



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_0 All) and for EST-derived markers (H_0 EST). Most other tree characteristics, including the number of 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

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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 (Dreßel and Jäger 2002; Podhorski 1956; 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 (Klemmt et al. 2013; Kurjatko et al. 2006; NMELV 2004) and can be admixed, e.g., in pure pine stands (Kurjatko et al. 2006; NMELV 2004). 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 (Dorji et al. 2019; Schütt et al. 2004; Stängle et al. 2014). The resulting three-dimensional point clouds allow an exact calculation of various tree characteristics such as crown size or crown dimension (Juchheim et al. 2017; Seidel et al. 2011) which are closely related to tree productivity and thus to timber production (Roloff 1991; Seidel et al. 2019). 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 (Burkardt et al. 2019; Höwler et al. 2017), can be computed. Finally, TLS-based approaches are also suitable to estimate competition intensity (Höwler et al. 2017; Metz et al. 2013). 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) (Agarwal et al. 2008; Varshney et al. 2005) 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:

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

Materials and methods

Study sites

We studied a total of 100 study trees in ten Northern 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 and 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.

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 284 mm (Brandenburg) to richer sites with nutrient rich loess and high precipitation rates of around 400 mm (Baden-Württemberg) (Table 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 $DBH \geq 7$ cm) and their respective distance to the target tree (within an

Table 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. ^a	Soil texture	MPG (mm) ^b	TMG (°C) ^c	Yield class ^c
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

^aGenetic Hap.: Haplotypes were assessed by Pettenkofer et al. (2019) in the same Northern red oak stands prior to our study

^bMPG: mean precipitation during the growing season (May–September)

^cTMG: mean temperature during the growing season (May–September) of the last 25 years provided by the Climate Data Centre (DWD Climate Data Center 1992–2018, 1992–2018); and yield-class: calculated based on the yield table for Northern red oak of Bauer (1953)

area of ca. 700 m² (r = 15 m) around each target tree) were included in the index calculation (Eq. 1).

$$\text{Hegyi-index} = \sum_{i=1}^n \frac{D_i}{D_j} \times \frac{1}{Dis_{ij}}, \quad (1)$$

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 surrounding 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 Cloud-Compare 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 (Figs. 1, 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 characteristics: 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 (Höwler et al. 2017; Seidel et al. 2011). PCGs

Fig. 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). O_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. **a** Tree with small branch angles (zenith) of first order branches; **b** tree with medium large branch angles (zenith) of first order branches, and **c** tree with large branch angles (zenith) of first order branches

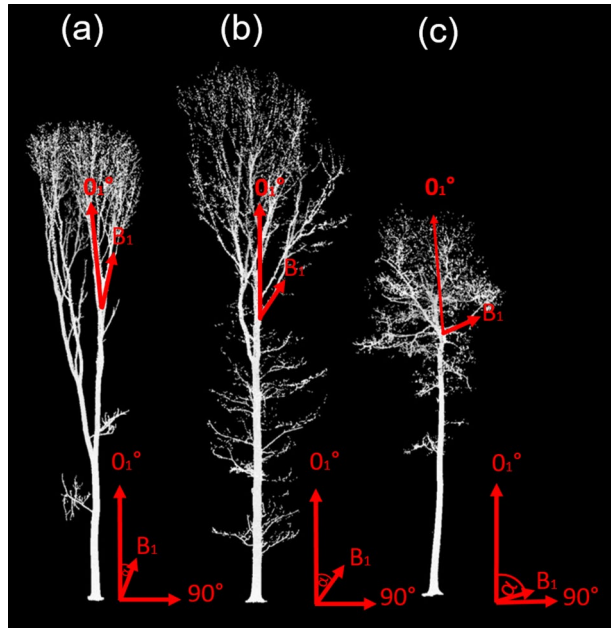
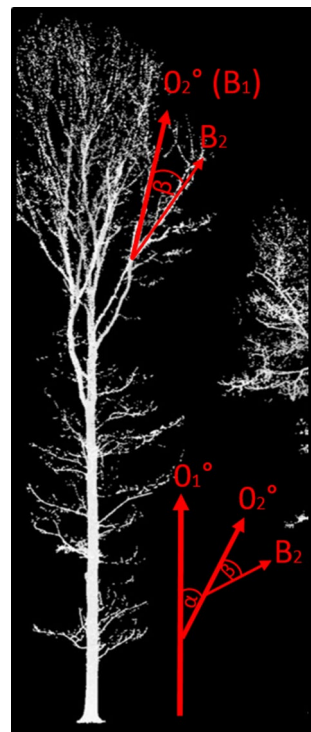


Fig. 2 Graphical visualisation of the mean branch angle zenith of second order branches based on the point cloud of the target trees derived from terrestrial laser scanning (TLS). From the sum of the second order branch angles per tree, mean value and median of the branch angles zenith were calculated. The branch angle range of second order branches was also computed, with O_2° (B_1) as reference point, B_2 as second order branch and β as the angle between the two variables O_2° (B_1) and B_2 second order



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. 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 (Burkardt et al. 2019; Höwler et al. 2017).

The following procedure was applied from the root collar to the level of the crown base to each 4 m 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” decomposition, which creates a circle to the points of each layer to factorize a matrix with “Q” as orthogonal and “R” as upper triangular matrix (Höwler et al. 2017; Seidel and Ammer 2014). 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 and 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_o All), for EST-derived markers (H_o EST) and for nSSRs (H_o Neutral). 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 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 (Hegy-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 function 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 (Table 2).

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

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

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 ($p < 0.01$) (Fig. 3), median branch angle zenith of

Table 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 groupwise 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. H _O Spec	Model	
					AIC	Adj.-R ²
BA _{mean} 1st	H _O EST	Idplot	− 65.33	− 22.53 (<i>p</i> < 0.01)	593.16	0.50
	H _O All	Idplot	71.81	− 28.27 (<i>p</i> = 0.01)	595.17	0.47
BA _{median} 1st	H _O EST	Idplot	62.87	− 26.42 (<i>p</i> < 0.01)	614.83	0.47
	H _O All	Idplot	68.69	− 30.31 (<i>p</i> = 0.02)	618.12	0.44
BA _{range} 1st	H _O EST	Idplot	179.82	− 26.78 (<i>p</i> < 0.001)	576.43	0.17
	H _O All	Idplot	186.55	− 30.69 (<i>p</i> < 0.01)	580.69	0.11
NB1st	H _O EST	Idplot	44.89	− 23.40 (<i>p</i> = 0.02)	641.25	0.29
BL _{sum} (ln)	H _O Neutral	Idplot	3.47	0.69 (<i>p</i> = 0.03)	75.32	0.18

first order branches (*p* < 0.01) and the number of first order branches (*p* = 0.02) significantly decreased with increasing heterozygosity H_OEST (Fig. 4). Mean branch angle zenith (*p* < 0.01), branch angle range (*p* < 0.01) (Fig. 3) and median branch angle zenith of first order branches also declined with increasing heterozygosity H_OAll (*p* < 0.01) (Table 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 2, Supplementary Table 4).

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 (Supplementary Table 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 (Supplementary Table 4).

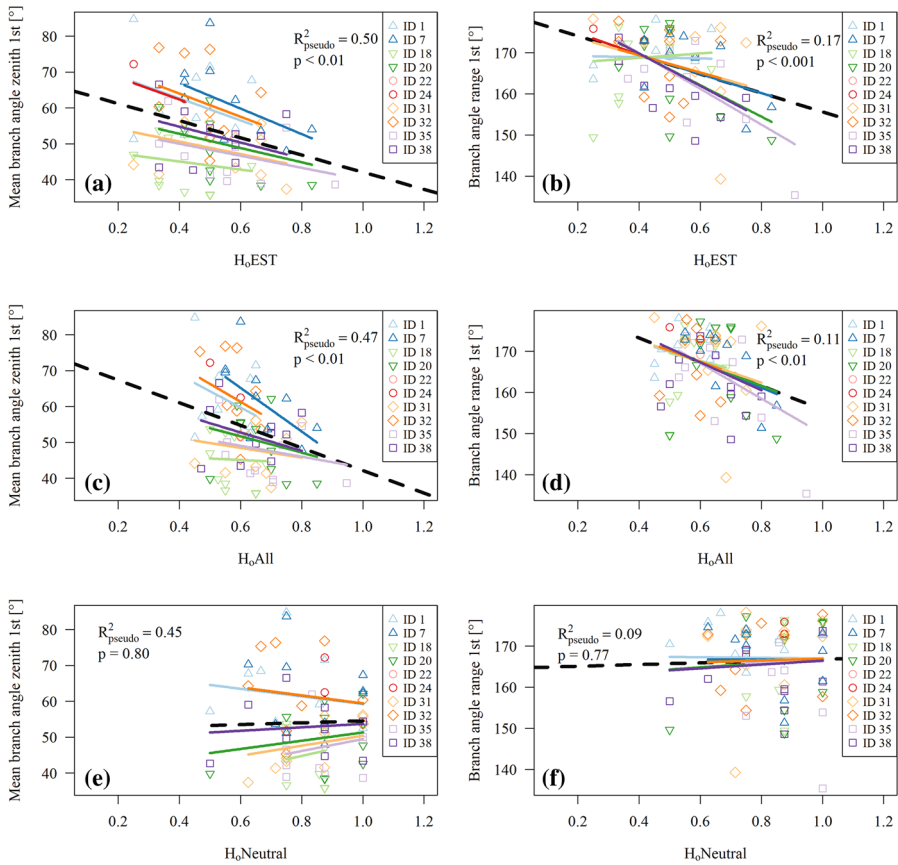


Fig. 3 Results of the linear mixed effect models: relationship between heterozygosity measured by EST-SSR markers “H₀EST” (a, b), heterozygosity measured by all markers “H₀All” (c, d) and heterozygosity measured by nSSR markers “H₀Neutral” (e, f) as independent variables, mean branch angle zenith 1st order (a, c, e) and branch angle range 1st order (b, d, f) 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

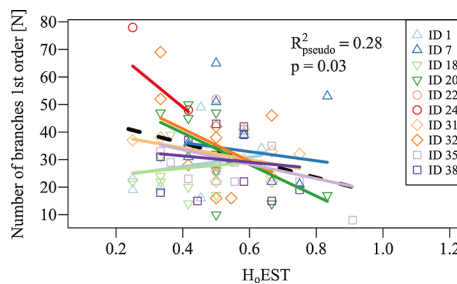


Fig. 4 Results of the linear mixed effect model: relationship between heterozygosity measured by EST-SSR markers “H₀EST” as independent variable and the number of first order branches as dependent variable on the ten study sites in Lower Saxony (ID 1: Dassel and ID 7: Rotenburg), North Rhine-Westphalia (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

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 (Supplementary Table 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 (Supplementary Table 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).

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).

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

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.

Table 3 Results of the Pearson correlation with branch angle range ($BA_{range1st}$), mean branch angle first order branches ($BA_{mean1st}$), median branch angle first order branches ($BA_{median1st}$) and mean branch length first order branches ($BL_{mean1st}$), maximum branch length first order branches (BL_{max1st}) and of branch length first order branches (BL_{sum1st}) and number of first order branches ($NB1st$)

	$BA_{range1st}$ <i>p</i> value	$BA_{mean1st}$	$BA_{median1st}$	$BA_{range1st}$ ρ value	$BA_{mean1st}$	$BA_{median1st}$
$BL_{mean1st}$	0.067	<i>0.000</i>	<i>0.000</i>	−0.204	−0.466	−0.436
BL_{max1st}	0.986	<i>0.001</i>	<i>0.001</i>	0.002	−0.347	−0.376
BL_{sum1st}	<i>0.000</i>	0.584	0.678	<i>0.424</i>	0.062	0.047
$NB1st$	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>	<i>0.480</i>	<i>0.496</i>	<i>0.475</i>

p values < 0.05 are shown in italics

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 (Grote and Pretzsch 2002; Kuuluvainen 1991), 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 intraspecific competition leads to a decrease in crown properties that are closely related to crown extension, crown size or crown dimensions (Bayer et al. 2013; Burkardt et al. 2019; Dieler and Pretzsch 2013; Dorji et al. 2019; Seidel et al. 2011; Thorpe et al. 2010). 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 (Burkardt et al. 2019; Höwler 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 eco-physiological factors, for instance light conditions in the crown, as well as on water and nutrients allocated to the branch (Gross and Pham-Nguyen 1987; Lanner 1976). 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.

Conclusions

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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Compliance with ethical standards

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

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