Influence of competition and other factors on crown and stem characteristics of northern red oak

Dissertation

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“Quidquid agis, prudenter agas et respice finem.”

Gesta Romanorum, c. 103

Summary

Native to northeastern America and southeastern Canada, northern red oak (*Q. rubra* L.) was introduced to Europe in 1691 and initially planted in parks and gardens. In the following centuries, three silvicultural cultivation periods in Europe demonstrated that northern red oak had both good growth and favorable silvicultural treatment options. The cultivation of native tree species, however, was always favored. Nowadays, the cultivation of non-native tree species is increasingly considered, since the consequences of climate change already range from losses of stand vitality to a dieback of entire forest areas, which causes the cultivation with native tree species to be subject to uncertainties. Northern red oak represents a tree species that is expected to withstand future climate conditions in Germany on suitable sites and reduce the risk of forestry operations. With an area share of 55000 ha, *Q. rubra* constitutes the most common non-native deciduous tree species. To date, there are few empirical studies on silvicultural treatment of northern red oak in Germany, and also, from the practitioners' point of view, there are various uncertainties regarding the intensity and frequency of interventions.

Therefore, the aim of this study was to investigate the influence of competition — which can be controlled by the intensity and frequency of silvicultural interventions — on crown and stem characteristics of northern red oak. The following hypotheses were proposed: 1. increasing competition results in shorter and more slender tree crowns; 2. increasing competition leads to fewer external stem characteristics, which are negatively related to the commercial timber value of northern red oak; 3. competition effects on stem and crown characteristics are superimposed by genetic variation; 4. stem form and number of bark anomalies—both indicating stem quality of northern red oak trees—differ between Canadian and German stands due to different silvicultural practices; 5. increasing tree competition is negatively related to external stem quality characteristics, and this relationship is constant under both management systems (shelterwood system vs. crop tree thinning).

The results of the study show that competition is the main factor influencing the tree morphology of northern red oak. Specifically, it was observed that various crown characteristics associated with both the vertical and horizontal crown extent become smaller with increasing competition. Thus, the first hypothesis of this study can be confirmed. The results suggest that the crown size is a good predictor of the level of competition faced by a given tree.

Light capturing depends on the crown extent, making a competition-induced reduction in crown size, such as crown radius, likely to affect growth performance and thus tree productivity. The second hypothesis can also be verified, as high competitive strength in *Q. rubra* resulted in a decrease in external (i.e., undesirable) stem characteristics, particularly stem non-circularity and the number of bark anomalies. The measure of the number of bark anomalies includes both branchiness and irregularities on the stem surface (stem injuries such as bark seams). Since branch-related wood defects are considered a major cause of declining stem quality in many tree species, this study confirms that northern red oak requires, similar to many other native tree species, higher levels of competition during the early stages of stand development to produce high quality timber. A relationship was also found between abiotic factors and stem and crown characteristics. The third hypothesis can be partially confirmed, as a correlation between genetic diversity (heterozygosity "EST" and "All") and first-order branch angle measures (branch angle (mean; median) and branch angle range) was detected. With increasing heterozygosity, branch angles of *Q. rubra* became steeper.

To verify the results, future studies may focus on identifying potential adaptive markers of northern red oak by modern high-throughput techniques such as RADseq (restriction site associated DNA sequencing) and on analyzing potential candidate genes for shaping crown morphology. A comparative assessment of external stem characteristics between the German and Canadian stands showed that values for the number of bark anomalies and stem non-circularity were significantly higher in the Canadian stands, whereas the stems in Germany were significantly more curved and crooked. We attribute the significant differences between countries to differences in silvicultural practices. Thus, the hypotheses 4 and 5 can also be confirmed.

For silvicultural treatment in northern red oak, which aims at achieving high quality timber, our results indicate that stands should be kept mainly at high stand densities in the initial development stages until the desired branch-free stem length has reached the desired height. Subsequent thinning should be moderate to heavy and at regular intervals for the highly phototropic Q. rubra, to promote crown size and thus productivity. The respective thinning intensity and frequency should always be adapted to the respective site conditions.

Zusammenfassung

Die in Nordostamerika und dem angrenzenden Südostkanada beheimatete Roteiche wurde 1691 nachweislich in Europa eingeführt und zunächst in Parks und Gärten angepflanzt. In den nachfolgenden Jahrhunderten fanden drei forstliche Anbauperioden statt, welche der Roteiche sowohl ein gutes Wachstum als auch günstige waldbauliche Behandlungsmöglichkeiten bescheinigten. Der Anbau heimischer Baumarten stand jedoch stets im Fokus der Forstwissenschaft. Aktuell führt der Klimawandel zu Vitalitätseinbußen bis hin zu einem flächigen Waldsterben, wodurch die Anbaueignung derzeit forstlich relevanter, heimischer Baumarten mit Unsicherheiten behaftet ist. Die Roteiche wird als eine Baumart eingeschätzt, die auf geeigneten Standorten zukünftige Klimaveränderungen in Deutschland aushalten und als Mischbaumart das Risiko für Forstbetriebe reduzieren kann. Mit einem Flächenanteil von 55.000 ha stellt *Q. rubra* die häufigste nichtheimische Laubbaumart dar, deren Holz schnell an Zuwachs gewinnt und für eine Vielzahl von Anwendungsmöglichkeiten genutzt werden kann. Bisher gibt es wenige empirische Untersuchungen zur waldbaulichen Behandlung der Roteiche in Deutschland und auch aus Sicht der Praktiker gibt es diverse Unsicherheiten bezüglich der Intensität und Häufigkeit der Eingriffe.

Ziel dieser Studie war es deshalb, den Einfluss von Konkurrenz - welche durch die Intensität und Häufigkeit waldbaulicher Eingriffe gesteuert werden kann - auf Kronen- und Stammmerkmale der Roteiche zu untersuchen. Hierbei wurden folgende Hypothesen aufgestellt: 1: Zunehmende Konkurrenz führt zu kürzeren und schlankeren Baumkronen; 2: Zunehmende Konkurrenz resultiert in einer geringeren Anzahl an äußeren Stammmerkmalen, die sich negativ auf die kommerzielle Holzqualität der Roteiche auswirken. 3: Konkurrenzeffekte auf Stamm- und Kronenmerkmale werden durch genetische Variation überlagert. 4: Die Stammform und die Anzahl der Rindenanomalien - beides Indikatoren für die Stammqualität - unterscheiden sich zwischen kanadischen und deutschen Beständen aufgrund unterschiedlicher waldbaulicher Behandlungen. 5. Zunehmende Konkurrenz zwischen Roteichen führt zu einer geringeren Anzahl an äußeren Stammmerkmalen, unabhängig vom Bewirtschaftungssystem (Großschirmschlag vs. Auslesedurchforstung). Die Ergebnisse der Untersuchung zeigen, dass Konkurrrenz der Hauptfaktor ist, der die Baummorphologie der Roteiche beeinflusst. Im Einzelnen wurde festgestellt, dass verschiedene Kronenmerkmale, die sowohl der vertikalen als auch der horizontalen Kronenausdehnung zugeordnet werden,

mit zunehmender Konkurrenz kleiner werden. Damit kann die erste Hypothese dieser Untersuchung bestätigt werden. Die Ergebnisse deuten darauf hin, dass die Kronenausdehnung ein guter Prädiktor für die Stärke der Konkurrenz ist, der der jeweilige Baum ausgesetzt ist. Der Grad der Lichterfassung von Bäumen ist von der Kronenausdehnung abhängig. Eine konkurrenzbedingte Verringerung der Kronengröße, kann sich negativ auf die Wachstumsleistung und damit auf die Produktivität des Baumes auswirken. Die zweite Hypothese kann ebenfalls verifiziert werden, da eine hohe Konkurrenzstärke bei *Q. rubra* zu einer Abnahme der äußeren (d. h. unerwünschten) Stammmerkmale führte, insbesondere der Unrundheit des Stammes und der Anzahl der Rindenanomalien. Das Maß für die Anzahl der Rindenanomalien umfasst sowohl die Astigkeit als auch Unregelmäßigkeiten auf der Stammoberfläche (Stammverletzungen, beispielweise ausgelöst durch Rücke- oder Fällschäden). Da astbedingte Holzfehler bei vielen Baumarten als Hauptursache für eine abnehmende Stammqualität angesehen werden, bestätigt diese Studie, dass die Roteiche, ähnlich wie viele andere heimische Baumarten, in den Phasen der frühen Bestandsentwicklung eine höhere Konkurrenzintensität benötigt, um qualitativ hochwertiges Holz zu produzieren. Ebenfalls wurde ein Zusammenhang zwischen abiotischen Faktoren und den Stamm- und Kronenmerkmalen gefunden. Die dritte Hypothese kann teilweise bestätigt werden, da ein Zusammenhang zwischen der genetischen Diversität (Heterozygotie „EST“ und „All“) und den Astwinkelmaßen erster Ordnung (Astwinkel (Mittelwert; Median) und der Astwinkelspanne festgestellt wurde. Mit zunehmender Heterozygotie wurden die Astwinkel der Roteichen steiler. Dieser Zusammenhang wurde erstmalig in einer Studie herausgefunden und ist damit überraschend. Zur Überprüfung der Ergebnisse sollten zukünftig potentiell adaptive Marker durch moderne Hochdurchsatztechniken wie RADseq (restriction site associated DNA sequencing) für die Roteiche identifiziert und potentielle Kandidatengene für die Gestaltung der Kronenmorphologie analysiert werden. Ein Vergleich der äußeren Stammmerkmale zwischen den deutschen und kanadischen Beständen zeigte für die Anzahl der Rindenfehler und die Stamm-Unrundheit signifikant höhere Werte in den kanadischen Beständen. Es zeigte sich, dass die deutschen Roteichenstämme eine schiefere und krummere Wuchsform aufwiesen. Die signifikanten Unterschiede zwischen den Ländern führen wir auf die unterschiedliche waldbauliche Behandlung zwischen Deutschland und Kanada zurück. Somit können auch die Hypothesen 4 und 5 bestätigt werden.

Für die waldbauliche Behandlung der Roteiche, die auf eine hohe Holzqualität abzielt, wird empfohlen, dass *Q. rubra* in den anfänglichen Entwicklungsstadien vorwiegend im Dichtstand aufgezogen wird. Bis durch die natürliche Astreinigung die gewünschte astfreie Stammlänge erreicht wird. Die anschließenden Durchforstungen sollten für die als sehr phototrop geltende Roteiche - zur Förderung der Kronengröße und damit der Produktivität- moderat bis stark und in regelmäßigen Abständen erfolgen. Die Durchforstungstärke und Häufigkeit ist den jeweiligen Standortsverhältnissen anzupassen.

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List of abbreviations

3D	Three-dimensional
AIC	Akaike's information criterion
Asymmetry	Crown asymmetry
BA	Basal area
Bark anom.	Bark anomalies
BA_{mean}1st	Mean branch angle of first order branches
BA_{median}1st	Median branch angle of first order branches
BA_{range}1st	Branch angle range of first order branches
Bl_{max}	Maximum branch length
BL_{mean}	Mean branch length
Bl_{median}	Median branch length
Bl_{sum}	Sum of branch length
CAN	Canada
CBH	Crown base height
CL	Crown length
CR_{mean}	Mean crown radius
CSA	Crown surface area
CV	Crown volume
DBH	Diameter at breast height
Dist.	Distance
Eq.	Equation
GER	Germany
Hegyi	Hegyi-index
H_OEST	Heterozygosity measured by EST-SSR markers
H_OAll	Heterozygosity measured by all markers used in this study
H_ONeutral	Heterozygosity measured by nSSR markers
I	Competitor tree
Int.	Interaction
J	Target tree
Ln	Logarithmus naturalis
Lme	Linear mixed-effects model
Lm	Linear model
LVP	Length of the vegetation period

Max. area	Maximum crown area
MPV	Mean precipitation during growing season
NB1st	Number of branches first order
Prec.	Mean annual precipitation
QSM	Quantitative structural model
SD	Standard deviation
SNC	Stem non-circularity
Sqrt	Squareroot
Temp.	Mean annual temperature
TLS	Terrestrial Laserscanning
TMV	Mean temperature during growing season
TTH	Total tree height
WTV	Wooden tree volume

Chapter 1

Introduction

1.1 Scientific motivation

Originating from eastern North America (Birchenko et al. 2009), northern red oak is now distributed on an area of about 360,000 ha across almost the entire European continent (Nicolescu et al. 2020). The largest area shares of *Q. rubra* are found in the Ukraine by 200,000 ha (Lavnyy and Savchyn 2017), Germany by 55,000 ha (Schmitz et al. 2014), France by 52,000 ha (Nicolescu et al. 2020 according to Merceron (2016)) and Poland by 15,000 ha (Gazda et al. 2016).

Introduced in France in 1691, *Q. rubra* was mainly planted in parks and gardens for aesthetic reasons (Hickel 1932). From that point, northern red oak spread rapidly to neighboring countries and also found its way into German avenues and parks. The first silvicultural cultivation trial of *Q. rubra* occurred here in the late 18th century (Wangenheim 1787; Beckmann 1790), followed by a second trial around 1880 (Booth 1882; Bauer 1953). Further extensive examinations in both silviculture and forest growth on northern red oak were conducted by Bauer (1953) and Göhre and Wagenknecht (1955) in the middle of the 20th century (Bauer 1953); however, the interest in this tree species decreased rapidly thereafter (Trauboth 2004). This is rather surprising, as all authors attribute to the northern red oak convenient silvicultural management options, as well as favourable growth and wood properties in Germany (Bauer 1953; Göhre and Wagenknecht 1955).

Nowadays, cultivating alien tree species is once again receiving increased attention. All climate projections for Germany show a rise in temperature with a simultaneous change in the seasonal distribution of precipitation with increased droughts, heavy rainfall, or storms (IPCC 2014; UBA 2015). The droughts recorded in Germany for 2018 and 2019 (Madruga de Brito et al. 2020) are recent evidence of the impacts of climate change (Grillakis 2019). The consequences can be observed in Germany as well as in large parts of Europe in regional production declines and loss of vitality up to forest dieback (Solberg 2004; Allen et al. 2010). For this reason, both in Germany and in many other countries, forest management is adapting to climate change by reconstituting pure stands into mixed and site-appropriate forest stands (Lüpke 2004; Forest Europe 2015; BMEL 2019). In contrast to previous generations, consisting mainly of pure coniferous trees, future forests will be predominantly composed of deciduous tree species (DHWR). Recently, even established deciduous tree species are considered to be at risk in the future due to new types of damage, mostly initiated by pest organisms (Tretter et al. 2019). Reasons for this include invasive species or a previous weakening of trees due to storms or droughts, which enables many damaging organisms to gain access to their host trees (Tarkka and Hildebrandt 2020). This makes the situation for future forest stands even more critical, since the number of tree species adapted to future climate conditions (to warmer and drier climates in particular) and native to our region is not large by global standards (Kölling 2013; Tretter et al. 2019). In forestry, the introduction of drought-tolerant but non-native tree species is thus also being considered (Asche 2007; Spathelf et al. 2008; Asche 2010), which has brought northern red oak back into greater focus for cultivation, along with other non-native tree species (Seidel and Kenk 2003; Klemmt et al. 2013). *Q. rubra* is expected to withstand future periods of drought and heat better compared to native white oak species (*Q. petraea* and *Q. robur*) (Timbal and Dreyer 1994; Dreßel and Jäger 2002; Gillner 2012) due to the lower water consumption of northern red oak (Nicolescu et al. 2020). The cultivation of this tree species might consequently reduce risks for forest owners and maintain the efficiency of forest operations (Spellmann et al. 2011).

Being the most common non-native deciduous tree species in Germany (Schmitz et al. 2014), northern red oak grows on poor sites with annual precipitation rates around 500 mm (Bauer 1953), which significantly undercuts the minimum precipitation values in its native range of 760 mm (Sander 1990; Thompson et al. 1999). In its natural distribution area, northern red oak colonizes a wide range of sites where mean annual precipitation can vary by 1,300 mm, mean annual temperatures by 11°C, or growing season length by 110 days (Sander 1990; Thompson et al. 1999). *Q. rubra* occurs on almost all soils and in a variety of mixed stands with hardwood or conifer species such as *Acer rubrum*, *Acer saccharum*, *Liriodendron tulipifera*, or *Pinus strobus* (Johnson et al. 2002; Nagel 2015). The broad climatic and site distribution in its area of origin suggests that northern red oak is also suitable for cultivation on a wide variety of sites in Germany, where it should be introduced primarily as an admixed tree species and at the expense of pure conifer stands (NMELV 2004; Kurjatko et al. 2006; Klemmt et al. 2013). For example, it should be introduced in strips in dry, poor sites in pure pine stands (and thus wildfire-prone areas) to prevent or at least reduce a potential fire spread (Otto 1976; Lange 1993; Wagner 1994; Nagel 2015). The cultivation of red oak is also recommended on sites with higher water content and at least moderate soil nutrient supply, as found in some parts of central and western Lower Saxony (NMELV 2004).

Northern red oak shows good growth performances in height and diameter, far exceeding that of *Q. petraea* and *Q. robur* native in Germany (Göhre and Wagenknecht 1955; Mitscherlich 1957; Spellmann 1994; Seidel and Kenk 2003). For example, 100-year-old *Quercus rubra* can surpass the upper heights of same-aged white oaks by 11 m - 14 m (Seidel and Kenk 2003). The fast growth of northern red oak results in target diameters of 60 – 70 cm within in a rotation period of 80-120 years, which is up to 100 years shorter than for native oak species (Seidel and Kenk 2003). According to Klemmt et al. (2013), the rapid growth is counteracted by a worse value performance (even up to 30% below the prices), due to the lack of xylem formation in the pores, which makes red oak wood unusable for barrel production. Nevertheless, northern red oak wood properties are estimated to be similar to those of native white oaks. For example, the bulk density is ± 0.68 g/cm³ and therefore relatively high (Konnerth et al. 2010). Strength properties are estimated to be even higher than those of native oak species (Göhre and Wagenknecht 1955). Thus, northern red oak can be used for a variety of applications, such as lumber, furniture, veneer, construction timber, mine wood, or firewood (Stähr and Peters 2004; Vansteenkiste et al. 2005).

1.2 Timber quality grading and basic influences on tree morphology

To determine whether a particular log is suitable for its intended use, a prior assessment of the timber quality is necessary. Timber quality depends on a variety of properties (such as branchiness, fiber length, or stem shape), which directly or indirectly affect the intended use and the particular end product (Gartner 2005; van Leeuwen et al. 2011). However, the concept of wood quality is used flexibly and varies depending on the suitability of a particular wood product for a particular purpose (Krajnc et al. 2019). Consequently, in the absence of a uniform definition of wood quality, the evaluation of the particular log would vary greatly depending on the expectations and requirements of individual customer groups (Kliger et al. 1995; Knoke et al. 2006). For this reason, a set of rules under private law for the timber and forestry industry has been formulated in Germany with the aim of ensuring a uniform, transparent and clearly defined language and trade usage in the German raw timber trade (Framework Agreement for the Raw Timber Trade in Germany (RVR 2015)). The raw wood is graded by species or species group and divided into four quality classes (A, B, C, D), where "A" stands for logs of excellent quality and "D" for logs of very low quality. Northern red oak wood quality evaluation is based on the quality grading of stems for native oak species. For oaks, this guideline includes characteristics such as knots (sound, rotten, or over-twisted), bending, radial cracks, or decay, which are either prohibited or allowed up to a certain size or extent in each quality class (RVR 2015).

Any factor that might influence tree growth can also impact wood structure and thus wood quality (Zobel and Jett 1995). Hence, stem characteristics are influenced by a variety of factors that include genetic predisposition as well as a variety of environmental factors, which in turn comprise site conditions or interactions between neighboring trees (Zobel and Jett 1995; Zingg and Ramp 2003; Seifert 2003; Richter 2010; Krajnc et al. 2019).

The influence of genetics on tree morphology is very complex. Genetic blueprinting and inheritance determine the expression of traits, but the strength of genetic control varies between species (Zobel and Jett 1995). Phenotypic plasticity further complicates the identification of the relationship between genes and their phenotypes, resulting in a more difficult detection of the underlying genes (Blue and Jensen 1988; Bruschi 2000). Different provenances of the same tree species can lead to differences in genetic constitution and associated phenotypic characteristics (Whittet et al. 2019). In particular, the parentage of introduced tree species is usually unknown, and their genetic and phenotypic traits often differ from the parent population after successful adaptation (Bossdorf et al. 2005), making it even more difficult to determine a particular genetic influence.

Environmental factors that can influence tree growth and thus wood quality include the relationship between neighboring trees, which comprises competitive (Kizuzewa 1996; Rouvinen et al. 1997) or facilitative effects (Ammer 2008) between the respective individuals (Assmann 1970; Strobel 1995; Lüpke and Spellmann 1997). Important factors in this context include initial spacing between trees, canopy architecture, or competitiveness with other tree species, as they are indicators of the availability of growing space, light, or shade (Barbeito et al. 2014). Large spacing between trees leads to a greater light availability for trees, larger crowns, and thus increased diameter and volume growth (e.g., Mäkinen and Hein 2006; Bartsch et al. 2019). A large neighboring tree can reduce growth potential, while a small neighbor can positively influence tree growth and stem quality of the respective tree (Tomé and Burkhart 1989).

Forest science therefore attempts to influence tree growth and wood quality profitably through tree species selection, determining plant spacing, or subsequent thinning interventions (Mäkinen and Hein 2006; Ammer 2008). These interventions modify stand density and thus the intensity of competition between trees (Cescatti and Piutti 1998; Aussenac 2000). Low thinning interventions keep competition intensity between trees high, which can lead to better stem quality (Hein 2008; Kirk and Berrill 2016), as well as to smaller crowns and limited radial tree growth (Mäkinen and Hein 2006; Oheimb et al. 2011), while heavy thinning leads to low competition intensities, which can cause the opposite effect (Sonderman and Rast 1988; Mäkinen 2002; Mäkinen and Hein 2006). Depending on the growth characteristics, light requirements, and age of each tree species, the intensity and frequency of thinning should be adjusted (Juodvalkis et al. 2005; Bartsch et al. 2019).

1.3 Cultivation history and silvicultural management of northern red oak

Northern red oak is one of the most important timber species in northeastern America (Vansteenkiste et al. 2005). According to FAS (2020), the value of exported red oak logs amounted to more than 100 million dollars for 2020. However, northern red oak timber quality itself can vary strongly, resulting in large price differences (Vansteenkiste et al. 2005; Marschall et al. 2014). In its natural range, oak species have a long history of cultivation (Johnson et al. 2002). Declines in northern red oak regeneration have been noted in recent decades (Sander 1979; Schlesinger et al. 1993) which may cause problems if less stemwood is expected to be available in subsequent generations while demand for red oak timber remains the same (Smith 1993). Therefore, numerous studies have focused particularly on silvicultural studies to support oak regeneration in general (Sander 1979; Johnson et al. 1989; Loftis 1990; Schlesinger et al. 1993; Dey and Parker 1996; Desmarais 1998). The present spread and expansion of *Q. rubra* can be attributed to the history of fires and to original land use systems (including logging, firewood harvesting, charcoal production, wood burning) (Abrams 1992; Dey 2002). Due to land use changes and increasing settlement, these disturbances occur much less frequently than in the past, which leads to a shifted competitive relationship between oaks and other tree species (Dey 2002). The lower shade tolerance of northern red oak regeneration compared to competitor tree species results in insufficient establishment of *Q. rubra* regeneration in its natural range (Sander 1979; Lorimer 1981). Therefore, attempts are being made to support northern red oak regeneration establishment through shelterwood cuttings (Johnson et al. 2002). In this method, no intervention is made for decades, until one or two thinnings are made throughout the entire rotation period (Pothier and Prévost 2002). The final removal of the overstory occurs when the desired seedlings can tolerate full light exposure and dominate the area; thus, the regeneration can be considered established (Hannah 1988; Loftis 1990).

In Germany, the importance of northern red oak for the timber industry is not yet high, which can be seen in the quantities offered on commercial timber submissions (e.g., Niedersächsische Landesforsten 2017; Parschau 2019; Niedersächsische Landesforsten 2021). Although its cultivation is recommended (NMELV 2004), extensive silvicultural experience with *Q. rubra* is not yet available here. There are extensive silvicultural guidelines on how native tree species should be treated in commercial forests and on which sites they should be naturally regenerated or planted (e.g., Dengler 1992, Niedersächsische Landesforsten 2014, 2016). For most non-native tree species - including northern red oak - there are still various uncertainties in this regard. While there is general agreement on the crop tree thinning approach, there are divided opinions on the intensity and frequency of those interventions (Nagel 2015). According to Lüdemann and Bernsmann (1998), tending in young stands need not be as intensive as in stands of native oak species. However, pruning seems to be necessary in the thicket/early pole stage, as vitality cannot continuously be associated with quality and removal of dominant but qualitatively poor trees is advised (Nagel 2015). While Nagel (2015) recommends early-starting heavy thinning beginning at tree heights of 14-16 m, which must be weakened after maximum volume growth performance has been reached, Göhre and Wagenknecht (1955) suggest more careful thinnings in early developmental stages.

While a preliminary evaluation of the outcome (the wood qualities and quantities) of the respective silvicultural system is performed on the standing tree by local experts, the accurate assessment of the stem quality and -volume is usually associated with felling and subsequent processing of the log (Bosela et al. 2016). When investigations need to be conducted on a standing tree, terrestrial laser scanning can represent a suitable method to record tree morphology (Dassot et al. 2012; Kretschmer et al. 2013; Höwler et al. 2017; Juchheim et al. 2017; Höwler et al. 2019) objectively (Liang et al. 2011) and non-destructively (Schütt et al. 2004; Stängle et al. 2014). Nearly every desired tree characteristic such as diameter at breast height (Simonse et al. 2003), tree height (Hopkinson et al. 2004; Seidel et al. 2015) or crown related measures such crown shapes, - volumes (Seidel et al. 2011) and branch angles (Juchheim et al. 2017) can be detected by using the terrestrial laser scanning approach. Also, external stem characteristics, such as bark anomalies as well as stem non-circularity (Höwler et al. 2017), lean or sweep (Juchheim et al. 2017)—providing information on external stem quality—can be detected. Due to the technological advancement of the terrestrial laser scanning application, the latest methods, such as the mobile laser scanner, promise an even higher efficiency (Lin and Hyyppa 2012) and thus easier and faster applications.

1.4 Objectives

The Agency for Renewable Resources (FNR) - a project agency of the German Federal Ministry of Food and Agriculture (BMEL) - supported this study under the funding priority "Sustainable Forest Management." The aim of this funding priority is to contribute through research and development to securing the supply of wood, the creation of value in forest ownership and wood-processing companies, and the preservation of commercial forests, which also serve the protective and recreational function.

Due to open questions concerning the silvicultural treatment of northern red oak, the most common non-native deciduous tree species in Germany, this study was particularly focusing on the influence of competition on tree morphology of northern red oak by terrestrial laser scanning (TLS). The aim was to find out whether *Q. rubra* can be treated similarly to many native deciduous tree species to achieve high quality timber. In addition, it aimed to investigate whether and to what extent other factors, such as genetics or site effects, can influence quality-related stem characteristics as well as crown structure and size. Another aim was to find out whether stem quality characteristics of northern red oaks in their natural distribution area differ from those in Germany and whether the differences can be attributed to the different silvicultural regimes. To do this, the following hypotheses were formulated:

1. Increased competition results in shorter and more slender tree crowns.
2. Increased competition results in fewer external stem characteristics that are negatively related to the commercial timber quality of northern red oak.
3. Competition effects on stem and crown characteristics are superimposed by genetic variation.

4. Stem form and the number of bark anomalies - both indicating stem quality of northern red oak trees - differ between Canadian and German stands due to different silvicultural practices.
5. Increasing tree competition is negatively related to external stem quality characteristics and this relationship is constant under both management systems (shelterwood system vs. crop tree thinning).

Even though mixed stands are recommended for future cultivation, we decided to examine pure northern red oak stands in Germany, in order to be able to extract the pure competition effects in absence of interspecific effects. Since no pure northern red oak stands could be found in Canada, red oak mixed stands with sugar maple or red maple were chosen.

1.5 Study site location

The investigations were conducted in Germany and in southeastern Canada, which is part of the natural distribution range of northern red oak.

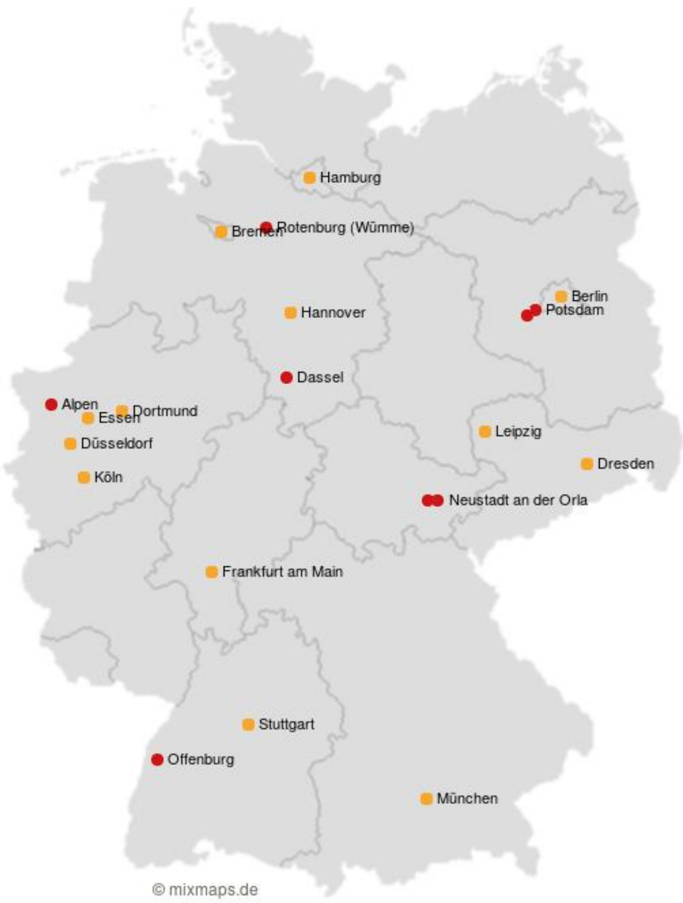

Figure 1-1: Map of the ten study sites in Germany. Stands indicated with only one marker within a region are located very close together. Lower Saxony (LS), North Rhine-Westphalia (NRW), Baden-Wuerttemberg (BWB), Thuringia (THU) and Brandenburg (BRB).

In order to cover a broad site spectrum in Germany (north-south and west-east gradient), a total of ten sample sites were investigated in five federal states: Baden-Württemberg (48°27'N; 7°51'E), North Rhine-Westphalia (51°32'N; 6°29'E), Lower Saxony (51°46'N; 9°35'E and 52°56'N; 9°22'E), Thuringia (50°45'N; 11°43'E and 50°46'N; 11°38'E) and Brandenburg (52°27'N; 13°4'E and 52°23'N; 13°5'E) (Figure 1-1). The ten study areas comprise a broad site amplitude, from rather nutrient-rich loamy loess soils with annual precipitation rates around 850 mm and annual average temperatures of 11.1 °C in Baden-Württemberg to poor sandy soils with relatively low precipitation rates of 600 mm and annual average temperatures of 9.8 °C in Brandenburg. Dassel (Sievershausen) is the site that receives the most 1192 mm precipitation, but also the coldest, with mean annual temperatures of 7.2 °C on a silty loam soil.

In Canada, the study sites are located in the southeast of the country, two each in Ontario near North Bay (46°22’N; 79°06’W and 46°39’N; 79°09’W), in Nova Scotia near Caledonia (44°31’N; 65°24’W and 44°29’N; 65°15’W), and another study site in Prince Edward Island near Charlottetown (46°16’N; 63°06’W) (Figure 1-2). On all study sites, the mean annual precipitation ranges between 1000 mm and 1300 mm, thus exceeding most of the precipitation values in Germany. The annual average temperatures in Ontario and Prince Edward Island are below the values in Germany with 4.3°C and 5.3 °C. Only the temperature of 8.5 °C in Nova Scotia rank in the lower third of the average temperatures in Germany (see also Table 4-1 in chapter 4).

Figure 1-2: Location of the five study sites in Canada, which were subjected to closer examination. Two sites each are located in Ontario near North Bay, two in Nova Scotia near Caledonia and one in Prince Edward Island near Charlottetown. The stands in Ontario and Nova Scotia were located geographically close to each other and were therefore marked as one site.

1.6 Study site and study tree selection

A full inventory of 40 northern red oak sites in Germany was conducted using the Field-Map-instrument and software package IFER (IFER; Monitoring and Mapping Solutions, Ltd., Czech Republic). The local position, diameter at the breast height (diameter ≥ 7 cm), the social position (tree classes according to Kraft (1884)) and vitality (alive, dead, broken alive or broken dead) of each tree was recorded. All sites were required to have the following criteria: (1) *Quercus rubra* trees had to be middle-aged (mature trees but not yet ready for harvest, in Germany between 55 and 85 years), (2) the site had to cover at least one hectare,

(3) the stands had to be more or less pure (minimum proportion of red oak: 80%), (4) the stands had to be on sites classified by local authorities as suitable for northern red oak cultivation.

For a more detailed silvicultural study, the two sample sites that demonstrated the highest haplotype diversity were selected for each one of the five investigated German federal states (10 study sites). On each of the ten study sites, ten (pre-) dominant trees (tree classes according to Kraft (1884)) were chosen as target trees, resulting in a sample size of 100 northern red oaks in Germany.

In order to identify study trees within the ten study sites, we used the GIS software (QGIS Development Team 2014) to manage spatial information on each tree's position obtained from Field-Map (IFER – Monitoring and Mapping Solutions, Ltd., Czech Republic). To minimize boundary effects, we placed a buffer zone of ten meters inside the boundary of each study site using xy-data. In the inner area, we randomly selected ten xy-coordinates and chose the closest (pre-) dominating tree for every random point (tree classes 1-2 according to Kraft (1884)) as "target tree". Figure 1-3 shows a graphical example of the target tree selection at one of the study sites.
The criteria for sample plot selection in Canada had to be adapted and softened compared to the criteria in Germany: (i) stands had to be middle-aged (mature trees but not yet ready for harvest), (ii) stands had to be at least one hectare in size, (iii) northern red oak had to be the main tree species (but no longer constitute at least 80% of the tree species), and (iiii) sites were considered representative of the natural range (NRCS 2002).

Due to time constraints, the sample tree selection in Canada did not occur on the basis of a previous full inventory with a subsequent random tree selection via QGIS. Instead, ten (pre-) dominant red oaks were selected directly in the stand at a distance of at least 10 m from each other and not in the border area of 10 m around the 10 m area (in order to adapt the sample tree selection in Canada to the German one as far as possible).

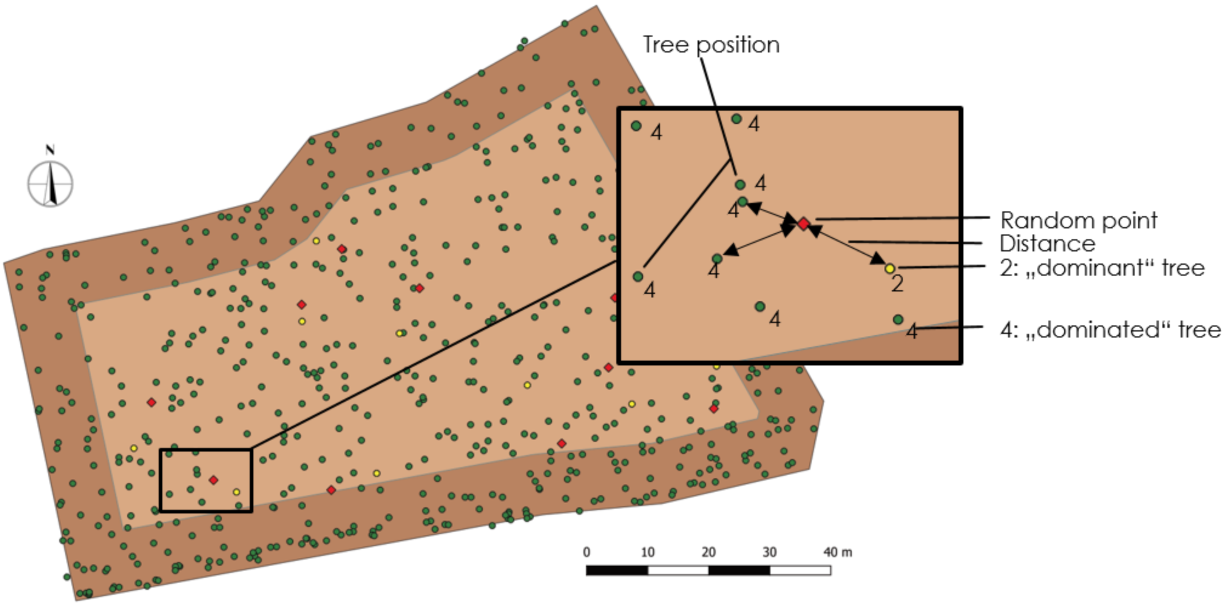

Figure 1-3: Graphical example of one study site and study tree selection in Baden-Wuerttemberg. Random point: Only one out of ten randomly selected points is shown for illustration purposes; Distance: Distance between random point and the respective study tree; 2: “dominant” tree: Dominant and nearest to the random point located tree, categorized to the tree class 2 according to Kraft (1884); 4:”dominated” tree: Dominated tree categorized to the tree class 4 according to Kraft (1884); Tree position: Local tree position on the study sites.

1.7 Technical equipment details applied for fieldwork

All 760 scans during this study were performed using a Focus 3D 120 laser scanner (Faro Technologies Inc., Lake Mary, FL, USA) mounted on a tripod (in 130 cm height above the ground). Detailed technical information regarding the Faro Scanner properties can be found in Table 1-1. The laser scanner emits and re-receives beams when they are reflected by an object nearby. More precisely, it is able to detect all objects in a field of view of up to 360° horizontally and 305° vertically and up to a distance of 120 m. By setting the angular step width to 0.035°, the spatial resolution included almost 44 million measurements per scan, which is equivalent to a resolution of 10.240 measurements per 360°. To capture the trees' three-dimensional structure, the scanning procedure was conducted on four or six positions around each target tree, depending on the surrounding vegetation density or crown visibility.

Table 1-1: Technical data sheet (Faro Technologies Inc., Lake Marry, Fl., USA).

Faro Focus 3D 120 properties:	
• Field of View: -Horizontally -Vertically	 360° 305°
• Coverage	0.6 m – 120 m
• Measurement rate	Up to 976.000 points/s
• Systematic distance error*	±2mm 10m and at 25m, at 90% and 10% reflectivity
• Laser class	3R (20mW laser output)
• Wave length	905 nm
• Spatial resolution (by angular step width to 0.035°	44 million measurements per scan = 10,240 measurements per 360 °
• Integrated color camera	Yes
• Working temperature	+5°C - 40°C

*The distance error is the maximum error in range measured by the scanner to a defined point on a level target surface

Field-Map represents a software and hardware technology that allows computer-aided acquisition of field data and processing of those data. The Field-Map—instrument and software package (IFER—Monitoring and Mapping Solutions, Ltd., Czech Republic) combines a mobile Getac T800 tablet computer and a TruPulse 360 R laser with an integrated foliage filter (to ensure a reaction of the laser lens only to high reflections), mounted on a monopod (technical data of both devices are provided in Table 1-2). Using Excel columns prepared previously and transferred to the mobile computer, the relevant information for each tree can be added in situ to the tablet computer. The local coordinates of each tree can be recorded by placing a reflector directly in front of the respective tree (in height of 130 cm) and recording it with the laser, which in turn transmits the data to the tablet computer via Bluetooth. By georeferencing the local coordinates, each tree can be found on the sites with an accuracy of 20 m in the stand. Geographical information systems such as QGIS can be used to read and process the information on the trees previously recorded in the inventory (IFER—Monitoring and Mapping Solutions, Ltd., Czech Republic)

Table 1-2: Technical properties of the Field-Map instruments, mounted on a tripod: namely the Getac T800 tablet computer and the Laser TruPulse 360 R.

Getac T800 tablet computer		TruPulse 360 R	
Weight:	950 g (incl. battery)	Weight:	385 g
Size:	22,7 x 15,1 x 2,4 cm	Size:	13 x 5 x 11 cm
Power supply:	Li-Ion battery 7.4V 4200mAh (up to 5 hours)	Power supply:	CR123A (3V) Lithium
Temp. range:	-21°C to +50°C	Temp. range:	-20 to +60°C
Resistance:	dust and rain (IP 65)	Resistance:	water and dust (IP 56)
Processor:	Intel® Atom Processor x7-Z8700	Accuracy (dist.):	±20 cm; typical
Memory:	4 GB DDR3L, 128 GB SSD	Accuracy (incl.):	±0.25°; typical
Display:	8.1” TFT LCD HD (1280 x 800), 600 nits LumiBond® display with Getac QuadraClear® sunlight readable technology	Accuracy (azim.):	±1 °; typical
		Range meas:	up to 1 000 m; typical
Origin:	China	Origin:	Japan

* Information provided by (IFER—Monitoring and Mapping Solutions, Ltd., Czech Republic).

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Chapter 2

Intraspecific competition affects crown and stem characteristics of non-native *Quercus rubra* L. stands in Germany

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Abstract

Accurate guidelines for silvicultural management of exotic tree species in Germany are sparse. For example, northern red oak (*Quercus rubra* L.) is the most commonly planted exotic deciduous tree species in Germany, but its response to varying levels of competition intensity has not yet been adequately explored. Here, we used terrestrial laser scanning to non-destructively examine the responses of stem and crown characteristics of *Quercus rubra* to intraspecific competition. A total of 100 dominant red oak trees were investigated in ten pure red oak stands, located in five federal states of Germany. The external stem quality characteristics namely stem non-circularity and bark anomalies decreased with increasing tree competition. Also, the crown characteristics crown volume, crown surface area, maximum crown area, crown length, and branch length declined by the degree of individual tree competition. We conclude that individual tree properties can be controlled by competition intensity, resulting in improved timber quality as shown for other tree species.

Keywords: northern red oak; terrestrial laser scanning; competition; crown characteristics; stem characteristics; silvicultural treatment

2.1 Introduction

Tree species selection and stand density control are usually the most important decisions forest managers can make. While the effects of silvicultural treatments that control competition intensity have been studied since the beginning of forest science (Cotta 1828; Bernhardt 1874; Kraft 1884) and are well known for native tree species (Cotta 1828; Bernhardt 1874; Kraft 1884; Burschel and Huss 2003; Eisenhauer and Sonnemann 2009), guidelines for exotic trees species are often lacking or are uncertain (Kölling 2013). Northern red oak (*Quercus rubra* L.) is the most commonly planted exotic deciduous tree species in Germany, covering 0.5% of its forested area (Stratmann and Warth 1987; Smith and Long 1989). Native to eastern USA and Canada (Sander 1990), red oak has been cultivated in Germany for more than a century.

Several studies have addressed silvicultural management of native oak species in Germany (Leibundgut 1945; Mosandl et al. 1991; Block et al. 2007). Studies of the management of red oak in Europe are, however, in contrast to North America (Sondermann and Rast 1987; Dey and Parker 1996; Dey et al. 2010), far more scarce, only a few management trials with red oak are available (Du Teissier Cros 1987; Rédei et al. 2010; Klemmt et al. 2013). Responses of *Quercus rubra* L. with respect to crown expansion and stem growth under varying competition intensities and different sites have not yet been fully explored outside their native range. While there is general agreement that thinning from above is a suitable treatment (Bauer 1953; Göhre and Wagenknecht 1955; Seidel and Kenk 2003; Nagel 2015), the discussion is ongoing regarding both the number of crop trees to be promoted and the degree of individual tree competition that promote timber quality (Seidel and Kenk 2003; Nagel 2015).

Terrestrial laser scanning (TLS) has recently been utilized as a tool to explore tree morphology in detail, including quality-related attributes of trees (Watt and Donoghue 2007; Newnham et al. 2015; Höwler et al. 2017; Seidel 2018; Seidel et al. 2019b). Several studies have demonstrated that various tree characteristics, such as diameter at breast height (Simonse et al. 2003), total tree height (Hopkinson et al. 2004; Seidel et al. 2015), or timber volume (Raumonen et al. 2013) can be derived from TLS. Additionally, Kretschmer et al. (2013) generated a method to identify bark irregularities, such as branch knots or branch scars, and recently Höwler et al. (2017) and Höwler et al. (2019) used TLS-based measures to describe external stem characteristics (i.e., bark anomalies, lean and sweep) of beech (*Fagus sylvatica* L.) trees in response to competition. Other studies have shown the potential of TLS to measure tree crown shapes under varying levels of intra- and interspecific competition (Seidel et al. 2011; Bayer et al. 2013; Metz et al. 2013; Juchheim et al. 2017).

Here we used TLS at different sites in Germany to investigate the morphological responses of red oaks to the competition. Although we are aware that red oak monocultures are no longer recommended in current silvicultural programs, we used pure stands in order to better understand competitive effects at a basic level without complex interspecific and species-specific implications (Bauer 1953).

The objective of our study was to contribute to improved management schemes for red oak. More specifically, we hypothesized that: (1) Increasing intraspecific competition results in shorter and more slender tree crowns, and (2) results in fewer external stem characteristics that are negatively related to the commercial timber quality of red oak.

2.2 Material and methods

Study Sites

Our study was conducted in five federal states of Germany: Brandenburg, Thuringia, Lower Saxony, North Rhine-Westphalia, and Baden-Wuerttemberg, and covered a broad geographical site range (Figure 2-1, Table 2-1). In each state, two study sites were chosen according to the following criteria: (1) *Quercus rubra* trees needed to be middle-aged (mature trees but not yet in their final harvesting period, here between 55–85 years), (2) the area should comprise at least one hectare, (3) stands should be more or less pure (minimum share of red oak: 80%), (4) stands had to be located on sites that local authorities had classified as suitable for red oak, and (5) stands should cover a wide range of genetic diversity (chloroplast DNA haplotypes, derived from a preceding study (Pettenkofer et al. 2019).

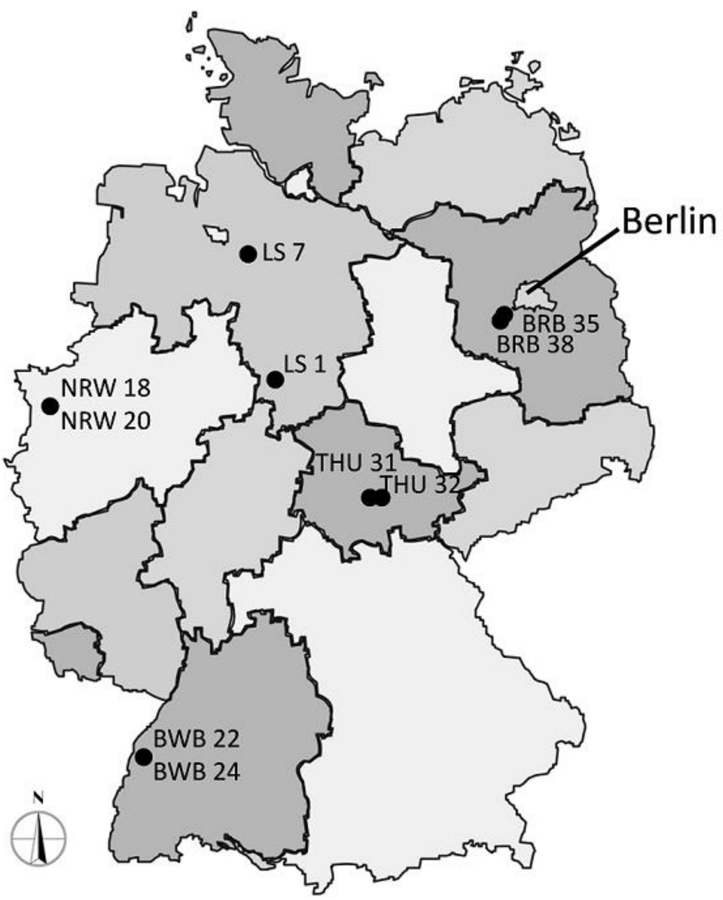

Figure 2-1: Location of the ten study sites in Germany. Stands indicated with only one marker within a region are located very close together. Lower Saxony (LS), North Rhine-Westphalia (NRW), Baden-Wuerttemberg (BWB), Thuringia (THU), Brandenburg (BRB).

Table 2-1: Main characteristics of the ten study sites and stands dominated by northern red oak in Germany: Lower Saxony (LS), North Rhine-Westphalia (NRW), Baden-Wuerttemberg (BWB), Thuringia (THU), Brandenburg (BRB).

Stand information	**LS**		**NRW**		**BWB**		**THU**		**BRB**	
District	Dassel	Rotenburg	Niederrhein	Niederrhein	Offenburg	Offenburg	Neustadt	Jena-Holzland	Potsdam	Potsdam
Department	Sievershausen	Diensthop	Leucht	Leucht	Schutterwald	Schutterwald	Strößwitz	Wolfersdorf	Güterfelde	Güterfelde
PlotID	1	7	18	20	22	24	31	32	35	38
Area size (ha)	1.0	0.9	0.8	1.3	0.8	1.0	1.0	1.1	1.0	1.0
latitude	51°46’47.34”N	52°56’46.74”N	51°32’14.11”N	51°32’19.68”N	48°27’13.11”N	48°27’9.64”N	50°45’37.95”N	50°46’19.900”N	52°27’13.29”N	52°22’57.95” N
longitude	9°35’25.30”E	9°21’58.43”E	6°29’26.77”E	6°29’50.10”E	7°51’32.91”E	7°51’37.01”E	11°43’31.84”E	11°38’27.95”E	13°4’37.92” E	13°5’43.83” E
Genetic Hap.*	A	A, B, C	A, B, C	A, E, B	A, C, E, B	A, C, B	A	A, B, C	A, C, O	A, B
soil texture	loessic loam	loamy sand	gravelly-, loamy sand	loamy sand	silty loam	silty loam	sand	sand	sand	sandy cover layers over boulder clay
Last thinning intervention	2013	2017	2017	2017	2013/2014	2013/2014	2013	2015	2014	2007
Crown thinning (m^{3,}*ha^{-1})	33.5	35	25	25	30–40	30–40	30	30	36	N/A
MPV (mm)**	468	346	354	359	397	397	350	341	291	284
TMV (°C)**	13.6	15.8	16.9	16.8	18.0	18.0	15.8	15.8	17.0	17.0
LVP (days)**	154	173	181	181	185	185	167	168	174	174
Elevation (m.a.s.l.)	524	69	68	72	148	148	392	372	47	38
Yield class**	3.3	2.2	1.6	1.6	0.8	0.6	0.6	1.2	2.8	1.6
Age (years)	66	67	58	68	67	60	57	82	63	67
mean stand height (m)	18.4	22.7	23.5	24.8	27.6	27.3	26.9	27.3	19.9	24.4
mean DBH (cm)**	20.3	20.6	28.1	27.7	20.3	22.8	26	27.8	18.6	21.8
Tree density (trees/area size)	706	662	334	447	583	550	415	673	731	614
BA (m^2) **	31.8	34.1	22.9	34.7	29.2	35.5	25.7	48.1	22.0	25.7

*Genetic Hap.: Haplotypes were assessed by Pettenkofer et al. (2019) in the same northern red oak stands prior to our study, ** MPV: Mean precipitation during the vegetation period (May–September) (DWD Climate Data Center-CDC 1988d - 2017), **TMV: Mean temperature during the vegetation period (May–September) (DWD Climate Data Center-CDC 1988c-2017), LVP: Length of the vegetation period (days), calculated based on the number of days between leaf emergence and leaf discoloration of *Quercus robur* (information for *Quercus rubra L*. was lacking) of the last 25 years provided by the Climate Data Centre (DWD Climate Data Center-CDC 1992a - 2018, 1992b -2018), yield-class: Calculated based on the yield table for red oak of Bauer (1953), DBH: Mean diameter at breast height, BA: Basal area, calculated as the sum of the cross-sectional areas (at breast height) of all stems ≥7 cm in DBH.

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Tree Inventory

We conducted a full inventory of all ten stands using the Field-Map—instrument and software package (IFER—Monitoring and Mapping Solutions, Ltd., Czech Republic). Tree coordinates, diameter at breast height (DBH) of every tree with a DBH ≥ 7 cm, social status (tree classes according to Kraft (1884)), and information on each tree's health status (alive, dead, broken alive, or broken dead) from visual assessment were recorded. For morphological assessments we randomly selected ten dominant red oak trees (tree classes 1–2 according to Kraft (1884)) per study site, resulting in a total of 100 "subject trees". The study trees were selected within a 10 m wide buffer zone along the border of the respective site.

The competitive status of each study tree was calculated based on an area of about 700 m^2 (r = 15 m) around each tree. All neighboring trees whose stems were located inside the 15 m radius were considered potential competitors. Since the measured maximum subject tree crown radius was ± 6.5 m, we assumed that the 15 m radius included all neighboring trees which could potentially influence the growth performance of the subject trees. In order to quantify competition intensity (Equ. 2-1) we used an Index adopted from Hegyi (1974).

Equ. 2-1 $$\text{Hegyi-Index} = \sum_{i=1}^{n} \frac{D_i}{D_j} \times \frac{1}{Dis_{ij}},$$

with subject tree j, competitor tree i, diameter at breast height (D (cm)) and the distance between subject tree j and the competitor trees i (Dis (m)).

Terrestrial Laserscanning

We used terrestrial laser scanning to describe the three-dimensional (3D) structure and external stem characteristics of each subject tree. All scans were performed between January and May 2018 in order to record the trees without their leaves. We used a Faro Focus 3D 120 laser scanner (Faro Technologies Inc., Lake Mary, FL, USA) mounted on a tripod at 1.3 m height above the ground. The scanner was set to capture a field of view of 360° horizontally and 300° vertically to a maximum distance of 120 m. The spatial resolution comprised nearly 44 million measurements per scan by setting the angular step width to 0.035°, which equates to a resolution of 10,240 measurements per 360°. Depending on the overall stand density and visibility in the surroundings of the subject tree, four to five scans were conducted (van der Zande et al. 2008). The mean distance between the position of the scanner and the subject tree depended on the crown proliferation. For spatial co-registration of all scans made in the surroundings of a subject tree, we used 15 to 25 artificial checkerboard targets (tie points on foil-coated DIN-A4 (21.0 cm x 29.7 cm) paper). As a result, a full 3D point cloud of each stem, including the crown of each subject tree, was available.

Post-processing of TLS Data

We exported the 3D point cloud of each subject tree as a .xyz-file (Cartesian coordinates) and imported the data into the CloudCompare Software (Cloud Compare 2.6, retrieved from http://www.cloudcompare.org/). Using CloudCompare, each subject tree was manually extracted from the total point cloud and also stored as a .xyz-file (Metz et al. 2013). For a more in-depth analysis of external stem characteristics that could be related to timber quality, the stem was separated from the individual tree point cloud using crown base height as the separation point between stem and crown. The 3D models of the stems were also exported as .xyz-files for further analysis.

Timber Quality Assessment

Using a newly developed algorithm written in the software Mathematica (Wolfram Research, Champaign, IL, USA) (Höwler et al. 2017), the 100 point clouds of the tree stems were virtually cut into 4 m long sections. Timber quality is commonly classified based on such sections in Germany according to the 'framework for trading wood' (RVR 2015). This framework defines which stem properties and wood attributes shall be evaluated and how timber is to be sorted into different quality grades.

To homogenize the spatial resolution point clouds of all trees, we used a point cloud grid (PCG) of 1.75 cm resolution for each stem section (Seidel et al. 2011; Höwler et al. 2017). Using PCGs, variations in point cloud densities among trees scanned with identical scan settings can be reduced (Höwler et al. 2017). Such variations naturally result from varying scanner-to-tree distances, varying overlap of data from different scan positions, and occlusion effects due to understory vegetation. An accuracy assessment of the approach is difficult but was attempted in Höwler et al. (2019), when bark anomalies were contrasted to internal wood characteristics.

Then, for every 4 m stem section the same approach was used: The homogenized point clouds were partitioned into horizontal layers of 1.75 cm thickness, representing "stem discs". These layers were processed in accordance to the "QR" decomposition that creates a circle to the points of each layer, factorizing a matrix with "Q" as the orthogonal and "R" as the upper triangular matrix (Höwler et al. 2017) (Seidel and Ammer 2014; Höwler et al. 2017). A minimum of 20 points has been considered to constitute a stable circle fit, as in further studies it has been proved as solid (Höwler et al. 2017). Afterward, the diameter, center coordinates and each height of every created circle were recorded (Höwler et al. 2017).

The measure “total lean” for every stem section was calculated based on horizontal differences between the lowest and the highest circle position. To guarantee a length-independent measurement of lean, the resulting value was divided by the total length of each stem section. “Total sweep” was defined as the ratio of the shortest distance between the centers of the lowest and highest circle (straight line) within a stem section and the distances between the centers of all circles of every stem section within a tree. To obtain sweep per meter, total sweep was corrected by the length of each stem section (Höwler et al. 2017).

In the following, we provide definitions for scan-based measures that were used for quality assessment of the external stem surface.

First, “stem non-circularity” was determined for each stem section based on the stem discs (see above). For each disc, we calculated the absolute differences between every point on the stem surface and the radius of the stem disc derived from the circle fit conducted for each disc (Höwler et al. 2017; Juchheim et al. 2017). As introduced by Höwler et al. (2017), p. 1607), “The mean of these absolute distances was calculated for each height layer. The median of all height layers was finally considered a measure of stem non-circularity of the stem section”. We also used the standard deviation of the stem non-circularity measure for all height layers per stem section as a measure of variability in stem non-circularity along the vertical stem axis (Höwler et al. 2017).

Secondly, we determined the mean distance between each point on the surface of a stem disc and the center of the respective stem disc. This measure was used to identify points that were either unusually far (larger than average distance + standard deviation) from the center of the stem disc (bumps) or unusually close (shorter than average − standard deviation of the stem disc) to the center (dents). We considered those points as “bark anomalies” (i.e., branch scars). “Bark anomalies thus count all points with a position that deviates “more than usual” from the fitted circle.”((Höwler et al. 2017), p. 1607), and it is highly adapted to the local conditions of the stem as each stem disc is considered individually (Höwler et al.

2017). To calculate bark anomalies per meter the number of bark anomalies was divided by the length of the stem sections (Höwler et al. 2017). Additionally, bark anomalies per square meter were computed based on the surface area of the respective stem sections to account for the differences of stem diameters.

Taking into account the RVR framework, lean and sweep are allusions of “simple sweep”. Bark anomalies comprise all branch caused defects (i.e., water sprouts, alive or dead branches). Crown characteristics are not included in the RVR Framework.

Tree Architecture

To describe tree architecture in terms of branching pattern we used Quantitative Structural Models (QSMs) deduced from the point clouds with the software Computree (Piboule et al. 2013) following the methodology introduced by Hackenberg et al. (2015). Hierarchical collections of cylinders were fitted to local details of the point cloud to describe the tree (Raumonen et al. 2013). From the cylinder models we derived measures of mean branch angle of first-order branches, mean branch angle of second-order branches, sum-, mean-, median-, maximum of branch lengths of first-order branches, tree stem volume, branch volume first-order, and—based on all cylinders of each tree—wooden tree volume (Figure 2-2).

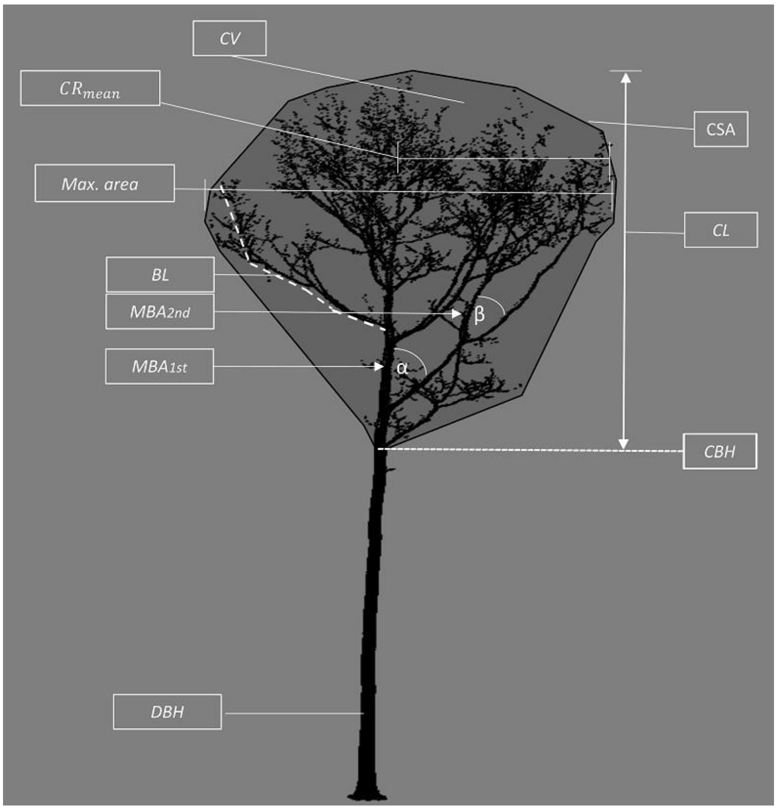

Figure 2-2: Graphical visualization of the most important tree characteristics analyzed for each subject tree: CV: Crown volume (m^3), CR_{mean}: Mean crown radius (m), max area: Maximum crown area (m^2), BL: Branch length (m), MBA1st: Mean branch angle first order (°), MBA2nd: Mean branch angle second-order (°), CSA: Crown surface area (m^2), CL: Crown length (m), CBH: Crown base height (m).

Tree Morphology

We also derived 12 measures of tree morphology and dimension directly from the point cloud of a given tree. This approach included the variables diameter at breast height (DBH) (Seidel et al. 2011), lean and sweep (Juchheim et al. 2017), stem non-circularity, bark anomalies (Höwler et al. 2017), crown base height (CBH) (Metz et al. 2013), maximum crown area (Seidel et al. 2015), crown surface area, crown volume, crown length (TTH-CBH), crown asymmetry (Seidel et al. 2011), and mean crown radius (Figure 2-2) (Seidel et al. 2015).

Statistical Analysis

We conducted all statistical analyses using the R Software environment (R Core Team 2018). We tested the data for normality using the Shapiro-Wilk Test. Variance homogeneity was tested using Levene's test.

The effect of competition intensity on both crown characteristics and stem quality attributes in every stem section (0 m–4 m (measured beginning from the root collar), 4 m–8 m, 8 m–12 m) were analysed using simple linear regression.

If needed, the independent or dependent variables were log-transformed to get normally distributed residuals and to depict nonlinear relationships with a linear model. Yield classes were used to assess whether the effect of competition on crown properties and stem quality was modified by site quality. Yield classes were derived from yield tables developed for red oak (Bauer 1953). High yield classes indicate poor site conditions while low values indicate better site conditions (Burschel and Huss 2003). In addition, linear mixed effect models were used to account for the hierarchical structure of the data, with idplot within federal states as a random factor. The random factor federal states did not significantly improve the models, so it was removed. The ID of the plots (idplot) (stand specific number) remained as a random factor and significantly improved the amount of variance explained. However, we decided to use simple linear regression models to show the overall effect of competition for the sake of simplicity and to present the results of the mixed effect models in the SI (site index) for comprehensiveness (Table S-2-2).

As some relations belong to basic knowledge (influence of competition on diameter at breast height, stem volume, branch volume, and wooden tree volume), they will not be discussed in the following (Figure S-2-2).

All models were fit with restricted maximum likelihood (REML). For all statistical analyses, we used a significance level of $p < 0.05$. However, since the use of *p*-values has recently been criticized (Wasserstein et al. 2019), only obvious and biologically reasonable relationships were considered in the Discussion.

2.3 Results

Distribution of the number of bark anomalies per meter (median ± SD (standard deviation)) decreased from the lowest stem section (0 m–4 m) to the top section (8 m–12 m) (0 m–4 m: 932.9 + 201.7, 4 m–8 m: 534.5 + 127.3, 8 m–12 m: 271.5 ± 87.3). The values for mean stem non-circularity decreased from the first section (0 m–4m: 0.009 ± 0.003) to the second section (4 m–8 m: 0.007 ± 0.002). Between the second section and last sections, the values for stem non-circularity were almost equal (8 m–12 m: 0.007 ± 0.002).

Two external stem characteristics and seven crown characteristics were significantly related to competition intensity. The two stem quality attributes stem non-circularity (section 0 m–4 m ($p < 0.001$), 4 m–8 m ($p < 0.001$) and 8 m–12 m ($p < 0.001$)) and bark anomalies (section 0 m–4 m ($p < 0.001$) and 4 m–8 m ($p = 0.001$)) significantly declined with increasing competition (Figure 2-3). At a given level of competition, both measures had higher values at better sites (Table S-2-1). Also, bark anomalies per square meter were significantly related to competition. In section 0 m–4 m the number of bark anomalies decreased with increasing competition indices ($p < 0.01$). Whereas in the sections 4 m–8 m ($p = 0.05$) and 8 m–12 m ($p < 0.05$) the number of bark anomalies per square meter increased with increasing competition (Figure 2-3). For lean and sweep no significant relationship with competition was observed (Figure S-2-1).

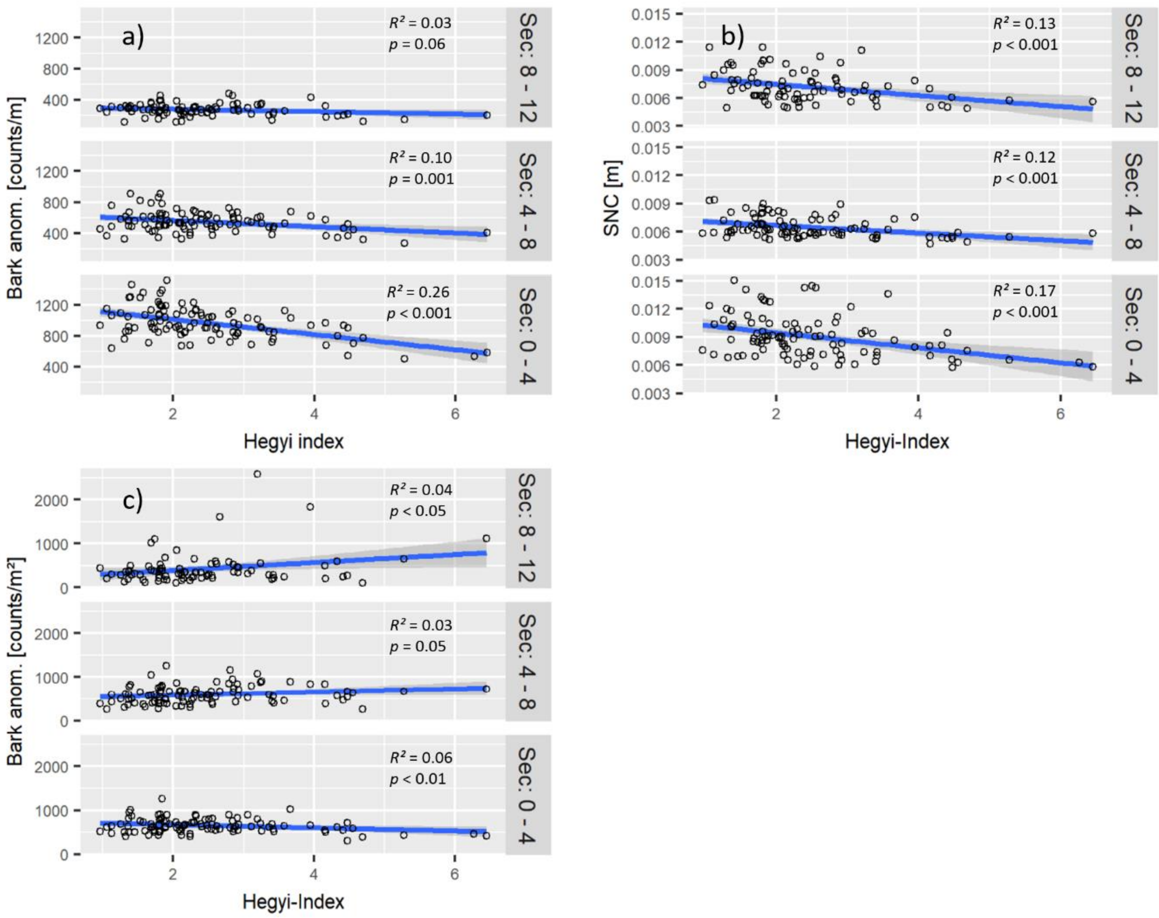

Figure 2-3: Linear models of competition intensity (Hegyi-Index) and the stem quality attributes bark anomalies (Bark anom.) ((a) counts/m and (c) counts/m^2) and stem non-circularity (SNC) ((b) in m) along the stem sections 0 m–4 m (Sec: 0–4), 4 m–8 m (Sec: 4–8), 8 m–12 m (Sec: 8–12) as cumulative values for all 100 tested trees.

The seven crown attributes crown volume ($p < 0.001$), crown surface area ($p < 0.001$), mean crown radius ($p < 0.001$), maximum crown area ($p < 0.001$), maximum branch length ($p < 0.001$), sum of branch length ($p < 0.001$), and crown length ($p < 0.001$) decreased with increasing competition intensity (range = 0.97 − 6.45, min and max) (Figure 2-4).

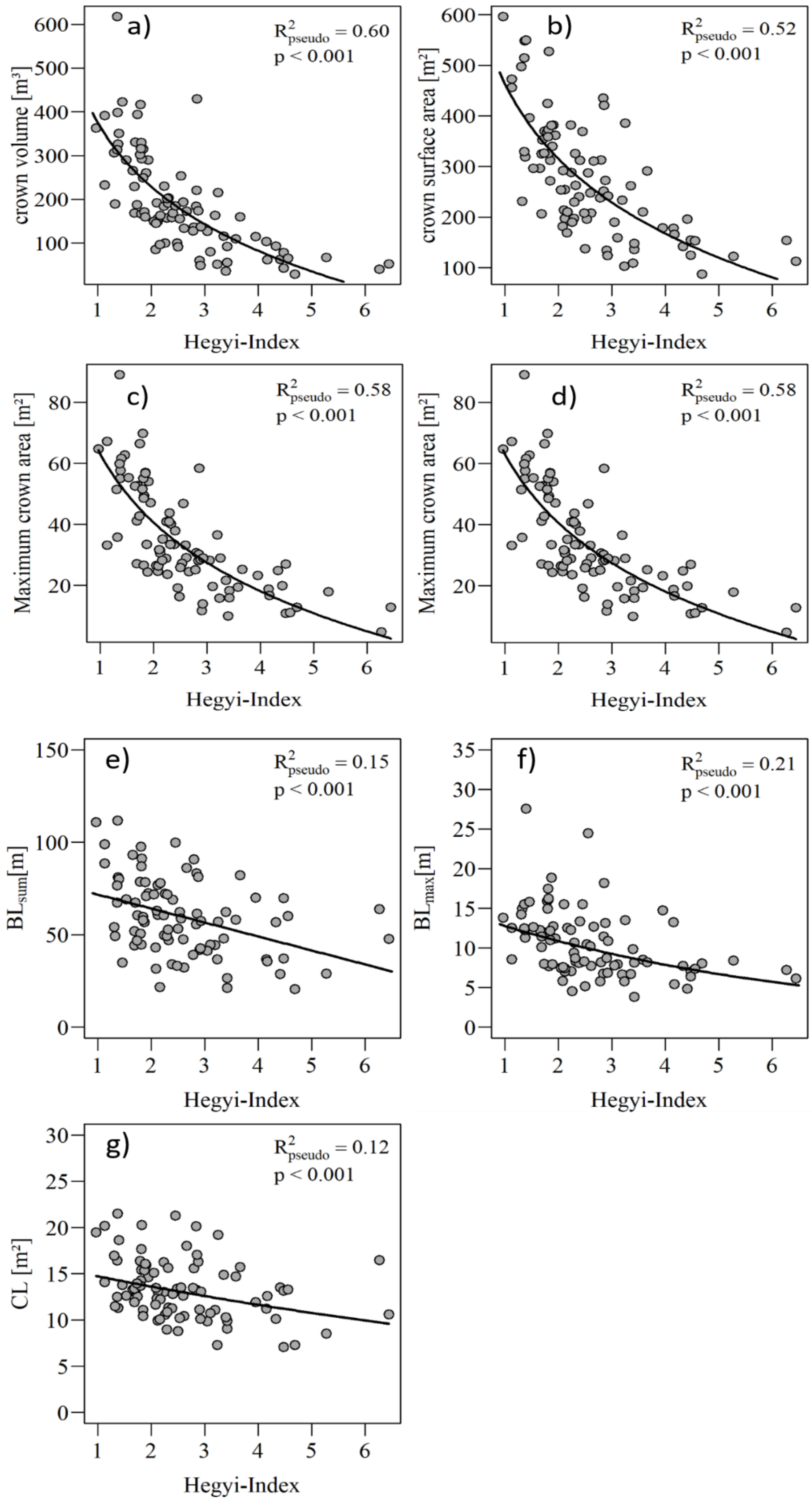

Figure 2-4: Relationship between competition intensity (Hegyi-Index) and the crown characteristics: (a) Crown volume (CV), (b) crown surface area (CSA), (c) mean crown radius (CR_{mean}), (d) maximum crown area (max area), (e) sum of the branch length (BLsum), (f) maximum branch length (BLmax), and (g) crown length (CL).

We found no significant relation between competition and the crown attributes mean branch length, median branch length, mean branch angle of first-order branches, mean branch angle of second-order branches, crown asymmetry, and crown base height (Figure S-2-2).

The tree attributes diameter at breast height ($p < 0.001$), stem volume ($p < 0.001$), branch volume first order ($p < 0.001$) and wooden tree volume ($p < 0.001$) decreased with increasing competition (Figure S-2-2).

Apart from the competition, crown surface area, mean crown radius, maximum branch length, and sum of branch length were also significantly influenced by the site index. In three out of four cases crown attributes increased with site quality (Table S-2-1).

2.4 Discussion

Effect of Competition Intensity on Crown Attributes

The results of this study show that competition plays an important role in shaping both the morphology and the architecture of red oak trees. Horizontal crown extension (mean crown radius and maximum crown area), vertical crown extension (crown length), and the complete three-dimensional crown extension (crown volume and crown surface area) decreased with increased competition. Maximum branch length, accounting for a large part of the crown volume, was also reduced by increased competition. These findings are in line with previous studies of deciduous trees, suggesting that crown extension can be used as a predictor of the degree of competition a tree has experienced during its development (Roloff 2001; Purves et al. 2007; Thorpe et al. 2010; Dieler and Pretzsch 2013). For example, Mäkinen and Hein (2006) showed that branch lengths of Norway spruce trees were affected by high competition intensities and led to smaller crowns, including shorter crown lengths.

Crown extension reflects the availability of above-ground resources (Pretzsch and Schütze 2005; Purves et al. 2007). In turn, the resource acquisition capacity of trees is negatively affected by increasing competition. Consequently, increased competition leads to a reduction in crown length (Brown et al. 2004; Lang et al. 2010), which is due to the loss of branches in the lower crown areas as a result of low light availability in the lower crown sections (Mäkelä and Vanninen 1998). Vertical crown extension, however, is the driving force of productivity, since it determines leaf area and impacts light interception and the microclimate of the canopy (Prescott 2002; Purves et al. 2007; Hardiman et al. 2013; Jucker et al. 2015).

We found the expected negative relationship between crown extension and competition even though we could only quantify the present competition status, which does not necessarily correspond to the situation in past decades. If, for example, a recent thinning intervention had reduced competition of our study trees, their crown shape still would have been strongly affected by the previous tree neighborhood. It seems that actual competition status is therefore closely related to crown attributes that are relevant for productivity (Assmann 1970).

Effect of Competition Intensity on Stem Quality Characteristics

The external stem quality characteristics number of bark anomalies and stem non-circularity decreased with increasing competition. Irregularities on the stem surface originate from both former branches and multiple stem injuries (e.g., bark seams) (Richter 2010). This study confirmed previous findings that increasing stand density leads to reduced branchiness (Ballard and Long 1988; Gottschalk and Fosbroke 1995; Mäkinen 1999; Mäkinen 2002; Mäkinen and Hein 2006). Thus, for red oak high competition intensities are also necessary to improve timber quality (Sondermann 1984; Hunter 1999; Fischer 2000; Höwler et al. 2017), as increasing branchiness is thought to reduce the stem quality and value of many tree species (Fischer 2000; Burschel and Huss 2003; RVR 2015). Recovered bark wounds, which were included in our assessment of the number of bark anomalies, can have negative impacts on inner stem quality (e.g., white rot) of oak (Schulz 1973) leading to reduced timber value. Thus, the number of bark anomalies is a reasonable measure for predicting inner timber quality (Höwler et al. 2017).

It has to be considered that bark anomalies may also include recovered bark wounds, which can be caused by harvesting machines during a thinning intervention. The intensity of damage depends on several factors i.e., stand density, machine type or environmental conditions (Hassler and Grushecky 1999; Akay et al. 2006). Bark wounds can be observed 10 years or 20 years after harvest (Seablom and Reed 2005). Further studies about the impact of stem wounds in the number of bark anomalies are necessary. Another possible effect of harvest events is the phototropic growth of red oak (Bauer 1953), that can result in swept and leaned stems after strong release. The results of this study did not show any significant results with the stem characteristics lean and sweep, so we suggest, that there was no strong release during past thinning interventions.

In order to correct the absolute number of bark anomalies by stem dimensions, we calculated the number of bark anomalies per m^2 as well. We found our expectations confirmed that the upper stem sections did not profit from the higher competition in terms of stem quality because here the diameter increment was not high enough to quickly cover the scars from former branches. Stem non-circularity decreased with increasing competition, revealing another positive effect of higher competition intensities (Zingg and Ramp 2003; Höwler et al. 2017). Dean (2003) found that stem non-circularity can lead to an overestimation by up to 10% of mature tree stem volume for *Sequoiadendron giganteum, Eucalyptus regnans* and *Quercus robur,* which in turn reduces the timber yield of the stem strength classes.

Effect of Site Conditions

Site conditions generally reflected both total timber yields and height growth in forest stands. Thus, we used yield classes to classify the site conditions.

Both stem quality attributes and all crown characteristics were related to competition intensity and yield classes. At a given level of competition, higher values of bark anomalies and stem non-circularity and hence poorer stem quality were found on better sites. We assume that this finding is due to differences in growth. On good sites, trees grow faster, resulting in larger stem and branch diameters. After self-pruning, branch occlusion may take longer or may be more pronounced for these large branches as expressed by the measures bark anomalies and stem non-circularity.

The interaction term that included the three crown characteristics crown surface area, maximum branch length and the sum of branch length resulted in stronger responses to competition intensity under good than under poor site conditions. In line with the stress-gradient-hypothesis (Bertness and Callaway 1994; Maestre et al. 2009) it seems that on good sites competition for resources is greater than on less good sites (lower yield classes)

Silvicultural Recommendations

We found significant effects of competition intensity on external stem quality attributes specifically stem non-circularity and bark anomalies. High competition intensities led to better stem qualities with respect to both measures. Several other tree characteristics (e.g., mean crown radius or crown volume) were also affected by competition intensities. To obtain higher timber quality, our results indicate that red oaks need rather high stand densities to produce fewer external stem defects. External stem quality characteristics are strongly related to internal stem quality (Sterba et al. 2006; Höwler et al. 2019). With higher competition intensities, intended diameters of subject trees may be reached later, but stem qualities will be higher (Sondermann and Rast 1987). Once the desired branch-free log lengths are reached, it is essential to release future crop trees from the competition in order to direct diameter increment primarily to these trees.

As this study captured only a snapshot of the relationship of competition to morphology, longer time series of red oak thinning trials under different site conditions would be desirable. Such experiments would make it possible to assign direct growth responses, which could then be related to a release from the competition. The effect of competition from other tree species in mixed red oak stands is another field that should be explored by future studies on red oak outside its natural range.

2.5 Conclusion

We examined the effect of competition intensity on tree and crown characteristics of northern red oak. Crown dimensions decreased with increasing competition, but stem quality was, in general, better in denser stands. We conclude that increased competition was the main driver of enhanced stem quality and reduced crown size.

European northern red oak stands could be managed similarly to many native broadleaved tree species. In Germany this would mean applying low thinning intensities in young stands until self-pruning has reached the desired height, followed by heavy thinning from above in order to support crown extension of selected subject trees and hence growth.

2.6 Supplementary

The following are available online at www.mdpi.com/xxx/s1. Table S-2-1: Relationship between tree characteristics, competition intensity (Hegyi-Index) and site Index (yield class; the lower the class, the better the site); Table S-2-2: Results of the linear mixed effect model with competition as independent, idplot (site effect) as random factor; Figure S-2-1: Linear models of competition intensity (Hegyi-Index) and the stem quality attributes sweep and lean along the stem sections; Figure S-2-2: Relationsship between competition intensity (Hegyi-Index) and various tree characteristics.

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Supplementary Materials:

Table S-2-1: Relationship between tree characteristics, competition intensity (Hegyi-Index) and site Index (yield class; the lower the class, the better the site); Adj-R^2: Adjusted R^2; AIC: Akaike-Information-Criterion; P-value; Int: Interaction between Hegyi-Index and yield classes.

Tree characteristics	Model	Adj R^2	AIC	P-value
Bark anomalies Sec: 0-4 m	y = 1257.37 - 87.54 * Hegyi - 45.79 * yield c.	0.29	1315.50	Hegyi < 0.001 Yield c. = 0.03
Stem-non-circularity (ln) Sec: 0-4 m	y = -4.37 - 0.08 * Hegyi - 0.09 * yield c.	0.26	-12.32	Hegyi < 0.001 Yield c. < 0.001
Crown surface area	y = 636.98 - 131.39 * Hegyi - 90.92 * yield c. + 29.78* Hegyi * yield c.	0.49	1023.27	Hegyi < 0.001 Yield c.: = 0.003 Int: = 0.004
Mean crown radius	y = 3.92 - 0.61 * Hegyi + 0.27 * yield c.	0.59	149.22	Hegyi: p < 0.001 Yield class: p < 0.001
Sum of the branch length	Y = 111.83 – 21.75 * Hegyi - 15.35 * yield c. + 6.59 * Hegyi * yield c.	0.22	760.01	Hegyi: p < 0.001 Yield c.: p = 0.02 Int. = 0.004
Maximum branch length (ln)	Y = 3.34 - 0.35 * Hegyi - 0.34 * yield c. + 0.10*Hegyi * yield c.	0.27	57.18	Hegyi: p < 0.001 Yield c.: p = 0.004 Int.= 0.02

Table S-2-2: Results of the linear mixed effect model with competition as independent, idplot (site effect) as random factor, bark anomalies in section 0-4 m, bark anomalies in section 4 – 8 m, bark anomalies in section 8 – 12 m (ln), bark anomalies in section 0-4 m per m² (ln), bark anomalies in section 4 – 8 m per m², bark anomalies in section 8 – 12 m (ln) per m², stem-non-circularity in section 0-4 m, stem-non-circularity in sec: 4-8 m (ln), stem-non-circularity in section 8-12 m (ln), lean in section 0-4 m (ln), lean in section 4-8 m, lean in section 8-12 m (sqrt), sweep in section 0-4 m, sweep in section 4-8 m (sqrt), sweep in sec 8-12 m (ln), diameter ast breast height (DBH), crown base height (CBH), stem volume (ln), wooden tree volume (ln) (WTV), branch volume 1. order (sqrt), crown length, crown surface area, crown volume, maximum crown area, mean crown radius, maximum branch length, sum of the branch length, mean branch length (ln), median branch length, mean branch angle 1. order, mean branch angle 2. Order and crown asymmetry as dependent variables, parameter estimate, marginal-R^2, conditional-R^2, random R^2 and probability of error p for the model. Significant relations ($p<0.05$) are highlighted in bold.

Tree characteristics	Estimate	Marginal R^2*	Conditional R^2*	Random R^2*	P-value
Bark anomalies Sec: 0-4 m	-96.50	0.26	0.46	0.20	**0**
Bark anomalies Sec: 4 – 8 m	-41.74	0.11	0.26	0.15	**0.006**
Bark anomalies Sec: 8 – 12 m	-30.9379	0.07	0.19	0.12	**0.02**
Bark anomalies Sec: 0-4 m per m² (ln)	-0.07	0.08	0.12	0.04	**<0.01**
Bark anomalies Sec: 4 – 8 m per m²	20.62	0.01	0.21	0.20	0.40
Bark anomalies Sec: 8 – 12 m per m² (ln)	-0.00	0.00	0.32	0.32	0.96
Stem-non-circularity (ln) Sec: 0-4 m	-0.10	0.17	0.42	0.25	**< 0.001**
Stem-non-circularity (ln) Sec: 4-8 m	0.06	0.10	0.10	0.00	**0.002**
Stem-non-circularity (ln) Sec: 8-12 m	-0.09	0.14	0.14	0.00	**<0.001**
Lean Sec: 0-4 m (ln)	-0.09	0.02	0.02	0.00	0.12
Lean Sec: 4-8 m	0.00	0.00	0.23	0.23	0.65

Lean Sec: 8-12 m (sqrt)	0.00	0.00	0.17	0.17	0.82
Sweep Sec: 0-4 m	0.00	0.01	0.02	0.01	0.68
Sweep Sec: 4-8 m (sqrt)	0.02	0.03	0.12	0.09	0.14
Sweep Sec: 8-12 m (ln)	0.13	0.01	0.06	0.05	0.36
DBH	-5.71	0.49	0.79	0.30	**0**
CBH	-0.32	0.01	0.46	0.45	0.50
Stem volume (ln)	-0.31	0.48	0.86	0.38	**0**
WTV (ln)	-0.33	0.52	0.82	0.30	**0**
Branch volume 1. Order (sqrt)	0.10	0.24	0.35	0.11	**0**
Crown length	-0.90	0.10	0.16	0.06	**0.01**
Crown surface area	-67.59	0.41	0.55	0.14	**0**
Crown volume	-0.48	0.63	0.67	0.03	**0**
Maximum crown area	-11.22	0.52	0.53	0.01	**0**
Mean crown radius	-0.64	0.59	0.67	0.08	**0**
Maximum branch length	-1.56	0.16	0.41	0.25	**0.002**
sum of the branch length	-8.97	0.21	0.32	0.11	**<0.001**
mean branch length (ln)	-0.31	0.14	0.56	0.42	**0.001**
Median branch length	-0.15	0.04	0.52	0.48	0.08
Mean branch angle 1. order	-1.44	0.02	0.38	0.36	0.26
Mean branch angle 2. order	0.28	0.00	0.49	0.49	0.83
Crown asymmetry	0.02	0.00	0.24	0.24	0.26

*****Marginal R²: Variance explained by the fixed effects,*Conditional R²: Variance explained by both, fixed and random effects (variance of the complete model), *Random R² (Conditional-R2 – Marginal-R²).

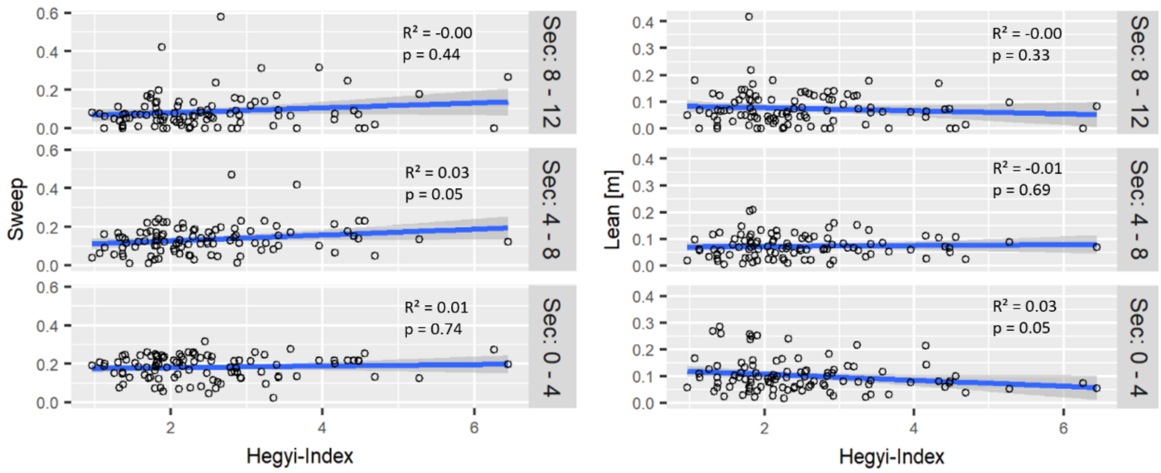
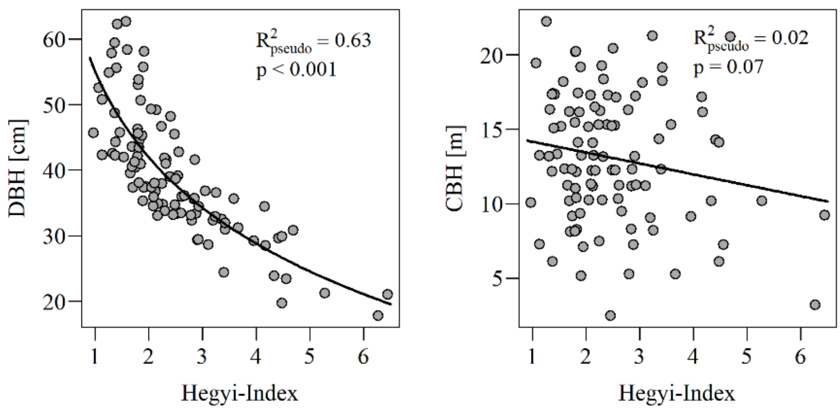


Figure S-2-1: Linear models of competition intensity (Hegyi-Index) and the stem quality attributes sweep and lean along the stem sections 0-4 m (Sec: 0-4), 4-8 m (Sec: 4-8), 8-12 m (Sec: 8-12) as cumulative values for all 100 tested trees.



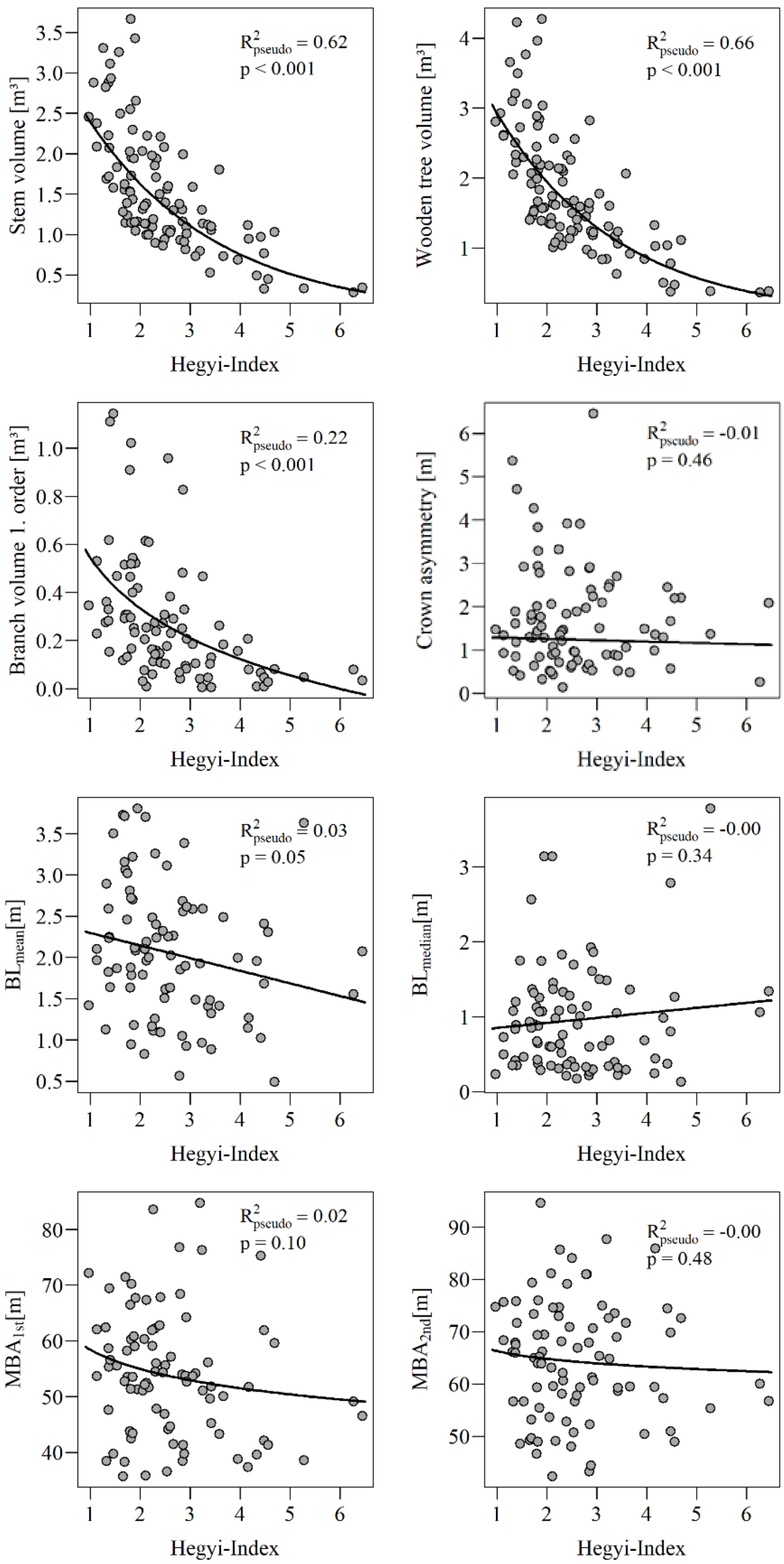


Figure S-2-2: Relationsship between competition intensity (Hegyi-Index) and various tree characteristics, namely diatmeter at breast height (DBH), crown base height (CBH), stem volume, wooden tree volume, branch volume 1. order, crown asymmetry, mean branch length (BLmean), median branch length (BLmedian), mean branch angle 1. Order (MBA1st) and mean branch angle 2. Order (MBA2nd).

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Chapter 3

Influence of heterozygosity and competition on morphological tree characteristics of *Quercus rubra* L. - a new single-tree based approach

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Abstract

In Europe, the non-native Northern red oak (*Quercus rubra* L.) is widely recommended for future cultivation. However, outside its natural range, Northern red oak has to date been insufficiently studied both in terms of silviculture and genetics. To clarify this, we studied the architecture of 92 (pre-) dominant Northern red oak trees in five German federal states using the non-destructive terrestrial laser scanning method (TLS). In addition, individual-based heterozygosity was calculated based on microsatellite data obtained by analyzing twelve potentially adaptive genic (EST derived markers) and eight putatively selectively neutral nuclear microsatellite markers. With these data the individual heterozygosity of the sample trees was calculated.

Mean or median branch angles as well as branch angle ranges of first order branches decreased with individual heterozygosity calculated group-wise for all markers (H_oAll) and for EST-derived markers (H_oEST). Most other tree characteristics, including the number of stem bark anomalies and mean stem-non-circularity and crown characteristics such as crown volume, crown surface area, or mean branch length of first order branches responded exclusively to competition. We conclude that competition, not genetics, is the main driver of Northern red oak stem and crown characteristics. Thus, stem quality and crown dimension can primarily be controlled by silvicultural interventions. The significant relationship between Northern red oak branch angle traits and individual tree heterozygosity was unexpected, and at this time we do not have any validated explanation for this. This issue needs to be further investigated.

Keywords: Northern red oak, individual-based heterozygosity, competition, branch angle measures, stem quality

3.1 Introduction

In Europe, cultivation of Northern red oak (*Quercus rubra* L.), a non-native tree species, has become increasingly popular since it expands the portfolio of forest enterprises and is thought to minimize management risks (Spellmann et al. 2011). A native of North America, northern red oak is now found in large parts of Europe (Podhorski 1956; Dreßel and Jäger 2002; Rédei et al. 2010). Its main areas of cultivation include Belgium (Vansteenkiste et al. 2005), France (Magni Diaz 2004), and Germany (Dreßel and Jäger 2002). In Germany it is the most common non-native deciduous tree species, covering an area of 55,000 ha

(Schmitz et al. 2014). Due to numerous advantages such as its rapid growth, drought, and storm resistance, Northern red oak is recommended for future cultivation (NMELV 2004; Kurjatko et al. 2006; Klemmt et al. 2013) and can be admixed, e.g., in pure pine stands (NMELV 2004; Kurjatko et al. 2006). Nevertheless, the response of Northern red oak to silvicultural interventions has not yet been adequately investigated outside of its natural distribution range (Burkardt et al. 2019). For example, questions such as how often Northern red oak stands are to be thinned and how intensively thinnings should be carried out are currently under debate (Nagel 2015). Generally speaking, thinnings are intended to reduce stand density and thus the competition intensity between trees (Kirk and Berrill 2016). Individual tree growth of future crop trees with this intervention should increase since they are released from competition (Burschel and Huss 2003). However, since branchiness of trees increases when competition is reduced by crown thinning, trade-offs exist between stem quality and diameter growth (Sonderman and Rast 1988). Therefore, optimised approaches are required to achieve both good stem quality and high yields.

To assess tree morphology objectively (Liang et al. 2011) and in a non-destructive way, terrestrial laser scanning (TSL) has been shown to be an appropriate method (Schütt et al. 2004; Stängle et al. 2014; Dorji et al. 2019). The resulting three-dimensional point clouds allow an exact calculation of various tree characteristics such as crown size or crown dimension (Seidel et al. 2011; Juchheim et al. 2017) which are closely related to tree productivity and thus to timber production (Roloff 1991; Seidel et al. 2019a). Also, external stem characteristics such as lean or curved stems (Juchheim et al. 2017) and the number of branches and bark anomalies, which indicate stem quality (Höwler et al. 2017; Burkardt et al. 2019), can be computed. Finally, TLS-based approaches are also suitable to estimate competition intensity (Metz et al. 2013; Höwler et al. 2017). Terrestrial laser scanning cannot, however, account for the genetic controls on tree morphology and physiology.

The expression of tree characteristics is determined by genetic blueprint and inheritance, but the degree of genetic control differs between species (Zobel and Jett 1995). Gene sequencing technology has improved within the last decades by providing a wide selection of new gene markers (Paux et al. 2012). The most often utilized gene marker types are simple sequence repeats (SSRs) (Varshney et al. 2005; Agarwal et al. 2008) and can be classified into expressed sequence tag derived (EST-SSR) and nuclear simple sequence repeats (nSSR). EST-markers can provide insights into the link between phenotypic and genotypic variation

(Gupta and Varshney 2000). The exact link between genes and their phenotypes remains somewhat unclear due to species' phenotypic plasticity, which complicates detection of underlying genes (Blue and Jensen 1988; Bruschi 2000). Because it is proportional to the amount of genetic variance at a locus, heterozygosity is an appropriate measure to examine the amount of genetic variation (Allendorf 1986). In population genetics, heterozygosity is usually studied when the genetic variation (i.e., following a genetic bottleneck or introduction of a species) is of interest. While Savolainen and Hedrick (1995) could not find any link between heterozygosity and fitness in *Pinus sylvestris* populations, Mitton et al. (1981) found a link between high levels of heterozygosity and high growth variability in aspen and ponderosa pine (Mitton et al. 1981). However, there are few examples whereby heterozygosity has been studied at the individual tree level (Yezerinac et al. 1992). Bergmann and Ruetz (1991) compared clones of *Picea abies* with randomly selected forest trees and found differences in the distribution of individual tree heterozygosity between the two groups.

To our knowledge there are no studies that have comparatively tested the influence of single tree heterozygosity and competition on tree characteristics of Northern red oak. In order to close this knowledge gap, the objective of our study was to explore which of the two properties influencing tree morphology is of more importance. More specifically, we hypothesized that:

- Increasing competition results in reduced tree dimensions, more precisely in smaller crowns, fewer branches and fewer external stem characteristics of *Quercus rubra* L.
- Competition effects on stem and crown characteristics are superimposed by genetic variation.

3.2 Material and Methods

Study sites

We studied a total of 100 study trees in ten red-oak stands located in five federal states within Germany (two each in Brandenburg, Thuringia, Lower Saxony, North Rhine-Westphalia and Baden-Württemberg). The sites were selected based on the following criteria: (1) stands should consist of at least 80% Northern red oak (basal area share), (2) stand age should be between 55-85 years (middle-aged), (3) stand size should be ≥ 1 ha, (4) stands should show preferably large haplotype diversity (see Pettenkofer et al. 2019) and

(5) sites should be classified as suitable for further cultivation of this species by local authorities.

Table 3-1: Main characteristics of the ten study sites dominated by Northern red oak in Germany: FD: Federal states namely: Lower Saxony (LS), North Rhine-Westphalia (NRW), Baden-Württemberg (BWB), Thuringia (THU), Brandenburg (BRB).

FD	District	PlotID	Latitude	Longitude	Genetic Hap.*	Soil texture	MPG (mm)*	TMG (°C)*	Yield class*
LS	Dassel	1	51°46'47"N	9°35'25"E	A	loessic loam	468	13.6	3.3
LS	Rotenburg	7	52°56'46"N	9°21'58"E	A, B, C	loamy sand	346	15.8	1.6
NRW	Niederrhein	18	51°32'14"N	6°29'26"E	A, B, C	gravelly-, loamy sand	354	16.9	1.6
NRW	Niederrhein	20	51°32'19"N	6°29'50"E	A, E, B	loamy sand	359	16.8	1.6
BWB	Offenburg	22	48°27'13"N	7°51'32"E	A, C, E, B	silty loam	397	18.0	0.8
BWB	Offenburg	24	48°27'9"N	7°51'37"E	A, C, B	silty loam	397	18.0	0.6
THU	Neustadt	31	50°45'37"N	11°43'31"E	A, C	sand	350	15.8	0.6
THU	Jena-Holzland	32	50°46'19"N	11°38'27"E	A, B, C	sand	341	15.8	1.2
BRB	Potsdam	35	52°27'13"N	13°4'37"E	A, C, O	sand	291	17.0	2.8
BWB	Potsdam	38	52°22'57"N	13°5'43"E	A, B	sandy cover layers over boulder clay	284	17.0	1.6

*Genetic Hap.: Haplotypes were assessed by Pettenkofer et al. (2019) in the same Northern red oak stands prior to our study; *MPG: mean precipitation during the growing season (May-September), *TMG: mean temperature during the growing season (May-September) of the last 25 years provided by the Climate Data Centre (DWD Climate Data Center-CDC 1992a - 2018, 1992b -2018); and yield-class: calculated based on the yield table for Northern red oak of Bauer (1953).

Silvicultural Measurements

A full tree inventory was conducted on all 10 study sites using the Field-Map instrument and software package (IFER – Monitoring and Mapping Solutions, Ltd., Czech Republic). We recorded each tree’s coordinates, diameter at breast height and dominance (tree classes 1-5 according to Kraft (1884)). For the analyses of tree morphology, ten dominant or (pre-) dominant study trees (tree classes 1-2 according to Kraft (1884)) were randomly selected within each of the ten study sites (for further information see Burkardt et al. 2019).

The sites covered a wide geographical and edaphic range, ranging from rather unfavourable sandy sites with low precipitation rates during the growing season of around 285 mm (Brandenburg) to richer sites with nutrient rich loess and high precipitation rates of around 400 mm (Baden-Württemberg) (Table 3-1).

To calculate the competition intensity to which each of the 10 target trees was exposed, we used the competition index according to Hegyi (1974). Both the diameter of all neighbouring trees (with DBH ≥ 7 cm) and their respective distance to the target tree (within an area of ca. 700 m² (r = 15 m) around each target tree) were included in the index calculation (Equ. 3-1).

Equ. 3-1 $$\text{Hegyi-Index} = \sum_{i=1}^{n} \frac{D_i}{D_j} \times \frac{1}{Dis_{ij}},$$

with target tree *j,* competitor tree *i,* diameter at breast height (*D* in cm) and the distance between target tree and the competitor tree (*Dis* in m).

To assess stem and crown characteristics of the 10 target trees per site in a three-dimensional way, terrestrial laserscanning was applied using a Faro Focus 3D 120 laser scanner (Faro Technologies Inc., Lake Mary, Florida, USA). We applied the multiple scan approach (van der Zande et al. 2008), capturing each target tree from four or five directions (depending on stand density of the sourrounding neighbourhood). Between 15 and 25 artificial checkboard targets were mounted in the surroundings of the subject trees. Based on these targets, a spatial co-registration of the scans was performed using the software Faro Scene (Faro Technologies Inc, Lake Mary, FL, USA). The resulting three-dimensional point clouds had a registration error of less than 2 cm and included neighbouring trees and the surrounding vegetation up to a distance of 120 m.

Each target tree was manually extracted from the overall point cloud using the CloudCompare Software (Cloud Compare 2.6, retrieved from (http://www.cloudcompare.org/)) and saved as an .xyz-file (Cartesian coordinates). Additionally, the trunk (from the root collar to the crown base height) was isolated from the individual tree point cloud and exported as an xyz-file to ensure a detailed analysis of the external stem characteristics (Burkardt et al. 2019).

Two different methods were used to analyze tree morphology. Quantitative Structural Models (QSM) were applied to describe branching structures and were calculated with the software Computree (Piboule et al. 2013), in accordance with Hackenberg et al. (2015). In these QSM models, each tree was characterized by a hierarchical collection of cylinders adapted to the local information of each point cloud (Raumonen et al. 2013). Based on the QSM models, crown characteristics were computed as follows: mean branch angle of first order branches, mean branch angle of second order branches, median branch angle zenith of first order branches, median branch angle zenith of second order branches, branch angle range of first order branches, branch angle range of second order branches, median branch length of first order branches, median branch angle zenith of second order branches (Figure 3-1, Figure 3-2), mean- median- maximum-, and sum of branch length of first order branches.

Additionally, tree characteristics were derived directly from the point cloud of each tree. This included the following crown charateristics: crown base height (CBH) (Metz et al. 2013), maximum crown area, mean crown radius (Seidel et al. 2015), crown length (TTH-CBH), crown asymmetry, crown surface area, and crown volume (Seidel et al. 2011). Stem measurements directly deduced from the point cloud were lean, sweep (Juchheim et al. 2017), mean stem non-circularity, and bark anomalies (Höwler et al. 2017).

Timber quality assessment of the stems was based on newly developed algorithms in the software Mathematica (Wolfram Research, Champaign, Illinois, USA). Following the German guidelines for the raw timber trade (RVR 2015) for stem quality grading, the three-dimensional point clouds of the 100 stems of the target trees were virtually divided into 4 m long sections. These guidelines define tolerances for wood defects and categories of quality.

To homogenize the spatial resolution of the point clouds, a 1.75 cm point cloud grid (PCG) was processed for each stem section (Seidel et al. 2011; Höwler et al. 2017). PCGs are used to eliminate density variations in the point cloud that can result from trees scanned from varying distances or with different numbers of scans.

Figure 3-1: Graphical visualisation of the calculation of branch angle (zenith angle) of first order branches, based on the point cloud of the target trees derived from terrestrial laser scanning (TLS). $0_1°$ as main axis of a tree with B_1 as first order branch and α as the angle between the main axis and first order branches. From the sum of the first-order branch angles per tree, mean value and median of the branch angles zenith were calculated. The branch angle range of first order branches was also computed. Figure **a**: Tree with small branch angles (zenith) of first order branches; Figure **b**: Tree with medium large branch angles (zenith) of first order branches, and Figure c: Tree with large branch angles (zenith) of first order branches.

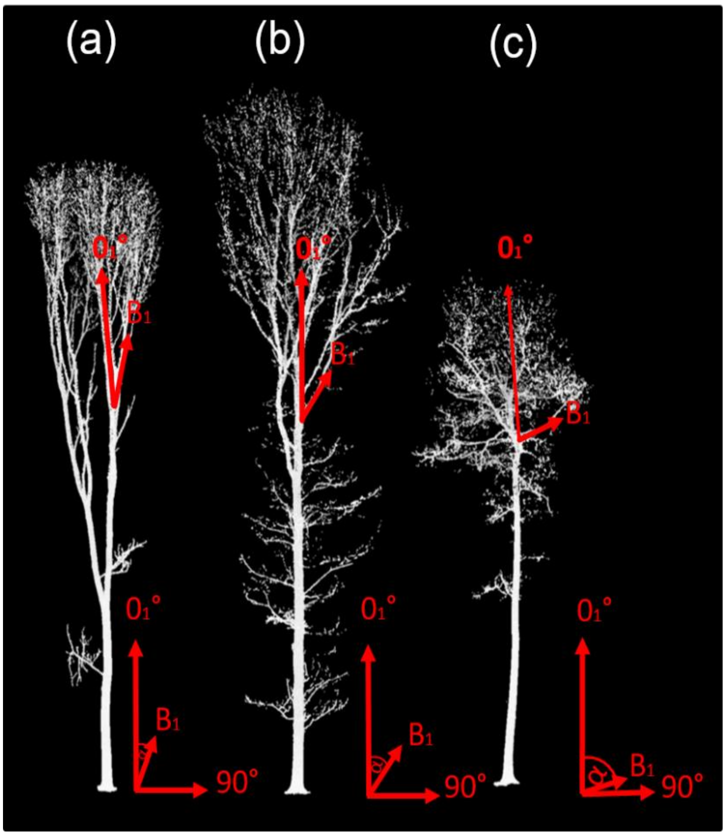
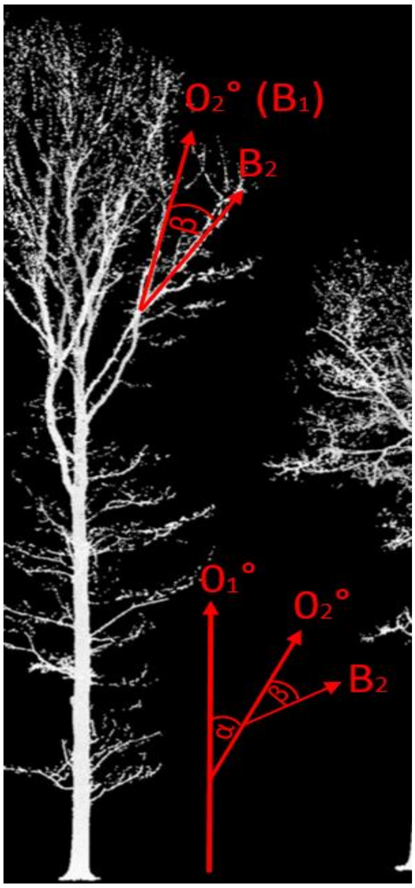


Figure 3-2**:** Graphical visualisation of the mean branch angle zenith of second order branches based on the point cloud of the target trees derived from terrestrial laser scanning (TLS). From the sum of the second order branch angles per tree, mean value and median of the branch angles zenith were calculated. The branch angle range of second order branches was also computed, with $0_2°$ (B_1) as reference point, B_2 as second order branch and β as the angle between the two variables $0_2°$ (B_1) and B_2 second order.



Examples are point density variations due to different scanner-to-tree distances, differences in scan-overlap due to different scan positions, or various understory vegetation heights or intensities (Höwler et al. 2017; Burkardt et al. 2019).

The following procedure was applied from the root collar to the level of the crown base to each 4m stem section. Horizontal layers of 1.75 cm thickness were created from the previously homogenized stem point clouds (Höwler et al. 2017; Juchheim et al. 2017). These layers were then processed using “QR” decomsposition, which creates a circle to the points of each layer to factorize a matrix with "Q" as orthogonal and "R" as upper triangular matrix (Seidel and Ammer 2014; Höwler et al. 2017). The diameter and height of each generated circle and the centre point coordinates were saved. Horizontal differences between the lowest and highest circle positions of each trunk were defined as the measure for "total lean". “Total lean" was divided by the stem length, to ensure a length-independent value of lean. “Total sweep” was derived by using the ratio of the distances between the centers of all circles of each trunk section and the smallest distance between the centers of the lowest and highest circles within a trunk section of a tree. By dividing “total sweep” by the respective stem length, "sweep per meter" was obtained (Höwler et al. 2017).

The number of “bark anomalies” per metre and “stem non-circularity” were calculated to assess stem surface quality.

The “stem non-circularity” was calculated for each stem section using stem discs. The absolute differences between each point on the stem surface and the radius of the stem disc (derived from the circular fit for each disc) were determined for each stem disc (Höwler et al. 2017). For each layer, the mean value was computed from these absolute distances. The “stem-non-circularity” was then defined by computing the median of all height layers (Höwler et al. 2017).

The mean distance between each point on the disc surface and the respective disc centre was also determined. This measure was used to identify points that were further away from the centre of the parent disc than the mean distance plus standard deviation, or less than the mean distance minus standard deviation. These deviations of points from a fitted circle were defined as “bark anomalies” and were calculated for each stem individually. "Bark anomalies per meter" were calculated by dividing the value by the stem length.

Genetic analyses

For this study, we included twelve potentially adaptive (expressed sequence tag-derived simple sequence repeat = EST SSR) and eight putative selective neutral nuclear microsatellite (nSSR) markers. The data obtained were part of a study conducted by Pettenkofer et al. (2020). EST-SSRs are located close to functional genes, in which variation is likely to be limited due to selection. They are more conserved than nSSR markers und thus show a higher transferability across species within genera. In contrast to this, nSSRs are highly polymorphic, being located in non-coding parts of the gene (Ellis and Burke 2007; Kalia et al. 2011). For this study, we calculated the individual tree-based heterozygosity group-wise for all markers (H_oAll), for EST-derived markers (H_oEST) and for nSSRs (H_oNeutral). The included EST markers were FIR013, FIR024, FIR028, FIR031, FIR035, FIR104, GOT021, GOT040, VIT023, VIT107, PIE040, PIE125 (Durand et al. 2010). For more information on the selected markers, see Pettenkofer et al. (2020) and Supplementary material (Table S-3-1).

When conducting microsatellite analyses, fragment lengths of the examined gene loci are obtained. There is either one (homozygote) or two different alleles (heterozygote) present for each marker in one individual. The occurrence of heterozygosity is known to affect the fitness of an individual and thus the survival of a population under changing environmental conditions (Hansson and Westerberg 2002). In this study, heterozygosity was computed on the individual level separately for all markers, for EST-markers, and for putatively neutral markers. The value for heterozygosity H_o reaches 1 when each examined marker of an individual has two different alleles. In contrast, $H_o = 0$ when there is only one allele for each marker found. In this study, only samples with sufficient data (>75% of all markers per sample) were included. Since the individual based heterozygosity could not be calculated for all trees, the total dataset in this study, including the silvicultural measures, was adjusted to the 92 trees for which genetic data was available. The computed value for heterozygosity was then compared with phenotypic traits such as stem- and crown characteristics.

Statistical analyses

All statistical analyses were implemented using the free statistics software ‘R’ (R Core Team 2018). Normal distribution of data was tested using the Shapiro-Wilk Test and variance homogeneity using Levene’s test. Some dependent variables were log- or sqrt-transformed to obtain normally distributed residuals. Assuming a linear relation, we investigated the relationship between competition (Hegyi-Index), heterozygosity measured by EST-SSR markers “H_OEST”, heterozygosity measured by all markers “H_OAll”, and heterozygosity measured by nSSR markers “H_ONeutral” as independent variables, and morphological tree characteristics as dependent variables. Plot-ID as was included in linear mixed effect models as random factor (lme fuction in “nlme” package). The update function in R was applied for model simplification by evaluating the parameter estimates and then deleting the least significant terms first by beginning with the top level interaction terms (Crawley 2007). We tested all stem characteristics of each stem section and all crown attributes for significance. In all examined relationships the random factor “idplot” enhanced the explained variance of the models.

Yield classes were derived for each study site using yield tables for Northern red oak (Bauer 1953). Better site conditions result in taller dominant trees at a given age (Burschel and Huss 2003). Linear models were used to assess whether yield classes alter the effect of heterozygosity or competition on Northern red oak tree characteristics.

We also calculated Pearson correlation coefficients for relationships between crown (including branch) characteristics.

For all statistical analyses we used a significance level of $p < 0.05$.

3.2 Results

Effect of single tree heterozygosity on stem and crown characteristics

Four crown characteristics were significantly related to heterozygosity measured by EST-SSR markers (H_OEST), which are located in expressed genes, and three crown attributes to heterozygosity measured group-wise for “All” markers (H_OAll). Mean branch angle zenith ($p < 0.01$), branch angle range ($p < 0.01$) (Figure 3-3), median branch angle zenith of first order branches ($p < 0.01$) and the number of first order branches ($p=0.02$) significantly decreased with increasing heterozygosity H_OEST (Figure 3-4).

Table 3-2: Results of the linear mixed effect models with the crown characteristics $BA_{mean}1st$: Mean branch angle of first order branches (°), $BA_{median}1st$: Median branch angle of first order branches (°), $BA_{range}1st$: Branch angle range of first order branches (°), NB1st: Number of first order branches (N), BL_{sum}: Sum of branch length of first order branches (N), H_oEST: Heterozygosity measured by EST-SSR markers, H_oAll: Heterozygosity measured group-wise by all markers, $H_ONeutral$: Heterozygosity measured by nSSR markers as independent variables (Indep.), Random factor: Idplot, Intercept: The intercept of the model, independent: Slope and p-value for each independent variable, Model: Akaike Information Criterion for the model, Adjusted R-Squared of the model (Adj. – R²).

Crown characteristics	Indep.	Random f.	Intercept	Indep.	Model	
				H_OSpec	AIC	Adj.- R^2
$BA_{mean}1st$	H_OEST	Idplot	-65.33	-22.53 (p<0.01)	593.16	0.50
	H_OAll	Idplot	71.81	-28.27 (p=0.01)	595.17	0.47
$BA_{median}1st$	H_OEST	Idplot	62.87	-26.42 (p<0.01)	614.83	0.47
	H_OAll	Idplot	68.69	-30.31 (p=0.02)	618.12	0.44
$BA_{range}1st$	H_OEST	Idplot	179.82	-26.78 (p<0.001)	576.43	0.17
	H_OAll	Idplot	186.55	-30.69 (p<0.01)	580.69	0.11
NB1st	H_OEST	Idplot	44.89	-23.40 (p=0.02)	641.25	0.29
BL_{sum} (ln)	$H_ONeutral$	Idplot	3.47	0.69 (p=0.03)	75.32	0.18

Mean branch angle zenith ($p < 0.01$), branch angle range ($p < 0.01$) (Figure 3-3) and median branch angle zenith of first order branches also declined with increasing heterozygosity H_OAll ($p < 0.01$) (Table 3-2).

Among all other tested branch and stem traits, only the sum of first order branches was related significantly to heterozygosity measured by nSSR markers ($H_ONeutral$), which are highly polymorphic and located in non-coding parts of the genome (Table 3-2, Table S-3-4).

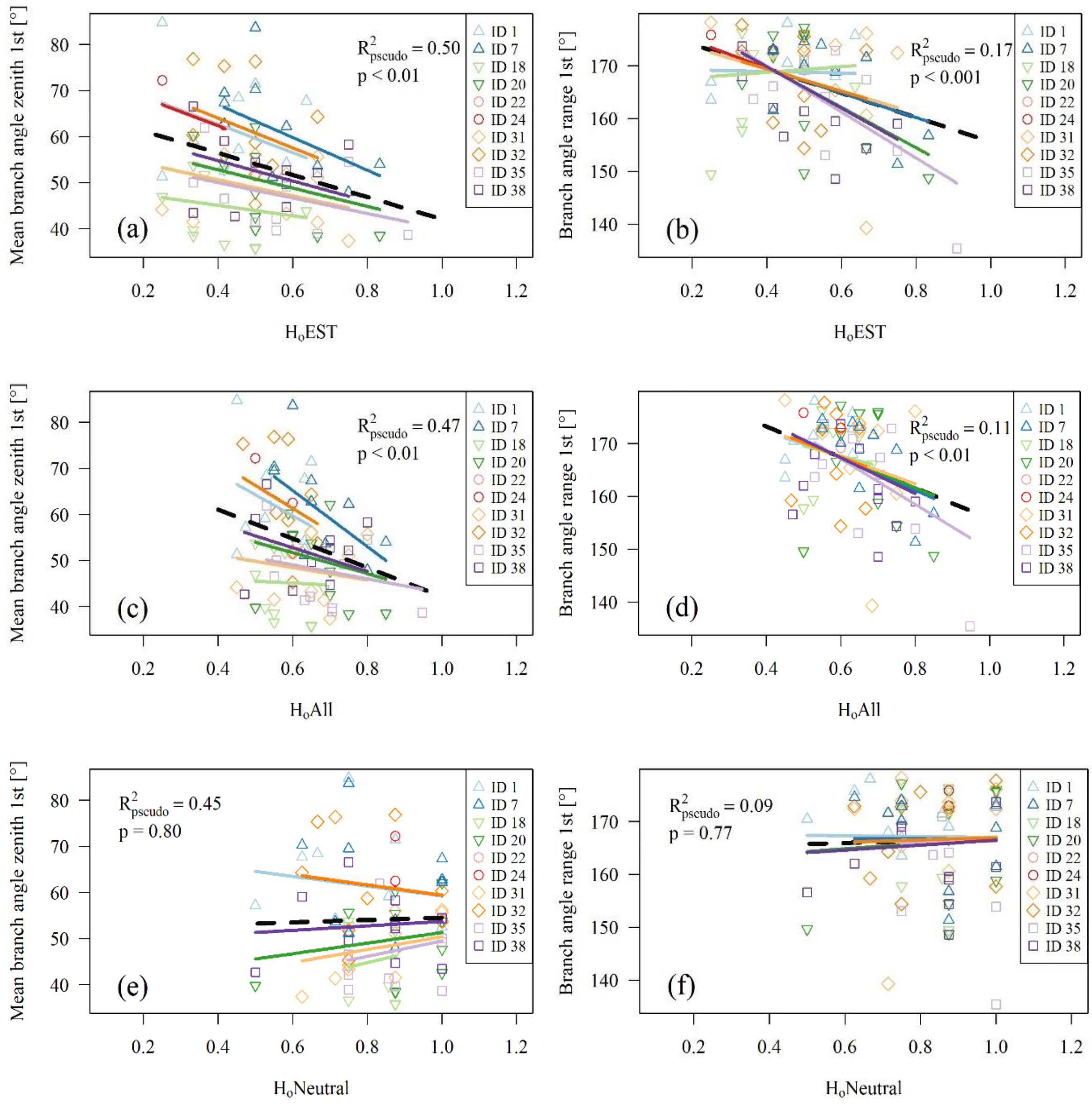


Figure 3-3: Results of the linear mixed effect models: Relationship between heterozygosity measured by EST-SSR markers "HoEST" (3a and 3b), heterozygosity measured by all markers "HoAll" (3c and 3d) and heterozygosity measured by nSSR markers "HoNeutral" (3e and 3f) as independent variables, mean branch angle zenith 1st order (3a, 3c, 3e) and branch angle range 1st order (3b, 3d, 3f) as dependent variables on the ten study sites in Lower Saxony (ID 1: Dassel and ID 7: Rotenburg), North Rhine-Westphalia (ID 18 and ID 20, Lower Rhine region), Baden-Württemberg (ID 22 and ID 24; next to Offenburg), Thuringia (ID 31 and ID 32; next to Neustadt Orla) and Brandenburg (ID 35 and ID 38; next to Potsdam) as random factor.

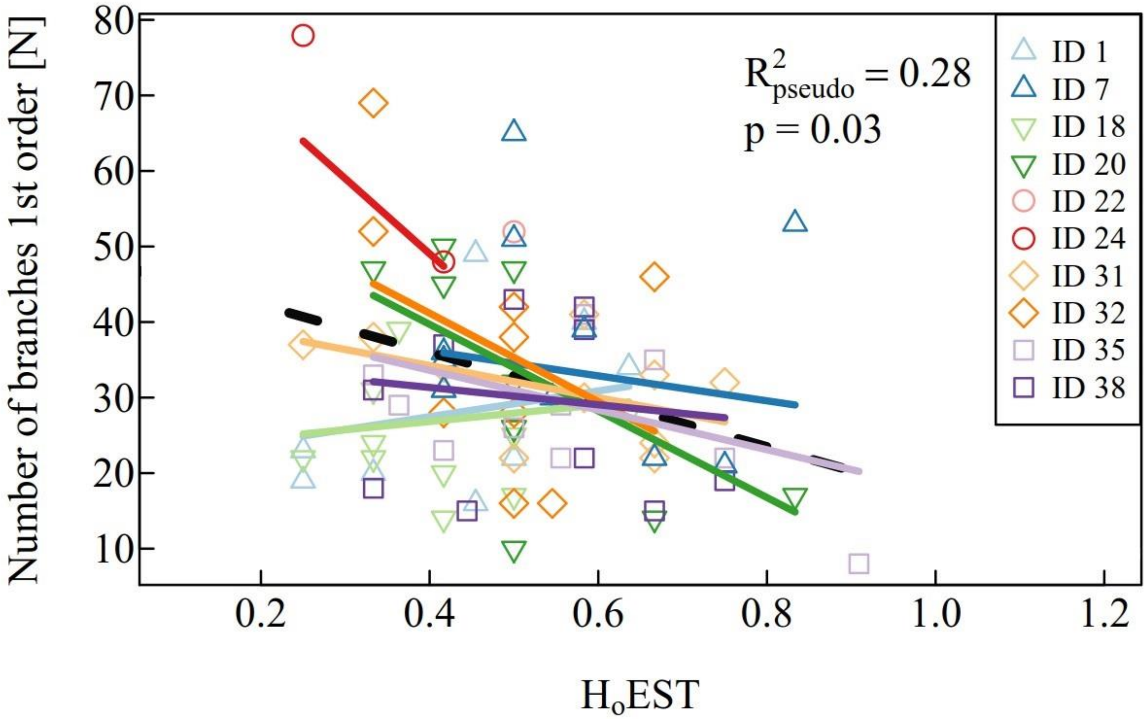


Figure 3-4: Results of the linear mixed effect model: Relationship between heterozygosity measured by EST-SSR markers "H_OEST" as independent variable and the number of first order branches as dependent variable on the ten study sites in Lower Saxony (ID 1: Dassel and ID 7: Rotenburg), North Rhine-Westphalia (ID 18 and ID 20, Lower Rhine region), Baden-Württemberg (ID 22 and ID 24; next to Offenburg), Thuringia (ID 31 and ID 32; next to Neustadt Orla) and Brandenburg (ID 35 and ID 38; next to Potsdam) as random factor.

Effect of competition and site conditions on crown and stem characteristics

Several crown characteristics were significantly related to competition intensity: crown volume, crown surface area, mean crown radius, maximum crown area, crown length, maximum branch length, mean branch length, and sum of branch length (Table S-3-4).

Other crown characteristics were not correlated with competition intensity: mean branch angle zenith of first order branches, mean branch angle zenith of second order branches, median branch angle zenith of first order branches, median branch angle zenith of second order branches, branch angle range of first order branches, branch angle range of second order branches, crown asymmetry, and number of first order branches (Table S-3-4).

Two of the four assessed stem characteristics were significantly related to competition intensity. The number of bark anomalies (0-4 m: $p < 0.01$; 4-8 m: $p= 0.03$ and 8-12 m: $p = 0.05$) and stem non-circularity of every stem section (0-4 m: $p < 0.01$, 4-8 m: $p < 0.01$ and 8-12 m: $p < 0.01$) decreased with increasing competition. Lean and sweep of every stem section was not significantly related to competition (Table S-3-3).

In addition to competition, the site index significantly influenced three crown characteristics and one stem characteristic. With increasing site quality, crown surface area, mean crown radius, and mean branch length of first order branches increased and mean stem-non circularity decreased (Table S-3-5).

Correlations between branch characteristics

Mean branch angle and median branch angle of first order branches were significantly correlated with mean branch length, maximum branch length of first order branches and with the number of first order branches. Branch angles decreased (branch angles got steeper) with increasing mean-and maximum branch length of first order branches. Also, first order branch angles decreased with a decreasing number of first order branches (Table 3-3).

Branch angle range of first order branches and sum of branch length first order branches, as well as branch angle range of first order branches and the number of first order branches were positively correlated (Table 3-3).

No other crown characteristics were significantly correlated with the branch angle measurements (Table S-3-2).

Table 3-3: Results of the Pearson correlation with branch angle range (BA_{range}1st), mean branch angle first order branches (BA_{mean}1st), median branch angle first order branches (BA_{median}1st) and mean branch length first oder branches (BL_{mean}1st), maximum branch length first oder branches (BL_{max}1st) and of branch length first order branches (BL_{sum}1st) and number of first order branches (NB 1st), p values < 0.05 are shown in italics

	BA_{range}1st	BA_{mean}1st	BA_{median}1st	BA_{range}1st	BA_{mean}1st	BA_{median}1st
		p value			ρ value	
BL_{mean}1st	0.067	*0.000*	*0.000*	-0.204	*-0.466*	*-0.436*
BL_{max}1st	0.986	*0.001*	*0.001*	0.002	*-0.347*	*-0.376*
BL_{sum}1st	*0.000*	0.584	0.678	*0.424*	0.062	0.047
NB1st	*0.000*	*0.000*	*0.000*	*0.480*	*0.496*	*0.475*

p values < 0.05 are shown in italics

3.3 Discussion

Effect of single tree heterozygosity on branch angle traits

The results of this study indicate that levels of heterozygosity play a role in shaping crown phenology of *Quercus rubra* since mean and median branch angle zenith as well as branch angle range of first order branches decreased with increasing heterozygosity "EST" and heterozygosity "All". This was a surprising finding, since if any relationship had been expected, the opposite would have been hypothesized; that increasing heterozygosity would be a driver of phenotypic plasticity.

Phenotypic plasticity may be defined as the propensity of an individual to react to a changing environment by changing its phenotype (Schlichting 1986). High phenotypic plasticity would reflect a strong effect of the environment on the individual's phenotype (Schlichting 1986).

Our results contradict the majority of other studies, which did not find a correlation between phenotypic plasticity and heterozygosity (Scheiner 1993). Instead, it seems as if heterozygosity is positively correlated with developmental stability, a characteristic that refers to the ability of an individual to buffer its development against environmental influences. However, this does not necessarily mean alterations in morphology (Palmer and Strobeck 1986; Scheiner 1993).

In our study, higher levels of heterozygosity did not result in larger crowns, which seems at first glance to be an evolutionary disadvantage. However, steep first order branches and thus low branch zenith angles may simply reflect trees' ability to avoid competition by neighboring trees. Since crown structure affects the photosynthetic performance of a tree (Kuuluvainen 1991; Grote and Pretzsch 2002), smaller crowns are likely to lead to lower leaf area and thus to lower photosynthetic performance (Assmann 1970). However, no significant relationships were found between tree characteristics attributed to crown extension and branch angle measurements. Thus, it seems that the steeper first order branch angles do not result in smaller crowns and hence productivity. The ability to reach a certain crown size even with small zenith branch angles may be a competitive advantage. However, this remains highly speculative, perhaps due to our choice of a marker system that may not be able to reveal adaptation, and needs further investigation. Pettenkofer et al. (2020) conducted an outlier analysis to reveal markers under selection, but none could be found within German Northern red oak stands. Furthermore, none of the markers appear to be located close to genes that may play an important role in shaping Northern red oak's crown morphology. In addition to identification of potentially adaptive markers in Northern red oak through modern high-throughput-techniques like RADseq (restriction site associated DNA sequencing), potential candidate genes for shaping crown morphology should be analyzed in future studies. We cannot rule out, therefore, the possibility that our finding should perhaps be considered an artefact.

Effect of competition intensity

Reduction in the degree of competition to which the remaining trees are exposed is an important objective of (crown-) thinning interventions that aim to promote the growth of selected future crop trees (Puettmann et al. 2009). In fact, thinning intensity differed in our stands. Thus, our sample includes trees exposed to high but also to low competition from neighbouring trees. Our results clearly indicate that even if genetic properties play a role (this needs to be clarified), neighborhood competition is the main driver affecting most crown and stem characteristics.

Eight crown characteristics of *Quercus rubra:* crown volume, crown surface area, mean crown radius, maximum crown area, crown length, mean-, maximum- and sum of branch length of first order branches, decreased with increasing competition. These results are consistent with studies of other tree species showing that high inter- or intra-specific competition leads to a decrease in crown properties that are closely related to crown extension, crown size or crown dimensions (Thorpe et al. 2010; Seidel et al. 2011; Bayer et al. 2013; Dieler and Pretzsch 2013; Burkardt et al. 2019; Dorji et al. 2019). Since the degree of light acquisition by trees corresponds to their crown extension (Purves et al. 2007) reductions in crown size, for example crown length, due to competition, affects growth performance (Burkardt et al. 2019). Resource acquisition capacity is an important factor influencing reproduction, survival, and competitiveness of a tree (Tilman 1982).

Depending on the goal, wood production may focus not only on timber quantity but also on wood quality (Burschel and Huss 2003). The results of this study indicate that for Northern red oak, high competition intensities led to a decrease in external (i.e., undesirable) stem characteristics such as stem non-circularity and number of bark anomalies. The measure of the number of bark anomalies includes both branchiness and irregularities on the stem surface (stem injuries such as bark seams) (Richter 2010). Hence, we confirm findings of previous studies of species other than Northern red oak which found that high stand densities led to lower branchiness and to higher self-pruning (Ballard and Long 1988; Mäkinen 2002; Mäkinen and Hein 2006). Branch related wood defects are considered main drivers of decreasing stem quality for several tree species (Sonderman and Rast 1988). Thus, this study verifies that as is the case for many other tree species, Northern red oak needs, at least in stages of early stand development, higher competition intensities to produce high quality timber (Sonderman and Rast 1988). In the property 'bark anomalies', all forms of bark wounds are included that can serve as gateways for bacteria or fungi (i.e., white rot), considered as potential timber quality degraders (Schulz 1973). The proportion of bark wounds in the number of bark anomalies has to be examined, but in general bark anomalies have been proven to be an appropriate measure for predicting both external and inner stem quality (Höwler et al. 2017; Burkardt et al. 2019).

Effect of environment/site conditions

While site quality was shown to have an impact on crown characteristics and stem non-circularity of Northern red oak (Burkardt et al. 2019), none of the branch angle measurements were influenced by yield classes. Interestingly however, some branch angle attributes could be related to branch length. Branch development depends on many environmental and ecophysiological factors, for instance light conditions in the crown, as well as on water and nutrients allocated to the branch (Lanner 1976; Gross and Pham-Nguyen 1987). Smaller branch angles may indicate stronger competition between the branches within the crown, possibly leading to higher branch lengths and to a lower number of first order branches. In this study only (pre-) dominant Northern red oak trees were investigated. To inspect the relationship between branch angle measurements and environment, further studies with trees in different canopy layers are needed.

3.4 Conclusion

The objective of this study was to investigate whether heterozygosity or neighborhood competition shapes stem and crown characteristics of Northern red oak target trees. Branch angle values decreased with increasing heterozygosity. Beyond speculation, there is not yet a mechanistic explanation for this, but the results suggest that branch angles of Northern red oak trees may be, at least to some degree, genetically influenced. This result is unique and should be investigated in further studies with more specific gene markers and perhaps also with more heterogeneous Northern red oak stand qualities.

We conclude that even if a genetic influence cannot be excluded, competition is the main factor controlling various crown and stem characteristics. For silviculture with Northern red oak aiming at high quality timber, our results suggest that stands should be kept rather dense until self-pruning has been achieved up to a desired stem length. As Northern red oak is known for its phototropic growth and responsiveness, subsequent thinning operations could be moderate but frequent in order to promote crown size and thus tree productivity.

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Authors' contributions: Conceptualization, K.B., T.V., D.S. and C.A.; data curation, K.B., formal analysis, K.B., D.S. and T.V., investigation, K.B., methodology, K.B., T.V., D.S., C.A. O.G.; project administration, C.A., T.V.and O.G.; supervision, T.V., D.S., and C.A.; writing—original draft, K.B. and T.P. (genetic analyses and parts of the effect of single tree heterozygosity on branch angle traits (discussion)), writing—review and editing, K.B., T.P., D.S., T.V., C.A, O.G., L.L..

3.5 Supplementary

Table S-3-1: Overview of the marker types used in this study

Marker	Description/Annotation	Source
FIR013	CONSTANS-like	Lind-Riehl et al. 2014
FIR024	DNA gyrase subunit a	Sullivan et al. 2013
FIR028	tropinone reductase, putative	Bodénès et al. 2012
FIR031	5-Adenylylsulfate reductase	Sullivan et al. 2013
FIR035	DNAJ heat shock N-terminal domain	Bodénès et al. 2012
FIR104	r2r3-myb transcription factor	Sullivan et al. 2013
GOT021	Histidine kinase 4-like	Sullivan et al. 2013, Lind & Gailing 2013
GOT040	40s ribosomal protein s16	Sullivan et al. 2013
VIT023	Integrase-type DNA-binding superfamily	Goicoechea et al. 2019
VIT107	lhca2 protein	Sullivan et al. 2013
PIE040	Basic leucine zipper transcription factor- like protein	Sullivan et al. 2013
PIE125	dnaj-like protein	Sullivan et al. 2013

Table S-3-2: Results of the Pearson correlation with branch angle range ($BA_{range\ 1st}$), mean branch angle first order branches ($BA_{mean1st}$), crown base height (CBH), maximum crown area (Max area), crown length (CL), and mean crown radius (CR_{mean})

Tree characteristics	BArange 1st	BAmean 1st	BArange 1st	BAmean 1st
	p-value		ρ-value	
CBH	1.00	0.54	0.00	0.07
Max area	0.11	0.26	0.18	0.13
CL	0.22	0.80	0.14	0.03
CR_{mean}	0.06	0.07	0.21	0.20

Table S-3-3: Results of the linear mixed effect models with the stem characteristics Bark anom.: Number of bark anomalies in the sections 0-4 m, 4-8 m, 8-12 m (counts/m), SNC: Stem non-circularity in the sections 0-4 m, 4-8 m, 8-12 m (m), lean in the sections 0-4 m, 4-8 m, 8-12 m (m) and sweep in the sections 0-4 m, 4-8 m, 8-12 m as dependent variables, H_OEST: Heterozygosity measured by EST-SSR markers, H_OAll: Heterozygosity measured by all markers, H_ONeutral: Heterozygosity measured by nSSR markers and Hegyi: Hegyi-Index as independent variables (Indep.), Random factor: Idplot, Intercept: The intercept of the model, Independent: The slope and p-value for each independent variable, Model: Akaike Information Criterion for the model, Adjusted R-Squared of the model (Adj. – R^2)

Stem quality characteristics	Indep.	Random f.	Intercept	Independent		Model	
				$H_o$spec	Hegyi	AIC	Adj.- R^2
Bark anom. (0-4 m)	H_OEST+Hegyi	Idplot	1238.68	-95.98 (p=0.40)	-92.74 (p<0.001)	1173.99	0.49
	H_OAll+Hegyi	Idplot	1262.96	-117.69 (p=0.46)	-93.79 (p<0.001)	1173.47	0.48
	H_ONeutral+Hegyi	Idplot	1201.34	-10.98 (p=0.93)	-94.63 (p<0.001)	1174.59	0.48
Bark anom. (4-8 m)	H_OEST+Hegyi	Idplot	643.28	-22.53 (p=0.79)	-34.75 (p=0.03)	897.75	0.41
	H_OAll+Hegyi	Idplot	617.97	24.65 (p=0.83)	-35.12 (p=0.03)	897.15	0.41
	H_ONeutral+Hegyi	Idplot	587.33	52.25 (p=0.55)	-33.79 (p<0.04)	897.44	0.41

Bark anom. (8-12 m)	H_OEST+Hegyi	Idplot	323.89	-18.83 (p=0.74)	-19.11 (p=0.05)	837.916	0.22
	H_OAll+Hegyi	Idplot	319.85	-7.67 (p=0.92)	19.29 (p=0.05)	837.40	0.22
	H_ONeu-tral+Hegyi	Idplot	308.74	6.80 (p=0.91)	-18.93 (p=0.05)	837.97	0.21
SNC (0-4 m) (ln)	H_OEST+Hegyi	Idplot	-4.45	-0.05 (p=0.76)	-0.10 (p<0.01)	3.68	0.43
	H_OAll+Hegyi	Idplot	-4.48	0.01 (p=0.95)	-0.10 (p=0.001)	3.10	0.43
	H_ONeu-tral+Hegyi	Idplot	0.16	0.12 (p=0.47)	-0.10 (p<0.01)	3.19	0.44
SNC (4-8 m) (ln)	H_OEST+Hegyi	Idplot	-4.88	-0.07 (p=0.59)	-0.05 (p<0.01)	-34.12	0.09
	H_OAll+Hegyi	Idplot	-4.83	-0.12 (p=0.50)	-0.05 (p<0.01)	-34.91	0.09
	H_ONeu-tral+Hegyi	idplot	-4.79	-0.14 (p=0.31)	-0.06 (p<0.01)	-35.03	0.11
SNC (8-12 m) (ln)	H_OEST+Hegyi	Idplot	-4.69	-0.13 (p=0.47)	-0.08 (p<0.01)	14.31	0.10
	H_OAll+Hegyi	Idplot	-4.67	-0.13 (p=0.60)	-0.08 (p<0.01)	13.56	0.10
	H_ONeu-tral+Hegyi	Idplot	-4.65	-0.12 (p=0.54)	-0.08 (p<0.01)	14.31	0.10
Lean (0-4 m)	H_OEST+Hegyi	Idplot	-2.33	0.10 (p=0.83)	-0.07 (p=0.23)	182.35	0.02
	H_OAll+Hegyi	Idplot	-2.25	-0.07 (p=0.90)	-0.07 (0.25)	181.75	0.02
	H_ONeu-tral+Hegyi	Idplot	-1.20	-0.35 (p=0.45)	-0.07 (p=0.23)	181.71	0.02
Lean (4-8 m) (sqrt)	H_OEST+Hegyi	Idplot	0.22	0.02 (p=0.69)	0.01 (p=0.28)	-155.30	0.30
	H_OAll+Hegyi	Idplot	0.17	0.09 (p=0.29)	0.01 (p=0.27)	-156.88	0.31
	H_ONeu-tral+Hegyi	Idplot	0.16	0.08 (p=0.22)	0.01 (p=0.20)	-156.72	0.31
Lean (8-12) (sqrt)	H_OEST+Hegyi	Idplot	0.25	0.02 (p=0.74)	0.01 (p=0.59)	-124.24	0.24
	H_OAll+Hegyi	Idplot	0.24	0.03 (p=0.79)	0.01 (p=0.57)	-124.83	0.24
	H_ONeutral +Hegyi	Idplot	0.28	-0.02 (p=0.75)	0.001 (p=0.58)	-124.32	0.24
Sweep (0-4 m)	H_OEST+Hegyi	Idplot	0.17	-0.02 (p=0.61)	0.01 (p=0.27)	-228.03	0.09
	H_OAll+Hegyi	Idplot	0.17	-0.00 (p=0.99)	0.01 (p=0.30)	-228.40	0.09
	H_ONeu-tral+Hegyi	Idplot	0.14	0.04 (p=0.45)	0.01 (0.01)	-228.43	0.08
Sweep (4-8 m)	H_OEST +Hegyi	Idplot	0.07	0.05 (0.22)	0.01 (p=0.16)	-213.40	0.33
	H_OAll +Hegyi	Idplot	0.03	0.11 (p=0.05)	0.01 (p=0.13)	-216.54	0.35
	H_ONeu-tral+Hegyi	Idplot	0.03	0.08 (p=0.05)	0.01 (p=0.08)	-215.76	0.36
Sweep (8-12 m) (ln)	H_OEST+Hegyi	Idplot	-3.40	1.16 (p=0.25)	0.17 (p=0.28)	277.55	0.06
	H_OAll +Hegyi	Idplot	-3.81	1.52	0.18	277.03	0.05

	H_ONeutral +Hegyi	Idplot	-2.97	(p=0.26 0.08 (p=0.94)	(p=0.23) 0.20 (p=0.19)	278.75	0.03

Table S-3-4: Results of the linear mixed effect models with the crown characteristics CV: Crown volume (m^3), CSA: Crown surface area (m^2), CR_{mean}: Mean crown radius (m), Max area: Maximum crown area (m^2), CL: Crown length (m), Asymmetry: Crown asymmetry (m), BL_{max}: Maximum branch length of first order branches (m), Bl_{mean}: Mean branch length of first order branches (m), BL_{median}: Median branch length of first order branches (m), BL_{sum}: Sum of branch length of first order branches (°), BA_{mean}1st: Mean branch angle of first order branches (°), BA_{median}1st: Median branch angle of first order branches (°), BA_{range}1st: Branch angle range of first order branches (°), BA_{mean}2nd: Mean branch angle of second order branches (°), BA_{median}2nd: Median branch angle of second order branches (°), BA_{range}2nd: Branch angle range of second order branches (°), and CBH: Crown base height (m) as dependent variables, H_OEST: Heterozygosity measured by EST-SSR markers, H_OAll: Heterozygosity measured by all markers, H_ONeutral: Heterozygosity measured by nSSR markers and Hegyi: Hegyi-Index as independent variables (Indep.), Random factor: Idplot, Intercept: The intercept of the model, independent: The slope and p-value for each independent variable, Model: Akaike Information Criterion for the model, Adjusted R-Squared of the model (Adj. – R^2)

Crown characteristics	Indep.	Random f.	Intercept	Independent		Model	
				H_OSpec	Hegyi	AIC	Adj.- R^2
CV (ln)	H_OEST+Hegyi	Idplot	6.30	-0.11 (p=0.73)	-0.46 (p<0.001)	102.74	0.63
	H_OAll+Hegyi	Idplot	6.23	0.03 (p=0.95)	-0.46 (p<0.001)	102.11	0.63
	H_ONeutral+Hegyi	Idplot	6.04	0.24 (0.49)	-0.45 (p<0.001)	102.18	0.63
CSA	H_OEST+Hegyi	Idplot	477.66	-65.26 (p=0.32)	-64.63 (p<0.001)	935.62	0.52
	H_OAll+Hegyi	Idplot	489.80	-67.82 (p=0.49)	-65.41 (p<0.001)	935.35	0.59
	H_ONeutral+Hegyi	Idplot	433.63	17.18 (p=0.82)	-65.87 (p<0.01)	936.31	0.50
CR_{mean}	H_OEST+Hegyi	Idplot	4.64	-0.40 (p=0.36)	-0.62 (p<0.001)	153.66	0.64
	H_OAll+Hegyi	Idplot	4.87	-0.67 (p=0.30)	-0.63 (p<0.001)	152.68	0.64
	H_ONeutral+Hegyi	Idplot	4.64	-0.21 (p=0.67)	-0.63 (p<0.001)	154.13	0.63
Max area (ln)	H_OEST+Hegyi	Idplot	4.40	0.03 (p=0.92)	-0.38 (p<0.001)	73.11	0.62
	H_OAll+Hegyi	Idplot	4.43	-0.02 (p=0.96)	-0.38 (p<0.001)	72.39	0.62
	H_ONeutral+Hegyi	Idplot	4.40	-0.03 (p=0.93)	-0.38 (p<0.001)	72.91	0.62
CL (ln)	H_OEST+Hegyi	Idplot	2.81	-0.18 (p=0.32)	-0.06 (p=0.02)	11.00	0.12
	H_OAll+Hegyi	Idplot	2.79	-0.09 (p=0.73)	-0.06 (p=0.01)	11.12	0.10
	H_ONeutral+Hegyi	idplot	2.61	0.14 (p=0.47)	-0.06 (p<0.01)	11.20	0.09
Asymmetry (ln)	H_OEST+Hegyi	Idplot	0.31	-0.04 (p=0.94)	-0.01 (p=0.94)	184.68	0.20
	H_OAll+Hegyi	Idplot	0.21	0.14 (p=0.85)	-0.01 (p=0.93)	183.90	0.20
	H_ONeutral+Hegyi	Idplot	0.20	0.11 (p=0.85)	-0.01 (p=0.95)	184.45	0.20
BL_{max} (ln)	H_OEST+Hegyi	Idplot	2.61	0.16 (p=0.53)	-0.16 (p<0.001)	60.36	0.41

	H_OAll+Hegyi	Idplot	2.62	0.11 (p=0.75)	-0.16 (p<0.001)	59.91	0.41
	H_ONeutral+Hegyi	Idplot	2.92	-0.27 (p=0.30)	-0.16 (p<0.001)	59.53	0.42
BL_{mean}	H_OEST+Hegyi	Idplot	2.29	0.92 (p=0.08)	-0.28 (p<0.01)	181.26	0.44
	H_OAll+Hegyi	Idplot	1.90	1.31 (p=0.09)	-0.27 (p<0.01)	180.68	0.03
	H_ONeutral+Hegyi	Idplot	2.29	0.47 (p=0.42)	-0.25 (p=0.01)	183.58	0.42
BL_{median} (ln)	H_OEST+Hegyi	Idplot	-0.18	0.21 (p=0.66)	-0.10 (p=0.27)	172.10	0.41
	H_OAll+Hegyi	Idplot	-0.28	0.33 (p=0.64)	-0.10 (p=0.28)	171.31	0.41
	H_ONeutral+Hegyi	Idplot	-0.37	0.33 (p=0.53)	-0.09 (p=0.33)	171.72	0.41
BL_{sum} (ln)	H_OEST+Hegyi	Idplot	4.60	-0.38 (p=0.16)	-0.14 (p<0.01)	73.78	0.30
	H_OAll+Hegyi	Idplot	4.50	-0.12 (p=0.75)	-0.15 (p=0.001)	74.95	0.28
	H_ONeutral+Hegyi	Idplot	3.90	0.60 (p=0.04)	-0.14 (p<0.01)	71.47	0.30
NB1st	H_OEST+Hegyi	Idplot	47.91	-22.58 (p=0.03)	-1.38 (p=0.42)	639.70	0.28
	H_OAll+Hegyi	Idplot	50.54	-20.95 (p=0.16)	-1.71 (p=0.32)	641.96	0.27
	H_ONeutral+Hegyi	Idplot	30.30	8.56 (p=0.45)	-1.71 (p=0.32)	643.91	0.20
BA_{mean}1st	H_OEST+Hegyi	Idplot	68.40	-21.96 (p<0.01)	-1.34 (p=0.32)	591.74	0.50
	H_OAll+Hegyi	Idplot	75.74	-28.06 (p=0.01)	-1.62 (p=0.23)	593.29	0.48
	H_ONeutral+Hegyi	Idplot	57.87	0.71 (p=0.93)	-1.67 (p=0.24)	600.52	0.44
BA_{median}1st	H_OEST+Hegyi	Idplot	65.05	-26.00 (p<0.01)	-0.95 (p=0.53)	613.76	0.48
	H_OAll+Hegyi	Idplot	71.82	-30.09 (p=0.02)	-1.30 (p=0.40)	616.71	0.44
	H_ONeutral+Hegyi	Idplot	48.40	5.62 (p=0.56)	-1.25 (p=0.44)	622.62	0.41
BA_{range}1st	H_OEST+Hegyi	Idplot	182.52	-25.43 (p<0.001)	-1.29 (p=0.16)	574.85	0.21
	H_OAll+Hegyi	Idplot	189.52	-30.69 (p<0.01)	-1.48 (p=0.10)	578.34	0.14
	H_ONeutral+Hegyi	Idplot	169.76	1.73 (p=0.83)	-1.80 (p=0.07)	588.21	0.07
BA_{mean}2nd	H_OEST+Hegyi	Idplot	68.29	-8.95 (p=0.20)	0.13 (p=0.92)	586.97	0.49
	H_OAll+Hegyi	Idplot	66.86	-4.25 (p=0.68)	-0.01 (p=1.00)	587.71	0.48
	H_ONeutral+Hegyi	Idplot	54.64	10.84 (p=0.15)	0.27 (p=0.84)	586.44	0.50
BA_{median}2nd	H_OEST+Hegyi	Idplot	65.91	-11.47 (p=0.16)	0.22 (p=0.88)	612.98	0.49
	H_OAll+Hegyi	Idplot	64.02	-5.34 (p=0.66)	0.06 (p=0.97)	613.98	0.47

	H_ONeutral+Hegyi	Idplot	48.41	13.92 (p=0.12)	1.54 (p=0.80)	612.37	0.49
BA_{range}2nd	H_OEST+Hegyi	Idplot	166.47	2.62 (p=0.77)	-0.56 (p=0.63)	620.11	0.01
	H_OAll+Hegyi	Idplot	156.55	18.21 (p=0.15)	-0.63 (p=0.58)	617.36	0.02
	H_ONeutral+Hegyi	idplot	150.06	20.84 (p=0.03)	-0.37 (p=0.74)	615.35	0.05
CBH	H_OEST+Hegyi	Idplot	13.71	1.34 (p=0.61)	-0.51 (p=0.32)	505.00	0.48
	H_OAll+Hegyi	Idplot	14.69	-0.63 (p=0.86)	-0.49 (p=0.34)	504.5	0.48
	H_ONeutral+Hegyi	idplot	17.02	-3.13 (p=0.24)	-0.55 (p=0.28)	503.83	0.49

Table S-3-5: Relationship between tree characteristics, competition intensity (Hegyi-Index), heterozygosity: H_OEST: Heterozygosity measured by EST-SSR markers, H_OAll: Heterozygosity measured by all markers, H_ONeutral: Heterozygosity measured by nSSR markers and site index (yield classes: Yield c.; The lower the class, the better the site); Adj-R^2: Adjusted R^2; AIC: Akaike-Information-Criterion; P-value; Int: Interaction between Hegyi-Index and yield classes. BA_{mean} 1st: Mean branch angle first order branches (°), BA_{median} 1st: Median branch angle first order branches (°), BA_{range} 1st: Branch angle range first order branches (°), NB1st: Number of first order branches, CSA: Crown surface area (m²), CR_{mean}: Mean crown radius (m), BL_{mean}: Mean branch length first order branches (m):, Bark anom.: Number of bark anomalies (counts/m), SNC: Stem non-circularity (m)

Tree characteristics	Model	Adj R^2	AIC	P-value
BA_{mean} 1st	y = 63.76 - 19.35 * H_OEST -2.01 * Hegyi + 2.54 * yield c.	0.09	623.56	H_OEST: P = 0.025 Hegyi: P = 0.085 Yield c.-: P = 0.095
	y = 73.36 – 30.02 * H_OAll - 2.15 * Hegyi + 2.48 * Yield c.	0.11	622.56	H_OAll: P = 0.015 Hegyi: P = 0.063 Yield c.: P = 0.101
	y = 60.49 – 6.48 * H_ONeutral -2.44 * Hegyi + 2.58 * Yield c.	0.04	628.42	H_ONeutral: P = 0.508 Hegyi: P = 0.041 Yield c.: P = 0.099
BA_{median} 1st	y = 59.44 – 22.92 * H_OEST -1.82 * Hegyi + 3.20 * Yield c.	0.10	643.108	H_OEST: P = 0.019 Hegyi: P = 0.166 Yield c.: P = 0.063
	y = 68.59 – 31.90 * H_OAll -2.01 * Hegyi + 3.15 * Yield c.	0.09	643.41	H_OAll: P = 0.022 Hegyi: P = 0.123 Yield c.: P = 0.067
	y = 50.82 – 2.05 * H_ONeutral -2.30 * Hegyi + 3.28 * Yield c.	0.03	648.92	H_ONeutral: P = 0.854 Hegyi: P = 0.088 Yield c.: P = 0.066
BA_{range} 1st	y = 182.33 - 25.39 * H_OEST - 1.20 * Hegyi - 0.04 * Yield c.	0.16	583.76	H_OEST: P < 0.001 Hegyi: P = 0.186 Yield c.: P = 0.973
	y = 189.63 – 30.71 * H_OAll -1.146 * Hegyi - 0.07 * Yield c.	0.12	588.02	H_OAll: P < 0.01 Hegyi: P = 0.115 Yield c.: P = 0.952
	y = 169.90 + 1.13 * H_ONeutral -1.73 * Hegyi + 0.06 * Yield c.	0.00	597.91	H_ONeutral: P = 0.889 Hegyi: P = 0.079 Yield c.: P = 0.962
NB1st	y = 48.30 – 18.26 * H_OEST - 0.99 * Hegyi – 2.68 * Yield c.	0.05	653.28	H_OEST: P = 0.076 Hegyi: P = 0.476 Yield c.: P = 0.142

	y = 50.110 – 16.46 * H_OAll – 1.23* Hegyi – 2.68 * Yield c.	0.03	655.29	H_OAll: P = 0.266 Hegyi: P = 0.380 Yield c.: P = 0.147
	y = 33.15 – 8.16 * H_ONeutral - 1.34 * Hegyi – 2.57 * Yield c.	0.02	656.08	H_ONeutral: P = 0.482 Hegyi: P = 0.340 Yield c.: P = 0.165
CSA	y = 618.65 – 23.48 * H_OEST - 122.31 * Hegyi – 80.36 * Yield c.+ 26.34 * Hegyi*Yield c.	0.44	956.63	H_OEST: P = 0.723 Hegyi: P < 0.001 Yield c.: P = 0.017 Int.: p = 0.017
	y = 625.32 – 23.30 * H_OAll – 123.71 * Hegyi – 81.83 * Yield c.+ 26.85 * Hegyi * Yield c.	0.44	956.70	H_OAll: P = 0.805 Hegyi: P <0.001 Yield c.: P = 0.015 Int.: P = 0.046
	y = 611.64 – 1.50 * H_ONeutral – 123. 66 * Hegyi – 81.41 * Yield c. + 26.73 * Hegyi * Yield c.	0.44	956.76	H_ONeutral: P = 0.984 Hegyi: P < 0.001 Yield c.: P = 0.018 Int: P = 0.018
CR_{mean}	y = 4.08 – 0.31 * H_OEST - 0.60 * Hegyi + 0.24 * Yield c.	0.56	143.91	H_OEST: P = 0.479 Hegyi: P < 0.001 Yield c.: P < 0.01
	y = 4.19 – 0.41* H_OAll – 0.60* Hegyi + 0.24 * Yield c.	0.56	143.99	H_OAll: P = 0.52 Hegyi: P < 0.001 Yield c.: P < 0.01
	y = 3.98 – 0.05 * H_ONeutral – 0.60 * Hegyi + 0.24 * Yield c.	0.59	143.98	H_ONeutral: P = 0.920 Hegyi: P < 0.001 Yield c.: P < 0.01
BL_{mean}	y = 1.83 + 0.60 * H_OEST - 0.19 * Hegyi + 0.26 * Yield c.	0.09	188.48	H_OEST: P = 0.304 Hegyi: P = 0.016 Yield c.: P = 0.014
	y = 1.40 + 1.14 * H_OAll – 0.19 * Hegyi + 0.26 * Yield c.	0.10	187.57	H_OAll: P = 0.234 Hegyi: P = 0.024 Yield c.: P = 0.014
	y = 1.45 + 0.77 * H_ONeutral - 0.18 * Hegyi – 0.26 * Yield c.	0.09	185.84	H_ONeutral: P = 0.482 Hegyi: P = 0.340 Yield c.: P = 0.165
Bark anom. Sec: 0-4 m	y = 1152.02 + 81.36 * H_OEST - 80.84 * Hegyi – 25.99 * Yield c.	0.23	1065.19	H_OEST: P = 0.530 Hegyi: P < 0.001 Yield c.: P = 0.261
	y = 1138.16 + 82.81 * H_OAll – 79.86 * Hegyi – 25.95 * Yield c.	0.22	1065.39	H_OAll: P = 0.655 Hegyi: P < 0.001 Yield c.: P = 0.262
	y = 1209.27 – 24.24 * H_ONeutral - 79.24 * Hegyi – 26.40 * Yield c.	0.22	1065.57	H_ONeutral: P = 0.867 Hegyi: P < 0.001 Yield c.: P = 0.255
SNC (ln): Sec 0-4 m	y = -4.53 + 0.05 * H_OEST - 0.06 * Hegyi – 0.06 * Yield c.	0.14	-19.36	H_OEST: P = 0.744 Hegyi: P < 0.01 Yield c.: P = 0.037
	y = 4.54 + 0.07 * H_OAll – 0.06 * Hegyi – 0.06 * Yield c.	0.14	-19.36	H_OAll: P = 0.751 Hegyi: P < 0.01 Yield c.: P = 0.038
	y = 4.55 + 0.05 * H_ONeutral – 0.06 * Hegyi – 0.06* Yield c.	0.14	-19.34	H_ONeutral: P = 0.767 Hegyi: P < 0.01 Yield c.: P = 0.038

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Chapter 4

Differences in stem form and bark anomalies of northern red oak trees in forest stands in Canada and Germany

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Abstract

Northern red oak (*Quercus rubra* L.) wood is valuable for a variety of applications not only in its natural distribution range in North America but also in Europe. Timber quality and stem diameter largely determine timber prices and respective uses. Silvicultural management is key to influencing tree growth and stem quality. In Germany, crop tree thinning is currently the standard treatment, while in Canada the shelterwood system is common practice. The objective of this study was to compare stem characteristics related to stem quality of northern red oaks from Canada with those from Germany to determine effects of different silvicultural treatments on stem quality. We examined stem characteristics from a total of 150 dominant northern red oaks in Canadian and German forest stands using the terrestrial laser scanning approach. Northern red oak stems in Canada (shelterwood system) were significantly straighter, whereas German stems (crop tree thinning approach) were significantly smoother on the surface and rounder on the upper parts of the stems (height 4 – 8 m). The number of bark anomalies decreased with increasing tree competition, indicating that competition is the main driver influencing external stem form and the occurrence or persistence of bark anomalies.

Keywords: *Quercus rubra*, tree stem quality, competition index, silviculture, terrestrial laser scanning

4.1 Introduction

Northern red oak timber is valued for its variety of applications (Nicolescu et al. 2020) and can command high timber prices (Northeast Timber Exchange, L.L.C 2021). Northern red oak timber is considered valuable not only in its natural range (Dey et al. 2008), but also in Europe (Göhre and Wagenknecht 1955), although in Europe oak species from the white oak group (in Germany mainly pedunculate oak and sessile oak) are usually preferred due to more desirable wood properties (e.g., wood durability, suitability for outdoor applications) (Klemmt et al. 2013). Yet, northern red oak is able to compensate for its lower price on the timber market by higher volume output within a shorter rotation period (Seidel and Kenk 2003). Northern red oak timber quality itself can vary greatly, resulting in broad price variability (Vansteenkiste et al. 2005; Marschall et al. 2014).

Timber quality and stem diameter are the main criteria determining end use and thus price (Bosela et al. 2016). Factors influencing tree growth may also impact wood structure and thus timber quality (Zobel and Jett 1995). Hence, silvicultural treatment, genetics, or site conditions can modify stem quality (Macdonald 2002). Tree species selection and stand density control are important decision-making factors in silviculture (Schall and Ammer 2013). Stand density, and thus competition intensity between individual trees, is one of the most important factors affecting stem quality characteristics, such as branchiness or bending (Hein 2008). High competition intensity can lead to reductions in stem quality properties (Hein 2008; Kirk and Berrill 2016), but is usually associated with restricted radial tree growth (Mäkinen and Hein 2006; Oheimb et al. 2011), while low competition intensity can have the opposite effect (Sonderman and Rast 1988). Differences in site conditions can also modify growth processes (Bertness and Callaway 1994), with competition considered one of the main factors influencing stem quality characteristics in northern red oak (Burkardt et al. 2019). Therefore, scientific research attempts to regulate stand density and thus competition intensity using different silvicultural methods to improve tree growth and stem quality (Sonderman and Rast 1988).

The deciduous forests of central and eastern Canada and the United States, where oak species are ecologically and economically important (Johnson et al. 2002), form much of the native range of northern red oak (*Quercus rubra* L.), a common dominant in many of the forests there (Birchenko et al. 2009). Northern red oak also grows outside its natural distribution range, in Ukraine (Lavnyy and Savchyn 2017), UK (Wilson et al. 2018), France (Timbal and Aussenac 1996), and Germany (Göhre and Wagenknecht 1955), where it was introduced from the late 17th to the 18th centuries, mostly as a park tree. Northern red oak accounts for 0.5% of the current forested area in Germany (Schmitz et al. 2014), making it the most common non-native broadleaved tree species in the country (Nagel 2015).

While several studies on silvicultural management of northern red oak have been conducted in its natural range (e.g.; Dey et al. 2008; Sonderman and Rast 1988), its silvicultural treatment has been less well studied in Europe (e.g.; Rédei et al. 2010; Nicolescu et al. 2020). To obtain high quality-timber, crop tree thinning of northern red oak stands is the standard treatment applied in Germany (Nagel 2015; Nicolescu et al. 2020), while the shelterwood system is commonly used in North America (Sonderman and Rast 1988; Ward 2002; Groninger and Long 2008).

The effectiveness of a silvicultural procedure is usually determined after harvesting and during timber sorting (Bosela et al. 2016). In some cases, it is necessary to assess timber quality on a standing tree, as in the case of selling timber "on the stump" (Bosela et al. 2016). Terrestrial laser scanning (TLS) has been proven to be a suitable method to objectively (Liang et al. 2011) and non-destructively (i.a., Stängle et al. 2014) record tree morphology, including stem quality characteristics (Höwler et al. 2017; Juchheim et al. 2017). For example, methods have been developed to identify bark irregularities such as branch scars or bars (Kretschmer et al. 2013), as well as differences in stem form (Juchheim et al. 2017). Höwler et al. (2017) defined stem surface irregularities as bark anomalies and related them to competition intensity in beech stands.

The objective of our study was to investigate the influence of two different management regimes using TLS data. We compare the North American shelterwood system with Central European crop tree thinning via their effects on timber quality of northern red oak.

We hypothesized that

1) Stem form and the number of bark anomalies - both indicating stem quality of northern red oak trees - differ between Canadian and German stands due to different silvicultural practices.
2) Increasing tree competition is negatively related to external stem quality characteristics and this relationship is constant under both management systems (shelterwood system vs. crop tree thinning).

4.2 Material and Methods

Study sites and sample trees

We assessed the external stem characteristics of 150 study trees (10 trees each in 15 stands) in five northern red oak stands located in five stands in Canada (two stands each in Ontario and Nova Scotia, one stand in Prince Edward Island) and in 10 federal states within Germany (two stands each in Brandenburg, Thuringia, Lower Saxony, North Rhine-Westphalia and Baden-Württemberg; the same tree database in Germany as decribed in Burkardt et al. (2019)) (Table 4-1).

The study site selection was made according to the following criteria: (i) stands had to be middle-aged (mature but not yet ready to harvest), (ii) stands should be minimum 1 ha in size, (iii) main tree species had to be northern red oak, and (iv) sites had to be considered representative of the natural distribution range (NRCS 2002); or, in Germany, recommended for future cultivation of northern red oak (i.a., NMELV 2004).

The geographically different study sites included dry sites such as Brandenburg (Germany) with mean annual precipitation of 560 mm and sites with high precipitation (e.g., more than 1300 mm in Nova Scotia, Canada). Annual average temperatures varied 4.3 °C and 11.1 °C; the length of vegetation period ranged between 154 days and 198 days (Table 4-1).

Table 4-1: Study site information for the Canadian (CAN) and German (GER) stands in eight regions.

Country	Plot ID	Region[a]	Stand Age[b] (yrs)	Latitude[b]	Longitude[b]	Soil texture[b,c]	Tree species (%)[b,d]	Prec. [mm][e]	Temp. [°C][e]	Grow. season length [days][e]	DBH (cm)[f]	Tree density (trees /ha)	Tree basal area [m²][g]
CAN	1	ON	100	46.38	79.11 W	Loamy sand	RO 56.3%; RM 28.2%; SM 9.4%; WP 3.2%; BF 3.2%	1044	4.3	156	38.2	925	48.8
CAN	2	ON	107	46.65	79.16 W	Loamy sand	RO 20.3%; SM70.3%; IW 8.1%; BC 1.4%	1044	4.3	156	40.7	814	46.2
CAN	3	NS	89	44.52	65.41 W	Loamy sand	RO 40%, WP 16%, RM 7%, WB 4%, BF 4%, BS 4%, lA 4%, RS 1%	1327	8.5	198	30.4	502	27.1
CAN	4	NS	86	44.49	65.26 W	Loamy sand	RO 38%, WP 25%, RM 21%, WB 10%, BS 6%, lA, 4%	1330	8.5	198	31.2	976	37.6
CAN	5	PEI	115	46.27	63.11 W	Loamy sand	Data not available	1073	5.3	148	35.7	1014	44.3
GER	6	LS	67	51.78	9.59E	Loessssig loam	RO: 100%	1192	7.2	154	35.3	706	21.7
GER	7	LS	68	52.95	9.37 E	Loamy sand	RO: 100%	775	9.5	173	40.4	735	24.7
GER	8	NRW	59	51.54	6.49 E	Gravelly- , loamy sand	RO: 100%	813	10.8	181	36.5	418	27.8
GER	9	NRW	69	51.54	6.50 E	Loamy sand	RO: 100%	826	10.7	181	44.7	344	29.0
GER	10	BW	68	48.45	7.86 E	Silty loam	RO: 90% AS: 10%	846	11.1	185	52.4	729	30.5
GER	11	BW	61	48.45	7.86 E	Silty loam	RO: 95% HB: 5%	846	11.1	185	51.7	550	29.8
GER	12	THU	58	50.76	11.73 E	sand	RO: 95% CB: 5%	668	8.8	167	37.0	415	32.7
GER	13	THU	83	50.77	11.64 E	sand	RO: 100%	656	8.9	168	33.7	612	32.1
GER	14	BR	64	52.45	13.07 E	sand	RO: 100%	592	9.8	174	25.1	731	21.7
GER	15	BR	68	52.38	13.10 E	sandy cover layer over boulder clay	RO: 100%	560	9.8	174	35.8	614	24.6

[a]LS, Lower Saxony; NRW, North Rhine–Westphalia; BW, Baden–Wurttemberg; THU, Thuringia; BR, Brandenburg; ON, Ontario; NS, Nova Scotia; and PEI, Prince Edward Island.
[b]For German sites, stand information is from Burkardt et al. (2019).
[c]For Canadian sites, details are from the Harmonized World Soil Database version 1.2.
[d]AS, ash; BC, black cherry; BF, balsam fir; BS, black spruce; CB, common birch; HB, hornbeam; IW, ironwood; LA, large-tooth aspen; RO, northern red oak; RM, red maple; RS, red spruce; SM, sugar maple; WB, white birch; WP, eastern white pine.
[e]Climate data for Germany are based on calculations of the Climate Data Center in Germany (DWD Climate Data Center 1988b–2017, 1988a–2017, 1992a–2018, 1992b–2018). For North Bay, Ontario, information is provided by local forest authorities (BAMS Growth and Yield Program 2020) and by Brown (2016). Data for Nova Scotia are provided by local forest authorities and Richards and Daigle (2011). For Prince Edward Island, data are based on Paradis et al. (2016).
[f]DBH, diameter at breast height; mean diameter of the target trees, 10 in each stand.
[g]Calculated based on the 10 m radius around each target tree.
hFrom BAMS Growth and Yield Program (2020).

Silvicultural management of northern red oak stands differs in Canada and Germany. In Canada, northern red oak stands are usually thinned only once and finally harvested in a shelterwod system for natural regeneration (Loftis 1990). In contrast, frequent crop tree thinning to promote individual target trees and final harvest at target diameters of 65 cm+ are applied in Germany (Nagel 2015).

To analyse external quality-related stem characteristics, 10 dominant target trees (tree classes 1 and 2 according to Kraft (1884)) were randomly selected within each of the 15 study sites. A competition index (Hegyi 1974) was calculated to determine the intensity of competition to which each target tree was exposed. For this, every neighbouring tree with a diameter at breast height (130 cm) ≥ 7 cm standing within a radius of 10 m around the target tree was included in the index calculation (Equ. 4-1).

Equ. 4-1 $$\textit{Hegyi-index} = \sum_{i=1}^{n} \frac{D_i}{D_j} \times \frac{1}{Dis_{ij}}$$

with subject tree *j,* competitor tree *i,* diameter at breast height (*D* in cm) and the distance between the target tree and the competitor tree (Dis in m).

Tree measurement and calculation of stem quality characteristics

Stems of the target trees were scanned with a terrestrial Faro Focus 3D 120 laser scanner (Faro Technologies Inc., Lake Mary, Florida, USA) to ensure a three-dimensional and objective assessment of target tree stems (Höwler et al. 2017). Four to six positions were recorded following the multiscan approach (van der Zande et al. 2008). For subsequent spatial co-registration of the scans with the software Faro Scene (Faro Technologies Inc, Lake Marry, USA), 15-25 targets were placed around each target tree as tie points. From each coregistered point cloud the target tree stems (from stem base to crown base height) were manually isolated using the CloudCompare software Cloud Compare 2.6, retrieved from (http://www.cloudcompare.org/)) and saved as an .xyz-file (Cartesian coordinates). The accuracy of this method was demonstrated in previous studies focusing on beech (Höwler et al. 2017; 2019).

We used several stem quality criteria (e.g., straightness, roundness, bark anomalies) commonly used for such assessments (RVR 2015) and calculated a laser-based surrogate. First, the external stem characteristics *bending* and *sweep* as indices of the straightness of the lower stem parts as described in Höwler et al. (2017) were calculated. To do this, the stem point clouds were initially separated into stem discs of 1.75 cm horizontal thickness. The distance between the lowermost fitted stem disc (stem base) and the uppermost fitted stem disc (crown base height) was defined as stem length (a in Fig. 4-1). *Lean* was calculated based on the horizontal difference between the midpoints of the lowermost and uppermost stem sections (computed for 0 m- 4 m and 4 m - 8 m) (d in Fig. 4-1). To obtain *lean per meter* for better comparison among stems of different lengths, the value was divided by the total length of the section to obtain a length-independent measure. The ratio between the shortest distance between the centers of the lowest and highest stem discs (b in Fig. 4-1) and the sum of the shortest distances between the centers of all consecutive stem discs (c in Fig. 4-1) along the vertical axis was defined as *sweep*. This measure was also converted to *sweep* per metre by dividing *sweep* by the length of the stem section (4 m each).

Figure 4-1: Schematic draft of the stem characteristics calculation based on the point clouds of the terrestrial laser scans. a, b, c and d were used to calculate lean and sweep according to Höwler et al. (2017). Grafical representation of an bark scar included in the calculation of the number of bark anomalies (Bark anom.).

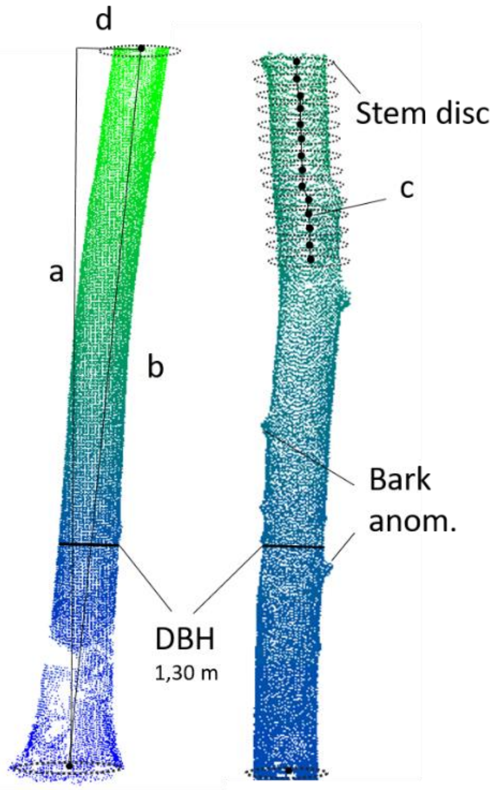


Figure 4-2: Range of competition intensities (Hegyi-Index) on the 15 study sites with site ID 1 and 2: Ontario; 3 and 4: Nova Scotia; 5: Prince Edward Island; 6 and 7: Lower Saxony; 8 and 9: North-Rhine Westfalia; 10 and 11: Baden-Württemberg; 12 and 13: Thuringia; 14 and 15: Brandenburg.

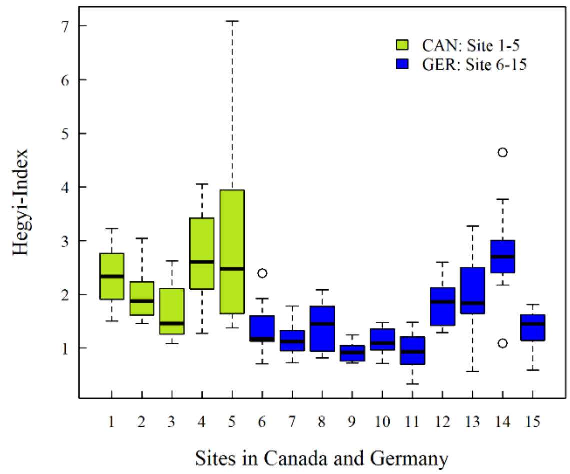


Table 4-2: Significance of the differences between the stem characteristics bark anomalies, stem non-circularity, bending and sweep in the sections 0 - 4 m and 4 - 8 m of both Canadian (n=49) and German northern red oak trees (n=94) according to the T-test and F-test.

Section	Bark anomalies [counts/m]	Stem non-circularity [m]	Bending [m]	Sweep [m]
0-4 m	p = 0.052	p = 0.87	*p < 0.01*	*p < 0.01*
4-8 m	*p < 0.01*	*p < 0.01*	*p = 0.03*	p = 0.95

P values < 0.05 are marked in italics.

In addition, *stem non-circularity* and the *number of bark anomalies* as additonal stem quality attributes introduced by Höwler et al. (2017) were calculated using Mathematica (Wolfram Research, Champaign, Illinois, USA). *Bark anomalies* were calculated to indicate irregularities such as bumps or scars on the stem surface, either of which indicates stem damage (Richter 2010; Höwler et al. 2017). The three-dimensional point clouds of the 150 stems were divided into sections of 4 m length to comply with the German sorting guidelines for log quality (general agreement for the German raw timber market (RVR 2015), which defines tolerances for wood defects and quality categories. In addition, the 4 m divisions allowed a more accurate assessment of the quality of individual stem sections. To eliminate density fluctuations in the point cloud, the spatial resolution of the point clouds for each stem section was homogenized using a 1.75 cm point cloud grid (Höwler et al. 2017). For details on the calculation of stem characteristics see Höwler et al. (2017), Juchheim et al. (2017) and Burkardt et al. (2019).

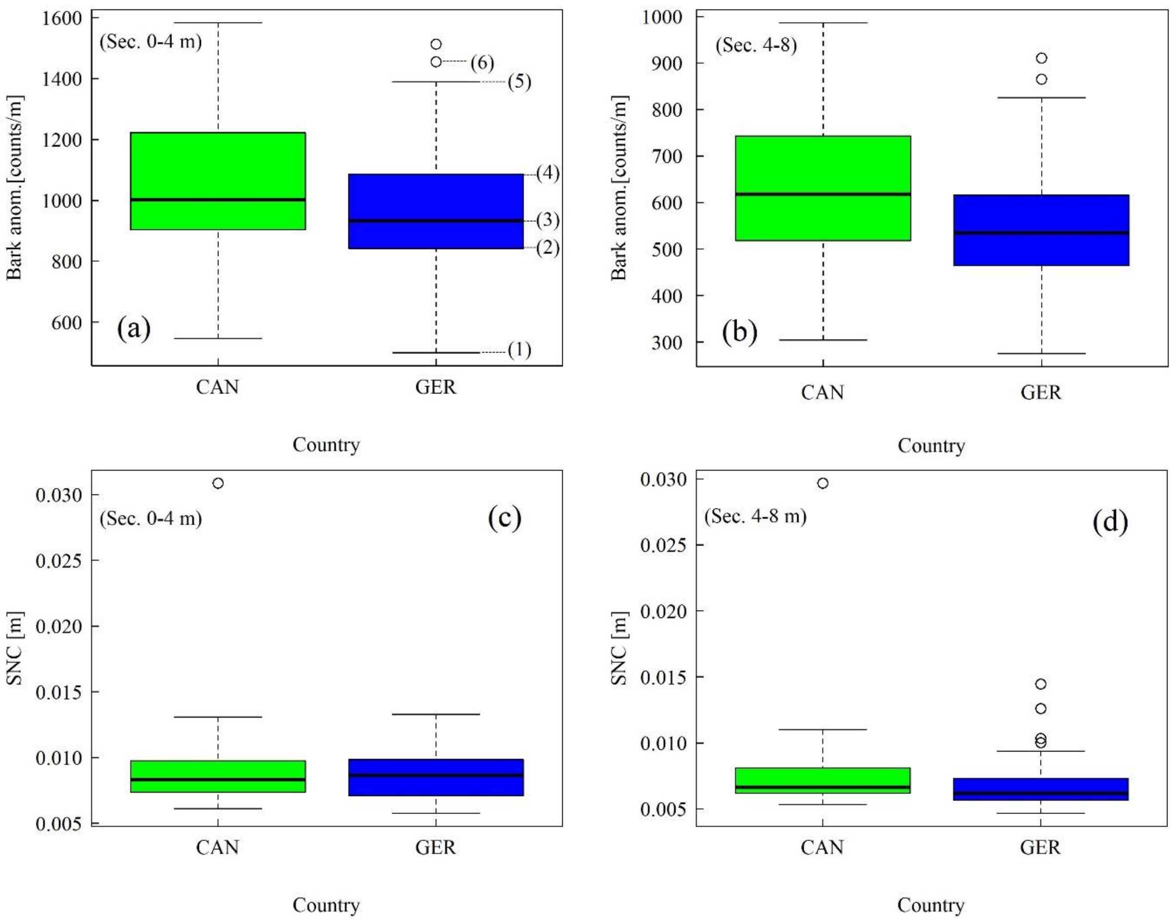
Statistical analyses

All statistical analyses were conducted with the open access statistics software R (R Core Team 2018). The Shapiro-Wilk test was used to check for normal distribution and Levene's test to check for variance homogeneity. To confirm equality of variances between the two countries (Canada with the shelterwood system and Germany with crop tree thinning), the F-test (to compare equality of variances between two samples in "R") was utilized. Depending on the data distribution, the Mann-Whitney U test or the T-test were applied to compare the means of the two groups. To obtain normally distributed residuals of stem non-circularity or sweep, we used square root or log-transformation. Competition intensity and local climatic effects, in this case mean annual precipitation and mean annual temperature, and country (Canada and Germany, as surrogates for the management approaches), were examined to capture unknown differences between the two countries (management approaches) as independent factors explaining the external stem features *stem-non-circularity*, *number of bark anomalies*, *sweep,* and *bending* as dependent variables in a multiple linear regression model. To avoid multicollinearity, the dependent variable *growing season* was excluded from the calculations, as it was highly correlated with *mean annual temperature*. Temperature and precipitation rates were available to cover the site conditions (local climatic effects). Detailed soil data were not available for every forest stand and therefore could not be included in our analyses. The significance level for all statistical analyses was $p < 0.05$.

4.3 Results

Competition intensity was significantly higher in Canadian northern red oak stands than in German stands ($p < 0.001$; Canada: 2.4 ± 1.1; Germany: 1.5 ± 0.7). A detailed overview of competition intensities on each study site is shown in Figure 4-2.

In Canada, stem quality was negatively influenced by higher numbers of bark anomalies and higher stem non-circularity values compared to northern red oak trees in Germany (Table 4-2, Figure 4-3). These differences were only significant for upper stem sections (4 - 8 m). Conversely, stem quality in Germany was lower in terms of bending (0 – 4 m and 4 – 8 m) and sweep (0 – 4 m) (Table 4-2, Figure 4-3).



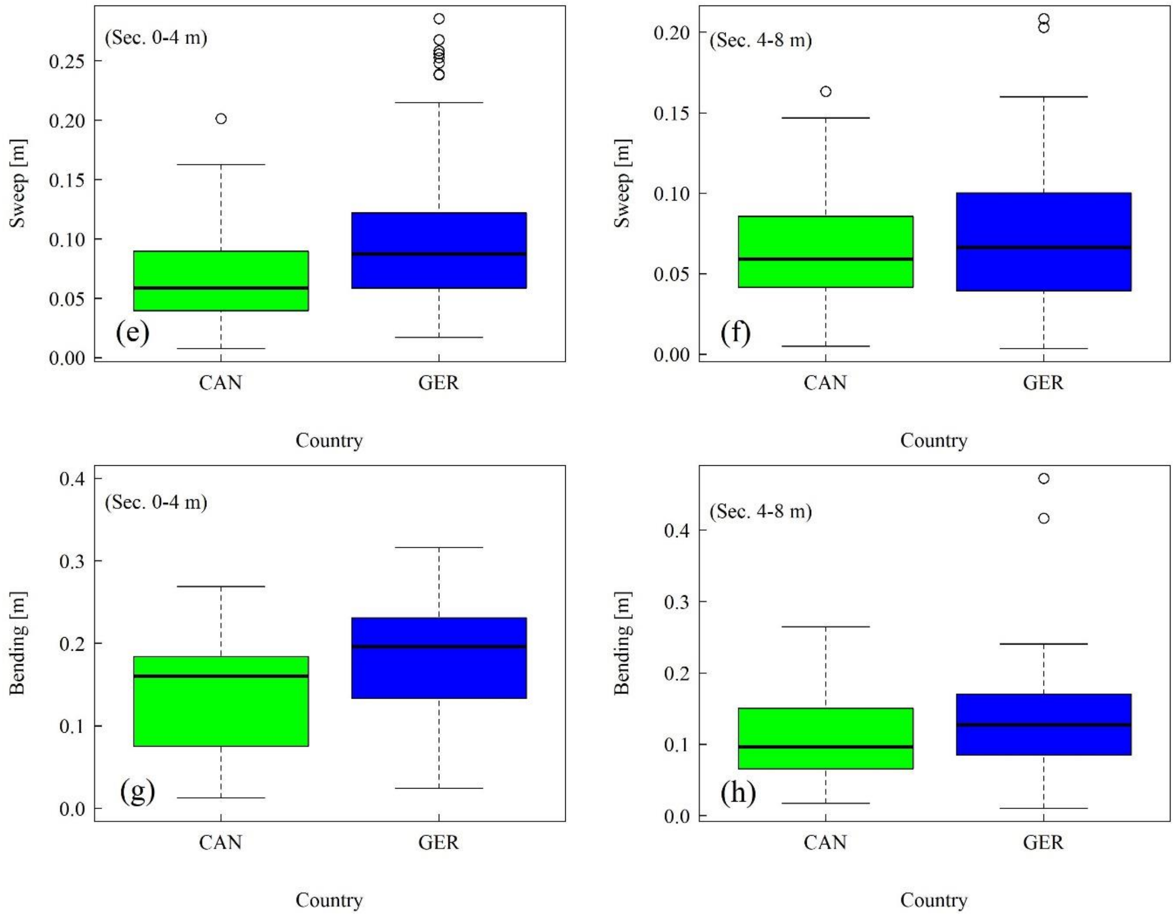


Figure 4-3: Range of the external stem characteristics number of bark anomalies (bark anom.) (section 0-4 m (a), section 4-8 m (b)), stem non-circularity (SNC) (section 0-4 m (c), section 4 – 8 m (d)), sweep (section 0 – 4 m (e); section 4-8 m (f)) and bending (section 0 – 4 m (g), section 4-8 m) between Canadian (CAN) and German (GER) northern red oak stands (N = 143, each). Figure a: The numbers 1-6 shows the values visualised by an boxplot; 1: minimum; 2: first quartile; 3: median; 4: third quartile; 5: maximum; 6: outlier of the values.

Table 4-3: Relationships between the number of bark anomalies (Bark anom.) in the stem section 0 m - 4 m (n=143) and 4 m - 8 m (n=142) as dependent variables, Heygi index (Hegyi), and local climatic effects, namely countries (Country), mean annual temperature (Temp.) and mean annual precipitation (Prec.) as independent variables of the multiple linear regression model. Model equation (Model), adjusted R-squared (Adj. R^2), Akaike Information Criterion of the model (AIC) and P value for each independent variable, Country:Temp represent the P value of the interaction term.

Stem characteristics	Model	Adj R^2	AIC	P-value
Bark anom [counts/m], section: 0-4 m	Y = -85.8 - 113.4 x Hegyi + 917.6 x Country + 132.3 x Temp – 101.5 x Country x Temp	0.36	1987.0	Hegyi: P < 0.001 Country: P < 0.001 Temp.: P < 0.001 Country: Temp.: P < 0.001
Bark anom. [counts/m], section: 4 - 8 m	Y = 577.9 - 76.4 x Hegyi + 215.0 x Country - 0.17 x Prec.	0.26	1851.3	Hegyi: P < 0.001 Country: P < 0.001 Prec.: P = 0.01

The number of bark anomalies (in section 0-4 m) was significantly related to competition intensity, country as proxy for silvicultural approach, and mean annual temperature (Table 4-3). With increasing competition intensity, the number of bark anomalies decreased in both Canadian and German stands ($p < 0.001$). With decreasing temperatures, a higher number of bark anomalies was observed in Canada ($p < 0.001$), while in Germany the opposite was found ($p < 0.001$) (Table 4-3). In the case of section 4-8 m, a significant relationship between the number of bark anomalies, competition, country, and mean annual precipitation was observed. We found significant negative correlations between competition intensity and number of bark anomalies ($p < 0.001$) as well as between precipitation and number of bark anomalies ($p = 0.01$) in both Canada and Germany (Table 4-3).The number of bark anomalies is shown here to demonstrate the relationships among stem quality characteristics, different stem sections, the two countries, competition, and local climatic effects (i.e., differences between the two countries' mean annual temperatures and precipitation). Results on stem non-circularity, sweep, and bending of all sections can be found in the supplement (Table S-4-1).

4.4 Discussion

Our results indicate that stem quality in the Canadian stands (shelterwood management) was negatively influenced by higher numbers of bark anomalies and higher stem non-circularity values compared to northern red oak trees in Germany managed with crop tree thinning. The number of bark anomalies includes all irregularities that could have resulted from former branches and old wounds (Richter 2010). Both theory and earlier studies suggest that increasing competition should result in a decreasing number of bark anomalies (Höwler et al. 2017). This relationship was confirmed within both management systems (CAN and GER). The higher number of bark anomalies and greater stem non-circularity with higher competition intensity in Canada may be due to shelterwood management. In Germany, the crop tree thinning method aims to promote individual valuable trees by careful but frequent removal of potential competitors. This involves a pre-selection of high-quality target trees at younger ages; the dominant trees examined in this study may have had better initial stem quality as compared to the non-treated northern red oaks in Canada (at the same levels of competition). In addition, continuous reduction in stand density and thus in competition intensity aims at improving tree growth. This could thus lead to faster branch occlusion processes, which would result in the observed lower number of bark anomalies in Germany.

In contrast, the shelterwood system, as commonly applied in Canada, has the primary goal of establishing natural regeneration. No interventions are performed over decades until a single thinning is followed by a final harvest (Hannah 1988; Loftis 1990). High stand density and thus, high competition intensity reduces radial tree growth (Mäkinen and Hein 2006). Consequently, trees that have been grown densely over decades might require more time for branch occlusion (due to reduced secondary growth) after natural self-pruning. This could explain the higher number of bark anomalies in Canadian stands. However, high stand density in Canada may also have resulted in straighter stems; light conditions in Canada change only gradually in the absence of frequent silvicultural interventions. In contrast, with the regular thinning approach in Germany, an increased risk of northern red oak growing into lateral light shafts could result in less straight stems.

It must be considered that pure northern red oak stands in Germany have higher intraspecific competition when compared to the naturally regenerated northern red oak stands in Canada, where there is an admixture of sugar maple and white pine. It is not clear, however, whether the Hegyi index, which quantifies competition intensity, but which does not include tree species identity or tree height, over- or underestimates the actual competition in Canadian stands. Overestimation would occur if the competitive pressure by the admixed species was lower than that by conspecific neighbours; underestimation would be expected if interspecific competition was stronger than intraspecific interference.

In addition to the management effects addressed in our study, other factors can also affect quality-related tree characteristics. Recent studies have shown that external stem quality characteristics (Burkardt et al. 2019) or tree growth (Pederson et al. 2004; Tardif and Conciatori 2006; Rollinson et al. 2016) are influenced by more complex environmental processes than can be explained by competition alone. To inspect the relationship between external stem features, competition and local effects, further studies should also include nutrient availability in the soil, species identities of tree species mixtures, as well as climatic differences. The latter was also supported by our study, in which it was indicated that precipitation and temperature may have significant effects on timber quality attributes, even though our results were inconsistent (see supplement Table S-4-1). Furthermore, genetic differences may also impact tree growth, depending on seed origin and local climate in the respective stand. Further studies should therefore include results of provenance trails.

4.5 Conclusion

We investigated the influence of two different management regimes via TLS (shelterwood system vs. crop tree thinning). We examined whether there are significant differences between quality-related stem characteristics of Canadian (shelterwood system) and German (crop tree thinning) northern red oak stands. We also tested how such characteristics change under conditions of individual tree competition and local climatic effects. We conclude that tree competition is the main driver influencing external stem characteristics and therefore enhanced stem quality in both Canadian and German stands. As recommended in previous studies (Burkardt et al. 2019), red oak should be kept rather dense in its early developmental stages to obtain desired branch free stem length. The results of our study suggest that stands should then be thinned in order to increase radial tree growth and thereby accelerate branch occlusion processes in order to eliminate irregularities in stem surfaces as rapidly as possible. According to the results of stem forms in the Canadian stands, these interventions could initially be conducted more cautiously than assumed previously to achieve straighter stem forms.

Competing interests : The authors declare there are no competing interests.

Contributors' statement: Conceptualization, K.B., T.V., D.S. and C.A.; data curation, K.B., formal analysis, K.B., D.S. and T.V., investigation, K.B., methodology, K.B., T.V., D.S. and C.A.; project administration, C.A. and T.V.; supervision, T.V., D.S., and C.A.; writing—original draft, K.B.; writing—review and editing, K.B., D.S., T.V. and C.A.

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4.6 Supplementary

Table S-4-1**:** Relationship between the stem characteristics number of bark anomalies (Bark anom.), stem non-circularity (SNC), bending and sweep in the stem sections 0 m – 4 m or 4-8 m, Heygi-Index and local effects, namely mean annual temperature (Temp.), mean annual precipitation (Prec.) and country (Canada and Germany). Model equation (Model), adjusted R-squared (Adj. R^2), Akaike Information Criterion of the model (AIC) and P-value for each independent variable, Country:Temp and Country:Prec represent the P-value for the interaction between the two variables.

Stem characteristics	Model	Adj R^2	AIC	P-value
SNC [m], section 0 - 4 m (sqrt)	Y = 0.1162 - 0.0053 x Hegyi - 0.0014 x Temp.	0.11	-875.4	Hegyi: P < 0.001 Temp.: P < 0.01
SNC [m], section 4 - 8 m (ln)	Y = -11.66 - 0.06 x Hegyi + 0.06 x Country - 0.43 x Temp. + 0.01 x Prec. + 0.47 x Country x Temp. - 0.01 x Country x Prec.	0.17	-18.8	Hegyi: P < 0.01 Country: P < 0.01 Temp.: P < 0.01 Prec.: P < 0.001 Country:Temp: P < 0.01 Country:Prec: P < 0.001
Bending, section 0 - 4 m	Y = 0.8383 - 0.0002 x Prec.	0.05	-10.0	Prec.: P < 0.01
Bending, section 4 - 8 m	Y = 0.7454 - 0.0003 x Prec.	0.11	-44.7	Prec.: P < 0.001
Sweep [m], section 0 - 4 m (sqrt)	Y = 0.2413 + 0.0335 x Country	0.02	-289.1	Prec.: P = 0.04
Sweep [m], section 4 - 8 m (sqrt)	Y = 0.3005 - 0.0000 x Prec.	0.02	-332.2	Prec.: P = 0.05

4.7 References

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Chapter 5

Synthesis

5. Synthesis

Each tree represents a highly complex structured organism, which can be defined by the shape of the stem and the crown including the individual crown structures with needles or leaves (Seidel 2011). Genetics, as well as site conditions and competition between neighboring trees, can alter tree morphology (Zobel and Jett 1995; Zingg and Ramp 2003). Competition between trees can be considered a major driver for influencing tree growth and stem quality (Zingg and Ramp 2003; Höwler et al. 2017). Silvicultural interventions can cost-effectively alter neighborhood competition in order to influence both stem quality and tree growth (Zingg and Ramp 2003; Ammer 2008). Therefore, comprehensive silvicultural management guidelines exist for native tree species in Germany. For various non-native tree species, there is often still uncertainty in this regard (Burkardt et al. 2019). In order to achieve detailed information on how the non-native northern red oak responds to silvicultural interventions considering various factors in Germany, the following research questions were object of investigation:

(1) Does intraspecific competition influence crown characteristics of northern red oak?
(2) Can intraspecific competition impact external stem characteristics that are related to stem quality?
(3) Are there any additional factors, which might influence the stem or crown characteristics of northern red oak?
(4) Is it possible to link tree characteristics to genetic traits of *Q. rubra*?
(5) Does stem quality differ between stands from Germany and the natural range and what could be the reasons for this?
(6) Can the results of this study provide further information on how to manage northern red oak in Germany?

5.1 Effect of competition on crown and stem characteristics

Effect of competition on crown characteristics:

Increasing intraspecific competition leads to a decrease of several crown dimensions, namely mean crown radius, maximum crown area, branch length (sum, maximum, and mean), crown length, crown volume, and crown surface area (see chapter 2 and 3). Even when other potentialyl influencing factors were taken into account, this relationship was significant (see chapters 2 and 3). Hence, I see my first hypotheses confirmed: Increasing competition intensity results in shorter and more slender crowns. These results are consistent with studies for both coniferous and deciduous species in finding a relation between a high competitive strength and smaller vertical and horizontal crown extensions (Miller 2000; Roloff 2001; Paulo et al. 2002; Mäkinen and Hein 2006; Thorpe et al. 2010). One of the most important regulators of tree growth is the light captured by the canopy (Pacala et al. 1996). High competition results in a reduced crown length (Mäkinen and Hein 2006) as branches of the lower crown regions die due to insufficient light availabilities, leading to a reduced assimilative vertical crown area (Assmann 1970). Consequently, high competition result in a fewer number of branches in the crown (Mäkinen and Hein 2006), and likely to less light assimilation and conversion as less leaf mass is available in the lower crown area. Young trees can usually compensate for the loss in the lower crown by continuing to grow in height and thus crown growth more effectively than older trees (Assmann 1970). Horizontal crown expansion is also reduced by mechanical abrasion of branches between immediate competitors (Putz et al. 1984; Rudnicki et al. 2001). High competition intensity consequently changes crown structures (Kellomäki 1980) and reduces crown size (Mäkinen and Hein 2006). Due to high competition and thus less light availability in the crown area, the proportion of shade branches becomes larger, which in turn are less efficient at capturing light for photosynthesis compared to light branches (Assmann 1970; Oliver and Larson 1996). Thus, the crown is an indicator of aboveground resource acquisition (Purves et al. 2007), and strong competition can reduce stand productivity (Hemery et al. 2005). Crown structure determines both light uptake (Kuuluvainen and Pukkala 1987), water uptake (Pretzsch 2010), and microclimate for underlying vegetation (Prescott 2002), so that changes in competition affect not only the tree itself but also the immediate environment. However, smaller crowns are not necessarily associated with lower productivity. This depends on the situation in the stand and on the strategy of the respective tree species to occupy free canopy space and to use the available resources effectively (Smith and Long 1989; Jack and Long 1992; Oliver and Larson 1996).

No relationship was found between crown asymmetry and competition (chapter 2; Table S-2-2). Crown asymmetry is caused by inconsistent space conditions due to varied competition intensities of different directions (Seidel 2011). Thereby, the trees are able to balance the resource allocation in reducing the crown growth in the direction of the competitors, but increasing it in areas with more resource availability (Muth and Bazzaz 2003). This finding is in contrast to my assumption and to the findings of Rock (2004), who have found a change in crown centricity (crown asymmetry) with increasing one-sided competition in oaks. However, it should be noted that the influence of birch on northern red oak crowns was studied and not between northern red oaks itself. For our study, this could indicate that competition from all sides was either always equal, or northern red oak does not show its phototropic properties in the formation of asymmetric crowns, at least in our study.

Effect of competition on stem quality characteristics

The number of bark anomalies and stem non-circularity decreased with increasing competition intensity, independent if intra- (chapters 2 and 3) or interspecific competition was observed (see chapter 4). A series of studies has also found a relation between high stand densities and a reduced branchiness for several deciduous and coniferous tree species (Ballard and Long 1988; Sonderman and Rast 1988; Mäkinen 1999; Mäkinen and Hein 2006; Höwler et al. 2017). A study of the second-log branches of *Sequoia sempervirens* and *Pseudotsuga menzisii* showed that high stand density was associated with a smaller diameter of the largest second log branches. With increasing neighbor proximity, the branch diameters of the observed tree became smaller (Kirk and Berrill 2016). Similar results were observed by Sonderman and Rast (1988) in northern red oak stands, which had fewer and smaller live and dead branches when light thinnings (leading to high stand density) compared to heavy thinnings (leading to low stand density) were applied. Strong competition leads to faster natural self-pruning and thus to potentially faster branch occlusion processes. Two facts must be considered here. First, it is tree species dependent how fast and how strong branches are formed in the stem area. In general, fast growing tree species also form large branches more quickly, which take longer to occlude the wounds than small branches (Schulz 1961). Depending on the size of the preceding branch, these branch fragments are still visible as bulges on the stem surface for decades (Schulz 1961). Second, results from Canada suggest that long-term strong competition (decades of high stand density) might not be conducive to the number of bark anomalies and thus to stem quality due to an inadequate light supply, resulting in smaller crowns and a reduced secondary thickness growth and thus to delayed branch occlusion processes (see chapter 4).

In the measurement of the number of bark anomalies, all irregularities in the stem cross-sections are included. Thus, this measure stands as a representative of all branches, regardless of whether they are alive, dead, or still showing as branch scars. The measurement of bark anomalies also includes wounds, such as those caused by felling or pruning (Burkardt et al. 2019). These wounds can still reduce quality after closure (Hecht et al. 2015) and might be particularly fatal, as they can lead to secondary damage inside (including slime flow in oak), which can later no longer be assessed from the outside (Schulz 1961). In addition, knots interrupt fiber decomposition and thus the strength of the wood (Mäkinen and Hein 2006; Richter 2010). It is possible to relate the width and height of a given branch to its depth within the stem and thus infer the internal quality (Schulz 1961). Thus, the unevenness on the stem surface can be an indication of the internal wood quality (Höwler et al. 2019). Therefore, the results suggest that also for *Q. rubra,* strong competition intensities are necessary to improve timber quality.

Stem non-circularity decreased with increased competition (chapter 2, 3 and 4), indicating increasing timber quality (Zingg and Ramp 2003). Tree ring development not proceeding equally in all directions often results in oval logs (Gabriel et al. 2001). This might be a result of one-sided competition leading to a reduced growth on the stem side that is exposed to strong competition (Gabriel et al. 2001). High competition could reduce radial growth to such an extent that inhomogeneous growth of annual rings caused by one-sided competition may no longer be as significant, thus reducing stem non-circularity values. Lower stem non-circularity results in a greater yield of subsequent processing steps than logs with higher stem non-circularity values (Dean 2003; Richter 2010; Pulkkinen 2012). One has to consider that the calculation of stem non-circularity is based on horizontal layers, which can incorrectly lead to an elliptical calculation for leaned round stems (Höwler et al. 2017). For this reason, errors in the calculation of both stem non-circularity and the number of bark defects cannot be completely excluded.

5.2 Effect of other factors on stem and crown characteristics

Effect of site conditions

Site conditions were significantly related to crown (chapters 2 and 3) and stem characteristics of northern red oak, regardless of whether yield classes, mean annual temperatures or precipitation rates were object of investigation (chapters 2, 3 and 4). Yield classes reflect the yield performance on a site and thus site conditions, with 1 representing the best performance and 3 the worst (Burschel and Huss 2003). The stem characteristics, namely the number of bark anomalies and stem non-circularity appeared to be higher on good sites, suggesting that this may have been due to faster tree growth and thus branch growth. Thicker branches require a longer time to be occluded after branch dropping, resulting in a higher number of bark anomalies (chapters 2 and 3). On good sites, the tree might also react more rapidly to its immediate environment (one-sided competition) in growth, which could explain the higher stem non-circularity values on better sites (see also section above influence of competition on stem characteristics).

We also found a stronger response of several crown characteristics to competition on good sites in Germany (chapter 2 and 3). This is consistent with the stress gradient hypothesis, which states that competition for resources is greater at good sites than at poor sites (Bertness and Callaway 1994; Maestre et al. 2009). Under low competition intensities, there still seem to be sufficient resources available to the tree, as reflected by large crown characteristics. Under higher competitive pressures, this relationship appears to reverse rapidly, with crown features becoming smaller on better sites due to higher competition for resources.

Including data from Canadian stands, stem traits showed significant correlations with climate variables in both German and Canadian stands, although the results did not show a consistent trend (chapter 4). For example, higher numbers of bark defects were detected in Germany with increases in temperature, while the opposite was found in Canada. For bending and sweep, we did not find differences between countries; however, the stems appear to become straighter with increasing precipitation. These results should not be given so much importance, as no more detailed information on site quality was considered here. As the relation between the growth of northern red oaks and climate is also depending on other factors (Rollinson 2016), it should be noted that the site has some influence on the stem characteristics of northern red oak, but for a more accurate assessment, further studies including comprehensive site conditions are necessary.

Effect of genetics

So far, few studies exist attempting to link genetic aspects with silvicultural characteristics on a single tree basis (Burkardt et al. 2020). Four branch angle measures namely mean branch angle zenith first order, median branch angle zenith first order, branch angle range first order, and the number of branches first order decreased with increasing heterozygosity ("EST" and heterozygosity "All"), suggesting that crown structure might be modified by genetics (chapter 3). As described in chapter 3, the results of the study contradict the assumption that increasing heterozygosity leads to higher phenotypic plasticity, which would explain a wider variety of branch angles. Higher heterozygosity might be associated to higher developmental stability (Dobzhansky and Wallace 1953; Lerner 1954; Dobzhansky and Levene 1955) and less fluctual asymmetry (Palmer and Strobeck 1986). Individuals, being “developmental stable”, are attributed to have a higher resistance against genetic or environmental disturbances during the trees’ development (Waddington 1942; Møller and Swaddle 1997). Furthermore, developmental stability is said to suppress phenotypic variation within individuals (Hallgrímsson et al. 2002). However, studies that have found a link between heterozygosity and developmental stability for trees are scarce. Fluctuating asymmetry is of interest because it indicates that an individual deviates from ideal, perfect bilateral symmetry (Palmer and Strobeck 1986), likely caused by environmental stresses, developmental instability, and genetic problems during tree development. Although no correlation was found between heterozygosity and crown asymmetry in this study - a measure we used indicating increasing crown symmetry as values decrease (Table S-5-1) - this result need not be considered of great significance. Tree crown is influenced by several factors, as shown for example by Muth and Bazzaz (2003) or Seidel et al. (2011), who found a correlation between neighborhood asymmetry and tree crown displacement. The trees were able to increase their crowns in the direction of greater resource availability and less competition (e.g.; Muth and Bazzaz 2003, Seidel et al. 2011). In particular, future studies could examine the symmetry of branch angles (for the different orders) in more detail to see if there is evidence of bilateral symmetry and whether and to what extent this can be linked to heterozygosity and branch angles. If small branch angles would be genetically predetermined, this might be an advantage to avoid competition by neighboring trees (Burkardt et al. 2020).

Another approach by Politov and Krutovskii (1994) suggests that increasing heterozygosity is associated with a growth advantage. They observed that older pines had higher levels of heterozygosity which is associated with growth heterosis. The authors explained it by suggesting that these trees were putting their energy into the major axis growth, which caused them to outcompete competitors. If faster growing trees were also those including narrower branch angles, this would give them an advantage over trees with a wide branch angle.

5.3 Additional analyses

Average annual diameter growth

Determining the tree species' suitability for future climates, it is essential to know how the growth response of the respective tree species has been to past climates and how future climates will affect tree growth (Nitschke et al. 2017). The annual radial growth response is often used to obtain relationships between tree species, climate changes, biotic factors, or site conditions (Fritts and Swetnam 1989; Pichler and Oberhuber 2007). Therefore, mean annual radial growth (average over the entire tree age) and mean annual radial growth for 2018 and 2019 of northern red oak target trees were calculated (see supplementary; additional analyses (Table S-5-2). Both values were then related to mean annual temperatures and precipitation during the growing season (Table 5-1) to examine whether there were differences between the mean radial growth response of northern red oak (total tree age) and the mean radial growth response in the dry years of 2018 and 2019 and the mean temperature and precipitation rates prevailing at the time. Northern red oak showed a high radial growth, although both an increase in temperature and a decrease in precipitation was measured on all study plots (Table S-5-3). Both the mean radial growth (total tree age) and the mean radial growth for 2018 and 2019 showed a significant increase with increasing mean temperature and precipitation during the growing season. However, a weaker relationship was observed between mean annual diameter growth and the climate variables in 2018 and 2019 (Table 5-1).

These findings indicate that northern red oaks might manage the climatic conditions on the study sites and climate changes as recorded in 2018 and 2019 (less precipitation with simultaneously higher temperatures) at least in the short term. These results stand in line with the expectations of several studies indicating that northern red oak can tolerate drought events (Sander 1990; Dreßel and Jäger 2002; Gillner 2012).

Table 5-1: Results of the multiple linear regression models. Relation between the mean annual radial growth (total age), and mean temperatures (temp30) and precipitation rates (prec30) during the growing season (30 year interval); relation between mean annual radial growth for 2018 and 2019 and mean temperatures (temp2) and precipitation rates (prec2) during the growing season for 2018 and 2019.

Radial growth	Model	Adj R²	AIC	P-value
Radial growth (total tree age)	Y = -1.543 + 0.083 * temp30 + 0.002 * prec30	0.54	145.67	Temp30: P < 0.001 Prec30: P < 0.001
Radial growth (for 2018 and 2019)	Y = -3.319 + 0.172 * temp2 + 0.003 * prec2	0.28	50.71	Temp2: P < 0.001 Prec2: P < 0.001

Since only estimates and not exact calculations of northern red oak radial growth were made in this study (no increment borings were made nor were log slices taken), the results presented here are of limited significance. In future studies, further growth investigations on northern red oak should be performed in order to be able to make better forecasts regarding the future climate tolerance of northern red oak in Germany.

5.4 Limits of the study und improvement ideas

The Hegyi index used in this study is easy to calculate and is considered a good representative of the actual competition intensity (Bachmann 1998). As only the diameter at breast height and the distance between the target trees and their competitors is included in this index, no information is provided about the tree species identity and the crown characteristics of the respective tree. In the Canadian northern red oak mixed stands, a different index accounting for tree species would have been advantageous because actual competition effects from tree species that are different from those caused by red oak could be stronger or weaker than measured by the current competition value (see chapter 4). Competition indices including tree species identity and crown shapes (i.a., Pretzsch 1995 and Metz et al. 2013) could remove these uncertainties regarding tree species effects and also increase the explanatory power in the German pure stands due to additional crown information.

In this study, precise information on soil properties was not available, although these, in combination with climatic factors, are an important evaluation criterion of site quality (Bartsch et al. 2019). Since site quality is known to contribute significantly to plant growth success, soil analyses should be investigated in future silvicultural studies. Important soil information would include soil water balance or pH-value in the mineral soil and nutrient concentrations (especially Ca, Mg, K or P) in the soil solution, providing information on the nutritional situation of a plant (Bartsch et al. 2019).

The results of the influence of heterozygosity ("EST," "All") on branch angle measures in the section "Influence of other factors on stem and crown characteristics" and chapter 3 should be viewed with caution, and interpretation of the results is highly speculative. No genetic markers likely to occur under selection were found in an outlier analysis of German northern red oak stands (Pettenkofer et al. 2020), nor do the markers used in the study appear to be close to genes that could give an important role in shaping crown size and structure (Burkardt et al. 2020). For more accurate statements in the future, potentially adaptive markers should be identified by modern high-set techniques and genes should be analyzed that may be responsible for shaping the crown size or structure of northern red oak (Burkardt et al. 2020).

Since mixed stands are preferable over monocultures, I recommend that future studies should include mixed stands with a clear assignment of tree species identities. In this context, a comparison of the influence of intra- and interspecific competition on tree morphology of northern red oak should be applicable, taking into account site quality and climate. The investigation should be enlarged to further federal states (extension of the north-south and west-east gradient) for a more comprehensive coverage of sites in Germany.

5.5 Relevance of the findings for forest management and conclusion

We found our expectations confirmed that intraspecific competition is the main determinant of crown and stem characteristics in northern red oaks (research questions 1 and 2). Although we observed an influence between tree morphology and other factors (such as site variables or genetic diversity (research question 3), competition appears to be the main driver determining crown and quality-related stem characteristics (chapters 2, 3, and 4). I underline the statements from all three studies (chapters 2, 3, and 4) that northern red oak can be treated similarly to our native tree species to produce quality timber (Nagel 2015; Nicolescu et al. 2020). The crop tree thinning is a common practice here, which aims to support individual valuable trees by releasing them from potential competitors at regular intervals (Burschel and Huss 2003). The results of our study suggest that northern red oak initially requires high stand densities to achieve a desired branch-free stem length. No target tree number can be derived from our studies, however according to the recommendation of various authors, 80-120 potential target trees should already be selected during the first thinning intervention (Seidel and Kenk 2003; Nagel 2015). Subsequent treatments should be conducted moderately to heavily at frequent intervals to ensure crown expansion and thus tree growth of northern red oak (see chapters 2, 3, and 4). Stem form results for Canadian northern red oaks indicate that initial interventions should be applied weaklier and more cautiously than previously thought, in order to obtain straighter stem forms (chapter 4).

Strong interventions can lead to a more rapid closure of cut wounds (Sandi et al. 2012; Nicolescu et al. 2013; Nicolescu et al. 2020). However, it must be noted that faster growth, whether triggered by better sites or by release, also increases the risk of developing larger branch diameters, requiring longer time to be occluded over after branch dropping. Conversely, the results of higher numbers of bark anomalies and stem non-circularity in Canadian northern red oak stands (research question 4) suggest that decades of high stand density may limit radial tree growth to the extent that dead branch or wound closure mechanisms are slowed. It should be noted that the shelterwood system commonly applied in Canada is primarily used to establish natural regeneration and not, as in Germany, to achieve quality timber (Matthews 1989; Smith et al. 1997). There is neither a pre-selection of high-quality trees nor a consequent release of those valuable trees. A pre-selection of high-quality target trees at younger ages, as is common in Germany, could already lead to an initial better stem quality of the trees compared to the untreated northern red oaks in Canada. However, another result of dense stands could be the straighter stems in Canada. Since light conditions change only gradually without any interventions in Canada, there might be no reason for the phototropic northern red oak to grow leaned and sweeped, merely growing straight upward toward the light source. In contrast, the regular releases in Germany pose the risk that red oak might grow into lateral light shafts, resulting in less straight stems. Future studies need to verify to what extent genetic aspects have an influence on stem shapes and how large the difference in bending and curvature between the German and the Canadian stems actually is for the utilization of the wood, and to what extent these characteristics influence pricing.

The results of this work provide new insights into the effects of silvicultural management intensity on the three-dimensional tree structure of a non-native tree species. In this study, a recently developed terrestrial laser scanning (TLS) approach for assessing external stem quality characteristics of beech (Höwler 2020) was adapted to external stem characteristics of northern red oak. Automated methods for determining crown characteristics, such as crown volume, branch angles, or lengths, were used to obtain data on the internal crown structure of *Q. rubra.* In addition, to my knowledge, this work is the first study that has linked TLS-based data to the genetic measure of heterozygosity in northern red oak. Many of the measured characteristics are difficult or impossible to detect using conventional field measurements (Juchheim 2020). The TLS was shown to be capable of examining both crown and stem characteristics in a non-destructive way, joining a wide variety of studies that have described the TLS as a useful tool that ensures a quantitative, objective (Liang et al. 2011), and non-destructive detection of objects (e.g., Schütt et al. 2004; Stängle et al. 2014; Juchheim 2020; Höwler 2020). Linking silvicultural measures generated from the TLS approach with genetic measures revealed by the latest gene sequencing technologies represents another opportunity to link silvicultural topics across disciplines further to understand the complex mechanisms that constitute tree morphology. Currently, point clouds from tripod-based laser scanners (as used in our study) are already being replaced by mobile and handheld laser scanners (e.g.; Del Perugia et al. 2019), which further increases the likelihood of the laser scanning method being used in practice to support or facilitate various field operations in the future.

5.6 References

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6. Appendix

Genetic analyses

Table S-5-1: Results of the linear regression. Relationship between crown asymmetry (Asymmetry), heterozygosity EST (“H_OEST”), heterozygosity All (“H_OAll”) and heterozygosity Neutral (“H_ONeutral); R^2; AIC: Akaike-Information-Criterion; P-value.

Crown characteristics	Model	R^2	AIC	P-value
Asymmetry (ln)	y = 0.284 – 0.046 * H_OEST	-0.01	178.53	H_OEST = 0.93
Asymmetry (ln)	y = 0.156 + 0.167 * H_OAll	-0.01	178.49	H_OAll = 0.83
Asymmetry (ln)	y = 0.145 + 0.141 * H_ONeutral	-0.01	178.48	H_ONeutral = 0.82

Additional analyses

To test whether radial growth was affected by the 2018 and 2019 droughts in Germany, we calculated the mean annual radial growth of the Q. rubra taget trees between past decades and within the two drought years 2018 and 2019 (Table S-5-2). The mean annual radial growth (total tree age) was calculated by the ratio of breast height diameter to tree age including values for 2017. The mean annual diameter growth for 2018 and 2019 was calculated based on the difference between the diameter measured in the early 2018 and in early 2020 (before the respective growing season has started). This value was then divided by the factor two to obtain mean radial growth for the dry years 2018 and 2019. The mean temperature and mean precipitation during the growing season (May including September) for the last 30 years (including 2017; the time span of 30 years is often indicated for evaluating the standard climate (Arguez and Vose 2011)) and for 2018 and 2019 for each of the ten study sites were also calculated (Table S-5-3).

Table S-5-2: Mean annual radial growth (total tree age); mean annual radial growth for 2018 and 2019 and the difference between mean annual radial growth (total tree age) and mean radial growth for 2018 and 2019.

Idplot	Mean annual radial growth (cm) (total age)	Mean annual radial growth (cm) 2018-2019	Differences between mean annual radial growth (cm)	Differences between mean annual radial growth percentage (%)
1	0.57	0.88	0.32	56
7	0.61	0.90	0.29	48
18	0.62	0.78	0.16	26
20	0.65	0.69	0.05	8
22	0.81	1.43	0.62	76
24	0.88	1.29	0.41	47
31	0.66	0.82	0.16	24
32	0.41	0.85	0.44	107
35	0.40	0.74	0.34	85
38	0.53	0.75	0.22	42

Table S-5-3: Climate conditions on the ten northern red oak study sites in Germany in the Federal States (FS): Lower Saxony (LS), North Rhine-Westfalia (NRW), Baden-Württemberg (BWB), Thuringia (THU) and Brandenburg (BRB): 1: Dassel, 9: Rotenburg an der Wümme, 30 and 33: Niederrhein Leucht, 42 and 44: Offenburg, 65 Neustadt an der Orla, 66: Wolfersdorf, 70 und 73: Potsdam. Mean temperature (Mean temp.), mean precipitation (Mean prec.) during the growing season and length of the growing season (Grow. season) (May – until and including September) calculated for the time span between 1988 and 2017 (1. period), 2018 and 2019 (2. period) and the difference between the 1. and 2. period for all three climate variables.

ID	FS	Period 1: 1988-2017			Period 2: 2018-2019			Difference between period 1 and period 2		
		Mean temp. (°C)	Mean prec. (mm)	Grow. season (days)	Mean temp (°C)	Mean prec. (mm)	Grow. season (days)	Mean temp. (°C)	Mean prec. (mm)	Grow. season (days)
1	NS	13.5	446	154	14.5	437	158	+1.0	-9	+4
7	LS	15.8	337	173	16.7	302	179	+0.9	-35	+6
18	NRW	16.8	352	181	17.8	252	192	+1.0	-100	+11
20	NRW	16.8	357	181	17.8	254	191	+1.0	-103	+10
22	BWB	17.9	395	185	18.9	350	192	+1.0	-45	+7
24	BWB	17.9	395	185	18.9	350	192	+1.0	-45	+7
31	THU	15.7	336	167	17.0	294	172	+1.3	-42	+5
32	THU	15.7	327	168	17.0	283	172	+1.3	-44	+4
35	BRB	17.0	288	174	18.1	267	180	+1.1	-21	+6
38	BRB	17.0	279	174	18.3	261	180	+1.3	-18	+6

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DECLARATION OF CONSENT

I hereby declare that I am the sole author of this dissertation entitled “Influence of competition and other factors on crown and stem characteristics of northern red oak”. All references and data sources that were used in the dissertation have been appropriately acknowledged. I furthermore declare that this work has not been submitted elsewhere in any form as part of another dissertation procedure.

Göttingen, 01.03.2022

Katharina Burkardt