Environmental and Genetic Control of Functional Traits in a Provenance Trial of Oak (*Quercus robur*)

Master thesis

Student: Nevena Momirović

International Master in Horticultural Science
Supervisor: Univ. Prof. Mag. Dr. Peter Hietz
Institute of Botany
Department of Integrative Biology and Biodiversity Research
University of Natural Resources and Life Sciences, Vienna

Vienna, 2019

Acknowledgements

Firstly, I would like to thank to my Supervisor, Prof. Dr. Peter Hietz, for his support and guidance, and the will to always share his knowledge and expert advice. I would also like to thank my Co-supervisor, Prof. Dr. Francesco Spinelli from the University of Bologna, for his kind support.

I had help from my kind colleagues from the Institute of Botany which were a great team on the project. Special thanks go to so called “Oak people”: Dr. Kanin Rungwattana, Dr. Guillaume Theroux-Rancourt, Dr. Susanne Schefknecht and MSc. Natascha Luijken.

I’d also like to thank BFW, the Austrian Research Centre for Forests, which established the provenance trial and particularly Dr. Jan-Peter George, who helped with the collection of material and access to the sites and provided previously collected information and measurements.

Last, but not the least, I would like to thank my family for the support and motivation. They cherished my love for plants since early age, and always were my truest inspiration.

Abstract

Tree growth and other characteristics are shaped by their genes and the environment, and to understand their response to the environment is important for management and prediction of the response under future environments. This response is also shaped by their genes, resulting in a gene - environment interaction. In provenance trials, plants collected from various locations are planted in a common garden so that differences observed among provenances are largely due to genetics. When the same provenances are planted at sites with different environments, this permits to distinguish environmental from genetic effects as well as their interactions. Using the 11-year-old trial of ten pedunculate oak (*Quercus robur*) provenances from Central Europe planted in three locations in Austria, we investigated the intra-specific variation of wood and leaf traits as well as tree growth. Wood anatomical traits (vessel area, the fraction of the cross-section occupied by vessels and the theoretical hydraulic conductivity) were predominantly under genetic control while wood density and wood water content depended mainly on the site (environment). In leaves, measures of leaf shape (leaf area and length-to-width ratio) were largely under genetic control whereas measures related to leaf anatomy (specific leaf area - SLA and leaf dry matter content - LDMC) differed by site. Height and diameter growth were affected by both, but stronger by the environment. Significant site – provenance interactions were found only in wood density and height growth. There were correlations among wood traits and among leaf traits but none between wood and leaf traits, and tree growth was related to wood density, leaf shape, SLA and LDMC. Interestingly, the annual rainfall of the provenance locations was only weakly related to the xylem vessel area and LDMC, but the mean temperature of the place of origin was significantly related to the vessel fraction, leaf shape and SLA. These results deepen our understanding of the genetic and ontogenetic adaptations to different environments and help to select trees for breeding and planting under various present and future climates.

Zusammenfassung

Wachstum und andere Eigenschaften von Bäumen werden von Genen und Umwelt bestimmt. Für ein Waldmanagement, besonders auch unter dem Klimawandel, ist auch wichtig zu verstehen, wie die Reaktion auf die Umwelt genetisch kontrolliert wird. In Provenienzversuchen werden Pflanzen unterschiedlicher Herkünfte unter gleichen Umweltbedingungen gepflanzt, womit Unterschiede großteils genetisch bedingt sind. Wenn in einem Versuch die gleichen Provenienzen an verschiedenen Standorten gepflanzt werden, können genetische von Umwelteffekten unterschieden und deren Interaktion gezeigt werden. Im Rahmen dieser Arbeit wurde von einem zehnjährigen Versuch mit zehn Stieleichen (*Quercus robur*)-Provenienzen aus Mitteleuropa, die an drei Standorten in Österreich gepflanzt wurden, Holz- und Blattmerkmale sowie Baumwachstum untersucht. Holzanatomische Eigenschaften (Tracheengröße, Anteil der Tracheen am Querschnitt und theoretische hydraulische Leitfähigkeit) werden überwiegend genetisch kontrolliert, aber Holzdichte und –wassergehalt v.a. von der Umwelt. Bei Blättern ist die Blattform (Größe und das Längen/Breiten Verhältnis) großteils von der Provenienz und Eigenschaften, die mit der Blattanatomie zusammenhängen (spezifische Blattfläche – SLA und Trockengewicht/Sättigungsgewicht – LDMC), von der Umwelt (Standort) kontrolliert. Wachstum wird auch von der Provenienz, aber stärker vom Standort bestimmt. Herkunft – Standort Interaktionen fanden sich nur für Holzdichte und Höhenwachstum. Während verschiedene signifikante Korrelationen innerhalb der Holz- und innerhalb der Blattmerkmale gefunden wurden, ergab sich kein Zusammenhang zwischen Holz- und Blattmerkmalen. Das Wachstum war mit der Holzdichte, der Blattform, SLA und LDMC korreliert. Interessanterweise stand der Jahresniederschlag am Herkunftsort nur in einem schwachen Zusammenhang mit der Tracheengröße und dem LDMC, wohingegen die Jahresmitteltemperatur signifikant mit der Gefäßfraktion, der Blattform und dem SLA korreliert. Diese Ergebnisse vertiefen unser Verständnis der genetischen und ontogenetischen Anpassungen an verschiedene Umgebungen und können helfen, Bäume für verschiedene gegenwärtige und zukünfti.

Table of Contents

Abbreviations

Table 1. List of functional traits investigated within the oak provenance trial

Abbreviation	Trait	Unit
VD	Vessel density	mm^{-2}
VA	Vessel area	µm^{2}
PV	Proportion of size occupied by vessels	%
K_h	Theoretical hydraulic conductivity	kg m s^{-1} MPa^{-1} x 10^{5}
WC	Water content	g/cm^{3}
WD	Wood density	g/cm^{3}
AR	Aspect ratio	/
LA	Leaf area	mm^{2}
SLA	Specific leaf area	mm^{2}/g
LDMC	Leaf dry matter content	mg/g
DBH	Tree diameter	Cm
Height	Tree height	Cm

Table 2. List of oak provenances studied in the trial

Provenance	Abbreviation
Geinberg (AT)	Ge (AT)
Linz (AT)	Li (AT)
Braunsberger Wald (AT)	BW (AT)
Rainfeld (AT)	Ra (AT)
Luising (AT)	Lu (AT)
Klagenfurt (AT)	Kla (AT)
Hluboka (CZ)	Hlu (CZ)
Kutina (HR)	Ku (HR)
Murska Suma (SLO)	MS (SLO)
Velika Gorica (HR)	VG (HR)

1. INTRODUCTION

1.1 Botanical background (Quercus L.)

1.1.1 Distribution and classification

Genus *Quercus* represents woody angiosperms that belong to the beech family *Fagaceae*, subfamily *Quercoideadeae*, and comprises of more than 400 tree and shrub species, distributed among contrasting climates, from temperate and subtropical forests, to Mediterranean evergreen woodlands (Manos et al. 1999; Kremer et al. 2012). Most of *Quercus* species are widely distributed throughout the Northern Hemisphere (Nixon 1993), contributing largely to deciduous forest ecosystems of this area. According to Gil-Pelegrín et al. (2017), *Quercus* L. is in fact, regarded as the most diverse Northern Temperate tree genus. Oak trees populate a great range of habitats, such as well-drained upland or montane areas, where they might be the dominant trees, as in temperate seasonally dry forests (Aldrich & Cavender-Bares, 2011). The ample geographical range extent of *Quercus* distribution suggests its high taxonomic complexity and substantial genetic diversity.

Figure 1. Modern distribution of genus *Quercus* (Barrón et al. 2017), adopted and modified from Camus (1936-1938) and Manos et al. (1999)

The general classification of oak species is based on morphological features, such as foliar and fruit characteristics (Nixon, 1993), as well as pollen morphology (Gil-Pelegrín et al. 2017). Nixon's classification (1993), which was adopted and modified from Camus (1936-1938), recognizes two subgenera within the *Quercus* genus: *Cyclobalanopsis* and *Quercus*, according to more explicit morphological cladistics analysis.

Cyclobalanopsis genera include the cycle-cup oaks and show more of tropical-subtropical distribution, dating from the Cenozoic (Gil-Pelegrín et al. 2017). They are situated mostly in Southeast-Asian region and its fruit morphology is different (Manos et al. 1999), characterized by apical position of aborted ovules.

The second mentioned subgenus *Quercus* represent all the remaining oaks and recognizes three sections within: *Lobatae* (red oaks, group indigenous to North and South America), *Protobalanus* (golden-cup or intermediate oaks from western North America) and *Quercus* (white or scale-cup oaks, typical for Eastern and Western Hemispheres) (Nixon 1993; and Manos et al. 1999). Nixon (1993) stated that, while division into *Lobatae* and *Protobalanus* sections was natural, the section *Quercus* was artificial and heterogeneous. He modified this by merging *Cerris* section – the black oaks (comprising *Cerris* and *Ilex* oaks) with *Euquercus* (with remaining *Illex* and white oaks), on the basis of basal position of aborted ovules in these oak groups.

However, traditional concept has been recently informally replaced by an updated infrageneric classification (*Figure 2*), based on morphological traits as well as on geographic regions of origin (Denk et al. 2017). New classification comprises two subgenera and eight sections, with two new distinct phylogenetic lineages: sections *Virentes* and *Ponticae*.

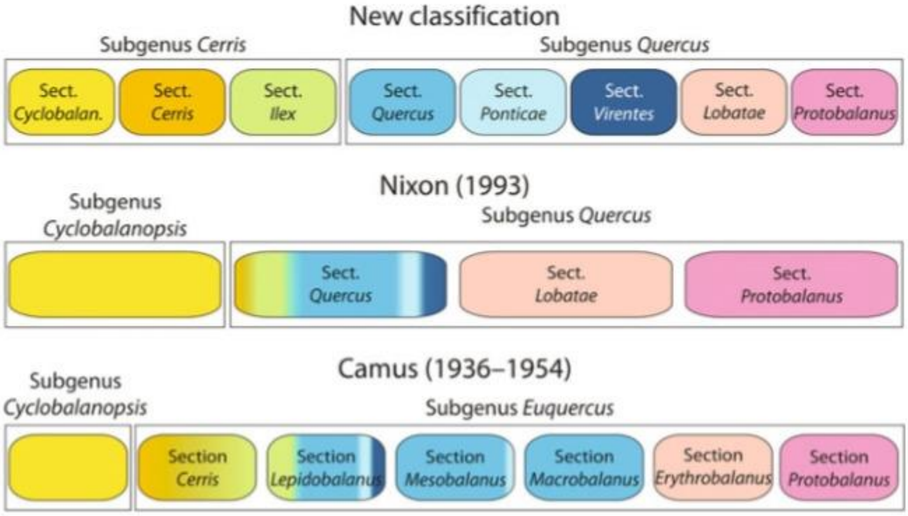

Figure 2. Recent modifications of *Quercus* taxonomic schemes, with new infrageneric classification above (Denk et al. 2017)

1.1.1.1 Quercus robur

The oak species of our interest - *Q. robur*, belongs to the white oaks of North and Central America and Eurasia, along with *Q. alba* and *Q. virginiana*. Their distribution on Northern hemisphere is represented as section *Quercus s.s*. in *Figure 3*. *Q. robur* is also known as European, French or English, pedunculate oak and it is, along with *Q. petraea*, studied to the largest extent of all the oaks. The fact that almost half (46.5%) of the world's oak cultivars or groups are from either *Q. robur* or *Q. petraea,* emphasizes the significance of these species and longer breeding tradition they have in Europe (Aldrich & Cavender-Bares, 2011).

Despite the fact that oak trees are generally one of the most recognizable trees at genus level, they are quite hard to distinguish at species level. The ability of *Quercus* species to form hybrids in nature (Burger 1975, Van Valen 1976) truly contributes to the difficulty of distinguishing clearly between them. This is common for European oaks as well, whereas *Q. robur* and *Q. petraea* seem to overlap in species phenotypes. Muir & Schlotterer (2005) suggest that they share ancestral polymorphism, which is why they genetically overlap.

However, according to Petit et al. (2004), it seems that *Q. robur* was a pioneer species with higher seed dispersal capacity than *Q. petraea,* which appeared later.

In comparison to *Quercus petraea, Q. robur* prefer more wet and rich soils, which tend to be more alkaline (Saintagne et al. 2004). It also prefers more humid habitats and may tolerate periodic flooding. This suggests higher water requirements needed by *Q. robur* in comparison to *Q. petraea,* which is reflected in lower water use efficiency (Ponton et al. 2002) and its higher sensitivity to soil water deficit (Vivin et al. 1993).

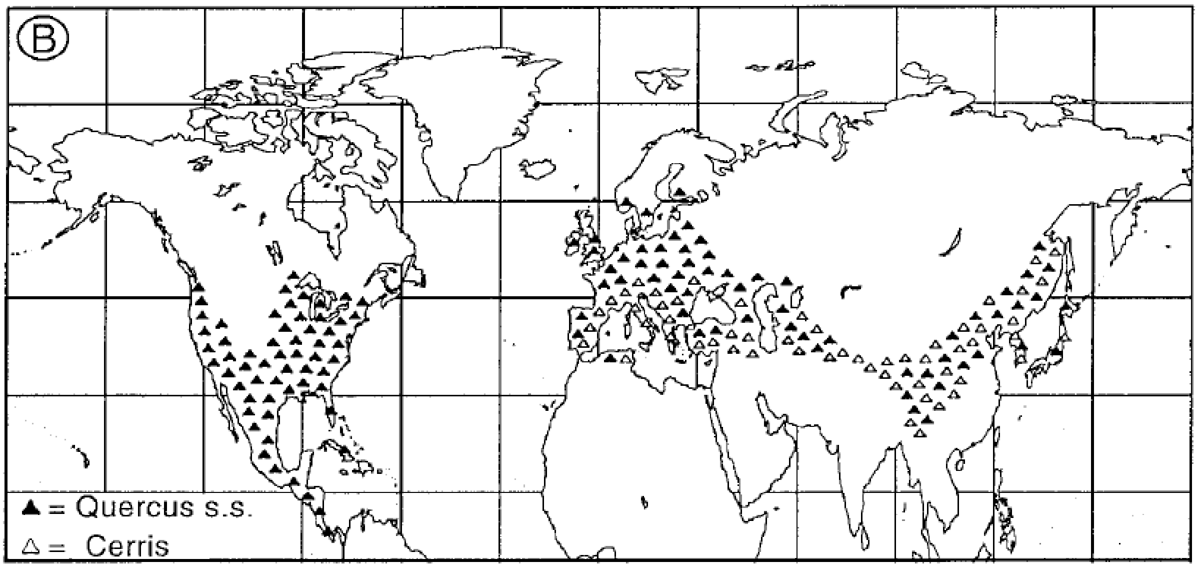

Figure 3. Distribution of subgenus *Quercus* (here indicated as Quercus s.s.), including *Q. robur*, in the Northern Hemisphere, modified from Camus (1936-54) and Nixon (1985)

1.1.2 Historical background

The genus *Quercus* has always been significantly related with humans from the cultural, symbolical and mythological aspect, continually reported throughout history since ancient times. Gil-Pelegrín et al. (2017) emphasizes this relation when saying that oak trees have always been closely related to mankind. The first records of *Quercus* date from the late Palaeocene, ca. 66 million years ago (Barrón et al. 2017). There are some evidences in archaeological sites suggesting that *Homo sapiens* used oak acorns even then as once “edible species”. This was the case found in Acheulean archealogical site of Gesher Benot Ya’aqov in Israel, from Middle Pleistocene 780,000 years ago (Goren-Inbar et al, 2000). According to Goren-Inbar, acorns from oak were used as food for the humans that inhabited this area, in particular referring to *Q. caliprinos* and *Q. ithaburiensis*. In addition to this theory, archaeologists documented the acorn consumption by humans since that period (Chassé 2016) and it was later reported until 18th century and even after, during great famine periods (García-Gómez et al. 2002).

Oaks represented indigenous dietary resource also for the natives of south-eastern USA (Fagan, 2004), among many other benefits they provided. Local cultures cherished strong relation with the oak populations, referring to them as “bread or tree of life” (Anderson, 2007).

Nowadays, oak woodlands provide many benefits for the inhabitants of “Middle Hills” of Central Himalaya, taking into account firewood, forage for the cattle, and compost from the leaves etc. (Shrestra et al. 2013, Singh and Singh 1986). Moreover, banj oak (*Q. leucotriphora)* was known as “people’s species” for its great significance to the people of this region (Singh and Singh, 1986).

Also oak wood has been used for a millennia (De’Athe et al. 2013; Out 2017; Ruiz-Alfonso et al. 2017), firstly as firewood and later, as key material for naval construction in the past (Giachi et al. 2017). Reboredo & Pais (2014) report oak timber as main raw material in the 15th and 16th century, used by the Portuguese fleets.

1.1.3 Range of significance

The genus *Quercus* includes some of the most widespread and economically important wood species. Partly, its economic significance derives from great strength and hardness, elasticity and durability of wood, as well as resistance to pests due to its richness in tannin content. These characteristics are valued for oak’s commercial use, such as prized construction wood (e.g. ships in the past), hardwood timber, furniture making and flooring, barrels for aging of alcoholic beverages (Schonbeck & Frey 2005), among variety of other uses. Red oaks are more economically appreciated in the American market, while white oaks are traded all over the world (Aldrich & Cavender-Bares, 2011).

Oak barrels have a long tradition in winemaking, since they are part of the crucial practice of aging and ensuring high quality of wine. There is a general distinguish between oak used for wine barrels, with respect to its American (*Q. alba*) or European (*Q.robur* and *Q.petraea)* origin. Each of them is appreciated for their particular contribution to the wine colour, taste and aroma, giving different characteristics to the final product (Chira & Teissedre, 2015). According to Schonbeck & Frey (2005), oak barrels contribute to the antioxidative activity of the wine as well. Wine cork provides long storage and durability of wine, and it is made of oak bark (*Q. suber*), thus emphasizing the importance of *Quercus* in the winemaking process. Yeast (*Saccharomyces cerevisiae*) is used for flavouring during fermentation and aging. Since oak bark contains notable amount of tannin, oak tree can be additionally used for tanning leather.

Oaks have mycorrhizal symbioses with fungi, among which truffles (genus *Tuber*) are the most economic important ones. *Q. ilex* is the most common host, crucial for the truffle production (Gil-Pelegrín, 2017). In addition, it is worth mentioning that oak trees are hosts for the gall wasps as well. Acorns serve as food source to the wildlife such as deers or boars, as well as squirrels that also serve seed dispersion. Oak leaves also sustain diverse herbivores, whereas silk moths *Antheraea yamamai* have been of economic use (Oishi et al. 2005).

1.1.4 Morphology and ecology

In general, oaks can be trees of up to 20-30 (or 55) m height, or in the form of shrubs. They can be evergreen or deciduous (Britton & Brown, 1913). *Quercus* species covering more southern areas tend to be evergreen, while more northern ones are winter-deciduous and lose their leaves in autumn, or change colour into bright gold (Schonbeck & Frey, 2005). These two leaf habits represent a direct consequence of different paleogeographical origins (Gil-Pelegrín et al. 2017). Fossil data testify that the ancestors of oaks were evergreen and then subsequently evolved into deciduous form (Manos & Stanford, 2001).

According to Britton & Brown (1913), oak bark is described as smooth or deeply furrowed, and particularly corky in some species. Terminal buds are spherical to ovoid, terete or angled. Oak wood is ring-porous or (semi) diffuse-porous.

Oak leaves have spiral arrangement and their lamina is mostly lobed, but can be unlobed as well. The leaf is margin entire, dentate or dentate with bristle-like extensions (Britton & Brown, 1913). Oak leaves are well known for their variation, across seasons and even within the same canopy (Blue & Jensen 1988; Bruschi et al. 2003).

Oak trees are monoecious, with the same tree carrying both male and female flowers, which are produced in spring. Male flowers are organized in catkins, while female ones are in spikes. Wind is predominant mean of pollination (Aldrich & Cavender-Bares, 2011) but oaks remain out-crossers, through established mechanisms of protandry or self-incompatibility.

The fruit of oak is called acorn and represents one-seeded nut. It lies in a cupule, a cup-shaped structure. Acorns usually contain one single or sometimes two seeds and are formed in the first (all North-American white oaks – section *Quercus*) or in second year (most North American red oaks – section *Lobatae*), usually in September - October. Acorns are nowadays often used in organic agriculture, for animal feed, due to their nutritional value and richness in starch, sugar, protein, lipid, resin and tannin content. Seeds are large and easily dispersed by animals, where squirrels in particular have an important role in acorn dispersal and hoarding (Aldrich & Cavender-Bares, 2011). Grey squirrels have the ability to distinguish between the dormant red and germinating white oak acorns, and tend to keep the red ones and feed on the white ones. The squirrel preferences, which probably occur because of acorn fat and tannin content, are suggested to be associated with more quick dispersion of red oaks compared to the white ones (Steele & Koprowski 2001). This might also be the reason why red oaks are less genetically differentiated than the white ones (see section 1.1.1).

The lifespan of oak trees may reach hundreds of years (Burns & Honkala 1990), and they also take relatively long to reach maturity, and it takes a long time to observe traits of interest in mature trees (Aldrich & Cavender-Bares J, 2011). This does not favour the process of oak evolution and domestication, nor is convenient for the breeders either, as 10 up to 15 years are required for evaluating a single crossbreed (Aldrich & Cavender-Bares, 2011). Therefore, many traditional breeding programs have been discontinued, and additional research is focused on new methods and technologies, such as quantitative genetics. Application of molecular genetic markers and QTL mapping for the traits of interest is rapidly improving oak selection (Aldrich & Cavender-Bares, 2011).

1.1.5 Physiology and phenology

Among deciduous tree species, oaks are generally considered as drought adapted (Abrams 1990). Several xeromorphic adaptations in leaf and wood structure, enabling them to withstand longer dry periods, classify oaks as very flexible towards drought (Vitasse et al. 2009).

Oaks are able to grow on sites with contrasting environmental conditions (Zimmerman et al. 2006). In comparison to some drought-sensitive species (e.g. *Fagus sylvatica*, *Picea abies* and *Abies alba*), oaks have lower risks of habitat loss due to climate change and might even benefit from it, by becoming very competitive with other tree species in the future. This is supported by the fact that oaks might survive at sites prone to drought and flood, which depends considerably on the oak species and the provenances.

Oaks have one of the deepest roots among tree species of North America (Kozlowski 1971, Spurr and Barnes 1980, Gale and Grigal 1987). In a recent study by Mauer, Houšková and Mikita (2017), root system of young *Q. robur* trees at the margins of regenerated stands, was reported to achieve 10.9 m depth. Their deep-penetrating roots help to maintain a high pre-dawn water potential, which is a primary adaptation to avoid desiccation during drought periods. In addition, oaks are able to rapidly resume assimilation after periods of limited water supply (Kuster et al. 2013).

Abrams and Kubiske (1990) have studied morphological leaf traits and reported that, in comparison with 21 other hardwood trees, several oak species had greater stomatal density and leaf thickness, as well as smaller guard cells. A higher number of smaller stomata is related to the better transpiration control, and also indicates a drought adaptation and high water-use efficiency of oak leaves. In addition, the overall leaf-size reduction has often been reported in Mediterranean oaks, as one of the key traits to withstand the water deficit (Peguero-Pina et al, 2014). Brodribb & Feild (2000) suggest that high hydraulic efficiency (or low hydraulic resistance) is related with high stomatal conductance and thus, indirectly with the photosynthetic capacity of a plant.

The xylem anatomy of temperate oaks is ring-porous with large early wood vessels (Zimmerman & Brown, 1977) which hydraulically supports the spring flush of leaves, by the fast sapflow rates at low hydraulic resistance. However, early-wood vessels are also more susceptible to cavitation (Tyree & Dixon, 1986), which occurs when an air bubble blocks the vessels or tracheids. For the rest of the season, or in dry periods, sustainable water flow is ensured through the latewood vessels, which are much narrower, hence more resistant to drought-induced embolisms (Aldrich & Cavender-Bares, 2011). According to Cochard & Tyree (1990), vessels are known to be very long in deciduous oaks.

It should be taken into account that all previously mentioned characteristics refer to the temperate oaks, while the subtropical and tropical species are diffuse porous without a change in vessel size throughout the seasons (Cavender-Bares & Holbrook 2001).

Oaks are good competitors on xeric sites where canopies are open. By contrast, oaks are not shade tolerant, and hence are very poor competitors on mesic sites with closed canopies.

Some phenological patterns of oaks, modified by drought and warming, are mentioned in the study reported by Kuster et al. (2014). Photoperiod and temperature are key environmental factors that control the phenology of oaks. The growing season usually begins in April, which certainly differs among the regions, although combination of high temperatures and air warming may trigger an even earlier bud burst. Nevertheless, advanced phenological development is in direct contrast with the ability of *Quercus* to flush several times during the growing season, since early onset effects the discontinuation of an earlier intra-annual shoot growth. However, the duration of shoot growth might be under strong ontogenetic control, not only controlled by environmental factors. In their study, Kuster et al. (2014) report that leaf unfolding and senescence in *Q. robur* and *Q. petraea* seedlings had not been influenced by drought, although reduced water availability affected the intra-annual shoot growth by reducing the number of flushes. Moreover, drought delayed an onset of a second flush later in the growing season, when water availability actually becomes more limited than in spring (Morin et al. 2010). Kuster et al. (2014) observed both *Q. petraea* and *Q. robur* in their study, where the latter species had more flushes in the growing season and had longer growth period.

Recent study about drought impact on leaf phenology and spring frost susceptibility in *Q. robur* (Čehulić et al. 2019) provides another perspective regarding the phenology altered by drought. In their provenance trial, oak seedlings were influenced by drought in terms of flushing phenology, which was either delayed or advanced, regarding on the time span when plants suffered from water deficit. Interestingly, this phenomenon was previously described in beech (Yonekura et al. 2004), that is, a “carry-over” effect plants reflect after being under water stress. The study showed a delay in oak bud burst in the subsequent year, in case they suffered drought at the beginning of the vegetation period (i.e. early spring), while in case of drought treatment applied more towards season peak (i.e. middle of the summer), then advanced flushing would happen in the subsequent year. Additionally, plants in the trial exhibited a delay in senescence, a commonly known physiological response to drought (Mijnsbrugge et al. 2016). The discrepancy in bud burst affected by water stress was reported in few other studies. Kuster et al. (2014) reports an advanced oak bud burst induced by drought, while Mijnsbrugge et al. (2016) reports oppositely - a delayed bud burst in oak imposed by drought in the previous years. This phenomenon in flushing phenology can be explained as epigenetic response or modification induced by environmental stresses. However, it remains unclear why these phenological shifts happen in opposite directions.

1.2 Provenance trials

In general, provenance refers to the origin of population of species that come from a certain location. “Provenance” represents an original, native, geographic source of species and may come from pollen, seed or propagules (Schmidt 1997). Consequently, provenance trials, or forestry common garden experiments, represent a special type of plantation experiment, which enables us to understand how trees with different origin are adapted to different environmental conditions, through genetic adaptation and phenotypic plasticity.

In order to establish such a trial, seeds are collected first from different locations of interest and thereafter planted together in a systematic experimental design, on either one or multiple sites. Intra- and inter- specific competitiveness are not taken into account, since seedlings are spatially organized in this type of trials.

Multiple site provenance trials might be used for studying plastic responses (e.g. phenology of trees) of populations in new environments (Kramer 1995; Shutyaev & Giertych, 1997; Vitasse et al. 2010), with respect to sites differing in environmental conditions such as temperature or water availability. In addition, provenance trials may help to evaluate the pre-existing adaptations in the gene pool (Aldrich & Cavender-Bares, 2011). In other words, provenance trial conducted on one site might identify the genetic effects, whereas planting the same genotypes on different sites might distinguish the genetic x environmental effects.

Data from provenance trial experiments are analysed to gain a better understanding of how species adapt to certain environmental conditions in general. Trait variation in a provenance trial might imply evolutionary adaptations that are inherited and reflect the climate conditions effect (Alberto et al. 2013).

Anatomical and physiological differences among the individuals in the trial show how they might have genetically adapted to different climates. Thus, provenance trial experiments may help us reveal the genetic background and differences among planted species or genotypes, as well as allow to select for plants of superior qualities. In this way, plants might be selected for specific purposes (e.g. wood production) or specific locations (e.g. plants adapted to local climate). Nevertheless, provenance trials may also serve for studying the ways plants adapt throughout space and time.

Provenance trials often represent the first step in domestication of tree species in a given environment. Some believe (Mátyás, 1996) that provenance studies might become key solution in assisting oaks in their adaptation to ever-changing climate. The possibility of using data from provenance trials on phenotypic plasticity and local adaptation for models predicting the future distribution might be of great significance to reduce extinction risk in southern populations (Morin & Thuiller, 2009).

1.3 Phenotypic plasticity and adaptive response

Along with environmental changes throughout the history, plants are constantly adapting through evolution and through phenotypic plasticity. Trees are generally ideal for studying the adaptive evolution of species, as they are geographically widely distributed through different areas, landscapes and climate conditions (Eckert & Dyer, 2012). Phenotypic plasticity is described as "the capacity of given genotype to express different phenotypes under different environmental conditions" (Pigliucci, 2001). Phenotypic plasticity is an adaptive response towards varying environmental conditions (Abrams 1994), and thus also a primary mechanism by which plants respond to climate change (Matesanz et al. 2010). However, phenotypic plasticity is not only an environmental phenomenon; it derives from a complex interaction of both genotype and environment (Pigliucci, 2001). Moreover, Pigliucci suggests that it is not an instant reaction, but a result of the longer ontogenetic development of an organism. Phenotypic plasticity can have a short-term or long-term response, where the latter one contributes to the maintenance of genetic variation (Matesanz et al. 2010). The establishment and persistence of plant populations in new environments or in range shifts strongly depends on their plasticity and adaptive response.

In a situation where there is no genetic variation present, any phenotypic change reported in a new environment might be considered as consequence of phenotypic plasticity (Alberto et al. 2013). Plasticity is adaptive only when plants achieve greater fitness in new environments or maintain their fitness in a stressful environment. In other words, plasticity needs to have an impact on plant fitness advantage, in order to be adaptive, as well as to improve plant survival and reproduction (Matesanz et al. 2010). The plasticity of life-history traits or traits relevant for morphology, physiology and reproduction will be crucial for adaptation to climate change in the future (Alberto et al. 2013). Phenological shifts, delaying or advancing the bud burst in response to the new conditions, are one of the most reported forms of phenotypic plasticity. The plastic responses towards environmental factors such as drought, temperature, light, or CO_2 might be morphological and physiological; and include changes on leaf level (e.g. increase in stomatal conductance or water-use-efficiency), as well as whole-plant responses (e.g. growth patterns, biomass allocation).

Consequently, phenotypic plasticity is an important mechanism to fight global change and may help in maintaining population fitness despite the on-going changes (Matesanz et al. 2010). This concept is supported by the fact that oak traits related to climate specialization (e.g. growth rates, vulnerability to drought) evolved during time, while no changes were recorded in terms of fruit and flower morphology evolution (Manos et al. 1999).

The ability to adaptively alter morphological and physiological functional traits to environmental variations without genomic alterations (Niklas 1997, Agrawal 2001), is very well described in *Quercus*, both physiologically and morphologically (Bostad et al. 2003, Quero et al. 2006). Trees in general have high adaptive response to environment, which they owe to their large populations and high genetic variability, with the potential for natural selection and the evolution of better adapted genotypes (Alberto et al. 2013). In addition, tree populations have high dispersal capacities which increase their adaptive potential. Adaptive response to drought would be i.e. the increase in water use efficiency (WUE) in provenances from an arid place of origin, grown under the same climatic conditions.

Phenotypic plasticity is moreover a trait itself and is subject to natural selection as well (Pigliucci & Byrd, 1998) and can evolve as a response to environmental variation. More plasticity might also mean less intense selection, which suggests that populations are evolving more slowly. However, decreased selection might be compensated by increased phenotypic plasticity, in order to respond to the changing climate. Besides, if over a longer period of time, selection favors a phenotype that is most successful e.g. in terms of drought tolerance in arid conditions, other phenotypes might be entirely removed and thus, genetic variation from the population is lost (Matesanz et al. 2010).

1.4 Functional traits

According to Escudero & Valladares (2016), the functional trait approach provides a direct functional explanation for understanding the patterns of species distribution and variation. Functional traits represent a distinguishing quality or characteristic of an organism. It is a genetically determined morphological, physiological, phenological or biochemical characteristic, which is expressed in the phenotype and is important for an organism's response to the environment (Violle et al. 2007).

However, single traits might be misleading indicators of species distribution. The advanced approach of looking at the set of traits, instead of exploring them individually, might ensure a better general overview, as well decrease the risk of bias (Rungwattana et al. 2018). Sometimes many traits are under the complex polygenic genetic architecture (e.g. cold tolerance, growth, and phenology) which makes it hard to detect the causal genetic variation (Ma et al. 2010).

Villar et al (2006) show that *Quercus* has been an interesting study case for researchers, especially in terms of analysis of traits which are involved in growth processes. This might be due to the high variability of functional traits found in *Quercus* genus. It is one of the first species used for research studies for topics on tree functioning, such as water-conduction pathway of trees and xylem conductivity (Cochard & Tyree 1990; Lo Gullo & Salleo 1993).

1.4.1 Wood functional traits

Among the others, commonly measured and easily comparable wood traits are: vessel density, vessel area, vessel fraction, theoretical hydraulic conductivity, wood density and wood water content. Vessel elements and tracheids, known as "conduits", take part in transporting the water from roots to leaves.

Vessel density

Vessel density takes into account the amount of vessels found in the sample (mm^{-2}). Lower density might imply larger vessels or vice versa. Higher density might indicate smaller vessel diameter, more capable of handling cavitation which occurs at higher xylem tensions (lower water potential). Hence, smaller vessel diameters are characteristic of xeric plants of drier regions, while wet adapted plants have large vessel diameters which makes them more susceptible to water column disruption, reducing the xylem hydraulic conductivity.

Vessel area

The trait represents the measured vessel area within a sample (µm^2). Larger cells conduct water more quickly than the smaller ones, that is, hydraulic conductivity increases by the power of four, with increasing the lumen diameter (according to Hagen-Poiseuille law).

Vessel fraction

It represents the fraction of size occupied by the vessels (mm^2).

Hydraulic conductivity

Hydraulic conductivity represents a trait correlated with drought resistance. Theoretical K_h is a good proxy for measuring conductivity directly, using the vessel size and the Hagen-Poiseuille law. The water transport efficiency within a plant is directly related to the hydraulic conductivity of the xylem, which is defined by the conduit size (Martínez-Cabrera & Estrada-Ruiz E, 2014). The higher the conductivity, the less is cavitation resistance and higher the water availability. Thus, in environments with high water availability, hydraulic capacity is also increased by decreasing the water flow resistance in the xylem. By contrast, plants from arid habitats tend to have smaller vessel diameters, which may increase their cavitation resistance. If cavitation occurs, the water column breaks which reduces the xylem hydraulic conductivity and the overall plant water trasport (Martínez-Cabrera & Estrada-Ruiz E, 2014). The significance of this particular trait was explained by Brodribb and Feild (2000): high hydraulic efficiency (or low hydraulic resistance) is related with high stomatal conductance and thus, indirectly with the photosynthetic capacity of a plant. The conduit diameter has a strong influence on hydraulic conductivity since, according to the Hagen-Poiseuille law, the conductance of capillaries scales to the fourth power of the diameter (Giordano et al. 1978).

Mediteranean *Quercus* species of different drought tolerance have also been reported to differ in whole-plant hydraulic architecture (Meinzer et al. 2001) and the highest K_h was recorded in species adapted to more mesic environments.

The plant productivity is closely coupled with hydraulic efficiency, where high productivity can be reached only at the cost of hydraulic safety, that is, decrease of embolism resistance and cavitation occurence (Cochard et al. 2017). However, it is still unclear how these trade-offs are handled among different provenances of the same tree species and relationship between emolism resustance and growth rate remains undetected (Hajek et al. 2016).

Wood density

Wood density potentially has many functional roles, out of which mechanical support represents the first one. WD provides mechanical support to the tree, with denser wood being stiffer and less prone to breakage (Chave et al. 2009). Oak wood (*Quercus* L.) is generally dense (range ca. 0.5 – 0.9 g/cm^3), which allows for its high-quality uses. Cell walls contribute to positive wood density, parenchyma to low density, while vessel lumens account for zero density (Ziemińska et al. 2013). Additionally, denser woods are more resistant to pathogen attacks (Romero & Bolker 2008).

This trait is also associated with plant hydraulic strategies. Bucci et al. (2004) suggest that denser wood allow to operate at a more negative water potential and to have a higher cavitation resistance than the low-dense wood.

It is suggested that wood density is correlated to cavitation resistance, thus indicating the trait to be indirectly related with drought stress (Nardini, Battistuzzo & Savi, 2013). This trait is also correlated with the life-history strategies, where species with denser wood have lower mortality and higher growth rates (Poorter et al. 2010). Further, higher WD indicates biomechanical and hydraulic safety, while low density implies faster growth (Hacke et al. 2001).

Wood density is calculated as the oven-dry mass of wood divided by its green volume (g/cm3). It is measured easily and commonly used as a start point for species comparison (Poorter et al. 2010). Analogously to SLA for leaves, WD is related to many morphological and physiological stem traits (Poorter et al. 2010).

Water content

It is the amount of water found in a given piece of wood. Water content can be expressed as the percentage of the weight of the water compared to its oven-dry weight, or as (fresh weight – dry weight) / volume. The trait indicates the amount of water for storage and due to the wood physical constraint, there is a general trade-off between wood density and water content (Osunkoya et al. 2007).

1.4.2 Leaf functional traits

It is known that the leaf environment has a strong influence on functional traits (Cornelissen et al. 1996; Villar et al. 2006; Poorter et al. 2009). Therefore, we can expect differences in leaf anatomy and physiology between the provenances and sites observed.

We can associate leaf traits with history, distribution and resource requirements of given species (Hoffman et al, 2005). Among the leaf functional traits, some are commonly measured and widely reported, such as leaf area, specific leaf area and leaf dry matter content.

Leaf area (LA)

It represents the measured area of the leaf. Leaf area is included in the SLA measurements.

Leaf aspect ratio (AR)

This is a leaf shape indicator, used for leaf shape analysis and represents the major leaf axis divided by the minor axis of the particle's fitted ellipse (Li et al. 2018). This is a robust metric of overall length-to-width leaf ratio, whereas higher AR value indicates more elongated, less round leaf.

Specific leaf area (SLA)

"SLA represents one-sided area of a fresh leaf, divided by its dry mass" (Perez-Harguindeguy et al. 2013). In other words, SLA determines leaf area per unit leaf (dry) mass. Low SLA value may indicate a thick lamina, high tissue density or both.

Both leaf dry matter content and leaf thickness contribute to SLA value to different extent, and this is highly dependent on the plant species type. However, in woody plants, leaf thickness and LDMC are of similar influence for the SLA value. Leaf mass tends to increase more than the leaf area, while leaf is developing and gaining maturity age, therefore affecting the SLA to generally decrease.

Leaf dry matter content (LDMC)

LDMC represents dry mass over hydrated (fresh) leaf mass. It is related to average density (fresh mass per fresh volume) of the leaf tissue (Perez-Harguindeguy et al. 2013).

Both SLA and LMDC are easily measurable traits, and often reported in the literature. They indicate the leaf thickness and defence against pests (so called "leaf toughness") but also imply photosynthesis, light capture, etc. Leaves with high LDMC tend to be tougher and are considered as more resistant to herbivory and other physical damage, in comparison to leaves with lower LDMC (Perez-Harguindeguy et al. 2013).

2. RESEARCH OBJECTIVES

The aim of this work is analyse the intraspecific variation in wood and leaf traits in *Q. robur*, and to understand to which extent this variation is controlled by genotype (i.e. place of origin) or environment (i.e. site).

Different set of environmental conditions were taken into account, when evaluating the adaptive response of different *Q. robur* provenances. We have observed phenotypic plasticity based on anatomical and physiological differences among wood and leaf traits. Variation that comes as either a result of native, geographic location or genetic background might provide valuable answers in terms of adaptations towards new environmental conditions. Given that the three locations where trees were planted differ strongly in rainfall and thus exposure to drought, we further aimed to investigate if provenances differ in their response to drought. How were they different, based on wood and leaf trait results? Answers to these questions might contribute to design and species selection for future reforestation purposes.

Our main research objectives were to:

- distinguish genotypic (provenance) from environmental (site) effects on traits
- analyse correlations among traits
- test if traits are related to the climate at the origin of the provenance and
- to understand how oak trees adapted (evolved) to the climate (and particularly potential drought) of the places of origin

3. MATERIALS AND METHODS

3.1 Study site and plant material

Within the common garden experiment, ten oak provenances from 28 presented in the trial were selected for measurements of wood and leaf traits. The selected provenances originated from environmentally different parts of Europe (*Figure* 5), covering a broad range of geographic regions (i.e. Austria, Czech Republic, Croatia, and Slovenia). Seeds were collected from mother trees and seeds from one tree (half-sib) were planted with replicates at each trial site. We analyzed only one replicate per mother tree and site.

All provenances were planted at three common gardens in Austria: Weyerburg (WB), Wels (WL) and Weistrach (WR), as in *Figure 4*. The WL site is situated in Upper Austria (Oberösterreich), while the other two belong to Lower Austria (Niederösterreich). In terms of bioclimatic factors, sites mostly differed in mean annual temperature and annual precipitation, with WL being the most humid (1005 mm) and WB the driest site (641 mm), as in *Table 3*. Climate data from provenances place of origin (*Table 4*) span a narrow temperature range (7.4 to 10.0°C), but a wider range of rainfall (638 - 1066 mm). Interpolated climate data (for the period 1970 - 2000) was obtained from the WorldClim database (http://www.worldclim.org/bioclim) with 1km^2 resolution. Bioclimatic variables taken into account were mean annual temperature (*bio1*) and mean annual precipitation (*bio12*).

Common gardens were established in 2006/2007 and our research started in 2016. Trees were planted in a randomized block design (in three blocks), with the distance of 2m between the rows and 1m in the row itself. Oak trees were surrounded by other bordering trees that served as buffer zone to exclude the edge effect. In the experiment, we analysed 9 trees per provenance at each of the sites, leading to 270 sampled trees in total.

Table 3. Climate data at three sites in Austria (WB, WL and WR) including latitude, longitude, mean annual temperature (MAT) and mean annual precipitation (MAP)

Provenance	**Code**	**Latitude (°N)**	**Longitude (°E)**	**MAT (°C)**	**MAP (mm/year)**
Weyerburg	WB	48.557	16.171	8.8	641
Wels	WL	48.185	13.989	8.5	1005
Weistrach	WR	48.053	14.563	8.4	890

Figure 4. Location of the three sites in Austria: WB, WL and WR (source: Google Earth, accessed on February 10, 2019)

Table 4. Geographic origin and habitat characteristics of *Quercus robur* provenances, including latitude, longitude, mean annual temperature (MAT) and mean annual precipitation (MAP)

Provenance	**Country**	**Code**	**Latitude (°N)**	**Longitude (°E)**	**MAT (°C)**	**MAP (mm/year)**
Geinberg	AT	1	48.277	13.307	8.7	1066
Linz	AT	2	48.326	14.294	9.2	841
Braunsberger Wald	AT	6	48.473	16.333	9.1	638
Rainfeld	AT	8	48.042	15.732	7.4	785
Luising	AT	12	47.023	16.477	9.7	696
Klagenfurt	AT	14	46.63	14.35	8.0	988
Hluboka	CZ	17	49.09	14.444	7.4	764
Kutina	HR	18	45.433	16.683	10.9	915
Murska suma	SLO	19	46.498	16.511	10.1	810
Velika Gorica	HR	21	45.674	16.161	10.5	920

Figure 5. Geographic distribution of ten selected *Quercus robur* provenances studied in the trial (source: Google Earth, accessed on February 10, 2019)

3.2 Sampling and data collection

3.2.1 Wood samples

Wood samples were taken in February 2018, when threes were 12 years old, with a 5.1-mm increment borer and stored in tight 2.5 ml vials. In the laboratory, the bark and the sample beyond the center were removed, the length of the sample was measured with a caliper to 0.1 mm, and fresh weight was measured with a precision balance to 0.1 mg. After drying at 100 °C, dry weight was measured. Sample volume was calculated from the sample length and the diameter of the borer. Wood density was calculated as dry weight / volume and wood water content as (fresh weight – dry weight) / volume. Prior to cutting thin transverse sections of 30µm with a core microtome (WSL, Switzerland), samples were softened with ethylene diamine at 60°C. Sections were double stained with safranin solution and astrablue (Carl Roth, Germany), dehydrated with a graded alcohol series and subsequently embedded in Euparal medium (Carl Roth, Germany).

For digitalization, we used a DM5500B transmission light microscope equipped with an automatic stage, a DMC2900 camera and resolution of 864 pixels/mm. Vessels were marked manually with Adobe Photoshop CS2 (Version 9.0, Adobe Systems Incorporated, USA), and then measured automatically with ImageJ (v1.49p, http://rsb.info.nih.gov/ij).

We analysed 252 wood samples in total, since some were damaged during the sections preparation. The following parameters were calculated: vessel density per mm^2 (VD); mean area of individual vessels (VA); theoretical hydraulic conductivity (K_h), which was calculated from the vessel size and densities according to the Hagen–Poiseuille law (Giordano et al. 1978, Rungwattana et al. 2018,) and the following formula: $K_h = (\pi\rho_w/128\ \eta) \times VD \times Dh^4$. In the formula, η represents dynamic viscosity of water (1.002×10^{-3} Pa s at 20°C), ρ_w is the density of water (998.2 kg/m^3 at 20°) and $Dh = (\Sigma\ D^4/n)^{1/4}$, where D is the average of minor and major axes of the diameter of individual vessels.

3.2.2 Leaf samples

Prior to field sample collection, some SLA measurements have been taken in order to estimate leaf growth and maturation. This was done with the intention of predicting the optimal timeframe for real data collection. SLA was measured once a week since beginning of May until the sample collection in June. We used oak leaves from Türkenschanzpark for this purpose. Experiment showed variation in SLA during this period, with respect to change in leaf thickness and LDMC as function of SLA. SLA started to decrease by the end of this experiment, and we assumed leaves were sufficiently mature for field collection. In addition, we have experimented on few saturation methods and we found it best achieved when leaves were put between wet paper sheets. In this way, leaves had higher water content (data not presented).

Oak leaves from all three sites were collected on the 18th and 19th of June, 2018. Upper leading branches of oak trees were cut in the field with long-reaching telescopic pruning shears and collected in big plastic bags, with some water therein to keep them humid. Leaves were transported in this manner, until processed and put in cool storage.

Since SLA is strongly affected by the light intensity (Perez-Harguindeguy et al. 2013), attention was paid towards collecting sun exposed leaves, on the outer side of the canopy. We chose branches with more than 10, healthy and whole leaves, as far as possible without herbivore damage or fungi infection. Still, it was impossible to avoid such leaves from WB site, so the leaves with the least damage possible were chosen in these cases.

After collection, samples from 270 trees were processed according to the following protocol: 10 leaves per tree (from 9 to 11, depending on their condition) were selected for SLA and LDMC measurements. One extra leaf per sample was chosen for further stomatal density and leaf shape analysis, but these leaves and traits were not analysed as part of the current thesis. Following the results of the previous saturation tests, the ten leaves were placed in between wet paper sheets for 24h in a dark room, at 4°C. Subsequently, leaves were blotted dried and immediately measured for hydrated (fresh) weight to calculate the LDMC. Leaves were then scanned with flatbed scanner (ScanMaker 9800XL Plus, Microtek) for determination of LA, using the 150 dpi resolution. Within the experiment, we processed approximately 2700 leaves, of 7.3 m^2 area in total. The petioles were cut and measured before the scanning, and are thus not included in SLA calculations nor in the leaf shape analysis.

Upon scanning, leaves were dried in the oven at 60°C for at least 72h, in order to determine the leaf dry mass. This mass was used for both SLA and LDMC measurements. SLA (mm^2/g) was calculated as leaf dry mass / area and LDMC (mg/g) as dry weight / saturation weight. Additionally, leaf aspect ratio was calculated as leaf's length divided by its width.

We used ImageJ (from the US National Institutes of Health; http://www.nih.gov/) as image analysis software to process leaf area measurements. LA of each of the 10 individual scanned leaves was summed up and used to represent a single sample value within the SLA measurement.

3.2.3 Tree size

The tree height and diameter at 1.3 m was measured by BFW at the age of 10 years, between November 2016 and February 2017. BFW measured all trees in the trials and here we used the measurements of the 271 trees sampled for traits. Since trees were of the same age, size represented a comparative measure of growth rates.

3.3 Data analysis

Before running the ANOVA test, we checked if data satisfied the assumptions of normality. Since distribution of the data was rather normal (not ideal for VA, VD, K_h; but with marginal differences), there was no need to log-transform it.

We tested the effect of provenance and the site effect on functional traits of interest, by performing an ANOVA (analysis of variance) test. Data was analyzed with statistical package STATISTICA (version 8.0, analytical package, StatSoft. Inc, Tulsa, OK, USA).

We performed Tukey Honest Significant Difference post-hoc test, with intention to differ between groups of factors analyzed with ANOVA. Accordingly, groups's means were compared in order to distinguish which of them were specifically different from each other. Test was performed with Minitab 18.0 statistical software (www.minitab.com). According to grouping information, Tukey's HSD test results were represented with different letters, in case of significantly different means. Firstly, all provenances were compared within each site and their differences further labeled with upper case letters. Then, performance of each provenance was compared separately among all three locations, and those differences were labeled with lower case letters.

We calculated Pearson coefficient in different ways for the correlations among traits and correlations between traits and climate. To describe the nature of relationships among traits, we used trait values of each individual oak tree, which were considered as independent data points. However, for correlations between traits and climate parameters, we used the average trait values per provenance and site, rather than individual trees since all trees from one provenance represent the same climate.

4. RESULTS

Mean and variation of the traits analyzed are presented in *Table 5*. The coefficient of variation differed among the traits, from7.0 % in WC, to 38.7 % in K_h.

Table 5. Mean, range, standard deviation and coefficient of variation (SD/mean*100) of traits measured in oak provenances, grown at three sites in Austria

Trait	Unit	Mean	Max	Min	SD	CV (%)
Vessel density	mm^{-2}	47.3	93.2	22.8	12.4	26.1
Vessel area	μm^2	2573	5775	1221	721	28.0
Vessel fraction	%	11.64	24.22	6.92	2.69	23.1
Theoretical hydraulic conductivity	$kgm \cdot s^{-1} \cdot MPa^{-1}$ $x10^5$	9.27	25.17	3.23	3.59	38.7
Wood density	g/cm^3	0.578	0.741	0.513	0.043	7.4
Water content	g/cm^3	0.391	0.479	0.328	0.028	7.0
Leaf aspect ratio	/	1.89	2.60	1.45	0.21	11.1
Leaf area	mm^2	27273	60993	12938	8286	30.4
Specific leaf area	mm^2/g	14.37	31.12	8.60	3.33	23.2
Leaf dry matter content	mg/g	412	492	314	63	15.3
Tree diameter	cm	5.38	10.00	2.40	1.58	29.4
Tree height	cm	532	810	250	107	20.1

4.1 Wood Traits

4.1.1 Vessel density (VD)

Data analysis showed that neither the provenance, nor the site had a significant effect ($p>0.05$) on VD. Moreover, provenance x site interaction was not significant for the respective trait (*Table 6*).

Table 6. ANOVA testing the effect of provenance and site on vessel density

	Df	MS effect	F	p-level
Provenance	9	180.736	1.159	0.323
Site	2	27.938	0.179	0.836
Prov. x Site	18	116.244	0.746	0.761
Residuals	222	155.9		

Three provenances with the highest average VD were: Kla (AT) – 51.1, Li (AT) – 49.7 and BW (AT) - 48.6 vessels per mm^2. The lowest VD was recorded from Ra (AT) oak provenance, with 41.5 vessels per mm^2 (*Table 7).*

The site with highest average VD measured was WR – 47.8, followed by WB – 47.0, while lowest average VD was recorded at WL site, with 46.7 vessels per mm^2 (*Table 7*).

According to post-hoc Tukey test (*Table 7*), results showed no statistically significant differences in VD observed among oak provenances at the three sites.

Moreover, there were no significant differences in VD among the sites observed either (WB, WL and WR) (*Table 7*).

Figure 6. Vessel density (mm^{-2}): mean and standard error of ten oak provenances observed at three sites (WB – Weyerburg; WL - Wels; WR - Weistrach) in Austria

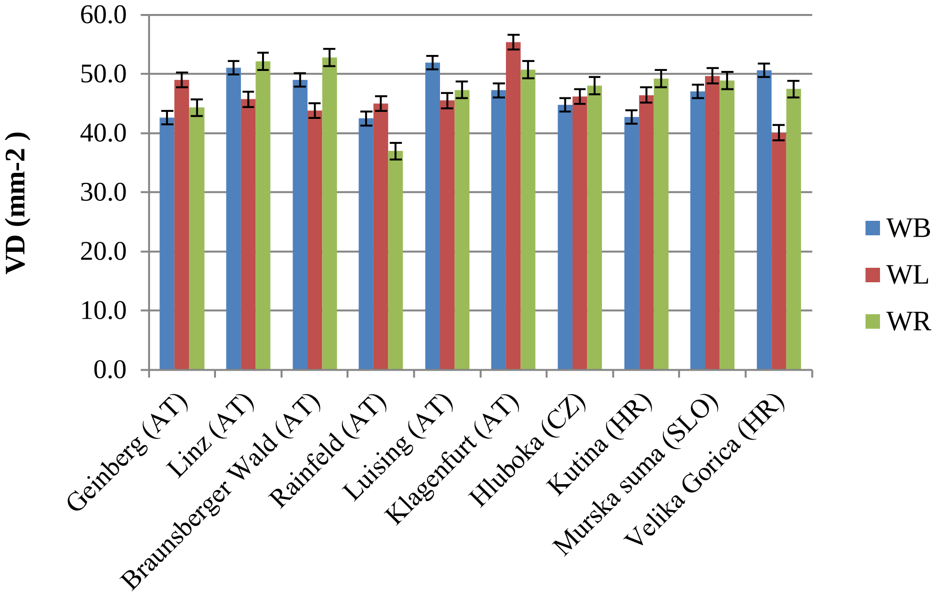

Table 7. Vessel density (mm^{-2}): mean ± standard deviation, range (min, max) and Tukey test results for ten oak provenanances grown at three sites in Austria; n = 252

Provenance	Site									Average
	WB			WL			WR			
Ge (AT)	42.6±6.7	(33.6 - 51.8)	Aa	49.0±6.5	(39.3 – 61.6)	Aa	44.3±7.8	(30.7 – 54.3)	Aa	45.3
Li (AT)	51.1±11.1	(37.7 – 64.9)	Aa	45.7±7.0	(36.4 – 60.6)	Aa	52.2±14.3	(35.6 – 81.5)	Aa	49.7
BW (AT)	49.0±14.4	(33.7 – 82.5)	Aa	43.9±17.2	(24.9 – 82.6)	Aa	52.8±19.8	(28.9 – 89.5)	Aa	48.6
Ra (AT)	42.5±8.1	(29.9 – 52.5)	Aa	45.0±17.3	(23.8 – 80.4)	Aa	37.0±9.9	(26.2 – 55.9)	Aa	41.5
Lu (AT)	51.9±11.4	(36.9 – 66.7)	Aa	45.5±16.8	(22.8 – 71.1)	Aa	47.3±12.2	(32.8 – 72.2)	Aa	48.3
Kla (AT)	47.3±5.9	(35.7 – 55.0)	Aa	55.4±19.2	(32.6 – 93.2)	Aa	50.8±17.8	(31.3 – 83.6)	Aa	51.1
Hlu (CZ)	44.8±11.6	(31.6 – 62.6)	Aa	46.2±9.3	(35.7 – 59.8)	Aa	48.0±6.5	(35.2 – 54.7)	Aa	46.3
Ku (HR)	42.8±10.0	(25.6 – 55.0)	Aa	46.5±12.0	(31.9 – 63.1)	Aa	49.3±6.9	(40.1 – 58.5)	Aa	46.2
MS (SLO)	47.1±10.8	(33.3 – 64.4)	Aa	49.7±19.0	(26.9 – 84.6)	Aa	48.9±13.5	(29.2 – 64.1)	Aa	48.6
VG (HR)	50.6±6.7	(40.7 – 58.8)	Aa	40.1±7.1	(32.6 – 49.8)	Aa	47.5±11.2	(32.1 – 65.7)	Aa	46.1
Average	47.0			46.7			47.8			47.2

Means followed by the same letter are not significantly different using Tukey's post-hoc test and with a 95.0% confidence level. Upper case letters refer to differences among sites (columns), while lower case letters refer to differences among provenances (rows).

4.1.2 Vessel area (VA)

Vessel area was significantly different among provenances (p = 0.009) observed in the trial, while site had no significant effect on VA. Moreover, provenance x site interaction had no significant effect on the VA (*Table 8*).

Table 8. ANOVA testing the effect of provenance and site on vessel area (p<0.05 in bold)

	Df	MS Effect	F	p-level
Provenance	**9**	**1.28E-06**	**2.515**	**0.009**
Site	2	7.69E-07	1.515	0.222
Prov. x Site	18	2.73E-07	0.538	0.938
Residuals	222	5.07E-07		

Three provenances with the highest average VA were the following ones: Lu (AT) – 2910, Ra (AT) - 2795, and VG (HR) with 2765 µm^2. The lowest VA however, was recorded from Hlu (CZ) oak provenance - with 2199 µm^2 (*Table 9*). The highest VA was recorded from WB – 2689 µm^2, followed by WR – 2541 µm^2, while lowest VA was recorded from WL, with 2506 µm^2 (*Table 9*).

Post-hoc Tukey test showed significant differences in VA among the provenances observed at three sites (WB, WL and WR). Hlu (CZ) oak provenance had the lowest VA at all locations. At WB site, Hlu was significantly lower than Ra (AT), Lu (AT) and VG (HR). At WL, Hlu (CZ) had a lower VA than Lu (AT) provenance, while at the WR site, it was lower than Ra (AT). (*Table 9*).

However, VA did not differ significantly among the sites observed in the trial (*Table 9*).

Figure 7. Vessel area (µm^2): mean and standard error of ten oak provenances observed at three sites (WB, WL andWR) in Austria.

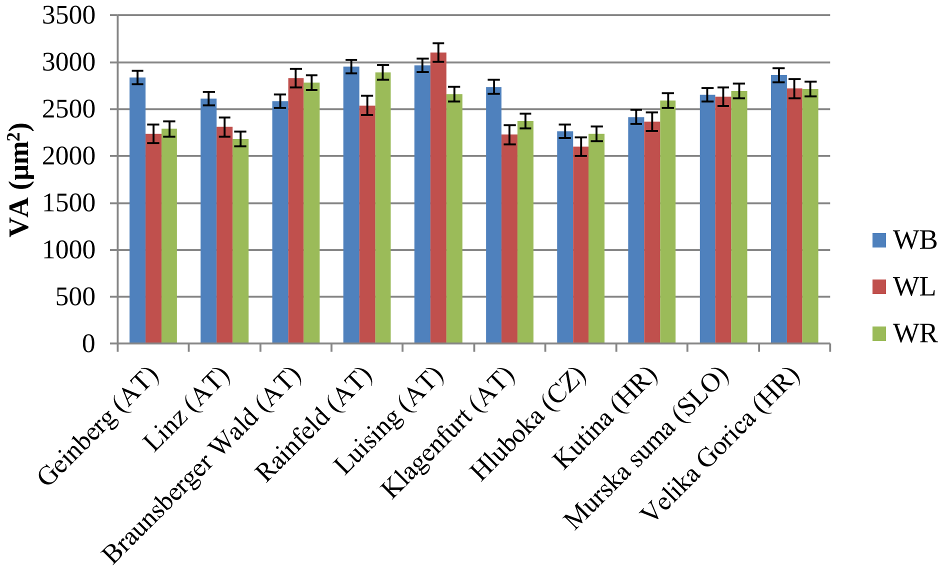

Table 9. Vessel area (μm^2): mean ± standard deviation, range (min, max) and Tukey test results of ten oak provenanances grown at three sites in Austria; n = 252

Provenance	Site									Average
	WB			WL			WR			
Ge (AT)	2837±739	(1851 - 4052)	ABa	2237±483	(1779- 3105)	ABa	2289 ±427	(1560 - 3017)	ABa	2454
Li (AT)	2611±673	(1785 - 3868)	ABa	2309 ±345	(2001 - 3040)	ABa	2181 ±352	(1548 - 2767)	Ba	2367
BW (AT)	2587 ±748	(1453 - 4136)	ABa	2828 ±985	(1357 - 4287)	ABa	2783 ±555	(1970 - 3388)	ABa	2733
Ra (AT)	2954±1094	(1765- 4724)	Aa	2540 ±859	(1734 - 4489)	ABa	2890±912	(1635- 4411)	Aa	2795
Lu (AT)	2967±985	(2062- 4922)	Aa	3102 ±1185	(1906- 5775)	Aa	2660±707	(1886 - 4217)	ABa	2910
Kla (AT)	2738 ±890	(1492 - 4275)	ABa	2227±669	(1222 - 3533)	ABa	2374±776	(1294- 3662)	ABa	2446
Hlu (CZ)	2262 ±605	(1477 - 3529)	Ba	2100±390	(1404- 2635)	Ba	2236±406	(1719 - 3014)	Ba	2199
Ku (HR)	2418±681	(1636 - 3631)	ABa	2365±693	(1526 - 3296)	ABa	2590±360	(2219- 3144)	ABa	2458
MS (SLO)	2655±486	(1939 - 3286)	ABa	2635±895	(1561 - 4418)	ABa	2694 ±759	(1786 - 4087)	ABa	2661
VG (HR)	2861±607	(2029- 3612)	Aa	2718±608	(2056 - 3687)	ABa	2715±429	(2156 - 3278)	ABa	2765
Average	2689			2506			2541			2579

Means followed by the same letter are not significantly different using Tukey's post-hoc test and with a 95.0% confidence level. Upper case letters refer to differences among sites (columns), while lower case letters refer to differences among provenances (rows).

4.1.3 Vessel fraction (PV)

Data analysis showed that PV significantly differed among the provenances, as well as among the sites observed, although the effect of provenance (p = 4.91E-05) was stronger than the one of site (p = 3.91E-03). There was no significant provenance x site interaction on PV (*Table 10*).

Table 10. ANOVA testing the effect of provenance and site on vessel fraction (p<0.05 in bold)

	Df	MS Effect	F	p-level
Provenance	**9**	**2.54E-03**	**4.204**	**4.91E-05**
Site	**2**	**3.43E-03**	**5.685**	**3.91E-03**
Prov. x Site	18	9.55E-04	1.582	0.066
Residuals	222	6.03E-04		

The three provenances with the highest average PV were Lu (AT) – 13.2%, VG (HR) – 12.7% and BW (AT) provenance with 12.5%. The lowest PV was recorded from Hlu (CZ) provenance, with 9.9% (*Table 11).* Average PV was highest at WB site - 12.2%, slightly lower at WR – 11.7 and lowest at WL, with the value of 11% (*Table 11*).

Post-hoc Tukey test showed the following results in terms of PV variation in the trial. At both WB and WL sites, Lu (AT) oak provenance had a significantly higher PV than the Hlu (CZ). At the WR site, BW (AT) provenance had a significantly higher PV compared to Ge (AT) provenance. (*Table 11).*

PV varied among the sites as well, especially in two cases. Li (AT) oak provenance had a significantly higher PV at WB compared to WL. In addition, Ku (HR) had a significantly higher PV at WR site compared to both WB and WL (*Table 11).*

Figure 8. Vessel fraction (%): mean and standard error for ten oak provenances observed at three sites (WB, WL andWR) in Austria

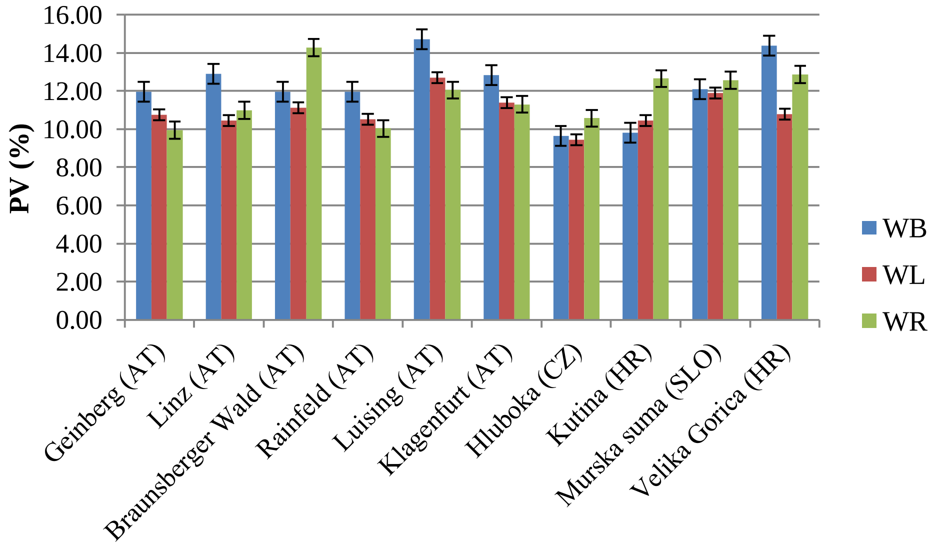

Table 11. Vessel fraction (%):mean ± standard deviation, range (min, max) and Tukey test results for ten oak provenanances grown at three sites in Austria; n = 252

Provenance	Site									Average
	WB			WL			WR			
Ge (AT)	11.96±3.17	(7.09 – 18.64)	ABCa	10.75±1.37	(9.05 – 13.84)	ABa	9.94±1.63	(8.41 – 13.74)	Ba	10.89
Li (AT)	12.90±2.40	(9.10 – 17.30)	ABCa	10.46±1.53	(8.42 – 12.84)	ABb	10.99±1.58	(8.63 – 12.81)	ABab	11.45
BW (AT)	11.97±1.86	(8.50 – 15.10)	ABCa	11.12±1.51	(8.46 – 14.23)	ABa	14.28±4.97	(8.45 – 24.22)	Aa	12.46
Ra (AT)	11.97±2.93	(7.50 – 17.10)	ABCa	10.51±2.37	(7.19 – 15.27)	ABa	10.04±1.69	(8.49 – 13.86)	ABa	10.84
Lu (AT)	14.73±3.06	(10.39 – 18.56)	Aa	12.70±2.29	(8.62 – 15.95)	Aa	12.05±2.07	(8.94 – 15.45)	ABa	13.16
Kla (AT)	12.82±4.18	(7.00 – 19.75)	ABCa	11.40±1.84	(7.49 – 13.88)	ABa	11.31±3.22	(7.09 – 16.14)	ABa	11.84
Hlu (CZ)	9.66±1.50	(6.96 – 11.23)	Ca	9.43±1.14	(8.39 - 11.23)	Ba	10.57±1.23	(8.30 - 11.69)	ABa	9.89
Ku (HR)	9.80±1.08	(8.92 - 11.65)	BCb	10.45±2.20	(6.92 – 14.61)	ABb	12.66±1.83	(9.64 – 15.83)	ABa	10.97
MS (SLO)	12.08±1.16	(10.79 – 13.66)	ABCa	11.91±2.19	(9.25 – 16.74)	ABa	12.56±2.94	(8.96 – 16.90)	ABa	12.19
VG (HR)	14.40±3.14	(8.96 – 19.71)	ABa	10.80±2.58	(7.29 – 14.92)	ABa	12.87±3.84	(8.77 – 20.80)	ABa	12.69
Average	12.23			10.95			11.73			11.64

Means followed by the same letter are not significantly different using Tukey’s post-hoc test and with a 95.0% confidence level. Upper case letters refer to differences among sites (columns), while lower case letters refer to differences among provenances (rows).

4.1.4 Theoretical hydraulic conductivity (K_h)

Statistical analysis showed that K_h was significantly different (p = 3.47E-04) among the provenances studied in the trial, but site and provenance x site interaction had no effect on the respective trait (*Table 12*).

Table 12. ANOVA testing the effect of provenance and site on theoretical hydraulic conductivity (p<0.05 in bold)

	Df	MS effect	F	p-level
Provenance	**9**	**4.20E-09**	**3.586**	**3.47E-04**
Site	2	3.03E-10	0.259	0.772
Prov. x Site	18	1.43E-09	1.220	0.246
Residuals	222	1.17E-09		

The three provenances with highest K_h were: Lu (AT) – 11.33, BW (AT) – 10.30 and Kla (AT) – 10.21 kg m s-1 MPa^{-1} x 10^5. The lowest Kh was recorded from Hlu (CZ) provenance, with only 7.17 kg m s^{-1} MPa^{-1} x 10^5 (*Table 13*). The site with the highest K_h was WB – 9.45, followed by WL – 9.13, while the lowest K_h was recorded at WR site, with 9.10 kg m s^{-1} MPa^{-1} x 10^5 (*Table 13*).

Post-hoc Tukey test showed no statistically significant differences in K_h among provenances observed at WB and WR sites. However, at WL site Lu (AT) oak provenance had a statistically significantly higher K_h than Hlu (CZ) (*Table 13*).

No statistically significant differences in K_h were found among the sites (*Table 13*).

Figure 9. Theoretical hydraulic conductivity K_h (kg m s^{-1} MPa^{-1} x 10^5): mean and standard error for ten oak provenances observed at three sites in Austria (WB, WL andWR)

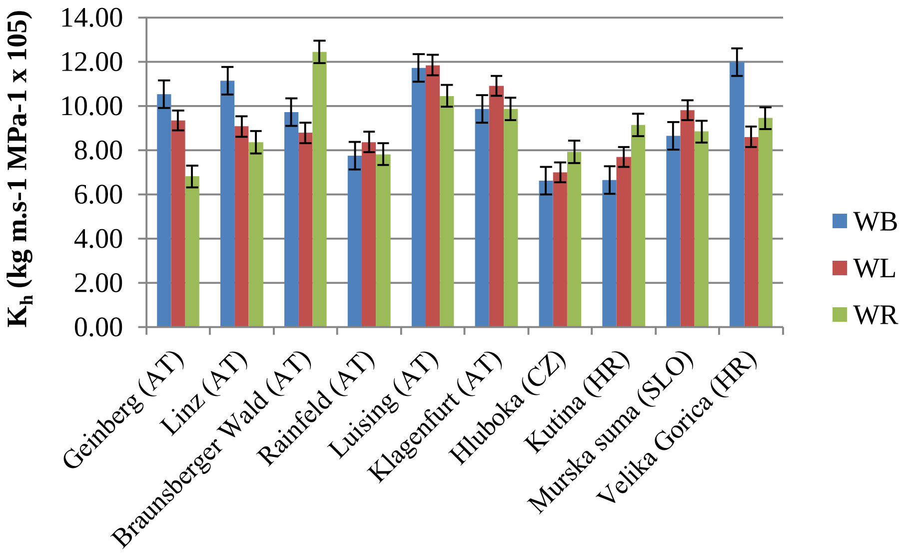

Table 13. Theoretical hydraulic conductivity (kg m s^{-1} MPa^{-1} x 10^5): mean ± standard deviation, range (min, max) and Tukey test results for ten oak provenanances grown at three sites in Austria; n = 252

Provenance	Site									Average
	WB			WL			WR			
Ge (AT)	10.52±5.11	(3.56 – 22.24)	Aa	9.33±1.65	(7.22 – 12.53)	ABa	6.80±2.02	(3.49 – 10.37)	Aa	8.88
Li (AT)	11.12±2.68	(8.22 – 16.55)	Aa	9.06±2.99	(5.31 – 15.22)	ABa	8.35±2.69	(4.33 – 12.08)	Aa	9.53
BW (AT)	9.70±4.06	(3.86 – 18.99)	Aa	8.77±1.87	(5.88 – 12.52)	ABa	12.44±6.23	(5.88 – 23.03)	Aa	10.30
Ra (AT)	7.74±2.56	(4.77 – 11.61)	Aa	8.36±2.15	(4.09 – 10.99)	ABa	7.81±2.43	(4.82 – 11.83)	Aa	7.97
Lu (AT)	11.71±3.94	(6.70 – 17.84)	Aa	11.84±3.75	(7.63 – 17.97)	Aa	10.45±4.26	(4.36 – 15.26)	Aa	11.33
Kla (AT)	9.85±4.23	(3.23 – 17.82)	Aa	10.90±3.60	(6.75 – 18.92)	ABa	9.86±4.91	(4.82 – 18.13)	Aa	10.21
Hlu (CZ)	6.61±1.99	(3.47 – 9.41)	Aa	6.98±1.92	(4.34 – 9.96)	Ba	7.92±1.92	(6.10 – 11.10)	Aa	7.17
Ku (HR)	6.63±2.60	(3.83 – 11.29)	Aa	7.69±1.40	(4.58 – 9.33)	ABa	9.13±3.11	(4.19 – 13.71)	Aa	7.82
MS (SLO)	8.63±2.22	(6.43 – 13.15)	Aa	9.79±3.80	(4.89 – 17.20)	ABa	8.83±2.05	(6.83 – 12.80)	Aa	9.08
VG (HR)	11.97±6.03	(4.85 – 25.17)	Aa	8.59±3.65	(3.40 – 14.38)	ABa	9.44±3.86	(3.86 – 15.23)	Aa	9.99
Average	9.45			9.13			9.10			9.23

Means followed by the same letter are not significantly different using Tukey's post-hoc test and with a 95.0% confidence level. Upper case letters refer to differences among sites (columns), while lower case letters refer to differences among provenances (rows).

4.1.5 Wood density (WD)

Statistical analysis showed that provenance had a marginally significant effect (p = 0.077) on the trait observed, while WD was significantly different among the sites (p = 1.77E-22). In addition, provenance x site interaction had a significant effect (p = 2.77E-05) on WD as well (*Table 14*).

Table 14. ANOVA testing the effect of provenance and site on wood density (p<0.05 in bold)

	Df	MS effect	F	p-level
Provenance	9	0.002	1.760	0.077
Site	**2**	**0.068**	**63.292**	**1.77E-22**
Prov. x Site	**18**	**0.003**	**3.189**	**2.77E-05**
Residuals	222	1.08E-03		

The three provenances with highest WD were: MS (SLO) – 0.589, Kla (AT) and Lu (AT) – 0.587 g/cm^3. The lowest WD value was recorded from Ge (AT) provenance – 0.565 g/cm^3 (*Table 15*). The site with highest WD was WB – 0.612, followed by WR – 0.567, while lowest average WD was obtained from WL site – 0.558 g/cm^3 (*Table 15*).

According to Tukey test results (*Table 15*), no statistically significant differences were found among oak provenances observed at WL and WR sites. However, at WB, WD was significantly higher in MS (SLO) provenance than in VG (HR) and Ge (AT). We assume that this provenance variation in WD resulted in a significance of provenance x site interaction.

In addition, Tukey test showed that WD differed among the sites and was always highest at WB (*Table 15*). Ge (AT) oak provenance had a significantly higher WD at WB and WR site, compared to the WL. Li (AT) had a significantly higher WD at WB compared to the WL. BW (AT), Lu (AT), Kla (AT), Hlu (CZ), Ku (HR) and MS (SLO) provenances had a significantly higher WD at the WB site, compared to both WL and WR.

Figure 10. Wood density (g/cm^3): mean and standard error for ten oak provenances observed at three sites in Austria (WB, WL andWR)

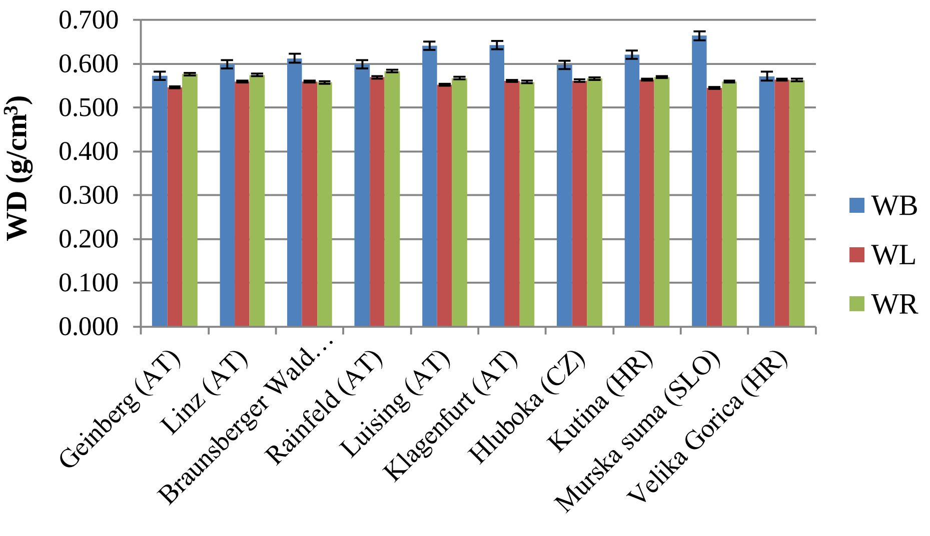

Table 15. Wood density (g/cm^3): mean ± standard deviation, range (min, max) and Tukey test results for ten oak provenanances grown at three sites in Austria; n = 252

Provenance	Site									Average
	WB			WL			WR			
Ge (AT)	0.572±0.019	(0.549 - 0.603)	Ba	0.546±0.019	(0.513 - 0.572)	Ab	0.576±0.020	(0.544 - 0.602)	Aa	0.565
Li (AT)	0.599±0.033	(0.559 - 0.664)	ABa	0.559±0.017	(0.535 - 0.592)	Ab	0.574±0.028	(0.538 - 0.607)	Aab	0.577
BW (AT)	0.612±0.058	(0.561 - 0.728)	ABa	0.560±0.018	(0.530 - 0.588)	Ab	0.558±0.018	(0.533 - 0.584)	Ab	0.577
Ra (AT)	0.599±0.049	(0.545 - 0.672)	ABa	0.569±0.021	(0.534 - 0.602)	Aa	0.583±0.021	(0.560 - 0.622)	Aa	0.584
Lu (AT)	0.641±0.042	(0.574 - 0.713)	ABa	0.552±0.024	(0.525 - 0.598)	Ab	0.567±0.021	(0.537 - 0.597)	Ab	0.587
Kla (AT)	0.643±0.060	(0.539 - 0.710)	ABa	0.561±0.023	(0.537 - 0.589)	Ab	0.558±0.020	(0.542 - 0.599)	Ab	0.587
Hlu (CZ)	0.598±0.023	(0.566 - 0.640)	ABa	0.561±0.030	(0.534 - 0.626)	Ab	0.566±0.013	(0.554 - 0.593)	Ab	0.575
Ku (HR)	0.621±0.044	(0.570 - 0.685)	ABa	0.563±0.014	(0.538 - 0.583)	Ab	0.569±0.025	(0.542 - 0.618)	Ab	0.585
MS (SLO)	0.664±0.067	(0.547 - 0.741)	Aa	0.545±0.020	(0.522 - 0.585)	Ab	0.559±0.038	(0.520 - 0.627)	Ab	0.589
VG (HR)	0.572±0.058	(0.518 - 0.665)	Ba	0.563±0.012	(0.543 - 0.579)	Aa	0.563±0.030	(0.527 - 0.612)	Aa	0.566
Average	0.612			0.558			0.567			0.579

Means followed by the same letter are not significantly different using Tukey's post-hoc test and with a 95.0% confidence level. Upper case letters refer to differences among sites (columns), while lower case letters refer to differences among provenances (rows).

4.1.6 Water content (WC)

Data analysis of water content measured in oak wood showed that WC varied significantly (p = 4.39E-03) among the provenances, but even more among the sites (p = 1.87E-05) studied in the trial. However, provenance x site interaction had no significant effect on this trait (*Table 16*.).

Table 16. ANOVA testing the effect of provenance and site on water content (p<0.05 in bold)

	Df	MS effect	F	p-level
Provenance	**9**	**1.81E-03**	**2.764**	**4.39E-03**
Site	**2**	**7.49E-03**	**11.440**	**1.87E-05**
Prov. x Site	18	7.39E-04	1.129	3.26E-01
Residuals	222	6.55E-04		

The three provenances with highest WC measured were: Kla (AT) and Lu (AT) – both 0.403, as well as BW (AT) with 0.397 g/cm^3. The lowest WC was recorded from VG (HR) oak provenance, with the total of 0.379 g/cm^3 (*Table 17*). The site with highest measured WC was WL – 0.401, followed by WB – 0.390, while WL recorded the lowest WC value of 0.383 g/cm^3 (*Table 17*).

Post-hoc Tukey test (given in *Table 17*) showed the following results of WC variation. Kla (AT) provenance had a significantly higher WC at WB site, compared to VG (HR). However, there were no statistically significant differences in WC among the provenances observed at WL and WR.

WC slightly differed among the sites as well. Both Hlu (CZ) and VG (HR) had a significantly higher WC at WL site compared to both WB and WR, while for other provenances, no significant differences among the sites were found (*Table 17*).

Figure 11. Water content (g/cm^3): mean and standard error for ten oak provenances observed at three sites in Austria (WB, WL and WR)

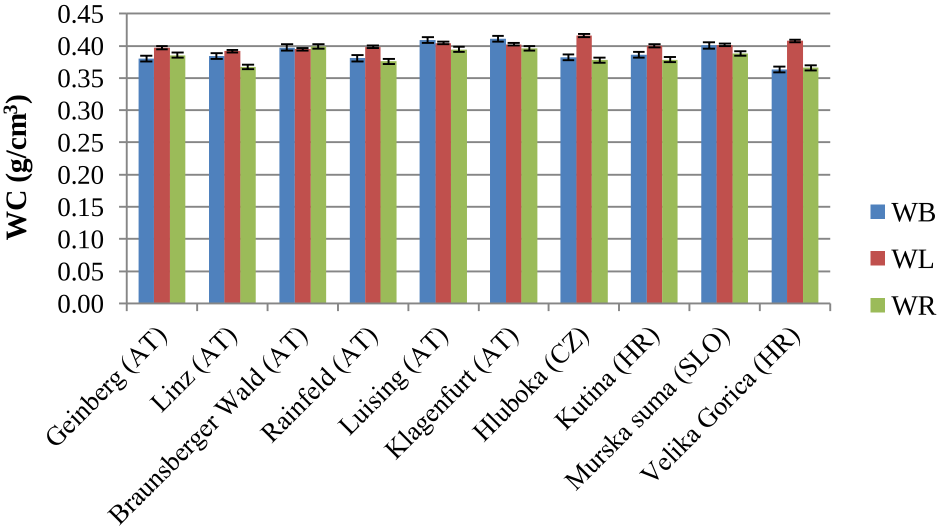

Table 17. Water content (g/cm^3): mean ± standard deviation, range (min, max) and Tukey test results for ten oak provenanances grown at three sites in Austria; n = 252

Provenance	Site									Average
	WB			WL			WR			
Ge (AT)	0.380±0.016	(0.361 – 0.411)	ABa	0.397±0.024	(0.371 – 0.433)	Aa	0.385±0.023	(0.350 – 0.414)	Aa	0.388
Li (AT)	0.384±0.016	(0.351 - 0.412)	ABa	0.392±0.029	(0.337 - 0.431)	Aa	0.367±0.021	(0.336 - 0.393)	Aa	0.381
BW (AT)	0.398±0.040	(0.329 - 0.453)	ABa	0.395±0.032	(0.350 - 0.461)	Aa	0.399±0.021	(0.373 - 0.435)	Aa	0.397
Ra (AT)	0.381±0.027	(0.347 - 0.413)	ABa	0.399±0.016	(0.366 - 0.422)	Aa	0.376±0.022	(0.340 - 0.415)	Aa	0.385
Lu (AT)	0.409±0.022	(0.369 - 0.444)	ABa	0.404±0.018	(0.374 - 0.433)	Aa	0.395±0.024	(0.371 - 0.441)	Aa	0.403
Kla (AT)	0.411±0.033	(0.364 - 0.450)	Aa	0.402±0.021	(0.373 - 0.446)	Aa	0.396±0.041	(0.352 - 0.479)	Aa	0.403
Hlu (CZ)	0.382±0.022	(0.354 - 0.424)	ABb	0.416±0.024	(0.389 - 0.464)	Aa	0.378±0.024	(0.352 - 0.409)	Ab	0.392
Ku (HR)	0.386±0.040	(0.355 - 0.455)	ABa	0.400±0.018	(0.369 - 0.422)	Aa	0.378±0.018	(0.361 - 0.406)	Aa	0.388
MS (SLO)	0.401±0.039	(0.335 - 0.471)	ABa	0.401±0.017	(0.373 - 0.424)	Aa	0.388±0.022	(0.353 - 0.425)	Aa	0.397
VG (HR)	0.363±0.033	(0.328 - 0.422)	Bb	0.408±0.021	(0.383 - 0.436)	Aa	0.366±0.018	(0.343 – 0.393)	Ab	0.379
Average	0.390			0.401			0.383			0.391

Means followed by the same letter are not significantly different using Tukey's post-hoc test and with a 95.0% confidence level. Upper case letters refer to differences among sites (columns), while lower case letters refer to differences among provenances (rows).

4.2 Leaf Traits

4.2.1 Leaf area (LA)

Data analysis showed that LA significantly differed (p = 0.008) among oak provenances studied in the trial. However, site as well as provenance x site interaction showed no significant effect on LA (*Table 20).*

Table 20. ANOVA testing the effect of provenance and site on leaf area (p<0.05 in bold)

	Df	MS effect	F	p-level
Provenance	**9**	**169097984**	**2.554**	**0.008**
Site	2	116800816	1.764	0.173
Prov. x Site	18	45996532	0.695	0.815
Residuals	240	66196968		

Three oak provenances with the highest average LA were: Lu (AT) – 32159, MS (SLO) – 29506 and Hlu (CZ) – 29019 mm^2, respectively. The lowest LA was recorded from VG (HR) provenance, with total of 24203 mm^2 (*Table 21*). Site with highest measured LA was WR - 28542 mm^2, followed by WL – 26942, while the lowest LA value was obtained at WB, with 26337 mm^2 (*Table 21*).

Post-hoc Tukey test results showed no significant differences in LA among the provenances observed at the WB and WL sites. However, oak provenances did differ at WR, e.g. Ge (AT) oak provenance had a significantly lower LA compared to Lu (AT), BW (AT) and Hlu (CZ) (*Table 21*). Tukey test did not record any statistically significant differences in LA among the sites observed (*Table 21*).

Figure 13. Leaf area (mm^2): mean and standard error for ten oak provenances observed at three sites in Austria (WB, WL and WR), in June 2018.

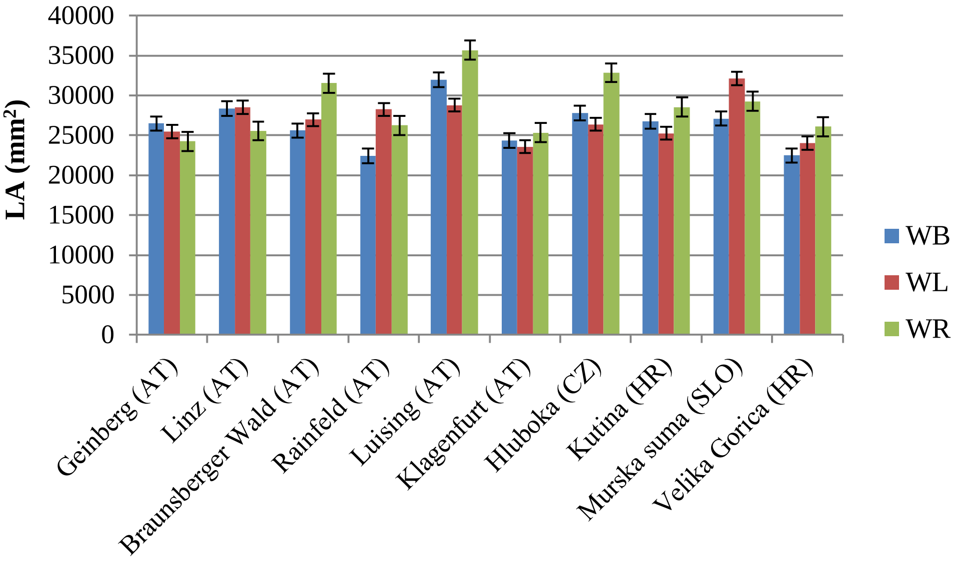

Table 21. Leaf area (mm^2), mean ± standard deviation, range (min, max) and Tukey test results for ten oak provenances grown at three sites in Austria, n = 270

Provenance (A)	Site (B)									Average
	WB			WL			WR			
Ge (AT)	26480±8095	(15723 – 36860)	Aa	25475±12693	(12938 – 56001)	Aa	24257±7203	(14385 – 40449)	Ba	25404
Li (AT)	28360±8646	(16444 – 43548)	Aa	28525±8721	(18755 – 45705)	Aa	25549±6082	(14570 – 36930)	ABa	27478
BW (AT)	25599±7805	(16203 – 37298)	Aa	26961±7309	(19060 – 44310)	Aa	31551±8762	(21362 – 44186)	Aa	28037
Ra (AT)	22426±5564	(14559 – 34038)	Aa	28250±5828	(18994 – 36141)	Aa	26244±5085	(19641 – 33226)	ABa	25640
Lu (AT)	31990±11823	(23369 – 60993)	Aa	28800±6598	(20517 – 42294)	Aa	35685±12414	(15720 – 51264)	Aa	32159
Kla (AT)	24359±5364	(17630 – 33375)	Aa	23586±7672	(14930 – 38951)	Aa	25351±6190	(18898 – 36403)	ABa	24432
Hlu (CZ)	27819±9677	(17822 – 50443)	Aa	26394±3509	(22729 – 31632)	Aa	32845±7943	(19383 – 45299)	Aa	29019
Ku (HR)	26747±10458	(15522 – 49096)	Aa	25276±10032	(13908 – 41533)	Aa	28548±8967	(17562 – 45662)	ABa	26857
MS (SLO)	27112±5842	(18277 – 36141)	Aa	32124±10200	(16813 – 47984)	Aa	29283±7431	(21098 – 41172)	ABa	29506
VG (HR)	22474±5588	(15516 – 32776)	Aa	24031±6055	(15763 – 34227)	Aa	26103±6963	(16827 – 37003)	ABa	24203
Average	26337			26942			28542			27273

Means followed by the same letter are not significantly different using Tukey's post-hoc test and with a 95.0% confidence level. Upper case letters refer to differences among sites (columns), while lower case letters refer to differences among provenances (rows).

4.2.2 Aspect ratio (AR)

Statistical analysis showed that leaf AR significantly differed (p = 1.51E-08) among the oak provenances compared in the trial. However, neither the site nor the provenance x site interaction, had a significant effect on the leaf aspect ratio (*Table 18*).

Table 18. ANOVA testing the effect of provenance and site on leaf aspect ratio (p<0.05 in bold)

	Df	MS effect	F	p-level
Provenance	**9**	**0.257**	**6.693**	**1.51E-08**
Site	2	0.110	2.863	0.059
Prov. x Site	18	0.033	0.872	0.613
Residuals	240	0.038		

The provenances with highest average AR were: Ku (HR) – 2.06, VG (HR) – 2.01, and both Lu (AT) and Hlu (CZ) with the same value of 1.96. The lowest AR recorded was from Ge (AT) oak provenance - 1.79 (*Table 19*). The site with the highest AR was WL – 1.92, followed by WB – 1.90, while the lowest AR was recorded at WR - 1.86 (*Table 19*).

Tukey test results showed no significant differences among the provenances observed at WL and WR sites. However, at the WB, AR from Ge (AT), Hlu (CZ), Ku (HR) and VG (HR) provenances, was significantly higher compared to Ra (AT) (*Table 19*).

According to the results, AR did not significantly differ among the three sites observed.

Figure 12. Leaf aspect ratio: mean and standard error for ten oak provenances observed at three sites in Austria (WB, WL and WR), in June 2018.

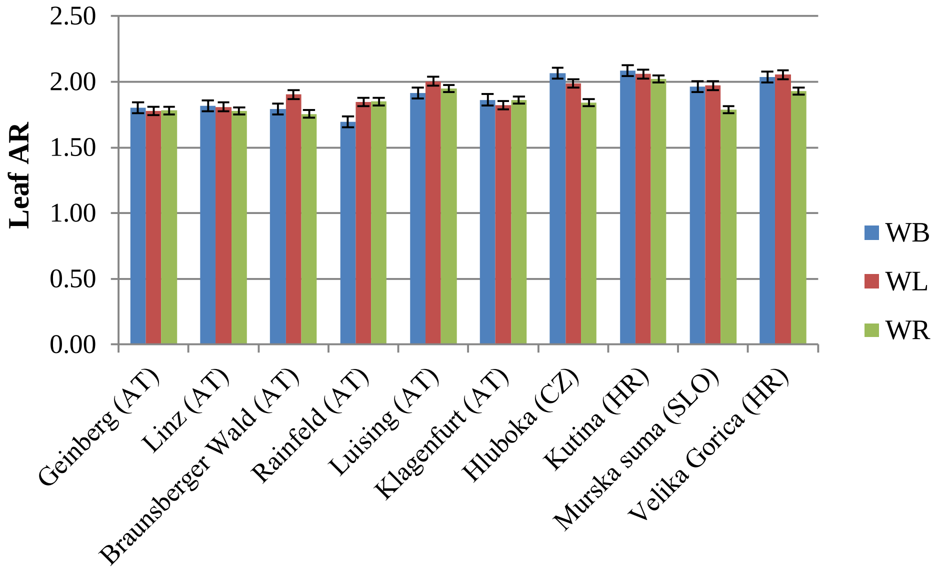

Table 19. Leaf aspect ratio: mean ± standard deviation, range (min, max) and Tukey test results for ten oak provenances grown at three sites in Austria; n = 270

Provenance	Site									Average
	WB			WL			WR			
Ge (AT)	1.80±0.22	(1.63 – 2.32)	Aa	1.78±0.12	(1.61 – 1.97)	Aa	1.78±0.10	(1.69 - 1.96)	Aa	1.79
Li (AT)	1.82±0.18	(1.60 – 2.11)	ABa	1.81±0.16	(1.48 - 2.08)	Aa	1.78±0.12	(1.51 – 1.90)	Aa	1.80
BW (AT)	1.79±0.21	(1.51 - 2.12)	ABa	1.90±0.17	(1.74 - 2.24)	Aa	1.76±0.21	(1.45 - 2.17)	Aa	1.82
Ra (AT)	1.70±0.12	(1.56 – 1.89)	Ba	1.85±0.12	(1.64 - 2.03)	Aa	1.85±0.21	(1.60 - 2.23)	Aa	1.80
Lu (AT)	1.91±0.17	(1.61 - 2.15)	ABa	2.00±0.15	(1.80 - 2.25)	Aa	1.95±0.28	(1.54 - 2.52)	Aa	1.96
Kla (AT)	1.86±0.20	(1.61 - 2.17)	ABa	1.82±0.25	(1.46 - 2.30)	Aa	1.86±0.17	(1.64 - 2.13)	Aa	1.85
Hlu (CZ)	2.06±0.18	(1.83 – 2.34)	Aa	1.99±0.27	(1.59 - 2.50)	Aa	1.84±0.17	(1.55 - 2.00)	Aa	1.96
Ku (HR)	2.09±0.30	(1.72 - 2.55)	Aa	2.06±0.18	(1.81 - 2.27)	Aa	2.02±0.28	(1.67 - 2.60)	Aa	2.06
MS (SLO)	1.96±0.23	(1.55 - 2.32)	ABa	1.97±0.16	(1.71 - 2.26)	Aa	1.79±0.17	(1.50 - 2.02)	Aa	1.91
VG (HR)	2.04±0.22	(1.77 - 2.36)	Aa	2.05±0.21	(1.71 - 2.41)	Aa	1.93±0.15	(1.73 - 2.21)	Aa	2.01
Average	1.90			1.92			1.86			1.89

Means followed by the same letter are not significantly different using Tukey’s post-hoc test and with a 95.0% confidence level. Upper case letters refer to differences among sites (columns), while lower case letters refer to differences among provenances (rows).

4.2.3 Specific leaf area (SLA)

SLA did not differ statistically among provenances (p = 0.25). However, SLA significantly differed among the sites (p = 4.20E-08) observed in this trial. Provenance x site interaction had no effect on the trait of interest (*Table 22*).

Table 22. ANOVA testing the effect of provenance and site on specific leaf area (p<0.05 in bold)

	Df	MS effect	F	p-level
Provenance	9	12.485	1.276	0.250
Site	**2**	**178.521**	**18.248**	**4.20E-08**
Prov. x Site	18	8.786	0.898	0.581
Residuals	240	9.783		

The three provenances with highest measured SLA were: MS (SLO) – 15.47, BW (AT) – 14.96 and VG (HR) – 14.76 mm^2/g, while lowest SLA came from Ra (AT) provenance, with 13.30 mm^2/g (*Table 23*). The site with the highest SLA was WL – 15.75, followed by WB – 14.43, while the lowest SLA (12.93 mm^2/g) was recorded was at WR site (*Table 23*).

According to the post-hoc Tukey test results, there were no significant differences among the provenances observed (*Table 23*).

SLA differed among sites and was usually lowest at the WR. Ge (AT) and Ku (HR) provenances had a statistically significantly higher SLA at WL site compared to the WR. Ra (AT) provenance had a significantly higher SLA at WB compared to the WR site (*Table 23*).

Figure 14. Specific leaf area (mm^2/g): mean and standard error for ten oak provenances observed at three sites in Austria (WB, WL and WR), in June 2018.

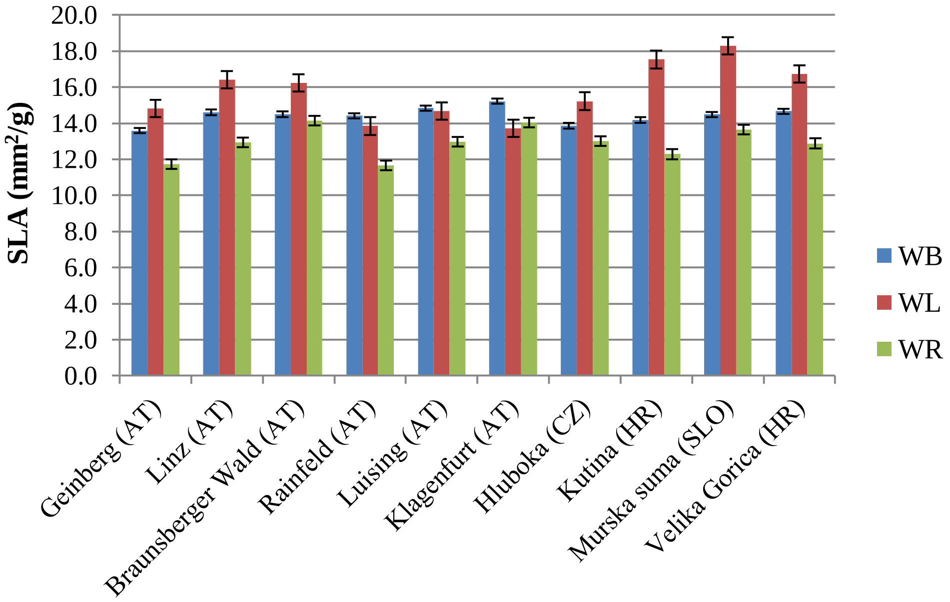

Table 23. Specific leaf area (mm^2/g): mean ± standard deviation, range (min, max) and Tukey test results for ten oak provenances grown at three sites in Austria; n = 270

Provenance (A)	Site (B)									Average
	WB			WL			WR			
Ge (AT)	13.59±1.56	(11.25 – 16.10)	Aab	14.81±3.61	(11.47 – 23.22)	Aa	11.73±1.03	(10.06 – 13.43)	Ab	13.38
Li (AT)	14.60±2.65	(10.78 – 18.09)	Aa	16.42±3.61	(10.67 – 21.35)	Aa	12.93±3.20	(8.60 - 18.06)	Aa	14.65
BW (AT)	14.50±2.43	(9.36 – 16.91)	Aa	16.23±3.84	(13.38 – 22.81)	Aa	14.14±4.20	(8.61 – 23.57)	Aa	14.96
Ra (AT)	14.41±1.19	(12.57 – 15.84)	Aa	13.84±2.54	(9.60 – 17.11)	Aab	11.66±1.75	(8.77 – 13.48)	Ab	13.30
Lu (AT)	14.84±3.58	(10.55 – 20.79)	Aa	14.68±2.58	(11.41- 18.77)	Aa	12.98±2.90	(9.68 – 19.59)	Aa	14.17
Kla (AT)	15.22±1.53	(13.00 – 17.90)	Aa	13.72±1.39	(11.37 – 15.27)	Aa	14.03±2.72	(10.06 – 17.88)	Aa	14.33
Hlu (CZ)	13.85±2.77	(9.74 – 19.09)	Aa	15.22±3.84	(10.97 – 22.47)	Aa	13.01±1.86	(10.20 – 16.09)	Aa	14.03
Ku (HR)	14.18±2.51	(9.85 - 19.10)	Aab	17.53±3.83	(12.67 – 25.04)	Aa	12.29±1.84	(9.47 – 14.68)	Ab	14.67
MS (SLO)	14.48±2.78	(11.11 – 19.24)	Aa	18.29±6.63	(11.30 – 31.12)	Aa	13.64±3.63	(9.36 – 20.89)	Aa	15.47
VG (HR)	14.66±1.98	(12.10 – 17.76)	Aa	16.73±5.83	(11.27 – 30.27)	Aa	12.88±2.35	(9.46 – 16.00)	Aa	14.76
Average	14.43			15.75			12.93			14.37

Means followed by the same letter are not significantly different using Tukey's post-hoc test and with a 95.0% confidence level. Upper case letters refer to differences among sites (columns), while lower case letters refer to differences among provenances (rows).

4.2.4 Leaf dry matter content (LDMC)

Statistical analysis showed that neither the oak provenance, nor the provenance x site interaction had a significant effect on the respective trait. However, LDMC significantly differed (p = 3.92E-09) among the sites observed in the trial (*Table 24*).

Table 24. ANOVA testing the effect of provenance and site on leaf dry matter content (p<0.05 in bold)

	Df	MS effect	F	p-level
Provenance	9	1685.531	0.736	0.675
Site	**2**	**48092.227**	**21.007**	**3.92E-09**
Prov. x Site	18	2893.819	1.264	0.213
Residuals	240	2289.342		

Three provenances with highest average LDMC were: VG (HR) - 425, Ku (HR) – 420 and Ge (AT) – 418 mg/g, while lowest LDMC was recorded from BW (AT) provenance, with 399 mg/g (*Table 25*). WR was the site with the highest LDMC - 425, followed by WB and slightly lower value of 421, while the lowest LDMC was recorded at WL - 390 mg/g.

Post-hoc Tukey test showed the following results in terms of LDMC variation among sites and provenances. At WB, Ku (HR) oak provenance had a significantly higher LDMC compared to Lu (AT). No significant differences in LDMC were found among oak provenances observed at WL and WR sites (*Table 25*).

LDMC differed among sites as well and was always lowest at WL, except in case of Lu (AT) and Kla (AT) provenances, where no significant differences were recorded (*Table 25*).

Figure 15. Leaf dry matter content (mg/g): mean and standard error for ten oak provenances observed at three sites in Austria (WB, WL and WR), in June 2018.

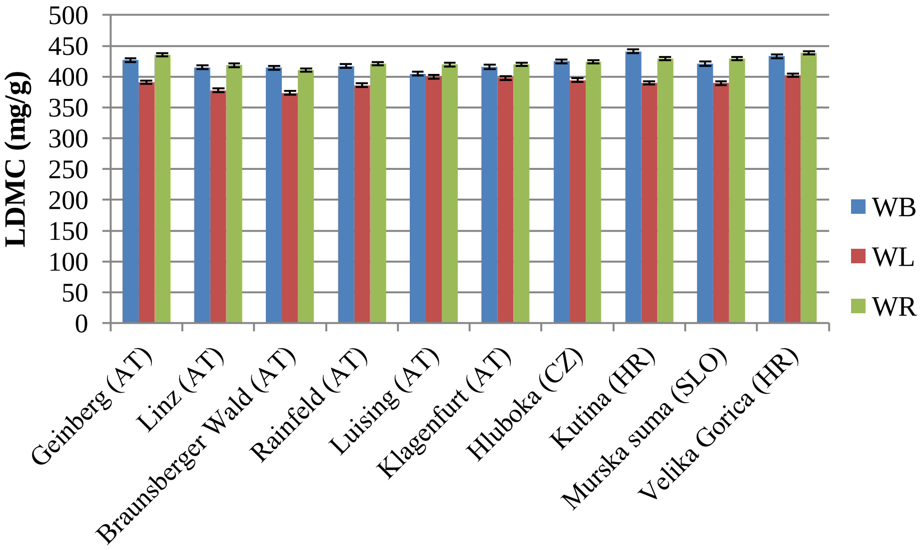

Table 25. Leaf dry matter content (mg/g): mean ± standard deviation, range (min, max) and Tukey test results for ten oak provenances grown at three sites in Austria; n = 265

Provenance (A)	Site (B)									Average
	WB			WL			WR			
Ge (AT)	427±143	(412 – 445)	Aba	391±24	(342 – 414)	Ab	435±12	(419 – 451)	Aa	418
Li (AT)	415±30	(378 – 462)	Aba	378±24	(347 – 419)	Ab	418±26	(372 – 448)	Aa	404
BW (AT)	414±20	(386 - 454)	Aba	374±35	(314 – 417)	Ab	410±40	(345 – 468)	Aab	399
Ra (AT)	417±9	(401 – 428)	Aba	386±27	(345 - 423)	Ab	421±21	(394 - 448)	Aa	408
Lu (AT)	405±34	(341 – 449)	Ba	400±23	(370 – 443)	Aa	420±38	(344 – 461)	Aa	408
Kla (AT)	416±17	(389 – 442)	Aba	398±13	(387 - 428)	Aa	420±30	(378 – 465)	Aa	411
Hlu (CZ)	425±142	(397 – 449)	Aba	394±32	(348 – 429)	Ab	424±16	(389 – 444)	Aa	414
Ku (HR)	441±16	(421 – 466)	Aa	390±26	(349 – 425)	Ab	430±20	(386 – 462)	Aa	420
MS (SLO)	421±17	(393 - 444)	Aba	389±172	(370 – 407)	Ab	429±32	(352 – 464)	Aa	413
VG (HR)	433±28	(400 – 492)	ABab	402±136	(366 - 429)	Ab	439±32	(404 - 492)	Aa	425
Average	421			390			425			412

Means followed by the same letter are not significantly different using Tukey's post-hoc test and with a 95.0% confidence level. Upper case letters refer to differences among sites (columns), while lower case letters refer to differences among provenances (rows).

4.3 Tree growth

4.3.1 Tree diameter (DBH)

Data analysis showed that DBH differed both among provenances and sites observed, whereas site effect (p = 1.96E-26) was stronger than the one of provenance (p = 3.21E-03). Provenance x site interaction had no effect on the respective trait (*Table 26*).

Table 26. ANOVA testing the effect of provenance and site on tree diameter (p<0.05 in bold)

	Df	MS effect	F	p-level
Provenance	**9**	**4.361**	**2.858**	**3.21E-03**
Site	**2**	**116.649**	**76.436**	**1.96E-26**
Prov. x Site	18	1.829	1.198	0.263
Residuals	241	1.526		

The three provenances with highest DBH were: Li (AT) – 5.99 Lu (AT) – 5.89 and Kla (AT) – 5.74 cm, while the lowest DBH was recorded from Ra (AT) provenance - 4.85 cm (*Table 27*). DBH was highest at WR site – 6.65, followed by WL – 4.96, while the lowest DBH was recorded at WB site – 4.50 cm (*Table 27*).

Post-hoc Tukey test results showed no significant differences among the provenances observed at WL and WR sites. At WB site however, both Austrian provenances Ge and Li had a significantly higher DBH compared to Ra (AT) and VG (HR) (*Table 27*).

DBH differed among sites and was always highest at WR. Ge (AT) oak provenance had significantly higher DBH at WR site, compared to WL, while BW (AT) and Kla (AT) provenances had higher DBH at WR, compared to the WB site. The rest of the provenances had a significantly higher DBH at WR, compared to both WB and WL sites (*Table 27.*).

Figure 16. Tree diameter (cm): mean and standard error for ten oak provenances observed at three sites in Austria (WB, WL and WR)

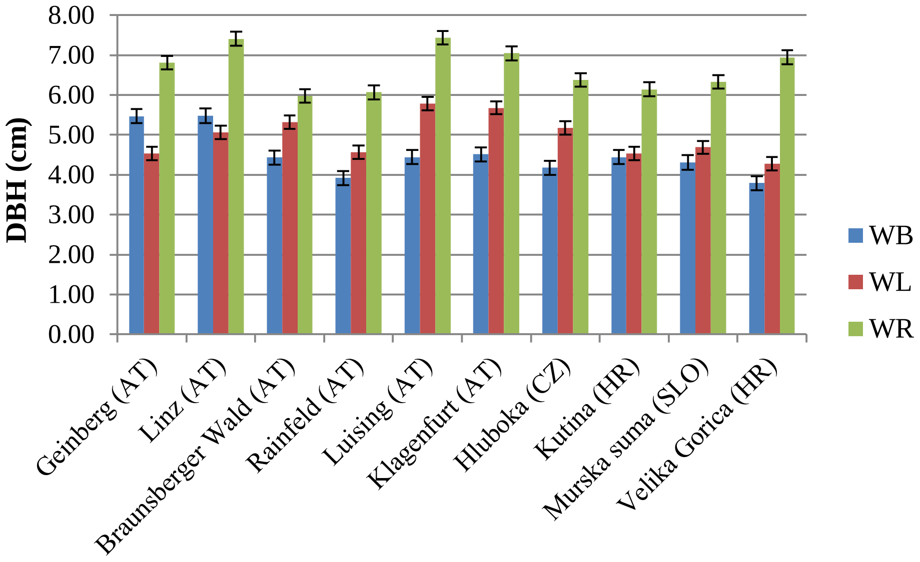

Table 27. Tree diameter (cm): mean ± standard deviation, range (min, max) and Tukey test results for ten oak provenances grown at three sites in Austria; n =271

Provenance (A)	Site (B)									Average
	WB			WL			WR			
Ge (AT)	5.5±0.9	(3.7 – 6.2)	Aab	4.5±1.1	(3.0 – 6.5)	Ab	6.8±1.6	(4.7 – 9.4)	Aa	5.6
Li (AT)	5.5±0.6	(4.6 - 6.5)	Ab	5.1±1.4	(2.9 – 7.2)	Ab	7.4±1.8	(4.0 – 10.0)	Aa	6.0
BW (AT)	4.4±1.3	(2.4 – 6.2)	ABb	5.3±1.4	(3.4 – 8.3)	Aab	6.0±1.0	(4.5 – 7.7)	Aa	5.2
Ra (AT)	3.9±1.1	(2.9 – 6.5)	Bb	4.6±1.3	(3.2 - 7.7)	Ab	6.1±1.1	(4.2 - 7.8)	Aa	4.9
Lu (AT)	4.4±0.5	(3.4 – 5.0)	ABb	5.8±1.5	(3.4 – 8.3)	Ab	7.4±1.4	(5.8 – 9.8)	Aa	5.9
Kla (AT)	4.5±1.2	(3.0 – 6.1)	ABb	5.7±1.2	(4.1 – 7.0)	Aab	7.0±1.8	(4.3 – 9.9)	Aa	5.7
Hlu (CZ)	4.2±0.7	(3.3 – 5.5)	ABb	5.2±1.0	(3.9 - 6.9)	Ab	6.4±1.1	(4.4 – 7.8)	Aa	5.2
Ku (HR)	4.4±0.7	(3.1 – 5.3)	ABb	4.5±0.9	(3.5 – 6.4)	Ab	6.1±1.8	(4.0 – 9.5)	Aa	5.0
MS (SLO)	4.3±1.2	(2.8 – 6.0)	ABb	4.7±0.7	(3.5 – 5.6)	Ab	6.3±1.5	(4.0 – 9.0)	Aa	5.1
VG (HR)	3.8±0.9	(2.4 – 5.2)	Bb	4.3±1.1	(3.1 – 6.9)	Ab	6.9±1.6	(5.1 - 10.0)	Aa	5.0
Average	4.5			5.0			6.7			5.4

Means followed by the same letter are not significantly different using Tukey's post-hoc test and with a 95.0% confidence level. Upper case letters refer to differences among sites (columns), while lower case letters refer to differences among provenances (rows).

4.3.2 Tree height

Tree height significantly differed among the oak provenances (p = 1.32E-09), but even more among the sites observed (p = 0). In addition, provenance x site interaction had a significant effect (p = 7.81E-03) on tree height as well (*Table 28).*

Table 28. ANOVA testing the effect of provenance and site on tree height (p<0.05 in bold)

	Df	MS effect	F	p-level
Provenance	**9**	**42508.250**	**7.457**	**1.32E-09**
Site	**2**	**552058.250**	**96.839**	**0**
Prov. x Site	**18**	**11758.389**	**2.063**	**7.81E-03**
Residuals	241	5700.807		

Trees from the following provenances were heighest: Li (AT) – 583 cm, Ge (AT) – 564 and Lu (AT) – 556 cm, while VG (HR) provenance had the lowest tree height, with only 462 cm (*Table 29*). Measured trees were heighest at WR site – 621, followed by WL – 498, while lowest height was recorded at WB – 476 cm (*Table 29*).

Post-hoc Tukey test showed the following differences in tree height among provenances and sites. At WB site, Ge (AT) and Li (AT) provenances were significantly higher than VG (HR). However, At WL, VG (HR) had a significantly lower tree height compared to Li (AT), Kla (AT) and Hlu (CZ) provenances. Further more, at WR site, Ku (HR) oak provenance had a significantly lower tree height compared to Ge (AT), Li (AT), and Lu (AT) (*Table 29*).

In addition, tree height significantly differed among the sites and was always highest at WR. Kla (AT) provenance had highest trees at WR compared to the WL site, but also significantly higher trees at WL site compared to WB (*Table 29*).

Figure 17. Tree height (cm): mean and standard error for ten oak provenances observed at three sites in Austria (WB, WL and WR)

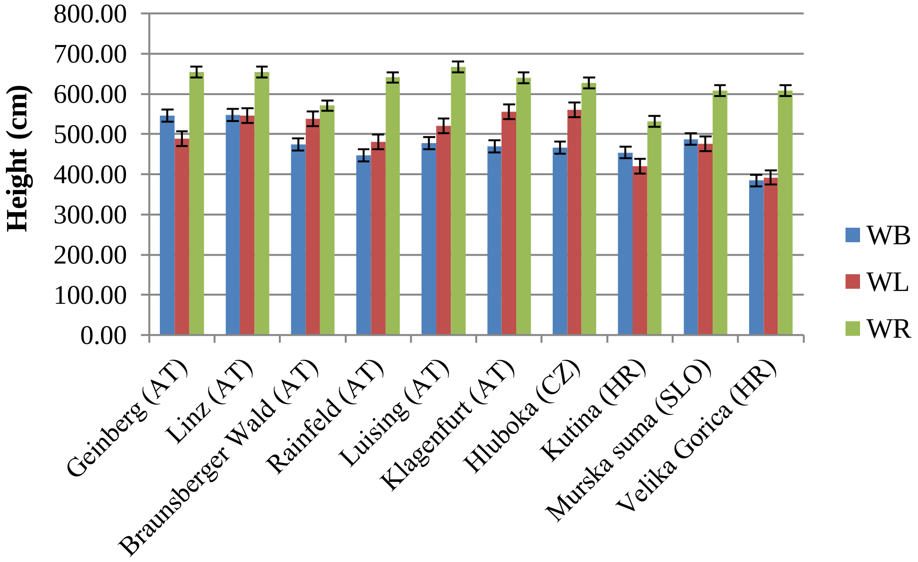

Table 29. Tree height (cm): mean ± standard deviation, range (min, max) and Tukey test results for ten oak provenances grown at three sites in Austria, in February 2017; n = 271

Provenance (A)	Site (B)									Average
	WB			WL			WR			
Ge (AT)	547±70	(470 – 690)	Ab	489±58	(400 - 590)	ABCb	655±67	(540 - 730)	Aa	564
Li (AT)	548±66	(460 - 690)	Ab	547±84	(350 - 650)	Ab	654 ±52	(570 – 700)	Aa	583
BW (AT)	474 ±92	(280 - 620)	ABb	538±59	(450 - 660)	ABab	571±74	(490 – 700)	ABa	528
Ra (AT)	448±86	(330 - 630)	ABb	481±120	(400 - 790)	ABCb	641±56	(570 - 740)	ABa	523
Lu (AT)	478±32	(430 - 530)	ABb	521±81	(400 – 700)	ABb	668±88	(560 - 810)	Aa	556
Kla (AT)	470±55	(360 - 540)	ABc	556±78	(430 - 650)	Ab	640±76	(540 - 760)	ABa	555
Hlu (CZ)	467±85	(340 - 610)	ABb	561±59	(470 - 640)	Aab	628±98	(400 - 760)	ABa	552
Ku (HR)	454±59	(350 - 530)	ABab	420±69	(320 - 520)	BCb	532±75	(430 - 630)	Ba	469
MS (SLO)	488±78	(380 – 600)	ABb	476±93	(370 - 650)	ABCb	609±65	(470 - 690)	ABa	524
VG (HR)	384±81	(250 - 520)	Bb	392±56	(320 – 470)	Cb	609±96	(490 – 750)	Aba	462
Average	476			498			621			532

Means followed by the same letter are not significantly different using Tukey’s post-hoc test and with a 95.0% confidence level. Upper case letters refer to differences among sites (columns), while lower case letters refer to differences among provenances (rows).

4.4 Correlations and regressions

For correlations among traits, data from individual trees (n = 252 – 270) were used. For correlations between traits and the climate at the location of origin, we used the mean of all measures from each provenance (n = 10) since using multiple datapoints from one provenance would present pseudo-replication. Because of the much lower number of datapoints, a much stronger relationship is necessary for the correlations to be significant, compared to correlations among traits. For bioclimatic data, we chose mean annual temperature (MAT) and annual precipitation (MAP). All correlations are summarized in *Table 30*.

Vessel area was strongly negatively correlated with VD (r = -0.598, p = 7.4E-26) and WC (r = -0.190, p = 0.002), but positively with PV (r = 0.473, p = 1.9E-15) and K_h (r = 0.401, p = 3.6E-11). Vessel density was significantly positively correlated with PV (r = 0.361, p = 3.5E-09) and K_h (r = 0.281, p = 5.7E-06) and also negatively with WD (r = -0.184, p = 0.003). Vessel fraction had a strong influence on K_h (r = 0.810, p = 8.0E-60). In addition, theoretical hydraulic conductivity was negatively correlated with WD (r = -0.188, p = 0.003). We found a significant correlation between WD and WC (r = 0.278, p = 7.3E-06).

Among leaf traits, the only significant correlation was between SLA and LDMC (r = -0.732, p = 8.9E-46). There was no correlation between wood and leaf traits.

Only a few traits appeared to be correlated with the tree size and thus growth. One of them was WD, which was correlated both with DBH (r = 0.182, p = 0.004) and height (r = 0.197, p= 0.002). There was a negative correlation between leaf AR with both DBH (r = -0.132, p = 0.030) and tree height (r = -0.186, p = 0.003). SLA had a significant negative correlation with both growth parameters, stronger for tree height (r = -0.242, p = 5.8E-05), and weaker for DBH (r = -0.198, p = 0.001). Moreover, LDMC was correlated with both traits, positively with DBH (r = 0.177, p = 0.004) as well as with tree height (r = 0.187, p = 0.002). As anticipated, here was a strong positive correlation between the tree diameter and tree height (r = 0.793, p = 8.1E-60). This relationship confirms that these two growth estimations strongly depend on each other.

Table 30. Pearson-Correlation of the wood/leaf traits and tree size parameters, measured for oak provenances in the trial. Correlation coefficient is in the left bottom half, while p-value is presented in the right top half; Significant correlations on the 0.05 level are underlined, **bold** on 0.01 level, and **both** on the 0.001 level of significance

	VA	*VD*	*PV*	*Kh*	*WD*	*WC*	*LA*	*AR*	*SLA*	*LDMC*	*Diameter*	*Height*	*MAT*	*MAP*
VA	1	7.4E-26	1.9E-15	3.6E-11	0.388	0.002	0.217	0.366	0.449	0.719	0.692	0.819	0.185	0.085
VD	**-0.598**	1	3.5E-09	5.7E-06	0.003	0.064	0.498	0.115	0.430	0.668	0.969	0.354	0.467	0.917
PV	**0.473**	**0.361**	1	8.0E-60	0.095	0.083	0.370	0.451	0.939	0.814	0.762	0.450	0.040	0.313
Kh	**0.401**	**0.281**	**0.810**	1	0.003	0.875	0.148	0.293	0.982	0.155	0.623	0.553	0.215	0.484
WD	0.055	**-0.184**	-0.105	**-0.188**	1	7.3E-06	0.960	0.723	0.283	0.095	0.004	0.002	0.645	0.346
WC	**-0.190**	0.117	-0.109	-0.010	**0.278**	1	0.729	0.075	0.172	0.094	0.767	0.812	0.978	0.614
LA	0.078	-0.043	0.057	0.091	-0.003	0.022	1	-0.089	0.102	0.123	0.429	0.377	0.236	0.215
AR	-0.057	0.100	0.048	0.066	0.022	0.112	0.143	1	0.977	0.759	0.030	0.003	0.016	0.667
SLA	0.048	-0.050	-0.005	-0.001	-0.068	0.086	-0.100	-0.002	1	8.9E-46	0.001	5.8E-05	0.047	0.257
LDMC	-0.023	0.027	0.015	-0.091	0.106	-0.106	-0.095	0.019	**-0.732**	1	0.004	0.002	0.198	0.052
Diameter	-0.025	0.002	-0.019	-0.031	**0.182**	-0.019	0.048	-0.132	**-0.198**	**0.177**	1	8.1E-60	0.946	0.505
Height	0.015	-0.059	-0.048	-0.038	**0.197**	-0.015	0.054	**-0.186**	**-0.242**	**0.187**	**0.793**	1	0.445	0.503
MAT	0.249	0.138	0.378	0.233	-0.088	0.005	0.223	0.438	0.365	0.242	-0.013	-0.145	1	0.719
MAP	-0.320	-0.020	-0.190	-0.133	-0.178	-0.096	-0.233	-0.082	-0.214	0.358	0.127	0.127	0.068	1

Legend: VA - vessel area; VD - vessel density; K_h – theoretical hydraulic conductivity; WD - wood density; WC - water content; AR – aspect ratio; LA - leaf area; SLA – specific leaf area; LDMC – leaf dry matter content; MAT – mean annual temperature; MAP – mean annual precipitation

Correlations with climate at the provenance locations

The temperature (MAT) was significantly correlated with PV (r = 0.378, p = 0.040), AR (r = 0.438, p = 0.016) and SLA (r = 0.365, p = 0.047).

No significant correlations were found between the precipitation rates (MAP) and the traits analyzed (*Table 26*), but VA marginally significantly (p = 0.085) decreased and LDMC increased (p = 0.052) with precipitation.

Because only averages were taken into account for the correlations between traits and bioclimatic variables, these marginal significance were expected.

5. DISCUSSION

5.1 Critical reflection on methods

The 250 years of common garden trials (Langlet 1971, Morgenstern 1996) have given us plenty of results and knowledge. Along with the extensive hybridization and tree breeding experience, selection is continuousy in progress of development. Even though *Quercus* is not as amenable to in vitro propagation as e.g. *Populus*, selection of oak traits is improving constantly, due to marker-assisted, transgenic breeding. Despite the long generation times, a few linkage maps have already been developed and are being utilized for QTL's for traits of interest in oak breeding (Aldrich & Cavender-Bares, 2011).

We underline that our study reflects the differences among oak provenances accumulated over 11 years of growth, but examines the differences in their wood and leaf traits measured over just one growing season. Even though a one-time evaluation was suitable for the scope of the study, inter-annual variations may have affected the results. In order to obtain a more complete perspective of trait plasticity in response to climate at the sites, several field seasons of monitoring would be required.

The entire climate – genotype relationship of *Quercus* (nearly all species in Europe) might be questioned regarding its origin, if we consider the expansion of tree breeding over the last century. Through time, foresters have interfered with the local genotypes by planting the non-local ones as well as breeding; hence their origins are not so distinct anymore. Due to many seed being transported and possibly mixed, the actual origin of nearly all trees is disputable. This mixture in European forests makes provenance studies somewhat problematic and not entirely reliable.

5.2 Phenotype and genotype dominance

Summary of all traits investigated in the provenance trial is represented in the following table. It is clear that for most of the wood traits studied in the trial, provenance effect was more significant than the one of site, whereas for leaf traits analyzed, provenance and site effect were equally distributed among the traits. For the tree growth, both provenance and site had a significant effect on the respective traits. Prov. x site interaction was usually not relevant for the traits of interest, except in case of WD and tree height.

Table 31. Significance (p-values) of provenance, site and prov. x site interaction, for all traits tested with ANOVA

Traits		**Provenance**	**Site**	**Prov. x Site**	**N**
Wood	VD	0.323	0.836	0.761	252
	VA	**9.23E-03**	0.222	0.938	252
	PV	**4.91E-05**	**3.91E-03**	0.066	252
	K_h	**3.47E-04**	0.772	0.246	252
	WD	0.077	**1.77E-22**	**2.77E-05**	252
	WC	**4.39E-03**	**1.87E-05**	0.326	252
Leaf	AR	**1.51E-08**	0.059	0.613	270
	LA	**8.06E-03**	0.173	0.815	270
	SLA	0.250	**4.20E-08**	0.581	270
	LDMC	0.675	**3.92E-09**	0.213	265
Growth	DBH	**3.21E-03**	**1.96E-26**	0.263	271
	Height	**1.32E-09**	**0**	**7.81E-03**	271

Effects of provenance and site on functional traits have been reported in numerous study cases (Robson et al. 2012; Eilmann et al. 2014; McKown et al. 2014; George et al. 2017; Rungwattana et al. 2018; etc.) Trait comparison in oak provenances indicates the influence of genetic predisposition and local environmental factors on the performance of these provenances under different site conditions. Significant provenance effect implies strong underlying genotype dominance. Site effect on the other hand, implies the phenotype is not strongly inherited, but modified by the local climate. Provenance trials that find a significant site effect, point to evolution in response to geographically variable selection. In their study on phenotypic trait variation and genetic structure in *Populus trichocarpa*, McKown et al. (2014) is pointing to the broad-sense heritability as a measurement of the overall population genetic structure. Heritability is explained as the proportion of the variation explained by the genotype (i.e. provenances). It can vary from 0 to 1, whereas values closer to 0 suggest low heritability, and values closer to 1 suggest more strong heritability. Therefore, low trait heritability indicates that phenotypic variation is higher than genotypic one (McKown. 2014).

In the beech provenance trial of Eilmann et al. (2014), they used variation in radial growth to account for environmental differences between the years. However, the theory that provenance performance is related to the genetic control was evidentially supported with a Bulgarian provenance (“Gotze Delchev”) from a drought-prone place of origin, which showed highest drought tolerance, earlier phenology and high photosynthetic activity, among others tested in the trial. Moreover, the consistency of its flushing under various climatic conditions for over 3 years indicates a very strong genetic control of leaf development. The

Bulgarian provenance “Gotze Delchev” and its ability to cope with drought was previously reported in a study by Robson et al. (2012), where it was demonstrated that provenances from Mediterranean and dry continental conditions at the south of Europe are among the least sensitive to water scarcity.

5.3 Trait variation

If we take into account the coefficient of variation (*Table 5*, see Chapter 4) which was 26.1% for VD, our results are consistent with other results (26.4%), in a study investigating the trait evolution in tropical rubber tree (Rungwattana et al. 2018). The mentioned study focused on wood trait assessment, while plenty of results seemed consistent to ours. CV of both VA and PV were very similar to the mentioned study. Further, K_h was very high in both studies, ranging from 35-38%. Our calculated WD was very low (7.4%) which was in accordance (<7%) with compared studied by Rungwattana et al. (2018). However, these two studies are not entirely comparable, since Rungwattana et al. investigated only the provenance effect and observed the traits at a single site, while we had three locations in total. Therefore, our CV should have been higher, due to additional variation between sites.

In a study by Oskunkoya et al. (2007), WD exhibited CV of 14.7%. In contrast, Poorter et al. (2010) found 66–89% of the total variation explained by WD. Then again, both previously mentioned studies were designed on multiple-species comparison and thus might not be perfectly comparable to ours.

Only growth showed substantial differences in both Rungwattana's and our results, ranging from 17.06% in study on tropical rubber tree, to 29.4% in the *Quercus* provenance trial.

5.3.1 Wood traits

Not many provenance trials were designed on intraspecific adaptations of wood traits, because more studies focused on foliar traits only. However, many studies suggest that most of the wood functional traits are predominantly under genetic predisposition. In their tree-ring study in beech, Eilmann et al. (2014) proved this hypothesis for a few wood properties, such as tree-ring width, mean vessel area, cumulative vessel area and conductive area. In their beech provenance trial from 2016, Hajek et al. confirmed the underlying genetic dominance for wood traits - both anatomical (vessel density) and hydraulic traits (hydraulic conductance), as well as for some foliar ones (mean leaf size). In their research, they found the traits to be closely related to the climate of the provenance origin, indicating the local adaptation and clear dominance of the genotype. However, this might be due to looking into entire range of beech from different locations.

Sometimes wood structure between the trees of different provenances might be similar when they are planted at the same site, even if their wood structure clearly differs at the places of origin (Zobel & van Buijtenen, 1989), which could explain the absence of provenance effect on few traits of this study, such as VD and WD.

Vessel density

The absence of provenance effect on VD was previously reported in a beech provenance demonstrated by Eilmann et al. (2014), which was in consistence with the findings of our study.

According to Hajek et al. (2016), vessel density is a trait significant for the adaptation of hydraulic system to different climates. In their study, none of the wood anatomical traits were in relation to the embolism resistance nor was the trade-off between hydraulic conductivity and embolism present. However, in our study we did find a strong positive correlation between VD and K_h. Provenances with highest VD, such as Kla and BW, also recorded highest K_h. In the mentioned study, VD is suggested to strongly increase with tree height, which was contrary to our results, where no such correlation was found. The design of the two studies differ because beech provenances were planted at one site only, and oak provenances were observed at tree sites.

Vessel area

In the study by Eilmann et al. (2014), provenance effect was significant at the 99% level accounting the mean vessel area. They observed several wood properties related to vessel size and found those were predominantly under genetic predisposition, which corresponds to the findings of our study.

In a beech provenance trial, Hajek et al. (2016) found a Spanish provenance more prone to dry sites with larger vessels. Even though this was contrary to expectation, it was not contributing to the better growth performance of this provenance. In our study, the lowest VA was recorded from Hlu provenance, which comes from the place with lowest precipitation (764 mm/year, *Table 4*). This observation is confirmed by a marginal correlation between VA and MAP ($p = 0.085$).

Vessel fraction

Lowest PV was recorded from Hlu provenance, which is probably related to the low VA found in this provenance as well. It seems that highest PV was recorded at the driest site WB, while most humid site WL recorded the lowest trait value, and this is probably related to the trade-off between hydraulic conductivity and hydraulic safety. It is suggested that smaller vessel fraction would also imply lower hydraulic efficiency and this is clearly demonstrated in case of Hlu provenance, which recorded the lowest K_h.

In addition, PV was positively correlated with the mean annual temperature from the provenance place of origin.

Theoretical hydraulic conductivity

In their provenance study, Hajek et al. (2016) report a significant connection between beech provenances of very dry climate origins and very wide vessels formation, resulting in high K_h compared to the other provenances when grown at humid sites with high precipitation rates. We did not find a correlation between K_h and MAT of the site of origin, but the two provenances from the lowest MAP (Lu and BW, *Table 4*) did have the highest K_h values (*Table 13*). Moreover, highest K_h was recorded at the driest site (WB).

In the study on growth response of *Q. ilex* to severe drought, Corcuera et al. (2003) suggest that water stress during the summer droughts may negatively affect hydraulic conductivity of the stems, besides reducing the plant growth. In addition, Robson et al. (2012) report a strong among-provenance correlation between tree height and K_h in the early summer. This was supported by the fact that provenances with lower hydraulic conductance also had lower water-use-efficiency as inferred from their more negative leaf δ13C. However, this was not the case in our findings, where K_h was not reduced at the driest sites.

Wood density & Water content

In their study, Mosedale et al. (1996) report that wood density was under the strong genetic control in both *Q. petraea* and *Q. robur*. WD was genetically controlled in a study by Corcuera et al. (2011) as well. However, in our findings, provenance effect had only a marginally significance ($p = 0.077$) on WD, but its influence was present through the significant provenance x site interaction effect.

Across species, WD was found to be negatively related to growth (Osunkoya et al. 2007; Chave et al. 2009; Poorter et al. 2010). Chave et al. (2009) explained the possible mechanism, that is, higher construction costs and lower xylem conductance influence lower photosynthetic potential and thus higher WD. We also found a negative correlation of wood density with both DBH and tree height. Study by Osunkoya et al. (2007) suggests that the negative correlation of WD with DBH increment implies that low WD allows for rapid growth. If we associate WD to growth (Poorter et al. 2010), whereas low WD indicates fast growth, we conclude that trees had grown fastest at WL site, which was also the most humid site in the trial. In contribution to the mentioned theory, our WD was highest at the driest site WB, where growth was reduced and we may assume that this allowed for investment in wood density instead.

However, this study might not be the most relevant one, since it investigates the functional traits and growth-mortality trade-off in tropical trees, thus including the multi-species comparison and not oak exceptionally.

Because provenance effect was absent for WD trait, it is not surprising that there was no correlation between this trait and climate at the place of origin. In their beech provenance trial, Aranda et al. (2015) also report that wood density was not related to the climate of origin. Moreover, WC had no correlations with bioclimatic data either.

As anticipated, there was a trade-off between WD and WC, as well as a significant correlation found between them. Since volumetric fraction of the cell-wall increases with wood (cellulose and lignin), the remaining space filled with either water or air, must decline accordingly (Osunkoya et al. 2007) due to this physical constraint. In our provenance trial, sites with lowest WD were at the same time sites with highest WC, and vice versa. Provenances with highest WC were Kla, Lu and BW subsequently, each originating from Upper Austria, and were apparently those that could have stored water the best. Lowest WC was recorded from VG, provenance from Croatia where mean annual temperature was higher (10.5ºC, *Table 4*).

5.3.2 Leaf traits

In a provenance trial conducted by Vitasse et al. (2009), *Q. petraea* was investigated among other species, and it appeared that provenance effect had influenced both on leaf phenology and growth. Also, senescence had occurred later in populations from colder provenances. Moreover, there was a positive correlation between growing-season length and growth rate, that is, oak trees that flushed earlier would also start the senescence earlier. Phenology was not investigated in our trial, but some possible patterns might have been explained by it.

Leaf area

Only provenance had affected the LA trait variation in the study. However, it seems that some pattern remains hidden here, since no correlation was found neither with MAT nor MAP. Highest LA was recorded from provenances, very variable in both temperature (7.4-10.1ºC) and precipitation (696-810 mm/year). Lowest LA was from provenance at the far south-edge of the provenance trial range.

Aspect ratio

We found a significant correlation between AR and the temperature from the provenance place of origin. The importance and meaning of this might be speculated in the following direction. Firstly, higher AR implies that leaves are more elongated. Given that the boundary layer conductance for convective heat exchange increases with decreasing of the leaf size, it can be suggested that more elongated leaves heat up less, which could be the explanation for this correlation. Accordingy, the lowest AR was recorded from Ge provenance with one of the lowest temperature at the place of origin (8.7 ºC, *Table 4*).

The chance of finding the correlation with climate was lower with n = 10 than if all trees were taken into account. We expected more correlation with MAP because rainfall gradient in the trial was substantially higher than the temperature range. However, temperature seemed to have higher effect on traits.

Specific leaf area

In our case, SLA was affected only by the site and was highest at the most humid one (WL). In his global-scale study on different leaf traits in trees and shrubs, Niinemets (2001) reported thats SLA was decreasing in more arid environments. Since few *Quercus* species were included in this study, we can conclude it is comparable to ours. However, these results are in contrast to the results of Cavender-Bares and Ramirez-Valiente (2017). In their research, SLA decreased at sites with higher precipitation-potential evapotransporation and was lowest at the wettest site.

If phenological traits was also investigated in this trial, maybe it would have provided further explanation regarding the site variation in SLA. In the study of McKown (2014), SLA differed significantly between the spring (earlier) leaves that were affected by their current phenological phase. However, once all leaves were fully developed (summer leaves), SLA was more uniform at site, which implies that site effect was also influenced by phenology.

Leaf dry matter content

Only site effect appeared significant for the trait variation in LDMC, while lowest value was recorded at the most humid site WL. This demonstrates a clear trade-off between SLA and LDMC, which we also confirmed by a strong negative correlation between these two traits.

5.3.3 Tree growth

In general, there is a strong relationship between wood traits and tree size (Lachenbruch, Moore & Evans, 2011). However, only WD from all the wood traits investigated was found as significantly correlated to the tree diameter and height. As anticipated, we found a strong positive correlation between DBH and tree height.

Results showed that both traits were significantly affected by both provenance and site. The best achievement was shown by Austrian provenances Li, Lu, Kla and Ge. Additionally, no correlation with MAT nor MAP was determinated.

5.4 Application for forest management

Trees are key species in most terrestrial ecosystems and provide a substantial role in the global carbon cycle. Nowadays, they suffer great challenges imposed by on-going climate change. Forest ecosystems are severely impaired by water availability, and while extreme climate events are expected to intensify in the future, tree populations are already jeopardized by drought and high air temperatures (Bréda et al, 2006). Large-scale tree declines will be substituted by artificial regeneration of the forests in greater amounts than before (Čehulić et al. 2019). According to Alberto et al. (2013), the intra-specific variation in functional traits, phenology and stress response represents the fundamental part of adaptive forest management. Furthermore, it has a substantial role in estimating the prospective species' range shifts, local adaptation of populations and moreover, the suitability of forest reproductive material that will be planted in the future (Alberto et al, 2013).

The aim of this research was to test the intra-specific wood and leaf trait variation in *Quercus robur*, at different environmental conditions. Our study on ten oak provenances from Europe revealed that most of the wood anatomical and leaf traits investigated are under the genetic control, according to the significant distinction among provenances, as well as in terms of their relation with climatic conditions at location of provenance origin.

Phenotypic trait assessment in oak common garden experiment has shown that most of functional traits investigated show high degree of phenotypic plasticity in response to different locations. In addition, provenance trial results are witnessing to local adaptation of *Q. robur*, which reflects in adaptive differentiation of functional traits in accordance with local environmental conditions at the trial sites.

High degree of intra-population genetic variability may indicate that species has a high potential capacity to overcome future changes in climate, primarily more frequent drought events. Therefore, special attention should be paid towards productive and possibly drought resistant provenances, as a basis for future breeding activities. Our analysis suggests that *Q. robur* possesses high genetic variation among and within provenances that can be used for breeding programs in the future. The present results support the importance of considering the existing genetic variation among oak provenances for the purpose of forest management and planning. Clearly, more provenance trial results and empirical information are needed to interpret the intra-specific variation in oak provenances and require further elucidation.

6. LIST OF REFERENCES

6.1 Literature

Abrams M.D. (1994): Genotypic and phenotypic variation as stress adaptations in temperate tree species: a review of several case studies. Tree Physiology, 14: 833-842.

Abrams M.D., Kubiske M.E. (1990): Leaf structural characteristics of 31 hardwood and conifer tree species in Central Wisconsin: influence of light regime and shade tolerance rank. Forest Ecology and Management, 31: 245-253.

Alberto F.J. ., Aitken S.N., Alía R., González-Martínez, S.C., Hänninen H., Kremer A., ... Savolainen O. (2013): Potential for evolutionary responses to climate change – evidence from tree populations. Global Change Biology, 19(6): 1645-1661.

Aldrich P.R. and Cavender-Bares J., (2011.): Genomics and breeding of oaks and their slightly less-domesticated wild oak relatives. In: C. Kole, editor. Wealth of Wild Species: Genetic, Genomic and Breeding Resources. Springer-Verlag, New York, pp 89-130.

Anderson M.K. (2007): Indigenous uses, management, and restoration of Oaks of the far western United States. Technical Note No 2. NRCS, National Plant Data Center, Washington DC.

Aranda I., Cano F.J., Gascó A., Cochard H., Nardini A., Mancha J.A., ... Sánchez-Gómez D. (2015): Variation in photosynthetic performance and hydraulic architecture across European beech (*Fagus sylvatica* L.) populations supports the case for local adaptation to water stress. Tree Physiology, 35: 34–46.

Barrón E., Averyanova A., Kvaček Z., Momohara A., Pigg K.B., Popova S., Postigo-Mijarra J.M., Tiffney B.H., Utescher T., Zhou Z.K. (2017): The Fossil History of Quercus. In: Oaks Physiological Ecology. Exploring the Functional Diversity of Genus *Quercus* L. Springer, Switzerland, pp 39-107.

Bostad P.V., Reich P., Lee T. (2003): Rapid temperature acclimation of leaf respiration rates in *Quercus alba* and *Quercus rubra*. Tree Physiology, 23: 969-976.

Blue M.P., Jensen R.J. (1988): Positional and seasonal variation in oak (*Quercus;* Fagaceae) leaf morphology. American Journal of Botany, 75: 939-947.

Bréda, N.; Huc, R.; Granier, A.; Dreyer, E. (2006): Temperate forest trees and stands under severe drought: A review of ecophysiological responses, adaptation processes and long-term consequences. Annals of Forest Science, 63: 625–644.

Britton N.L., Brown A. (1913): An illustrated flora of northern United States, Canada and British possessions. Scribner & Sons, New York.

Brodribb T.J., Feild T.S. (2000): Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from New Caledonian and Tasmanian rainforests. Plant, Cell & Environment, 23: 1381–1388.

Bruschi P., Grossoni P., Bussoti F. (2003): Within- and among- tree variation in leaf morphology of *Quercus petraea* (Matt.) Liebl natural populations. Trees: Structure and Function, 17: 164-172.

Bucci S.J., Goldstein G., Meinzer F.C., Scholz F.G., Franco A.C., Bustamante M. (2004): Functional convergence in hydraulic architecture and water relations of tropical savanna trees: from leaf to whole plant, Tree Physiology, vol. 24, pp 891-899.

Burger W.C. (1975): The species concept in *Quercus*. Taxon 24: 45-50.

Burns R.M., Honkala B.H. tech.coords (1990): Silvics of North America: 2. Hardwoods, vol 654, Agriculture handbook. US Department of Agriculture, Forest Service, Washington DC, USA.

Camus A. (1936–1938): Les Chênes. Monographie du genre Quercus. Tome I. Genre Quercus, sous-genre Cyclobalanopsis, sous-genre Euquercus (sections Cerris et Mesobalanus). Texte. Paul Lechevalier, Paris.

Cavender-Bares J., Holbrook N.M. (2001): Hydraulic properties and freezing–induced cavitation in sympatric evergreen and deciduous oaks with contrasting habitats. Plant, Cell & Environment, 24: 1243-1256.

Cavender-Bares J., Ramírez-Valiente J.R. (2017): Physiological Evidence from Common Garden Experiments for Local Adaptation and Adaptive Plasticity to Climate in American Live Oaks (Quercus Section Virentes): Implications for Conservation Under Global Change. In: Oaks Physiological Ecology. Exploring the Functional Diversity of Genus *Quercus* L. Springer, Switzerland, pp 107-137.

Chassé B. (2016): Eating acorns: what story do the distant, far and near past tell us, and why. International Oaks, 27: 107–135.

Chave J., Coomes D., Jansen S., Lewis S.L., Swenson N.G., Zanne A.E. (2009): Towards a worldwide wood economics spectrum. Ecology Letters , vol. 12, pg. 351-366.

Chira K., Teissedre P.L. (2015): Chemical and sensory evaluation of wine matured in oak barrel: effect of oak species involved and toasting process. European Food Research Technology, 240: 533–547.

Corcuera L., Camarero J.J., Gil-Pelegrín E. (2003): Effects of a severe drought on *Quercus ilex* radial growth and xylem anatomy. Trees, 18: 83–92.

Corcuera L., Cochard H., Gil-Pelegrín E., Notivol E. (2011): Phenotypic plasticity in mesic populations of *Pinus pinaster* improves resistance to xylem embolism (P50) under severe drought. Trees, 25: 1033–1042.

Cochard H., Tyree M.T. (1990): Xylem dysfunction in *Quercus*: vessel sizes, tyloses, cavitation and seasonal changes in embolism. Tree Physiology, 6: 393–407.

Cornelissen J.H.C., Castro Diez P., Hunt R. (1996): Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. Journal of Ecology, 84: 755-765.

Čehulić I., Sever K., Bogdan I.K., Jazbec A., Škvorc Ž., Bogdan S. (2019): Drought Impact on Leaf Phenology and Spring Frost Susceptibility in a *Quercus robur* L. Provenance Trial. Forests, 10(1): 50.

De'Athe R., Barnett C., Cooke N.N., Grimm J.M., Jones G.P., Leivers M., McKinley J.I., Pelling R., Schuster J., Stevens C.J., Foster W., James S.E. (2013): Early iron age metalworking and Iron Age/early Romano-British settlement evidence along the Barton Stacey to Lockerley gas pipeline. Proceedings of the Hampshire Field Club Archaeological Society, 68: 29–63.

Denk T., Grimm G.W., Manos P.S., Deng M., Hipp A.L. (2017): An updated infrageneric classification of the oaks: Review of the previous taxonomic schemes and synthesis of evolutionary patterns. In: Oaks Physiological Ecology. Exploring the Functional Diversity of Genus *Quercus* L. Springer, Switzerland, pp 13-39.

Eckert A.J., Dyer R.J. (2012): Defining the landscape of adaptive genetic diversity. Molecular Ecology 21: 2836-2838.

Eilmann, B., Sterck F., Wegner L., de Vries S.M.G., von Arx G., Mohren G.M.J., den Ouden J., Sass-Klaassen U. (2014): Wood structural differences between northern and southern beech provenances growing at a moderate site. Tree Physiology, 34(8): 882-893.

Escudero A., & Valladares F. (2016): Trait-based plant ecology: Moving towards a unifying species coexistence theory. Oecologia, 180: 919-922.

Fagan B.M. (2004): Before California: an archaeologist looks at our earliest inhabitants. Roman Altamira, Lanham MD.

Gale M.R., Grigal D.F. (1987): Vertical root distributions of northern tree species in relation to successional status. Canadian Journal of Forest Research, 17: 829-834.

García-Gómez E., Pereira-Sieso J., Ruiz-Taboada A. (2002): Aportaciones al uso de la bellota como recurso alimenticio por las comunidades campesinas. Cuadernos de la Sociedad Española de Ciencias Forestales, 14: 65–70.

Giachi G., Capretti C., Lazzeri S., Sozzi L., Paci S., Lippi M.M., Macchioni N. (2017): Identification of wood from Roman ships found in the docking site of Pisa (Italy). Journal of Cultural Heritage, 23: 176–184.

Gil-Pelegrín E., Peguero-Pina J.J., Sancho-Knapik D., (2017): Oaks and People: A Long Journey Together. In: Oaks Physiological Ecology. Exploring the Functional Diversity of Genus *Quercus* L. Springer, Switzerland, pp 1-13.

Gil-Pelegrín E., Peguero-Pina J.J., Sancho-Knapik D., (2017a): Oaks Under Mediterranean-Type Climates: Functional Response to Summer Aridity. In: Oaks Physiological Ecology. Exploring the Functional Diversity of Genus *Quercus* L. Springer, Switzerland, pp 137-195.

Giordano R., Salleo A., Salleo S., Wanderlingh F. (1978): Flow in xylem vessels and Poiseuille's law. Canadian Journal of Botany, 56: 333–338.

Goren-Inbar N., Feibel C.S., Verosub K.L., Melamed Y., Kislev M.E., Tchernov E., Saragusti I. (2000): Pleistocene Milestones on the Out-of-Africa Corridor at Gesher Benot Ya'aqov, Israel. Science, 289(5481): 944–947.

Hacke U.G., Sperry J.S., Pockman W.T., Davis S.D., McCulloh K.A. (2001): Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia, 126: 457–461.

Hajek P., Kurjak D., von Wühlisch G., Delzon S., & Schuldt B. (2016): Intraspecific variation in wood anatomical, hydraulic, and foliar traits in ten European beech provenances differing in growth yield. Frontiers in Plant Science, 7: 1–14.

Hoffmann A.A., Sgro C.M. (2011): Climate change and evolutionary adaptation. Nature, 470: 479–485.

Hoffmann W.A., Franco A.C., Moreira M.Z., Haridasan M. (2005): Specific leaf area explains differences in leaf traits between congeneric savanna and forest trees. Funcional Ecology, 19: 932-940.

Jordão A.M., Ricardo-da-Silva J.M., Laureano O., Adams A., Demyttenaere J., Verhé R., De Kimpe N. (2006): Volatile composition analysis by solid-phase microextraction applied to oak wood used in cooperage (*Quercus pyrenaica* and *Quercus petraea*): effect of botanical species and toasting process. Journal of Wood Science, 52: 514–521.

Kozlowski T.T. (1971): Growth and Development of Trees, Volume II: Cambial growth, root growth and reproductive growth. Academic Press, New York, 514.

Kramer K. (1995): Phenotypic plasticity of the phenology of 7 European tree species in relation to global warming. Plant, Cell & Environment, 18: 93-104.

Kuster T.M., Arend M., Gunthardt-Goerg M.S., Schulin R. (2013): Root growth of different oak provenances in two soils under drought stress and air warming conditions. Plant Soil, 369: 61–71.

Kuster T.M., Dobbertin M., Günthardt-Goerg M.S., Schaub M., Arend M. (2014): A phenological timetable of oak growth under experimental drought and air warming. PLoS ONE 9(2): e89724.

Lachenbruch B., Moore J.R., Evans R. (2011): Radial variation in wood structure and function in woody plants, and hypotheses for its occurrence. In F. C. C. Meinzer, B. Lachenbruch & T. E. E. Dawson (Eds.), Size and age related changes in tree structure and function. Dordrecht, the Netherlands: Springer, pp 121-164.

Langlet O. (1971): Two hundred years of genecology. Taxon, 20: 653-721.

Li M., An H., Angelovici R., Bagaza C., Batushansky A., Clark L., Coneva V., Donoghue M.J., Edwards E., Fajardo D., Fang H., Frank M.H., Gallaher T., Gebken S., Hill T., Jansky S., Kaur B., Klahs P.C., Klein L.L., Kuraparthy V., Londo J., Migicovsky Z., Miller A., Mohn R., Myles S., Otoni W.C., Pires J.C., Rieffer E., Schmerler S., Spriggs E., Topp C.N., Van Deynze A., Zhang K., Zhu L., Zink B.M., Chitwood D.H. (2018): Topological Data Analysis as a Morphometric Method: Using Persistent Homology to Demarcate a Leaf Morphospace. Frontiers in Plant Science, 9: 553.

Lo Gullo M.A., Salleo S. (1993): Different vulnerabilities of *Quercus ilex* L. to freeze- and summer drought-induced xylem embolism: an ecological interpretation. Plant, Cell & Environment, 16(5): 511–519.

Ma X.F., Hall D., St. Onge K.R., Jansson S., Ingvarsson P.K. (2010): Genetic differentiation, clinal variation and phenotypic associations with growth cessation across the *Populus tremula* photoperiodic pathway. Genetics, 186: 1033-1044.

Manos P.S., Doyle J.J., Nixon K.C. (1999): Phylogeny, biogeography and processes of molecular differentiation in *Quercus* subgenus *Quercus* (*Fagaceae*). Molecular Phylogenetics and Evolution, 12: 333-349.

Manos P.S., Stanford A.M. (2001): The historical biogeography of Fagaceae: tracking the tertiary history of temperate and subtropical forests of the northern hemisphere. International Journal of Plant Sciences, 162: S77-S93.

Martínez-Cabrera H.I., Estrada-Ruiz E. (2014): Wood Anatomy Reveals High Theoretical Hydraulic Conductivity and Low Resistance to Vessel Implosion in a Cretaceous Fossil Forest from Northern Mexico. PLoS ONE 9(10): e108866. https://doi.org/10.1371/journal.pone.0108866

Matesanz S., Gianoli E., Valladares F. (2010): Global change and the evolution of phenotypic plasticity in plants. Annals of the New York Academy of Sciences, 1206: 35-55.

Mátyás C. (1996): Climatic adaptation of tree: rediscovering provenance tests. Euphytica, 92: 45-54.

Mauer O., Houšková K., Mikita T. (2017): The root system of pedunculate oak (Quercus robur L.) at the margins of regenerated stands. Journal of Forest Science, 63: 22–33.

McKown A.D., Guy R.D., Klápště J., Geraldes A., Friedmann M., Cronk Q.C., El-Kassaby Y.A., Mansfield S.D., Douglas C.J. (2014): Geographical and environmental gradients shape phenotypic trait variation and genetic structure in *Populus trichocarpa*. New Phytologist 201: 1263–1276.

Meinzer F.C., Clearwater M.J.M., Goldstein G. (2001): Water transport in trees: current perspectives, new insights and some controversies. Environmental and Experimental Botany, 45: 239–262.

Mijnsbrugge K.,Turcsán A., Maes J., Duchêne N., Meeus S., Steppe K., Steenackers M. (2016): Repeated Summer Drought and Re-watering during the First Growing Year of Oak (*Quercus petraea*) Delay Autumn Senescence and Bud Burst in the Following Spring. Frontiers in Plant Science, 7: 419.

Morgenstern E.K. (1996): Geographic Variation in Forest Trees: Genetic Basis and Application of Knowledge in Silviculture. Vancouver: B.C., UBC Press.

Morin X., Thuiller W. (2009): Comparing niche and progress-based models to reduce prediction uncertainty in species range shifts under climate change. Ecology, 90: 1301-1311.

Morin X., Roy J., Sonie L., Chuine I. (2010): Changes in leaf phenology of three European oak species in response to experimental climate change. New Phytologist, 186: 900-910.

Mosedale J.R., Savill P.S. (1996): Variation of heartwood phenolics and oak lactones between the species and phonological types of *Quercus petraea* and *Q. robur*. Forestry, 69: 47-55.

Muir G., Schlotterer C. (2005): Evidence for shared ancestral polymorphism rather than recurrent gene flow at microsatellite loci differentiating two hybridizing oaks (*Quercus* spp.). Molecular Ecology, 14: 549-561.

Nardini A., Battistuzzo M., Savi T. (2013): Shoot desiccation and hydraulic failure in temperate woody angiosperms during an extreme summer drought. New Phytologist, 200(2): 322-9.

Niinemets, Ü. (2001). Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. Ecology, 82: 453-469.

Nixon, K.C. (1993): Infrageneric classification of *Quercus* (*Fagaceae*) and typification of sectional names. Annales des sciences forestières, 50, Suppl. 1: 25–34.

Oishi M., Yokota T., Teramoto N., Sato H. (2005): Japanese oak silk moth feeding preference for and performance on upper-crown and lower-crown leaves. Entomological Science, 9: 161-169.

Olson-Manning C.F., Wagner M.R., Mitchell-Olds T. (2012): Adaptive evolution: evaluating empirical support for theoretical predictions. Nature Reviews Genetics, 13: 867–877.

Osunkoya O., Sheng T.K., Mahmud N., Damit N. (2007): Variation in wood density, wood water content, stem growth and mortality among twenty-seven tree species in a tropical rainforest on Borneo Island. Austral Ecology 32(2): 191-201.

Out W.A. (2017): Wood usage at Dutch Neolithic wetland sites. Quaternary International, 436: 64–82.

Peguero-Pina J.J., Sancho-Knapik D., Barrón E., Camarero J.J., Vilagrosa A., Gil-Pelegrín E. (2014): Morphological and physiological divergences within *Quercus ilex* support the existence of different ecotypes depending on climatic dryness. Annals of Botany, 114: 301–313.

Perez-Harguindeguy N., Díaz S., Garnier E., Lavorel S., Poorter H., Jaureguiberry P., Bret-Harte M.S., Cornwell W.K., Craine J.M., Gurvich D.E., Urcelay C., Veneklaas E.J., Reich P.B., Poorter L., Wright I.J., Ray P., Enrico L., Pausas J.G., de Vos A.C., Buchmann N., Funes G., Quétier F., Hodgson J.G., Thompson K., Morgan H.D., ter Steege H., van der Heijden M.G.A., Sack L., Blonder B., Poschlod P., Vaieretti M. V., Conti G., Staver A.C., Aquino S., Cornelissen J.H.C. (CSIRO, 2013): New handbook for standardised measurement of plant functional traits worldwide. Australian Journal of Botany, 61: 167-234.

Petit R.J., Bodenes C., Ducousso A., Roussel G., Kremer A. (2004): Hybridization as a mechanism of invasion in oaks. New Phytologist, 161: 151-164.

Pigliucci M., Byrd N. (1998): Genetics and evolution of phenotypic plasticity to nutrient stress in Arabidopsis: drift, constraints or selection? Biological Journal of the Linnean Society, 64: 17-40.

Pigliucci M. (2001): The character concept in evolutionary biology, 363-388.

Pigliucci M. (2001): Phenotypic plasticity: Beyond Nature and Nurture. The John Hopkins University Press. Baltimore, MD.

Ponton S., Dupouey J.L., Bréda N., Dreyer E. (2002): Comparison of water-use efficiency of two sympatric oak species: genotype × environment interactions. Tree Physiology, 22: 413–422.

Poorter H., Niinemets U., Poorter L., Wright I.J., Villar R. (2009): Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. New Phytologist, 182: 656-588.

Poorter L., McDonald I., Alarcón A., Fichtler E., Licona J., Peña-Claros M., Sterck F., Villegas Z., Sass-Klaassen U. (2010): The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species, New Phytologist, vol. 18, pp 481-492.

Reboredo F., Pais J. (2014): Evolution of forest cover in Portugal: A review of the 12th–20th centuries. Journal of Forest Research, 25: 249–256.

Robson T.M., Sánchez-Gómez D., Cano F.J., Aranda I. (2012): Variation in functional leaf traits among beech provenances during a Spanish summer reflects the differences in their origin. Tree Genetics & Genomes, 8: 1111–1121.

Romero C., Bolker B.M. (2008): Effects of stem anatomical and structural traits on responses to stem damage: an experimental study in the Bolivian Amazon, Canadian Journal of Forest Research, vol. 38, pp 611-618.

Rungwattana K., Kasemsap P., Phumichai T., Kanpanon N., Rattanawong R., Hietz P. (2018): Trait evolution in tropical rubber (*Hevea brasiliensis*) trees is related to dry season intensity. Functional Ecology 00: 1-14.

Saintagne C., Bodenes C., Barrenche T., Pot D., Plomion C., Kremer A. (2004): Distribution of genomic regions differentiating oak species assessed by QTL detection. Heredity, 92: 20-30.

Schmidt, L. (1997): Tree improvement glossary. Danida Forest Seed Centre, Technical note. 46- 63.

Schonbeck, J., and R.J.Frey (2005): Oak. In J.L.Longe, The Gale Encyclopedia of Alternative Medicine. Farmington Hills, Mich: Thomson/Gale. ISBN 0787693960.

Shrestra K.B., Måren I.E., Arneberg E., Sah J.P., Vétaas O.R. (2013): Effect of anthropogenenic disturbance on plant species diversity in oak forests in Nepal, Central Himalaya. International Journal of Biodiversity Science, Ecosystem Services & Management, 9:21–29.

Shutyaev A.M., Giertych M. (1997): Height growth variation in a comprehensive Eurasian experiment of *Pinus sylvestris* L. Silvae genetica, 46:332-349.

Singh S.P., Singh J.S. (1986): Structure and function of the Central Himalayan oak forests. Proceedings of the Indian Academy of Sciences (Plant Science Section), 96:159–189.

Spurr S.H., B.V. Barnes (1980): Forest Ecology. John Wiley and Sons, New York, 687.

Steele M.A., Koprowski J.L. (2001): North America tree squirrels. Smithsonian Institution Press, Washington, DC, USA.

Tyree M.T., Dixon M.A. (1986): Water stress induced cavitation and embolisms in some woody plants. Physiologia Plantarum, 66:397-405.

Van Valen L. (1976): Ecological species, multispecies, and oaks. Taxon, 25:233-239.

Villar R., Ruiz-Robleto J., De Jong Y., Poorter H. (2006): Differences in construction costs and chemical composition between deciduous and evergreen woody species are small compared to differences among families. Plant, Cell & Environment, 29:1629-1643.

Violle C, Navas M.L., Vile D., Kazakou E., Fortunel C., Hummel I. et al. (2007): Let the concept of trait be functional! Oikos, 116:882-982.

Vitasse Y., Porte A.J., Kremer A., Michalet R., Delzon S. (2009): Responses of canopy duration to temperature changes in four temperate tree species: relative contributions of spring and autumn leaf phenology. Oecologia, 161:187–198.

Vitasse Y., Bresson C.C., Kremer A., Michalet R., Delzon S. (2010): Quantifying phenological plasticity to temperature in two temperate tree species. Functional Ecology, 24:1211-1218.

Vivin P., Aussenac G., Levy G. (1993): Differences in drought resistance among 3 deciduous oak species grown in large boxes. Annals of Forest Science, 50:221–233.

Yonekura T., Yoshidome M., Watanabe M., Honda Y., Ogiwara I., Izuta T. (2004): Carry-over effects of ozone and water stress on leaf phenological characteristics and bud frost hardiness of Fagus crenata seedlings. Trees, 18:581–588.

Ziemińska K., Butler D.W., Gleason S.M., Wright I.J., Westoby M. (2013): Fibre wall and lumen fractions drive wood density variation across 24 Australian angiosperms, AoB PLANTS, Volume 5, plt046, https://doi.org/10.1093/aobpla/plt046.

Zimmerman M.H., Brown C.L. (1977): Trees structure and function. Springer-Verlag, New York.

Zimmermann N.E., Bolliger J., Gehrig-Fasel J., Guisan A., Kienast F., Lischke H., Rickebusch S. and Wohlgemuth T. (2006): Wo wachsen die Bäume in 100 Jahren? In Wald und Klimawandel. Forum für Wissen. Ed. T. Wohlgemuth. WSL, Birmensdorf, Switzerland, pp 63–71. ISSN 1021–2256.

Zobel Bruce J., van Buijtenen J.P. (1989): Wood variation - its causes and control. Springer-Verlag Berlin Heidelberg, pp 33-69.

6.2 Online sources

Alberta Forest Genetics Council, University of Alberta, Department of Renewable Resources, https://sites.ualberta.ca/~ahamann/teaching/various/adaptation/4-genetic-testing.html

Google Earth, source: “Austria” (accessed on February 10, 2019)

URL: http://www.newworldencyclopedia.org/entry/Oak

WorldClim database, http://www.worldclim.org/bioclim (accessed in June 2018)

7. LIST OF FIGURES

8. LIST OF TABLES