that cultivating Japanese oak suitable for barrel production requires long-term forest management that maintains moderate competition.

From these results, it was shown that for white birch and Erman's birch, which had previously been limited to low-quality use, efficient production of general-purpose wood can be achieved by combining natural regeneration with active thinning. In contrast, for painted maple and Japanese oak, both late-successional species, management strategies for producing high-value wood differ for each species. Thus, the recommendation for active tending to ensure both quantity and quality, the fact that high-value production does not necessarily align with increased yield depending on species, and the potential to recover overlooked opportunities for profitability through revising thinning selection criteria, all underscore the need for hardwood silviculture that focuses explicitly on wood quality—an aspect insufficiently considered in conventional softwood-oriented management. This study, which integrates silviculture and wood science while taking into account species-specific wood properties and growth conditions in predominantly natural hardwood forests, provides fundamental knowledge for realizing forest management that ensures both stable supply and high value of hardwood resources.

References

Chapter 1

- Acker, J.V. 2021. Opportunities and challenges for hardwood based engineered wood products. 9th hardwood proceedings-part II. An underutilized resource: Hardwood oriented research. University of sopron press. pp-5-14.
- Akashi, N., Nitta, N., Ohno, Y. 2021. Effect of forest management on understory vascular plants in planted *Abies sachalinensis* forests. *For. Ecol. Manag.* 497: 119521. DOI: <https://doi.org/10.1016/j.foreco.2021.119521>.
- Akashi, N., Unno, A., Uno, H. 2022. The browsing ratio as an index of the impact of deer browsing on tree seedlings. *Trees, Forests and People.* 8: 100276. DOI: <https://doi.org/10.1016/j.tfp.2022.100276>.
- Alamo-Sanza, M., Nevares, I. 2018. Oak wine barrel as an active vessel: A critical review of past and current knowledge. *Crit. Rev. Food Sci. Nutr.* 58 (16): 2711-2726. DOI: 10.1080/10408398.2017.1330250.
- Asada, I., Yamazaki, H., Yoshida, T. 2017. Spatial patterns of oak (*Quercus crispula*) regeneration on scarification site around a conspecific overstory tree. *For. Ecol. Manag.* 393: 81-88. DOI: <http://dx.doi.org/10.1016/j.foreco.2017.03.011>.
- Barrette, J., Achim, A., Auty, D. 2023. Impact of Intensive Forest Management Practices on Wood Quality from Conifers: Literature Review and Reflection on Future Challenges. *Current Forestry Reports* 9: 101–130. DOI: <https://doi.org/10.1007/s40725-023-00181-6>.
- Bragg, D.C. 2006. Potential contributions of figured wood to the practice of sustainable forestry. *J. Sustain. For.* 23 (3): 67-81.

- Bragg, D.C., Mroz, G.D., Reed, D.D., Shetron SG., Stokke DD. 1997. Relationship between “birdseye” sugar maple (*Acer saccharum*) occurrence and its environment. *Can. J. For. Res.* 27: 1182-1191. DOI: <https://doi.org/10.1139/x97-032>.
- Bragg, D. C. 1995. Birdseye sugar maple’s geographic range and some implications for management. *North. J. Appl. For.* 12(2): 86–89. DOI: 10.1093/njaf/12.2.86.
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., West, G. B. 2004. Toward a metabolic theory of ecology. *Ecology* 85(7): 1771–1789. DOI: 10.1890/03-9000.
- Bruck, S. R., Parajuli, R., Chizmar, S., Sills, E. O. 2023. Impacts of COVID-19 pandemic policies on timber markets in the Southern United States. *J. For. Bus. Res.* 2(1): 130–167. DOI: 10.62320/jfbr.v2i1.25.
- Deblauwe, V. 2021. Life history, uses, trade and management of *Diospyros crassiflora* Hiern, the ebony tree of the Central African forests: A state of knowledge. *For. Ecol. Manag.* 481: 118655. DOI: 10.1016/j.foreco.2020.118655.
- Duong, D., Matsumura, J. 2018. Within-stem variations in mechanical properties of *Melia azedarach* planted in northern Vietnam. *J. Wood Sci.* 64: 329–337. DOI: 10.1007/s10086-018-1725-9.
- FAO. 2020. Global Forest Resources Assessment 2020: Main Report. Food and Agriculture Organization of the United Nations, Rome. DOI: 10.4060/ca9825en.
- Forestry Agency of Japan. 2023. Annual Report on Forest and Forestry in Japan 2023. Ministry of Agriculture, Forestry and Fisheries, Tokyo.
- Forestry Agency of Japan. 2024. Annual Report on Forest and Forestry in Japan 2024.

Ministry of Agriculture, Forestry and Fisheries, Tokyo.

- Gradel, A., Sukhbaatar, G., Karthe, D. 2017. Forest management and socio-economic challenges in Mongolia. *Geogr. Environ. Sustain.* 12(3): 133–166.
- Hart, J. F. 2010. A review of the effects of silviculture on wood quality. Univ. British Columbia thesis/report. DOI: 10.14288/1.0103111.
- Hasegawa, T., Mamada, R., Yamanaka, T., Shimazaki, B., Fujihara, T. 2018. Characteristic aromas of *Quercus crispula* (Japanese Oak). *Nat. Prod. Commun.* 13(4): 475–478. DOI: 10.1177/1934578X1801300424.
- Hata, T., Inoue, M. 2023. Investigation of the responses of the timber products industry and distributors to the 2010 timber crisis in Japan. *J. For. Econ.* 69(2): 1–12. DOI: 10.20818/jfe.69.2_1.
- Hayafune, M., Higuma, Y. 2025. Trends and issues in the research of the wood industry since the 2000s. *J. For. Econ.* 71(3): 29–43. DOI: 10.20818/jfe.71.3_29.
- Hirano, Y. 2023. Development of forest policy in Hokkaido. In K. Nakajima (Ed.), *Imperial Japan and forests: Environmental protection and resource development in modern East Asia* (pp. 123–145). Keiso Shobo, Tokyo.
- Hirata, A., Sakai, T., Takahashi, K., Sato, T., Tanouchi, H., Sugita, H., Tanaka, H. 2011. Effects of management, environment and landscape conditions on establishment of hardwood seedlings and saplings in central Japanese coniferous plantations. *For. Ecol. Manag.* 262(7): 1280–1288. DOI: 10.1016/j.foreco.2011.06.025.
- Hough, 1884
- Itô, H., Hino, T., Sakuma, D. 2012. Species abundance in floor vegetation of managed coppice and abandoned forest. *For. Ecol. Manag.* 269: 99–105. DOI: 10.1016/j.foreco.2011.12.017.

International Tropical Timber Organization (ITTO). 2023. ITTO Annual Report 2023.

ITTO, Yokohama.

Kasuya, N., Sumida, A., Ikeda, N., Ueno, Y., Ueno, Y., Miyafuji, H. 2025. Growth of young *Melia azedarach* trees in abandoned farmlands as planting sites in western Japan. *Trees, Forests and People* 20: 100822. DOI: 10.1016/j.tfp.2025.100822.

Kim, D., Gollihue, J., Poovathingal, S. J., DeBolt, S. 2024. Detailed three dimensional analyses of tyloses in oak used for bourbon and wine barrels through X-ray computed tomography. *Sci. Rep.* 14: 17044. DOI: <https://doi.org/10.1038/s41598-024-67298-x>.

Macdonald, E., Hubert, J. 2002. A review of the effects of silviculture on timber quality of Sitka spruce. *For.* 75(2): 107–138. DOI: 10.1093/forestry/75.2.107.

Masaki, T., Oguro, M., Yamashita, N., Otani, T., Utsugi, H. 2017. Reforestation following harvesting of conifer plantations in Japan: Current issues from silvicultural and ecological perspectives. *Reforesta* 3: 125–142. DOI: 10.21750/REFOR.3.11.35.

Matsumura, J., Inoue, M., Yokoo, K., Oda, K. 2006. Cultivation and utilization of Japanese fast growing trees with high capability for carbon stock I: Potential of *Melia azedarach*. *Journal of the Japan Wood Research Society.* 52: 77-82. DOI: <https://doi.org/10.2488/jwrs.52.77>.

Nakajima, T., Shiraishi, N., Kanomata, H., Fukuda, Y., Higuchi, H. 2017. A method to maximise forest profitability through optimal rotation period selection under various economic, site and silvicultural conditions. *N. Z. J. For. Sci.* 47: 4. DOI: 10.1186/s40490-016-0079-6.

Nakaya, A., Osaki, H., Ohno, Y., Yoshida, T. 2024. Tree and stand characteristics

- associated with the occurrence of false heartwood in individual Japanese white birch trees. *Can. J. For. Res.* 54: 601–610. DOI: 10.1139/cjfr-2023-0213.
- Nakaya, A., Murakami, S., Ohsaki, H., Ohno, Y., Yoshida, T. 2025. Growth characteristics of standing individual Japanese oak (*Quercus crispula*) qualifying for barrel timber in a secondary forest. *For. Ecol. Manag.* 598: 123183. DOI: 10.1016/j.foreco.2025.123183.
- Ohsaki, H., Murakami, S., Akitsu, H. 2019. The timber properties of birch grown in a plantation in Atsuma, Hokkaido. *Journal of the Japan Wood Research Society.* 65(4): 189–194. DOI: 10.2488/jwrs.65.189.
- Osumi, K. 2005. Reciprocal distribution of two congeneric trees, *Betula platyphylla* var. *japonica* and *Betula maximowicziana*, in a landscape dominated by anthropogenic disturbances in northeastern Japan. *J. Biogeogr.* 32: 2057–2068. DOI: 10.1111/j.1365-2699.2005.01368.x.
- Palanisamy, K., Gireesan, K., Nagarajan, V., Hegde, M. 2009. Selection and clonal multiplication of superior trees of teak (*Tectona grandis*) and preliminary evaluation of clones. *J. Trop. For. Sci.* 21(2): 168–174.
- Pillow, M.Y. 1955. Detection of figured wood in standing trees. Research Paper No. 2034. USDA Forest Service, Forest Products Laboratory, Madison, WI. 8 p.
- Quambusch, M., Bäucker, C., Haag, V., Meier-Dinkel, A., Liesebach, H. 2021. Growth performance and wood structure of wavy grain sycamore maple (*Acer pseudoplatanus* L.) in a progeny trial. *Ann. For. Sci.* 78: 15. DOI: <https://doi.org/10.1007/s13595-021-01035-6>.
- Sano, Y., Shibuya, M. 2015. Thinning effect on tree growth in secondary *Betula ermanii* stands on scarified sites. *J. Jpn. For. Soc.* 97(1): 25–29. DOI: 10.4005/jjfs.97.25.

- Savidge, RA. 2003. Tree growth and wood quality. In: Wood Quality and Its Biological Basis. Oxford: Blackwell Science, pp.1-29.
- Shimase, T. 2021. Status and prospects of locally grown birch (*Betula* sp.) wood demand in Hokkaido, Japan. *Boreal For. Res.* 69: 35–37.
- Suzuki, S.N., Sakaue, D., Goto, S., Owari, T. 2025. Management Practices for Natural Regeneration and Plantations. In: Owari, T., Suzuki, S.N., Tanaka, N., Fukui, D. (eds), *Integrative Forest Management and Silviculture: Harmonizing Conservation and Production*. Ecological Research Monographs, Springer, Singapore, pp. 151–174. DOI: 10.1007/978-981-95-1017-7_5.
- Terada, T., Yokohari, M., Bolthouse, J., Matsumoto, R. 2010. A citizen-based maintenance scheme for suburban satoyamas based on the Forest Working Plan. *Journal of Rural Planning Association* 29: 179–184. DOI: 10.2750/arp.29.179.
- Tomita, N., Murata, K., Nakamura, M., Akitsu, H., Ohsaki, H. 2020. Evaluation of the suitability of Dakekanba wood for baseball bats (Use of Dakekanba wood for baseball-bats). *Journal of Wood Science.* 66(1): 39–45. DOI: 10.2488/jwrs.66.39.
- Utsumi, M., Murata, K., Umemura, K., Yoshimura, T., Hattori, K., Nakamura, M. 2019. Mechanical properties and biological performance of particle board made of sendan (*Melia azedarach*). *BioResources* 14(2): 4100–4109. DOI: 10.15376/biores.14.2.4100-4109.
- Watanabe, S. 2003. Evaluation and Problems of Natural Forest Management. *Journal of the Japanese Forestry Society* 85(3): 273–281. DOI: 10.11519/jjfs1953.85.3_273.
- Woxblom, A., Nylinder, M. 2010. Industrial utilization of hardwood in Sweden.

Ecological Bulletins 53: 43–50.

- Yamaura, Y., Akashi, N., Unno, A., Ozaki, K., Tsushima, T., Nagasaka, A., Nagasaka, Y., & others. 2018. Retention Experiment for Plantation Forestry in Sorachi, Hokkaido (REFRESH): A large-scale experiment for retaining broad-leaved trees in conifer plantations. Bulletin of FFPRI (Forest and Forest Products Research Institute Bulletin) 17(1): 91–109.
- Yamazaki, H., and Yoshida, T. 2018. Significance and limitation of scarification treatments on early establishment of *Betula maximowicziana*, a tree species producing buried seeds: effects of surface soil retention. J. For. Res. 23(3): 166–172. Doi:10.1080/13416979.2018.1452458.
- Yamazaki, H., Yoshida, T. 2020. Various scarification treatments produce different regeneration potentials for trees and forbs through changing soil properties. Journal of Forest Research 25(1): 41–50. DOI: 10.1080/13416979.2019.1706798.
- Yoshida, T., Yamazaki, H., Miyamoto, T. 2022. Scarification with surface soil replacement can promote understory reinitiation as well as the growth of a secondary birch stand. Journal of Forest Research 28(1): 51–56. DOI: 10.1080/13416979.2022.2090669.

Chapter 2

- Aoyama, K., Yoshida, T., and Kamitani, T. 2009. An alternative of soil scarification treatment for forest restoration: effects of soil replacement. *J. For. Res.* **14**(1): 58–62. Doi:10.1007/s10310-008-0105-5.
- Arač, K., Orlović, J.K., and Diminić, D. 2021. Effect of fungus *Meripilus giganteus* (Pers.) P. Karst. On occurrence and development of false heartwood and rot in *Fagus sylvatica* L. round wood. *Croat. J. For. Eng.* **42**(3): 529–542. Doi:10.5552/crojfe.2021.885.
- Baral, S.K., Schneider, R., Pothier, D., and Berninger, F. 2013. Predicting sugar maple (*Acer saccharum*) discoloured wood characteristics. *Can. J. For. Res.* **43**(7): 649–657. Doi:10.1139/cjfr-2013-0017.
- Basham, J.T. 1991. Stem decay in living trees in Ontario's forests: a user's compendium and guide. Forestry Canada, Ontario Region, Sault Ste. Marie, Ontario, Information Report O-X-408.
- Belleville, B., Cloutier, A., and Achim, A. 2011. Detection of red heartwood in paper birch (*Betula papyrifera*) using external stem characteristics. *Can. J. For. Res.* **41**(7): 1491–1499. Doi:10.1139/x11-080.
- Beven, K.J., and Kirkby, M.J. 1979. A physically based, variable contributing area model of basin hydrology. *Hydrol. Sci. Bull.* **24**(1): 43–69. Doi:10.1080/02626667909491834.
- Campbell, W.A., and Davidson, R.W. 1941. Red heart of paper birch. *J. For.* **39**(1): 63–65. Doi:10.1093/jof/39.1.63.
- Chi, X., Tang, Z., Xie, Z., Guo, Q., Zhang, M., Ge, J., Xiong, G., and Fang, J. 2015. Effects of size, neighbors, and site condition on tree growth in a subtropical

- evergreen and deciduous broad-leaved mixed forest, China. *Ecol. Evol.* **5**(22): 5149–5161. Doi:10.1002/ece3.1665.
- Drouin, M., Beauregard, R., and Duchesne, I. 2009. Variability of wood color in paper birch in Quebec. *Wood Fiber Sci.* **41**(4): 333–345.
- Giroud, G., Cloutier, A., and Alteyrac, J.M. 2008. Occurrence, proportion, and vertical distribution of red heartwood in paper birch. *Can. J. For. Res.* **38**(7): 1996–2002. Doi:10.1139/X08-043.
- Giroud, G., Duchateau, E., Auger, I., Havreljuk, F., and Barrette, J. 2021. Regional variation in wood discoloration in paper birch trees. *Can. J. For. Res.* **51**(10): 1512–1520. Doi:10.1139/cjfr-2020-0475.
- Hallaksela, A.M., and Niemistö, P. 1998. Stem discoloration of planted silver birch. *Scand. J. For. Res.* **13**(1-4): 169–176. Doi:10.1080/02827589809382973.
- Hasenauer, H., and Monserud, R.A. 1996. A crown ratio model for Austrian forests. *For. Ecol. Manag.* **84**(1): 49–60. Doi:10.1016/0378-1127(96)03768-1.
- Havreljuk, F., Achim, A., and Pothier, D. 2013. Regional variation in the proportion of red heartwood in sugar maple and yellow birch. *Can. J. For. Res.* **43**(3): 278–287. Doi:10.1139/cjfr-2012-0479.
- Hemery, G.E., Savill, P.S., and Pryor, S.N. 2005. Applications of the crown diameter–stem diameter relationship for different species of broadleaved trees. *For. Ecol. Manag.* **215**(1): 285–294. Doi:10.1016/j.foreco.2005.05.016.
- Hofmann, T., Guran, R., Zitka, O., Visi-Rajczi, E., and Albert, L. 2022. Liquid chromatographic/mass spectrometric study on the role of beech (*Fagus sylvatica* L.) wood polyphenols in red heartwood formation. *Forests* **13**(1): 10. Doi:10.3390/f13010010.

- Hörnfeldt, R., Drouin, M., and Woxblom, L. 2010. False heartwood in beech *Fagus sylvatica*, birch *Betula pendula*, *B. papyrifera* and ash *Fraxinus excelsior* – an overview. *Ecol. Bull.* **53**: 61–76.
- Jönsson, M.T., Fraver, S., Jonsson, B.G., Dynesius, M., Rydgård, M., and Esseen, P.A. 2007. Eighteen years of tree mortality and structural change in an experimentally fragmented Norway spruce forest. *For. Ecol. Manag.* **242**(2): 306–313.
Doi:10.1016/j.foreco.2007.01.048.
- Knoke, T. 2003. Predicting red heartwood formation in beech trees (*Fagus sylvatica* L.). *Ecol. Model.* **169**(2): 295–312. Doi:10.1016/S0304-3800(03)00276-X.
- Knoke, T., and Wenderoth, S.S. 2001. Ein ansatz zur beschreibung von wahrscheinlichkeit und ausmaß der farbkernbildung bei buche (*Fagus sylvatica* L.). *forstwiss. Cent. Ver. Mit Tharandter Forstl. Jahrb.* **120**(1): 154–172.
Doi:10.1007/BF02796089.
- Koch, G. 2004. Eigenheiten des rotkerniges buchenholzesed. Bundesforschungsanstalt für Forst- und Holzwirtschaft, Hamburg, German.
- Kohler, H. 2006. Die farbverkernungssysteme der rotbucheed. Schwaigern Selbstverlag, Schwaigern, Germany.
- Lam, T.Y., and Maguire, D.A. 2012. Structural equation modeling: theory and applications in forest management. *Int. J. For. Res.* **2012**: 263953.
Doi:10.1155/2012/263953.
- Laughlin, D.C., and Fulé, P.Z. 2008. Wildland fire effects on understory plant communities in two fire-prone forests. *Can. J. For. Res.* **38**(1): 133–142.
Doi:10.1139/X07-118.
- Ohno, Y. 2011. Clarification of factors contributing to crown dieback of *Betula*

- maximowicziana* canopy trees in deciduous broad-leaved forests. Bull. Hokkaido For. Res. Inst. **48**: 1–46.
- Osumi, K. 2005. Reciprocal distribution of two congeneric trees, *Betula platyphylla* var. *japonica* and *Betula maximowicziana*, in a landscape dominated by anthropogenic disturbances in northeastern Japan. J. Biogeogr. **32**(12): 2057–2068. Doi:10.1111/j.1365-2699.2005.01368.x.
- Pape, R. 2002. Red heart in birch – origin, properties and utilization. Rep. No. 2.
- Pastur, G.M., Lencinas, M.V., Cellini, J.M., and Mundo, I. 2007. Diameter growth: can live trees decrease? Forestry **80**(1): 83–88. Doi:10.1093/forestry/cpl047.
- QGIS Development Team. 2021. QGIS geographic information system. Open source geospatial foundation project. <https://www.qgis.org/ja/site/>
- R Development Core Team. 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Available from <https://www.R-project.org/>[accessed 6 June 2022].
- Račko, V., and Čunderlík, I. 2002. Influence of some factors on beech false heartwood formation 1. Influence of tree age, ripewood ratio and stem diameter. Wood Res. **47**(2): 7–17.
- Račko, V., and Čunderlík, I. 2010. Which of the factors do significantly affect beech false heartwood formation?, *In* Hardwood science and technology, the 4th conference on hardwood research and utilization in Europe. University of Sopron, Hungary, Europe. Pp. 94–95.
- Razali, N.M., and Wah, Y.B. 2011. Power comparisons of Shapiro-Wilk, Kolmogorov-Smirnov, Lilliefors and Anderson-Darling tests. J. Stat. Model. Anal. **2**(1): 21–33.

- Rosseel, Y. 2012. Lavaan: an R package for structural equation modeling. *J. Stat. Softw.* **48**: 1–36. Doi:10.18637/jss.v048.i02.
- Sano, Y., Shibuya, M. 2015. Thinning effect on tree growth in secondary *Betula ermanii* stands on scarified sites. *J. Jpn. For. Soc.* **97**: 25–29.
- Schneider, C.A., Rasband, W.S., and Eliceiri, K.W. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* **9**(7): 671–675. Doi:10.1038/nmeth.2089.
- Shigo, A.L. 1984. Compartmentalization: A conceptual framework for understanding how trees grow and defend themselves. *Annu. Rev. Phytopathol.* **22**: 189–214. Doi.org/10.1146/annurev.py.22.090184.001201.
- Shigo, A.L. 1986. A new tree biology dictionary. Shigo and Trees, Associates, Durham, NH.
- Shigo, A.L., and Hillis, W.E. 1973. Heartwood, discolored wood, and microorganisms in living trees. *Annu. Rev. Phytopathol.* **11**(1): 197–222. Doi:10.1146/annurev.py.11.090173.001213.
- Shimase, T. 2021. Status and prospects of locally grown birch (*Betula* sp.) wood demand in Hokkaido, Japan. *Boreal For. Res.* **69**: 35–37.
- Siegle, H. 1967. Microbiological and biochemical aspects of heartwood stain in *Betula papyrifera* Marsh. *Can. J. Bot.* **45**(2): 147–154. Doi:10.1139/b67-011.
- Solomon, D, S., and Shigo, A, L. 1976. Discoloration and decay associated with pruning wounds on yellow birch. *Forest Science.* **22**(4): 391–392. Doi.org/10.1093/forestscience/22.4.391.
- Takahashi, K., Uemura, S., Suzuki, J.I., and Hara, T. 2003. Effects of understory dwarf bamboo on soil water and the growth of overstory trees in a dense secondary *Betula ermanii* forest, northern Japan. *Ecol. Res.* **18**(6): 767–774.

Doi:10.1007/s11284-003-0594-9.

Trendelenburg, R. 1939. Das holz als rohstoffed. Lehmanns Verlag, Munich, Germany.

Venet, J. 1986. Identification et classement des bois français. École Nationale du Génie Rurale, des Eaux et des Forêts, Nancy, France.

Waring, R.H., Newman, K.E.N., and Bell, J. 1981. Efficiency of tree crowns and stemwood production at different canopy leaf densities. *For. Int. J. For. Res.* **54**(2): 129–137. Doi:10.1093/forestry/54.2.129.

Wernsdörfer, H., Constant, T., Mothe, F., Badia, M.A., Nepveu, G., and Seeling, U. 2005. Detailed analysis of the geometric relationship between external traits and the shape of red heartwood in beech trees (*Fagus sylvatica* L.). *Trees* **19**(4): 482–491. Doi:10.1007/s00468-005-0410-y.

Wernsdörfer, H., Le Moguédec, G., Constant, T., Mothe, F., Nepveu, G., and Seeling, U. 2006. Modelling of the shape of red heartwood in beech trees (*Fagus sylvatica* L.) based on external tree characteristics. *Ann. For. Sci.* **63**(8): 905–913. Doi:10.1051/forest:2006074.

Wiedenbeck, J., Smith, K, T. 2019. Hardwood management, tree wound response, and wood product value. *The Forestry Chronicle.* **94**(3): 292-306.

Yamazaki, H., and Yoshida, T. 2018. Significance and limitation of scarification treatments on early establishment of *Betula maximowicziana*, a tree species producing buried seeds: effects of surface soil retention. *J. For. Res.* **23**(3): 166–172. Doi:10.1080/13416979.2018.1452458.

Chapter 3

- Aoyama K, Yoshida T, Harada. et al. Changes in carbon stock following soil scarification of non-wooded stands in Hokkaido, northern Japan. *J For Res* 2011;16:35–45. <https://doi.org/10.1007/s10310-010-0204-y>.
- Bergès L, Dupouey JL, Franc A. Long-term changes in wood density and radial growth of *Quercus petraea* Liebl. in northern France since the middle of the nineteenth century. *Trees* 2000;14:398–408. <https://doi.org/10.1007/s004680000055>.
- Bouriaud O, Rossi S, Lemoine M. et al. Influence of wood density in tree-ring-based annual productivity assessments and its errors in Norway spruce. *Biogeosciences* 2015;12:6205–6225. <https://doi.org/10.5194/bg-12-6205-2015>.
- Camarero JJ. Why Intra-annual density fluctuations should be formed at night? Implications for climate–growth relationships in seasonally dry conifer forests. *Forests* 2022;13:1425. <https://doi.org/10.3390/f13091425>.
- Camarero JJ, Serra-Maluquer X, Colangelo M. et al. Latewood intra-annual density fluctuations indicate wet summer conditions and enhanced canopy activity in a Mediterranean ring-porous oak. *IAWA Journal* 2024;45:213–226. 10.1163/22941932-bja10141.
- Cameron AD, Dunham R.A, Petty JA. The effects of heavy thinning on stem quality and timber properties of silver birch (*Betula pendula* Roth). *Forestry* 1995;68:275–286. <https://doi.org/10.1093/forestry/68.3.275>.
- Diaconu D, Wassenberg M, Spiecker H. Variability of European beech wood density as influenced by interactions between tree-ring growth and aspect. *For Ecosyst* 2016;3:6. 10.1186/s40663-016-0065-8.
- Dobrowolska E, Krzosek S. Density distribution in middle-sized silver birch wood

- (*Betula pendula* Roth). *Drewno* 2025;68:00065. <https://doi.org/10.53502/wood-204330>.
- Drane P, Sherwood J, Colosimo R. et al. A study of wood baseball bat breakage. *Procedia Eng* 2012;34:616–621. <https://doi.org/10.1016/j.proeng.2012.04.105>.
- Duncan RP, Stewart GH. The temporal and spatial analysis of tree age distributions. *Can J For Res* 1991;21:1703–1710. <https://doi.org/10.1139/x91-236>.
- Erdene-Ochir M, Kanzaki M, Nakai T. et al. Modelling of radial variations of wood properties in naturally regenerated trees of *Betula platyphylla*. *J Wood Sci* 2021;67:1–13. <https://doi.org/10.1186/s10086-021-01993-5>.
- Fischer A, Lindner M, Abs C. et al. Vegetation dynamics in central European forest ecosystems (near-natural as well as managed) after storm events. *Folia Geobot* 2002;37:17–32. <https://doi.org/10.1007/BF02803188>.
- Franceschini T, Berthier S, Maurin G. et al. Effect of ring width, cambial age, and climatic variables on the within-ring wood density profile of Norway spruce *Picea abies* (L.) Karst. *Trees* 2013;27:913–925. <https://doi.org/10.1007/s00468-013-0844-6>.
- Gastaldello P, Ruel JC, Paré D. Micro-variations in yellow birch (*Betula alleghaniensis*) growth conditions after patch scarification. *For Ecol Manag* 2007;238: 244–248. <https://doi.org/10.1016/j.foreco.2006.10.023>
- Giagli K, Vavřík H, Fajstavr M. et al. Stand factors affecting the wood density of naturally regenerated young silver birch growing at the lower altitude of the Czech Republic region. *Wood Res* 2019; 64:1011–1022. <https://repozitar.mendelu.cz/xmlui/handle/20.500.12698/1620>.
- Guilley É, Hervé JC, Huber F. et al. Modelling variability of within-ring density components in *Quercus petraea* Liebl. with mixed-effect models and simulating the

- influence of contrasting silvicultures on wood density. *Ann For Sci* 1999;54:449–458.
<https://doi.org/10.1051/forest:19990601>.
- Heräjärvi H. Variation of basic density and brinell hardness within mature finnish *Betula pendula* and *B. pubescens* stems. *Wood Fiber Sci* 2004;36:216–227.
- Humar M, Fabčič B, Zupančič M. et al. Influence of xylem growth ring width and wood density on durability of oak heartwood. *Int Biodeterior Biodegrad* 2008;62:368–371.
<https://doi.org/10.1016/j.ibiod.2008.03.010>.
- Hynynen J, Niemistö P, Viherä-Aarnio A. et al. Silviculture of birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.) in northern Europe. *Forestry* 2009;83:103–119.
<https://doi.org/10.1093/forestry/cpp035>
- Ito E, Hashimoto T, Aizawa S. et al. Association of soil physicochemical properties following scarification with regenerated birch growth in Hokkaido, northern Japan. *Bulletin of FFPRI* 2019;18:345–353. 10.20756/ffpri.18.4_345.
- Jones G, Ulan M, Liziniewicz M. et al. Relating estimates of wood properties of birch to stem form, age and species. *J For Res* 2024;35:14. <https://doi.org/10.1007/s11676-023-01669-4>.
- Kimberley MO, Cown DJ, McKinley RB. et al. Modelling variation in wood density within and among trees in stands of New Zealand-grown radiata pine. *N Z J For Sci* 2015;45: 22. <https://doi.org/10.1186/s40490-015-0053-8>.
- Lachowicz H, Bieniasz A, Wojtan R. Variability in the basic density of silver birch wood in Poland. *Silva Fennica* 2019;53: article id 9968. <https://doi.org/10.14214/sf.9968>.
- Louzada JLPC, Fonseca FMA. The heritability of wood density components in *Pinus pinaster* Ait. and the implications for tree breeding. *Ann For Sci* 2002;59:867–873.
<https://doi.org/10.1051/forest:2002085>.

- Moran PAP. Notes on continuous stochastic phenomena. *Biometrika* 1950;37:17–23.
<https://doi.org/10.1093/biomet/37.1-2.17>.
- Ohsaki H, Murakami S, Akitsu H. The Timber Properties of Birch Grown in a Plantation in Atsuma, Hokkaido. *J Jpn Wood Res Soc* 2019;65:189–194.
<https://doi.org/10.2488/jwrs.65.189>.
- R Development Core Team. R: A language and environment for statistical computing. R foundation for statistical computing 2023. <https://www.R-project.org/>.
- Rathgeber CBK. Conifer tree-ring density inter-annual variability – anatomical, physiological and environmental determinants. *New Phytol* 2017;216:621–625.
<https://doi.org/10.1111/nph.14763>.
- Rossel Y. Lavaan: An R Package for Structural Equation Modeling. *J Stat Softw* 2012;48:1–36. 10.18637/jss.v048.i02.
- Sano Y, Shibuya M. Thinning effect on tree growth in secondary *Betula ermanii* stands on scarified sites. *J Jpn For Soc* 2015;97:25–29. 10.4005/jjfs.97.25.
- Shimase T. The estimated volume of birch wood suitable for sawlogs or veneer logs in Hokkaido: An analysis of the detailed lists of standing timber sold via public auction by the Hokkaido Regional Forestry Bureau Office. *Boreal forest research* 2014;62:21–24. https://doi.org/10.24494/jfsh.62.0_21.
- Tomita N, Murata K, Nakamura M. et al. Use of dakekanba wood for baseball-bats. *J Jpn Wood Res Soc* 2020;66:39–45. <https://doi.org/10.2488/jwrs.66.39>.
- Viherä-Aarnio A, Velling P. Growth, wood density and bark thickness of silver birch originating from the Baltic countries and Finland in two Finnish provenance trials. *Silva Fennica* 2017;54:article id 7731. doi:10.14214/sf.7731.
- Wimmer R, DownesGM. Temporal variation of the ring-width–wood-density relationship

- in Norway spruce grown under two levels of anthropogenic disturbance. *IAWA J* 2003;24:53–61. 10.1163/22941932-90000320.
- Yoshida T, Yamazaki H, Miyamoto T. Scarification with surface soil replacement can promote understory reinitiation as well as the growth of a secondary birch stand. *J For Res* 2022;28:51–56. <https://doi.org/10.1080/13416979.2022.2091261>.
- Zalloni E, Luis M, Campelo F. et al. Climatic Signals from Intra-annual Density Fluctuation Frequency in Mediterranean Pines at a Regional Scale. *Front Plant Sci* 2016;7:579. 10.3389/fpls.2016.00579.
- Zamudio F, Baettyg R, Vergara A. et al. Genetic trends in wood density and radial growth with cambial age in a radiata pine progeny test. *Ann For Sci* 2002;59:541–549. 10.1051/forest:2005002.

Chapter 4

- Acker, J.V. 2021. Opportunities and challenges for hardwood based engineered wood products. *9th hardwood proceedings-part II. An underutilized resource: Hardwood oriented research*. University of sopron press. pp-5-14.
- Bäucker, C., Liesebach, H. 2018. From *in vitro* clones to high-quality timber production: the Project “Wavy Grain Maple”. German Russian Conference on Forest Genetics - Proceedings - Ahrensburg. 2017 November 21-23. Thünen Report 62. DOI: 10.3220/REP1539855736000.
- Beals, H.O., Davis, T.C. 1977. Figure in wood: an illustrated review. Alabama Agricultural Experiment Station (AAES) Reports. pp-6.
- Bragg, D.C., Mroz, G.D., Reed, D.D., Shetron SG., Stokke DD. 1997. Relationship between “birdseye” sugar maple (*Acer saccharum*) occurrence and its environment. *Can. J. For. Res.* 27: 1182-1191. DOI: <https://doi.org/10.1139/x97-032>.
- Bragg, D.C. 2006. Potential contributions of figured wood to the practice of sustainable forestry. *J. Sustain. For.* 23 (3): 67-81.
- Bollen, K.A., Noble, M.D. 2011. Structural equation models and the quantification of behavior. *PNAS*, 108(Suppl. 3), 15639–15646.
- Duncan, R.P, Stewart, G.H. 1991. The temporal and spatial analysis of tree age distributions. *Can. J. For. Res.* 21: 1703-1710. DOI: <https://doi.org/10.1139/x91-236>.
- Fan, Y., Chen, J., Shirkey, G., John, R., Wu, S.R, Park, H., Shao, C. 2016. Applications of structural equation modeling (SEM) in ecological studies: an updated review. *Ecol. Process.* 5: 19. DOI: <https://doi.org/10.1186/s13717-016-0063-3>.

- Hu, L., Bentler, P.M. 1999. Cutoff criteria for fit indexes in covariance structure analysis: Conventional criteria versus new alternatives. SEM. 6 (1): 1-55.
DOI: <https://doi.org/10.1080/10705519909540118>.
- Ibrahim, O.S., Mohammed, M.J. 2020. A comparison among robust estimation methods for structural equations modeling with ordinal categorical variables. IQJOSS. 17 (32): 132-149. DOI: 10.33899/iqjoss.2020.167418.
- Itô, H., Sumida, A., Isagi, Y., Kamo, K. 1997. The crown shape of an evergreen oak, *Quercus glauca*, in a hardwood community. J. For. Res. 2: 85-88. DOI: <https://doi.org/10.1007/BF02348474>.
- Kärkkäinen, K., Viherä-Aarnio, A., Vakkari, P., Hagqvist, R., Nieminen, K. 2017. Simple inheritance of a complex trait: figured wood in curly birch is caused by one semi-dominant and lethal Mendelian factor? Can. J. For. Res. 47: 991-995. DOI: [dx.doi.org/10.1139/cjfr-2017-0007](https://doi.org/10.1139/cjfr-2017-0007).
- Krajnc, L., Cufar, K., Brus, R. 2015. Characteristics and Geographical Distribution of Fiddleback Figure in Wood of *Acer pseudoplatanus* L. in Slovenia. Drvna Industrija. 66 (3). 213-220. DOI: 10.5552/drind.2015.1447.
- Lam, T.Y., Maguire, D.A. 2012. Structural Equation Modeling: Theory and Applications in Forest Management. Int. J. For. Res. Volume 2012. Article ID 263953. DOI: 10.1155/2012/263953.
- Laughlin, D.C., Fulé, P.Z. 2008. Wildland fire effects on understory plant communities in two fire-prone forests. Can. J. For. Res. 38: 133-142. DOI: 10.1139/X07-118.
- Li, C.H. 2016. Confirmatory factor analysis with ordinal data: Comparing robust maximum likelihood and diagonally weighted least squares. Behav. Res. 48:

- 936-949. DOI: 10.3758/s13428-015-0619-7.
- McKenna, J.R., Geyer, W.A., Woeste, K.E., Cassens, D.L. 2015. Propagating Figured Wood in Black Walnut. *Open. J. For.* 5: 518-525. DOI: <http://dx.doi.org/10.4236/ojf.2015.55045>.
- Moran, P.A.P. 1950. Notes on continuous stochastic phenomena. *Biometrika*. 37(1/2): 17-23. DOI: <https://doi.org/10.2307/2332142>.
- Panshin, A.J., Zeeuw, C. 1980. Textbook of wood technology. New York: McGraw-Hill Book Company.
- Pillow, M.Y. 1955. Detection of figured wood in standing trees. Research paper No. 2034. USDA ForestService, Forest products laboratory, Madison.
- Plourde, B.T., Boukili, V.K., Chazdon, R.L. 2015. Radial changes in wood specific gravity of tropical trees: inter- and intraspecific variation during secondary succession. *Func. Ecol.* 29: 111-120. DOI: 10.1111/1365-2435.12305.
- Puettmann, K., Wilson, S., Baker, S.C. 2015. Silvicultural alternatives to conventional even-aged forest management - What limits global adoption? *For. Ecosyst.* 2: 8. DOI: 10.1186/s40663-015-0031-x.
- Purba, C.Y.C., Dlouha J., Ruelle, J., Fournier, M. 2021. Mechanical properties of secondary quality beech (*Fagus sylvatica* L.) and oak (*Quercus petraea* (Matt.) Liebl.) obtained from thinning, and their relationship to structural parameters. *Ann. For. Sci.* 78: 81. DOI: <https://doi.org/10.1007/s13595-021-01103-x>.
- Quambusch, M., Bäucker, C., Haag, V., Meier-Dinkel, A., Liesebach, H. 2021. Growth performance and wood structure of wavy grain sycamore maple (*Acer pseudoplatanus* L.) in a progeny trial. *Ann. For. Sci.* 78: 15. DOI: <https://doi.org/10.1007/s13595-021-01035-6>.

- R Development Core Team. 2023. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Available from <https://www.R-project.org/>.
- Rossel, Y. 2012. Lavaan: An R Package for Structural Equation Modeling. *J. Stat. Softw.* 48 (2): 1-36. DOI: <https://doi.org/10.18637/jss.v048.i02>.
- Sarvašová, I., Sedmák, R., Sedmáková, D., Lukáčik, I. 2021. Differences in survival and phenotypic traits of curly birch preserved by heterovegetative propagation a case study from Central-East Europe. *Sci Rep.* 11: 8079. DOI: <https://doi.org/10.1038/s41598-021-87508-0>.
- Schütz, J.P., Saniga, M., Diaci, J., Vrška, T. 2016. Comparing close-to-nature silviculture with processes in pristine forests: lessons from Central Europe. *Ann. For. Sci.* 73: 911-921. DOI: [10.1007/s13595-016-0579-9](https://doi.org/10.1007/s13595-016-0579-9).
- Sedlar, T., Šefc, B., Stojnić, S., Sinković, T. 2021. Wood Quality Characterization of Sycamore Maple (*Acer pseudoplatanus* L.) and its Utilization in Wood Products Industries. *Croat. J. For. Eng.* 42: 3. DOI: [10.5552/crojfe.2021.1099](https://doi.org/10.5552/crojfe.2021.1099).
- Shimase, T. 2024. Trends in the precious hardwood roundwood market of Hokkaido, Japan, before and after the sticker shock of wood product prices occurred in 2021. *Boreal forest research.* 72 (0): 57-60. DOI: https://doi.org/10.24494/jfsh.72.0_57. Japanese.
- Šilhán, K. 2021. Spatial dendrogeomorphic sampling based on the specific tree growth responses induced by the landslide mechanism. *Quat Geochronol.* 61: 101132. DOI: <https://doi.org/10.1016/j.quageo.2020.101132>.
- Stanciu, M.D., Curtu, I., Moisan, E., Man, D., Savin, A., Dobrescu, G. 2015. Rheological Behaviour of Curly Maple Wood (*Acer Pseudoplatanus*) Used for

Back Side of Violin. *Pro Ligno*. 11(4). 73-80. DOI:

<http://www.proligno.ro/ro/articles/2015/201504>.

Takahashi, K. 2017. Regeneration Traits of Four Dominant Species in a Cool-Temperate Conifer-Hardwood Mixed Forest, Northern Japan. *Am. J. Plant Sci.* 8: 3313-3323. DOI: 10.4236/ajps.2017.813223.

Zevgolis, Y.G., Alsamail, M.Z., Akriotis, T., Dimitrakopoulos, P.G., Troumbis, A.Y. 2022. Detecting, quantifying, and mapping urban trees' structural defects using infrared thermography: Implications for tree risk assessment and management. *Urban For. Urban Green*. 75: 127691. DOI: <https://doi.org/10.1016/j.ufug.2022.127691>.

Chapter 5

- Aebischer, D. P., Denne, M. P. 1996. Spiral grain in relation to ring width and cambial age in European oak (*Quercus petraea* (Matt.) Liebl. and *Q. robur* L.). *Holzforschung*. **50** (4): 297-302. DOI: 10.1515/hfsg.1996.50.4.297
- Alamo-Sanza, M., Nevares, I. 2018. Oak wine barrel as an active vessel: A critical review of past and current knowledge. *Crit. Rev. Food Sci. Nutr.* **58** (16): 2711-2726. DOI: 10.1080/10408398.2017.1330250.
- Bacilieri, R., Labbe, T., and Kremer, A. 1995. Intraspecific genetic structure in a mixed population of *Quercus petraea* (Matt.) Liebl and *Q. robur* L. *Heredity*. **73**: 130-141. DOI: <https://doi.org/10.1038/hdy.1994.112>.
- Balducci, L., Cuny, H. E., Rathgeber, C. B. K., Deslauriers, A., Giovannelli, A., Rossi, S. 2016. Compensatory mechanisms mitigate the effect of warming and drought on wood formation. *Plant. Cell. Environ.* **39** (6): 1338-1352. <https://doi.org/10.1111/pce.12689>.
- Berg, E. E., Hamrick, E. J. 1995. Fine-scale genetic structure of a turkey oak forest. *Evolution*. **49** (1): 110-120. DOI: 10.1111/j.1558-5646.1995.tb05963.x.
- Beven, K. J., Kirkby, M. J. 1979. A physically based, variable contributing area model of basin hydrology. *Hydrol. Sci. J.* **24** (1): 43-69. DOI: 10.1080/02626667909491834.
- Bivand, R. S., Wong, D. W. S. 2018. Comparing implementations of global and local indicators of spatial association. *TEST*. **27**: 716-748. DOI: 10.1007/s11749-018-0599-x.
- Carabaña, M. V., González-Martínez, S. C., Hardy, O. J., Gil, L. 2007. Fine-scale spatial genetic structure in mixed oak stands with different levels of hybridization. *Mol.*

- Ecol. **16** (6): 1207-1219. DOI: 10.1111/j.1365-294X.2007.03231.x
- Danborg, F. 1994. Spiral grain in plantation trees of *Picea abies*. Can. J. For. Res. **24**: 1662-1671. DOI: 10.1139/x94-215.
- De Micco, V., Balzano, A., Wheeler, E. A., and Baas, P. 2016. Tyloses and gums: A review of structure, function and occurrence of vessel occlusions. IAWA. J. **37** (2): 186-205. DOI: 10.1163/22941932-20160130.
- Dufraisie, A., Coubray, S., Girardclos, O., Dupin, A., Lemoine, M. 2018. Contribution of tyloses quantification in earlywood oak vessels to archaeological charcoal analyses: Estimation of a minimum age and influences of physiological and environmental factors. Quat Int. **463** (Part B, 10): 250-257. DOI: <https://doi.org/10.1016/j.quaint.2017.03.070>.
- Gapare, W., Hathorn, A., Kain, D., Matheson, C., and Wu, H. 2007. Inheritance of spiral grain in the juvenile core of *Pinus radiata*. Can. J. For. Res. **37**: 116-127. DOI: 10.1139/X06-202.
- Geburek, T., Tripp-Knowles, P. 1994. Genetic architecture in bur oak, *Quercus macrocarpa* (Fagaceae), inferred by means of spatial autocorrelation analysis. Plant. Syst. Evol. **189**: 63-74. DOI: <https://doi.org/10.1007/BF00937578>.
- Gollihue, J., Pook, V. G., and DeBolt, S. 2021. Sources of variation in bourbon whiskey barrels: a review. J. Inst. Brew. **127**: 210-223. DOI: 10.1002/jib.660.
- Hallingbäck, H. R., Jansson, G., and Hannrup, B. 2010. Genetic correlations between spiral grain and growth and quality traits in *Picea abies*. Can. J. For. Res. **40**: 173-183. DOI: 10.1139/X09-173.
- Harris, J. M. 1989. Spiral grain and wave phenomena in wood formation. Springer series in Wood Science. Springer-Verlag Berlin Heidelberg.

- Johnson, P. S., Shifley, S. R., Rogers, R., Dey, D. C., and Kabrick, J. M. 2019. The ecology and silviculture of oaks. 3rd ed. Oxford: CAB Intl.
- Jose-Maldia, L. S., Matsumoto, A., Nagamitsu, T., Ueno, S., Tsumura, Y. 2024. Intraspecific genetic divergence of the subalpine shrubby variety *Quercus crispula* var. *horikawae* from the mountain tree variety *Q. crispula* var. *crispula* in Japan. *Plant. Species. Biol.* **39**: 113-125. DOI: 10.1111/1442-1984.12447.
- Kim, D., Gollihue, J., Poovathingal, S. J., and DeBolt, S. 2024. Detailed three-dimensional analyses of tyloses in oak used for bourbon and wine barrels through X-ray computed tomography. *Sci. Rep.* **14**: 17044. DOI: <https://doi.org/10.1038/s41598-024-67298-x>.
- Kishima, T. 1966. Review of tylosis formation in hardwood vessels. *Wood research.* **37**: 1-5.
- Kubler, H. 1988. Silvicultural control of mechanical stresses in trees. *Can. J. For. Res.* **18**: 1215-1225. DOI: <https://doi.org/10.1139/x88-188>.
- Kubler, H. 1991. Function of spiral grain in trees. *Trees.* **5**: 125-135. DOI:10.1007/BF00204333.
- Li, C., Yang, X., Chen, S., Huang, Y., Yang, Y., and Qiu, J. 2024. Comparative anatomical analysis of bark structure in 10 *Quercus* species. *Plants.* **13**: 1871. DOI: <https://doi.org/10.3390/plants13131871>.
- Medhurst, J., Ottenschlaeger, M., Wood, M., Harwood, C., Beadle, C., and Valencia, J. C. 2011. Stem eccentricity, crown dry mass distribution, and longitudinal growth strain of plantation-grown *Eucalyptus nitens* after thinning. *Can. J. For. Res.* **41**: 2209-2218. DOI:10.1139/X11-135.
- Mikami, S., Nagasaka, K. 1975. Selection for minimizing spiral grain in *Larix leptolepis*

- Gord. Bulletin of the Government Forest Experiment Station. **276**: 1-22.
- Misra, P. 1943. Correlation between excentricity and spiral grain in the wood of *Pinus longifolia*. Forestry. **17** (1): 67-80. DOI: <https://doi.org/10.1093/forestry/17.1.67>.
- Moore, J. R., Coen, D. J., and McKinley, R. B. 2015. Modelling spiral grain angle variation in New Zealand-grown radiata pine. N. Z. J. For. Sci. **45**: 15. DOI: 10.1186/s40490-015-0046-7.
- Moran, P. A. P. 1950. Notes on continuous stochastic phenomena. Biometrika. **37** (1/2). pp. 17-23. DOI: <https://doi.org/10.2307/2332142>.
- Mosedale, J. R. 1995. Effects of oak wood on the maturation of alcoholic beverages with particular reference to whisky. Forestry. **68** (3): 203-230. DOI: 10.1093/forestry/68.3.203.
- Murmanis, L. 1975. Formation of tyloses in felled *Quercus rubra* L. Wood Sci Technol. **9**: 3-14.
- Nakada, R. 2014. Wetwood in trees; Appearance and definition. J. Wood. Sci. **60** (2): 63-79. DOI: <https://doi.org/10.2488/jwrs.60.63>.
- Nakada, R., Hanaoka, S., Ohsaki, H., Murakami, S., and Akitsu, H. Intrafamily variation of grain spirality in a control-pollinated family of hybrid larch. Bulletin of FFPRI. **23** (1): 1-11. DOI: https://doi.org/10.20756/ffpri.23.1_1.
- Noguchi, Y. 2017. The Influence of Wood Species of Casks on Matured Whisky Aroma: Identification of Unique Character Imparted to Whisky by Casks Constructed of Japanese Oak. PhD Thesis, Heriot-Watt University, Edinburgh. <http://hdl.handle.net/10399/3276>.
- Ohkura, S. 1958. On the macroscopic features of twisted fiber in trees. J. Fac. Agri.

- Shinshu Univ. **8**: 59-100. (in Japanese).
- Ohkura, S. 1963. Torsion of wood stems and stresses due to torsion (translated title). J. Soc. Mater. Sci. Jpn. **12** (121): 740-744.
- Pape, R. 1999. Influence of thinning on spiral grain in Norway spruce grown on highly productive sites in southern Sweden. *Silva. Fennica*. **33** (1): 3-12. DOI: 10.14214/sf.666.
- Pérez-de-Lis, G., Rozas, V., Vázquez-Ruiz, R. A., García-González, I. 2018. Do ring-porous oaks prioritize earlywood vessel efficiency over safety? Environmental effects on vessel diameter and tyloses formation. *Agric. For. Meteorol.* **248**: 205-214. DOI: <https://doi.org/10.1016/j.agrformet.2017.09.022>
- QGIS Development Team. 2021. QGIS geographic information system. Open-source geospatial foundation project. <https://www.qgis.org/ja/site>.
- R Development Core Team. 2023. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Available from <https://www.R-project.org/>.
- Rauchfuss, J., Speer, J. H. 2006. Research report age dependence of spiral grain in white oaks (*Quercus alba* L.) in southwestern Illinois. *Tree-ring research*. **62** (1): 13-24. DOI: <https://doi.org/10.3959/1536-1098-62.1.13>.
- Rosseel, Y. 2012. Lavaan: An R package for structural equation modeling. *J. Stat. Softw.* **48**: 1-36. doi:10.18637/jss.v048.i02.
- Rubio-Bretón, P., Lorenzo, C., Salinas, M. R., Martínez, J., and Garde-Cerdán, T. 2013. Influence of oak barrel aging on the quality of red wines. *Oak: Ecology, Types and Management. Environmental science, engineering and technology*. pp: 59-86.

- Ruppitsch, W., Lebow, P., Lebow, S., Taylor, A. 2021. Role of tyloses in the durability of chestnut oak. *Wood. Fiber. Sci.* **53** (2): 126-146. DOI: 10.22382/wfs-2021-14.
- Sandurska, E., Ulaszewski, B., Meyza, K., Sztupecka, E., and Burczyk, J. 2024. Factors determining fine-scale spatial genetic structure within coexisting populations of common beech (*Fagus sylvatica* L.), pedunculate oak (*Quercus robur* L.), and sessile oak (*Q. petraea* (Matt.) Liebl.). *Ann. For. Sci.* **81**: 3. DOI: <https://doi.org/10.1186/s13595-023-01217-4>.
- Sano, Y., Fujikawa, S., Fukuzawa, K. 1995. Detection and features of wetwood in *Quercus mongolica* var. *grosseserrata*. *Trees.* **9**: 261-268. DOI: <https://doi.org/10.1007/BF00202016>.
- Sano, J. 1997. Age and size distribution in a long-term forest dynamics. *For Ecol Manage.* **92**: 39-44. DOI: [https://doi.org/10.1016/S0378-1127\(96\)03958-8](https://doi.org/10.1016/S0378-1127(96)03958-8).
- Shibata, H., Urakawa, R., Toda, H., Inagaki, Y., Tateno, R., Koba, K., Nakanishi, A., Fukuzawa, K., and Yamasaki A. 2011. Changes in nitrogen transformation in forest soil representing the climate gradient of the Japanese archipelago. *J. For. Res.* **16**: 374-385. DOI: 10.1007/s10310-011-0288-z.
- Tao, Y., García, J. F., Sun, D. W. 2014. Advances in wine aging technologies for enhancing wine quality and accelerating wine aging process. *Crit. Rev. Food. Sci. Nutr.* **54** (6): 817-835. DOI: <https://doi.org/10.1080/10408398.2011.609949>.
- Thinley, C., Palmer, G., Vanclay, J. K., and Henson, M. 2005. Spiral and interlocking grain in *Eucalyptus dunnii*. *Holz als Roh- und Werkstoff.* **63**: 372-379. DOI: 10.1007/s00107-005-0011-x.
- Thomas, J., Dijkstra, S. M., Harrington, J. J., and Collings, D. A. 2023. Induction of

- compression wood inhibits development of spiral grain in radiata pine. IAWA Journal. **44** (1): 36-62. DOI: 10.1163/22941932-bja10088.
- Ubukata, M., Itahana, N., and Kohono, K. 1999. Examination of the mating system of Mizunara (*Quercus mongolica* var. *grosseserrata*) in a natural stand based on spatial genetic structure and inbreeding depression. J. Jpn. For. Soc. **81**: 280-285.
- Warensjö, M. 2003. Compression wood in Scots pine and Norway spruce -Distribution in relation to external geometry and the impact on dimensional stability in sawn wood. 2003. Doctoral thesis. Swedish University of Agricultural Sciences.
- Wing, M. R., Knowles, A. J., Melbostad, S. R., and Jones, A. K. 2014. Spiral grain in bristlecone pines (*Pinus longaeva*) exhibits no correlation with environmental factors. Trees. **28**: 487-491. DOI: <https://doi.org/10.1007/s00468-013-0965-y>.
- Wu, H. X., Ivković, M., Gapare, W. J., Matheson, A. C., and Baltunis, B. S. 2008. Breeding for Wood Quality and Profit in Pinus Radiata: A Review of Genetic Parameter Estimates and Implications for Breeding and Deployment. 2008. N. Z. J. For. Sci. **38** (1): 56-87.
- Yadeta, K. A., Thomma, B. P. H. J. 2013. The xylem as battleground for plant hosts and vascular wilt pathogens. Front. Plant. Sci. **4**: 97. DOI: 10.3389/fpls.2013.00097.

Chapter 6

- Alamo-Sanza, M., Nevares, I. 2018. Oak wine barrel as an active vessel: A critical review of past and current knowledge. *Crit. Rev. Food Sci. Nutr.* 58 (16): 2711-2726. DOI: 10.1080/10408398.2017.1330250.
- Anzai, N., Shibuya, M., Saito, H., Miyamoto, T. 2023. Long-term dynamics of species diversity in natural secondary forest stands after severe windthrow damage. *Ecosphere* 14(7): e4600. DOI: 10.1002/ecs2.4600.
- Aoyama, K., Yoshida, T., Kamitani, T. 2009. An alternative of soil scarification treatment for forest restoration: effects of soil replacement. *J. For. Res.* 14(1): 58–62. Doi:10.1007/s10310-008-0105-5.
- Aoyama, K., Yoshida, T., Harada, A., Noguchi, M., Miya, H., Shibata, H. 2011. Changes in carbon stock following soil scarification of non-wooded stands in Hokkaido, northern Japan. *Journal of Forest Research* 16(1): 35–45. DOI: 10.1007/s10310-010-0204-y.
- Attocchi, G. 2013. Effects of pruning and stand density on the production of new epicormic shoots in young stands of pedunculate oak (*Quercus robur* L.). *Annals of Forest Science* 70(7): 663–673. DOI: 10.1007/s13595-013-0309-5.
- Baral, S.K., Schneider, R., Pothier, D., and Berninger, F. 2013. Predicting sugar maple (*Acer saccharum*) discoloured wood characteristics. *Can. J. For. Res.* 43(7): 649–657. Doi:10.1139/cjfr-2013-0017.
- Barrette, J., Achim, A., Auty, D. 2023. Impact of Intensive Forest Management Practices on Wood Quality from Conifers: Literature Review and Reflection on Future Challenges. *Current Forestry Reports* 9(2): 101–130. DOI: 10.1007/s40725-023-00181-6.

- Bäucker, C., Liesebach, H. 2018. From in vitro clones to high-quality timber production: the Project “Wavy Grain Maple”. German Russian Conference on Forest Genetics - Proceedings - Ahrensburg. 2017 November 21-23. Thünen Report 62. DOI: 10.3220/REP1539855736000.
- Belleville, B., Cloutier, A., and Achim, A. 2011. Detection of red heartwood in paper birch (*Betula papyrifera*) using external stem characteristics. *Can. J. For. Res.* 41(7): 1491–1499. Doi:10.1139/x11-080.
- Bragg, D.C. 2006. Potential contributions of figured wood to the practice of sustainable forestry. *J. Sustain. For.* 23 (3): 67-81.
- Cameron, A.D. 1996. Managing birch woodlands for the production of quality timber. *Forestry: An International Journal of Forest Research* 69(4): 357–371. DOI: 10.1093/forestry/69.4.357.
- Valbuena-Carabaña, M. V., González-Martínez, S. C., Hardy, O. J., Gil, L. 2007. Fine-scale spatial genetic structure in mixed oak stands with different levels of hybridization. *Molecular Ecology* 16(6): 1207–1219. DOI: 10.1111/j.1365-294X.2007.03231.x.
- Chen, S., Wang, Y., Yu, L., Zheng, T., Wang, S., Yue, Z., Kumari, S., Wei, H., Liu, G., Yang, C. 2021. Genome sequence and evolution of *Betula platyphylla*. *Horticulture Research* 8: 37. DOI: 10.1038/s41438-021-00481-7.
- Damayanti, R., Ozarska, B., Ilic, J., Pari, G., Dwianto, W., Indrawan, D. A., Krisdianto, K. 2020. Variation of heartwood proportion and wood colour from fast grown 5-year-old teak. *Wood Research* 65(1): 1–11.
- Dobrowolska, E., Wroniszewska, P., Jankowska, A. 2020. Density distribution in wood of European birch (*Betula pendula* Roth.). *Forests* 11(4): 445. DOI:

10.3390/f11040445.

Draper, M. C., Kern, C. C., Froese, R. E. 2021. Growth, yield, and financial return through six decades of various management approaches in a second-growth northern hardwood forest. *Forest Ecology and Management* 499: 119633. DOI: 10.1016/j.foreco.2021.119633.

Eilmann, B., Zweifel, R., Buchmann, N., Graf Pannatier, E., Rigling, A. 2011. Drought alters timing, quantity, and quality of wood formation in Scots pine. *Journal of Experimental Botany* 62(8): 2763–2771. DOI: 10.1093/jxb/erq443.

Forestry Agency, Research and Extension Division. 1981. *Broadleaf Forests and Their Management*. Chikyu-sha, Tokyo, Japan. 262 pp.

Forzieri, G., Jactel, H., Bianchi, A., Spinoni, J., Somasundaram, D., Feyen, L., Cescatti, A. 2024. Ecosystem heterogeneity is key to limiting the increasing climate-driven risks to European forests. *One Earth* 7(12): 2149–2164. DOI: 10.1016/j.oneear.2024.10.005.

Gerwein, J. B., Kesseli, R. V. 2006. Genetic diversity and population structure of *Quercus rubra* (Fagaceae) in old-growth and secondary forests in southern New England. *Rhodora* 108(933): 1–18. DOI: 10.3119/05-9.1.

Giroud, G., Cloutier, A., and Alteyrac, J.M. 2008. Occurrence, proportion, and vertical distribution of red heartwood in paper birch. *Can. J. For. Res.* 38(7): 1996–2002. Doi:10.1139/X08-043.

Gruber, A., Strobl, S., Veit, B., Oberhuber, W. 2010. Impact of drought on the temporal dynamics of wood formation in *Pinus sylvestris*. *Tree Physiology* 30(4): 490–501. DOI: 10.1093/treephys/tpq003.

Hurtado, P., Espelta, J. M., Jaime, L., Martínez-Vilalta, J., Kokolaki, M. S., Lindner, M.,

- Lloret, F. 2025. Biodiversity and Management as Central Players in the Network of Relationships Underlying Forest Resilience. *Global Change Biology* 31(5): e70196. DOI: 10.1111/gcb.70196.
- Inatsu, M., Yoshida, R., Karino, S., Takeuchi, S., Kobayashi, S. 2021. A high-resolution prediction system for birch pollen in Sapporo. *Agricultural and Forest Meteorology* 297: 108229. DOI: 10.1016/j.agrformet.2020.108229.
- Ishikawa, Y., Ito, K. 1988. The regeneration process in a mixed forest in central Hokkaido, Japan. *Vegetatio* 79(1-2): 75–84. DOI: 10.1007/BF00044850.
- Ito, K., Shibata, S., Koike, T. 2018. Utilization potential and market trends of broadleaf timber in northern Japan. Hokkaido Forest Research Report, Forestry and Forest Products Research Institute (FFPRI), Sapporo, Japan.
- Kärkkäinen, K., Viherä-Aarnio, A., Vakkari, P., Hagqvist, R., Nieminen, K. 2017. Simple inheritance of a complex trait: figured wood in curly birch is caused by one semi-dominant and lethal Mendelian factor? *Canadian Journal of Forest Research* 47: 991–995.
- Kerr, G. 1996. The effect of heavy or ‘free growth’ thinning on oak (*Quercus petraea* and *Quercus robur*). *Forestry: An International Journal of Forest Research* 69(4): 303–317. DOI: 10.1093/forestry/69.4.303.
- Kim, D., Gollihue, J., Poovathingal, S. J., and DeBolt, S. 2024. Detailed three dimensional analyses of tyloses in oak used for bourbon and wine barrels through X-ray computed tomography. *Sci. Rep.* 14: 17044. DOI: <https://doi.org/10.1038/s41598-024-67298-x>.
- Krajnc, L., Cufar, K., Brus, R. 2015. Characteristics and Geographical Distribution of Fiddleback Figure in Wood of *Acer pseudoplatanus* L. in Slovenia. *Drvena*

- Industrija. 66 (3). 213-220. DOI: 10.5552/drind.2015.1447.
- Kuuluvainen, T., Gauthier, S., Aakala, T. 2012. Natural forest dynamics in boreal Fennoscandia: A review and classification. *Forest Ecology and Management* 268: 83–95. DOI: 10.1016/j.foreco.2011.09.024.
- Kobayashi, M., Susloparova, E., Tsuyama, I., Shimase, T., Nakaba, S., Takahashi, N., Yoshida, T. 2021. Influence of soil properties on the heartwood colour of *Juglans mandshurica* var. *sachalinensis* in a cool temperate forest. *Journal of Wood Science* 67: 49. DOI: 10.1186/s10086-021-01981-9.
- Manel, S., Schwartz, M. K., Luikart, G., Taberlet, P. 2003. Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology & Evolution* 18(4): 189–197.
- Matsuzaki, J., Masumori, M., Tange, T. (2006). Stem phototropism of trees: a possible significant factor in determining stem inclination on forest slopes. *Annals of Botany* 98(3): 573–581. DOI: 10.1093/aob/mcl127.
- Mizutani, A., Higashi, W., Kaneko, M., Matsuyama, S. 2022. Soil nutrient and moisture environments and shoot growth of *Quercus crispula* canopy trees in two areas that experienced contrasting effects of deer overabundance over an 11-year period. *Journal of Forest Research* 27(6): 469–475. DOI: 10.1080/13416979.2022.2061395.
- McKenna, J. R., Geyer, W. A., Woeste, K. E., Cassens, D. L. 2015. Propagating Figured Wood in Black Walnut. *Open Journal of Forestry* 5: 518–525. DOI: 10.4236/ojf.2015.55045.
- Naji, H. R., Nia, M. F., Kiaei, M., Abdul-Hamid, H., Soltani, M., Faghihi, A. 2015. Effect of intensive planting density on tree growth, wood density and fiber properties

- of maple (*Acer velutinum* Boiss.). *iForest – Biogeosciences and Forestry* 9: 325-329. DOI: 10.3832/ifor1333-008.
- Nakada, R., Hanaoka, S., Ohsaki, H., Murakami, S., Akutsu, H. 2024. Intrafamily variation of grain spirality in a control-pollinated family of hybrid larch. *Bulletin of the Forestry and Forest Products Research Institute* 23(1): 1–11. DOI: 10.20756/ffpri.23.1_13.
- Nicolescu, V. N., Vor, T., Brus, R., et al. 2025. Management of sessile oak (*Quercus petraea* (Matt.) Liebl.), a major forest species in Europe. *Journal of Forest Research* 36:78. DOI: 10.1007/s11676-025-01868-1.
- Nocetti, M., Brunetti, M. 2024. Advancements in Wood Quality Assessment: Standing Tree Visual Evaluation—A Review. *Forests* 15(6): 943. DOI: 10.3390/f15060943.
- Ohkura, S. 1958. On the macroscopic features of twisted fibre in trees. *J. Fac. Agric., Shinshu Univ.* 8: 59-100.
- Osumi, K. 2005. Reciprocal distribution of two congeneric trees, *Betula platyphylla* var. *japonica* and *Betula maximowicziana*, in a landscape dominated by anthropogenic disturbances in northeastern Japan. *J. Biogeogr.* 32: 2057–2068. DOI: 10.1111/j.1365-2699.2005.01368.x.
- Pandey, S. 2021. Climatic influence on tree wood anatomy: a review. *Journal of Wood Science* 67: 24. DOI: 10.1186/s10086-021-01956-w.
- Pickering, M., Elia, A., Oton, G., Forzieri, G., Girardello, M., Migliavacca, M., Ceccherini, G. 2025. Enhanced structural diversity increases European forest resilience and potentially compensates for climate-driven declines. *Communications Earth & Environment* 6: 852. DOI:

10.1038/s43247-025-02592-8.

- Potterf, M., Eyvindson, K., Blattert, C., Triviño, M., Burner, R. C., Burgas, D., Mönkkönen, M. 2024. Diversification of forest management can mitigate wind damage risk and maintain biodiversity. *European Journal of Forest Research* 143(2): 419–436. DOI: 10.1007/s10342-023-01625-1.
- Puettmann, K. J., Wilson, S. C., Baker, S. C., Donoso, P. J., Drössler, L., Amente, G. A., Harvey, B. D., Knoke, T., Lu, Y., Nocentini, S., Putz, F. E., Yoshida, T., Bauhus, J. 2015. Silvicultural alternatives to conventional even-aged forest management — what limits global adoption? *Forest Ecosystems* 2:8. DOI: 10.1186/s40663-015-0031-x.
- Quambusch, M., Bäucker, C., Liesebach, H., Meier-Dinkel, A., Haag, V. 2021. Growth performance and wood structure of wavy grain sycamore maple (*Acer pseudoplatanus* L.) in a progeny trial. *Annals of Forest Science* 78: 15. DOI: 10.1007/s13595-021-01035-6.
- Río, M., Bravo-Oviedo, A., Pretzsch, H., Löf, M., Ruiz-Peinado, R. 2017. A review of thinning effects on Scots pine stands: From growth and yield to new challenges under global change. *Forest Systems* 26(2): eR03S. DOI: 10.5424/fs/2017262-11325.
- Ruņģis, D. E., Danusevičius, D., Kembrytė-Ilčiukienė, R., Jansone, L., Kempf, M., Jansons, Ā. 2025. Natural regeneration, genetic diversity, and provenance of introduced *Fagus sylvatica* L. stands in Latvia. *Forests* 16(1): 178. DOI: 10.3390/f16010178.
- Ruppitsch, W., Lebow, P., Lebow, S., Taylor, A. 2021. Role of tyloses in the durability of chestnut oak. *Wood. Fiber. Sci.* 53 (2): 126-146. DOI: 10.22382/wfs-2021-14.

- Rytter, L. 2013. Growth dynamics of hardwood stands during the precommercial thinning phase – Recovery of retained stems after competition release. *Forest Ecology and Management* 302: 264–272. DOI: 10.1016/j.foreco.2013.03.034.
- Sandurska, E., Ulaszewski, B., Meyza, K., Sztupecka, E., and Burczyk, J. 2024. Factors determining fine-scale spatial genetic structure within coexisting populations of common beech (*Fagus sylvatica* L.), pedunculate oak (*Quercus robur* L.), and sessile oak (*Q. petraea* (Matt.) Liebl.). *Ann. For. Sci.* 81: 3. DOI: <https://doi.org/10.1186/s13595-023-01217-4>.
- Sano, Y., Shibuya, M. 2015. Thinning Effect on Tree Growth in Secondary *Betula ermanii* Stands on Scarified Sites. *J. Jpn. For. Soc.* 97: 25-29. DOI: 10.4005/jjfs.97.25.
- Schütz, J.P., Saniga, M., Diaci, J., Vrška, T. 2016. Comparing close-to-nature silviculture with processes in pristine forests: lessons from Central Europe. *Ann. For. Sci.* 73: 911-921. DOI: 10.1007/s13595-016-0579-9.
- Seidler, T. G., Plotkin, J. B. 2006. Seed dispersal and spatial pattern in tropical trees. *PLoS Biology* 4(11): e344. DOI: 10.1371/journal.pbio.0040344.
- Shimase, T. 2014. Wood utilization and market characteristics of broadleaf species in Hokkaido: timber price and circulation. Hokkaido Research Center, Forestry and Forest Products Research Institute (FFPRI), Sapporo, Japan.
- Skovsgaard, J. P., Johansson, U., Holmström, E., Tune, R. M., Ols, C., Attocchi, G. 2021. Effects of thinning practice, high pruning and slash management on crop tree and stand growth in young even-aged stands of planted silver birch (*Betula pendula* Roth). *Forests* 12(2): 225. DOI: 10.3390/f12020225.
- Tanimoto, T. 1990. *Ecology of Broadleaf Forest Management*. Soubun, Tokyo, Japan. 245 pp.

- Tomita, N., Murata, K., Nakamura, M., Akitsu, H., Ohsaki, H. 2020. Evaluation of the suitability of Dakekanba wood for baseball bats (Use of Dakekanba wood for baseball-bats). *Journal of Wood Science*. 66(1): 39–45. DOI: 10.2488/jwrs.66.39.
- Ubukata, M., Itahana, N., and Kohono, K. 1999. Examination of the mating system of Mizunara (*Quercus mongolica* var. *grosseserrata*) in a natural stand based on spatial genetic structure and inbreeding depression. *J. Jpn. For. Soc.* 81: 280-285.
- Vekemans, X., Hardy, O. J. 2004. New insights from fine-scale spatial genetic structure analyses in plant populations. *Molecular Ecology* 13: 921–935. DOI: 10.1046/j.1365-294X.2004.02076.x.
- Viherä-Aarnio A, Velling P. 2017. Growth, wood density and bark thickness of silver birch originating from the Baltic countries and Finland in two Finnish provenance trials. *Silva Fennica*. 54: article id 7731. DOI: 10.14214/sf.7731.
- Yamazaki, H., and Yoshida, T. 2018. Significance and limitation of scarification treatments on early establishment of *Betula maximowicziana*, a tree species producing buried seeds: effects of surface soil retention. *J. For. Res.* 23(3): 166-172. Doi:10.1080/13416979.2018.1452458.
- Żukowska, W. B., Lewandowski, A. 2025. Genetic structure and divergence of marginal populations of black poplar (*Populus nigra* L.) in Poland. *Scientific Reports* 15: 3014. DOI: 10.1038/s41598-025-86994-w.

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