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Response of Pedunculate Oak (*Quercus robur* L.) to Adverse Environmental and Weather Conditions in Genetic and Dendrochronological Studies

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Abstract: Pedunculate oak (*Quercus robur* L.) is widely distributed in Europe and plays a critical ecological role. Studying how it responds to stressors such as drought, extreme temperatures, pests and phytopathogen helps reveal the species' capacity to adapt to climate change. Genetic and dendrochronological data (tree-ring analysis) provide insights into historical resilience, a historical record of how trees have responded to past environmental stressors, revealing which traits and genetic variants are linked to climate adaptation and how they may contribute to future resilience in changing environments. By examining the width, density, and dynamics of tree rings in *Q. robur*, researchers can correlate periods of growth suppression or enhanced growth with specific environmental conditions. This information helps predict how forests might respond to future climatic events and supports conservation and management strategies. By identifying genetic markers associated with stress tolerance, forest managers can prioritize the conservation of populations with higher adaptive potential. This is particularly important as *Q. robur* is an economically and ecologically valuable species. One of the main objectives of the review to summarize also publications on *Q. robur* genetic diversity and adaptive traits that can guide reforestation efforts and help develop climate-resilient oak populations. The review is focused on genetic and dendrochronological studies that offer complementary perspectives on tree response mechanisms. Genetic studies reveal adaptive genetic diversity and inheritance patterns, while dendrochronology provides a phenotypic record of responses over time. Combining these fields creates a holistic understanding of how *Q. robur* responds to stress, useful for fields ranging from ecology to forest genetics. Hopefully, this review helps understand *Q. robur*'s resilience mechanisms, support adaptive management practices, and enable sustainable forest planning in the face of environmental challenges.

Keywords: adaptation; climate; dendrochronology; dendrogenomics; environment; epigenetics; genetics; genomics; plasticity; *Quercus robur*; resilience; pedunculate oak; stress

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1. Introduction

The genus *Quercus* includes about 450 species of both deciduous and evergreen forest trees, the majority of which are distributed mainly from northern latitudes to the tropics [1] (Bellusci et al. 2023). The pedunculate oak (*Quercus robur* L.), also known as the English or European oak, occupies a large area of in Europe [2] (Eaton et al. 2016) and plays a significant role both ecologically and economically [3] (Mölder et al. 2019). It is a keystone species that provides vital habitat and resources for many other organisms from insects and birds to mammals and fungi. Over 2,300 species have been associated with oaks, including specific insects, such as moths, butterflies, and beetles, that rely on oak leaves, acorns, or bark [4] (Mitchell et al. 2019). These trees are excellent habitats, particularly for woodland birds, bats, wild boar and small mammals. The acorns provide food for animals like squirrels, jays, and deer, while older trees with hollow trunks create nesting and roosting sites for bats and birds. As oak leaves decompose, they enrich the soil with organic matter, benefiting the entire forest floor ecosystem. Oak leaf litter also supports many detritivores (decomposer organisms) that break down dead organic material, which in turn supports soil health and fertility.

Oak trees store substantial amounts of carbon in their wood, leaves, and roots, helping reduce greenhouse gases in the atmosphere and mitigating global climate warming. Their large canopies also help in regulating local microclimates by providing shade and retaining moisture in the surrounding area. Oaks play also an important role in water regulation by absorbing rainfall, reducing runoff, and maintaining soil structure, which helps prevent erosion.

Oak wood is highly valued for its durability, strength, and attractive grain. *Q. robur* wood is used in furniture, flooring, barrels (for wine and whiskey aging), and high-quality construction materials. Its resistance to moisture and decay also makes it suitable for outdoor use, including fencing and shipbuilding.

Large, ancient oaks are often landmarks and attract tourists for recreational activities like hiking, birdwatching, and photography. This contributes to local economies, especially in areas known for scenic oak woodlands.

Although less common today, oak wood has historically been used as firewood and charcoal due to its high energy content and slow-burning nature. In some regions, it still remains a preferred wood for sustainable fuel. The bark and leaves of the oak have been traditionally used for their tannins, which have medicinal applications in treating skin issues and inflammation. Additionally, the oak has cultural significance in many European countries, symbolizing strength, endurance, and longevity.

Overall, the *Q. robur*'s ecological contributions help sustain biodiversity and ecosystem balance, while its economic value supports industries from timber production to tourism. However, the *Q. robur* forests are threatened and declining in many areas due to a combination of bad weather conditions, phytopathogens, pest outbreaks and repeated severe defoliation likely associated with climate change [5–16] (Oosterbaan & Leffef 1987; Thomas et al. 2002; Neagu 2010; Lione et al. 2012; Matisons et al. 2013; Keča et al. 2016; Conte et al. 2019; Losseau et al. 2020; Schroeder et al. 2021; Macháčová et al. 2022; Kowsari et al. 2023; Gribbe et al. 2024). That is why it is extremely important to study response of *Q. robur* to adverse environmental and weather conditions and to search for its adaptive potential using genetic, genomic and dendrochronological methods and, especially, interdisciplinary approaches, such as dendrogenomics [17] (Krutovsky 2022). Available genomic, transcriptomic, and experimental resources for oaks, including *Q. robur*, and applications of these resources to genetic linkage and Quantitative Trait Locus (QTL) mapping and to population genomic analyses such as association mapping (Genome-wide Association Analyses, GWAS), landscape genetics, population epigenomics, paleogenomics, and phylogenomics studies are reviewed also in [18] (Gailing et al. 2021). This review also emphasizes the application of genomic tools for exploring

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local adaptation, adaptive divergence, and interspecific hybridization and introgression in oaks. It particularly focuses on recent population genomics approaches that address the genomic basis of adaptive trait variation and local adaptation. Additionally, it examines the roles of interspecific hybridization and epigenetic changes in facilitating rapid local adaptation, lineage divergence, and speciation, alongside the temporal scale of adaptive genomic shifts. Prospective advancements in genome-wide variation studies, such as whole-genome resequencing at the population level, high-resolution population epigenomics, genomic vulnerability assessments, and strategies for conservation and sustainable management of oak populations amid environmental changes, are briefly discussed [18] (Gailing et al. 2021). Here, we present a summary on *Q. robur*, focusing on its response to adverse environmental and weather conditions in genetic and dendrochronological studies.

2. Nuclear Genome of *Q. robur*

Q. robur has a diploid set of 24 chromosomes (2n=2x=24) [19] (Gadella & Kliphuis 1973). Triploids among *Q. robur* trees were found only in a few cases [20–22] (Butorina, 1993; Naujoks et al. 1995; Dzialuk et al. 2007). An additional B chromosome was observed in some studies (2n=2x=24+1B) [23,24] (Zoldos et al. 1997; Zoldos et al. 1998). Analyses of the karyotypes of the genera *Quercus*, *Lithocarpus*, *Castanopsis* and *Castanea* [25,26] (Mehra et al. 1972; D'Emerico et al. 1995) and *Fagus* [27,28] (Ohri and Ahuja 1990, 1991) by different research groups showed that the number of chromosomes in the Fagaceae family is generally stable and amounts to 2n = 24. The oak karyotype contains two types of chromosomes: 7 pairs of metacentric and 5 pairs of submetacentric [29] (Wang, 1986). Current oak chromosomes evolved through multiple fusions, fissions, and rearrangements after an ancestral triplication event [30] Cao et al. 2024). No secondary constriction or satellites were detected, but regular association of the nucleolus with one of the chromosome pairs was detected in meiotic observations. Based on this, it can be assumed that the nucleolus-forming regions are located in the telomeric regions of this chromosome [31] (Natividade, 1937).

The DNA content in different species of the genus *Quercus* varies per 1C from 0.5 pg (490 Mbp) in *Q. sessilis* to 1.22 pg (1,195 Mbp) in *Q. austrochinchinensis* with a mean of 0.95 (± 0.13) pg (924 ± 131 Mbp) for 29 species according to [32] (Leitch et al. 2019). The DNA content of *Q. robur* per 1C was 0.90 pg (882 Mbp) [33] (Favre and Brown,1996). According to [34] (Kremer et al. 2007) the DNA content among 28 species of the genus *Quercus* varies per 1C from 0.59 pg (565 Mbp) in *Q. velutina* to 1 pg (980 Mbp) in *Q. coccifera* and *Q. suber*. The studied species include representatives of all four main subgenera or sections: 11 species of the subgenus *Erythrobalanus* (red oak), 12 species of the subgenus *Lepidobalanus* (white oak), three species of the subgenus *Cerris* and two - subgenus *Sclerophyllodrys*. The average DNA content was 0.79 pg (759 Mbp) for the subgenus *Erythrobalanus*, 0.85 pg (0.785 Mbp) for *Lepidobalanus*, 0.87 pg for *Cerris*. Both species *Q. coccifera* and *Q. ilex* of the subgenus *Sclerophyllodrys* had a maximum genome size of 1 pg (980 Mbp). They are evergreen plants and belong to the botanical group of the subgenus *Sclerophyllodrys* according to the classification [35] (Schwarz et al. 1964). But according to another classification [36] (Camus 1936) they belong to two different subgenera: *Q. ilex* belongs to the subgenus *Lepidobablanus*, and *Q. coccifera* to the subgenus *Cerris*. Molecular genetic analysis also included these two evergreen oak species in different subgenera [37,38] (Manos, Steele, 1997; Xu, 2004), confirming the previously made taxonomic division of the *Sclerophyllodrys* group [35] (Schwarz et al. 1964).

The earlier studies on the genetic linkage mapping of *Q. robur* are described in [39–44] (Barreneche et al. 1998, 2004; Gailing 2008; Gailing et al. 2008; Bodénès et al. 2012, 2016) and summarized in [45] (Quercus PORTAL). The densest genetic linkage map for the genus *Quercus* is based on 4,261 single-nucleotide polymorphism (SNP) markers obtained by genotyping more than 1,000 full-sibs from two intraspecific (*Q. robur*: 3PxA4, *Q. petraea*: QS28xQS21) and two interspecific full-sib families of *Q. petraea* and *Q. robur* (11PxQS29 and 11PxQS28) by using an 8K gene-based SNP array [46] (Lepoittevin et al. 2015). A single composite map was constructed by merging the eight parental maps using LPMerge software [47] (Endelman & Plomion, 2014). This is spanning 742 cM over the 12 linkage groups (LGs) of the oak genome. Overall, 82% of the SNPs successfully genotyped were polymorphic in at least one of the four pedigrees and 63% were mapped as framework markers on the parental genetic maps [44] (Bodénès et al. 2016). This oak map establishes a foundation for genome-wide analysis at the centimorgan level, supporting studies on evolutionary relationships among related species, genomic scans of species and population divergence, and the positional identification of quantitative trait loci (QTLs) through co-localization with gene-based markers. It also aids in identifying chromosomal rearrangements [44] (Bodénès et al. 2016).

The development of the next-generation sequencing (NGS) techniques greatly promoted the whole genome sequencing, including oaks. First complete assembly and annotation of the *Q. robur* genome consisted in a total of 17,910 scaffolds (>2 Kb each) corresponding to ~1.354 Gbp/2C [48] (Plomion et al. 2016; the European Nucleotide Archive accession number ERP006803; available also online at https://www.oakgenome.fr/index4f22.html?page_id=244, accessed on 14 October, 2024). The second version contained 8,827 scaffolds covering 1.455 Gbp [49] (Plomion et al. 2018) and 871 scaffolds assigned to the 12 linkage groups of the genetic map covering 716.6 Mb and containing 23,220 genes [50]. The current genome assembles of *Q. robur* available at the NCBI GenBank database are presented in Table 1.

Table 1. Genome assembles of *Q. robur* available at the NCBI GenBank database.

Assembly (Type)	**GenBank Accession #**	**Level**	**Release**	**WGS Accession**	**Scaffold Count**	**Genome Size, Mbp**	**Submitter**
ASM301314v1 (haploid)	GCA_003013145.1	Scaffold	Mar, 2018	PVWZ01	84,416	719.6	Swiss Institute of Bioinformatics
dhQueRobu3.1 (principal haplotype of diploid)	GCA_932294415.1 (NCBI RefSeq)	Chromosome	Mar, 2022	CAKOAN01	95	789.2	Wellcome Sanger Institute
dhQueRobu3.1 (alternate haplotype of diploid)	GCA_932294425.1	Scaffold	Mar, 2022	CAKOAP01	1,219	762.4	Wellcome Sanger Institute
Q_robur_v1	GCA_900291515.1	Scaffold	Mar, 2018	OLKR01	550	814.3	Genoscope CEA

3. Chloroplast Genome of *Q. robur*

The chloroplast genome of the *Q. robur* has been studied extensively due to its significance in understanding the evolutionary history, genetic diversity, and adaptation of this species across Europe. The chloroplast genome of *Q. robur* is typical of angiosperms, featuring a circular structure with approximately 160,000 base pairs. It contains the standard set of genes necessary for photosynthesis and other chloroplast functions, along with inverted repeat regions that help maintain genomic stability [51] (Dumolin et al. 1995).

Research on the chloroplast genome has revealed geographic structuring, with different haplotypes fixed in regional populations [52] (Semerikova et al. 2021). This structuring provides insight into how *Q. robur* recolonized Europe following the last Ice Age [53] (Ducousso & Bordacs, 2004). Chloroplast DNA variation in *Q. robur* shows a clear east-west gradient, suggesting multiple refugial sources and migration pathways. This geographic pattern also helps explain the resilience and adaptability of the species to various climates and habitats in Europe.

The chloroplast genome’s high differentiation among populations contrasts with the nuclear genome, which tends to show more within-population diversity [53] (Ducousso & Bordacs, 2004).

This differentiation has important implications for conservation, as it emphasizes the need for preserving regional genetic diversity to maintain resilience in *Q. robur* populations. Conservation strategies often recommend using local genetic material for reforestation and avoiding the introduction of non-local genotypes, which could disrupt local adaptations.

Chloroplast DNA markers from *Q. robur* have been used in population genetics to understand interspecies hybridization, notably with *Q. petraea*. These markers are essential for distinguishing species and assessing the genetic purity of populations, which is crucial in forestry and conservation management [54] (Blanc-Jolivet & Liesebach, 2015).

The chloroplast genome of *Q. robur* is a crucial aspect of its genetic makeup, providing insights into the species' adaptation, evolution, and phylogeography. This chloroplast genome, transmitted maternally, helps trace lineage and historical distribution across Europe, particularly as this oak species migrated northward after the last Ice Age. Chloroplast DNA variation in *Q. robur* shows geographic structuring, with certain chloroplast haplotypes becoming fixed in specific populations due to limited gene flow through seeds and high regional differentiation in chloroplast genomes compared to nuclear genomes. This structure has contributed to the east-west genetic gradient observed in the species and is important for understanding historical migration routes and the oak's adaptability to different environments.

One significant application of understanding chloroplast DNA in *Q. robur* is its role in conservation genetics. As climate changes and habitat fragmentation continue, the genomic diversity within chloroplasts supports resilience and adaptation, guiding conservation efforts. Effective management practices, such as promoting local seed use for regeneration, help maintain this diversity and prevent the introduction of non-native genotypes, which could disrupt local adaptations in *Q. robur* populations.

Additionally, the high level of phenotypic variation tied to the chloroplast genome helps *Q. robur* thrive in diverse environments, from rocky slopes to sand dunes and peat bogs. This adaptability is partly due to chloroplast variations supporting efficient photosynthesis and other cellular functions, which are essential for survival in different ecological niches.

The genetic insights gained from the chloroplast genome highlight the importance of preserving genetic diversity within oak populations, particularly as threats from pathogens, pests, and climate pressures increase. These findings suggest a continued focus on genetic conservation and sustainable management practices to ensure the resilience of oak forests in Europe.

In summary, the chloroplast genome of *Q. robur* plays a vital role in tracing historical migration, supporting biodiversity conservation, and providing insights into the evolutionary resilience of this ecologically important tree. For more detailed information, see studies on chloroplast DNA variation and phylogeography in *Q. robur* by [55,56] (Petit et al. 1993; Petit & Vendramin 2007).

4. Mitochondrial Genome of *Q. robur*

The mitochondrial genome of oak species is supposedly comparatively complex, particularly due to the large size of plant mitochondrial genomes and the presence of numerous non-coding regions. Currently, the complete mitochondrial genome assemblies are only for four oak species: *Q. robur* of 390,906 bp (the NCBI GenBank accession number:OW028777.1), Chinese cork oak (*Q. variabilis*) of 412,886 bp [57] (Bi et al. 2019) (the NCBI GenBank accession number MN199236.1) and of 419,744 bp [58] (Wang et al. 2023) (the NCBI GenBank accession number CP129458.1), Japanese sawtooth oak (*Q. acutissima*) of 448,982 bp [59] (Liu et al. 2022) (the NCBI GenBank accession number MZ636519.1), and cork oak (*Q. suber*) of 531,858 bp [60] (Usié et al. 2023). The mitogenome of *Q. acutissima* is presented by three distinguished contigs including a single linear molecule and two circular molecules with 448,982 bp total length [59] (Liu et al. 2022). It contains 51 genes, including 32 protein-coding, 16 tRNA and 3 rRNA genes. The complete mitochondrial genome of *Q. variabilis* is supposedly circular and contains slightly more genes – 60 in total, including 36 protein-coding, 21 tRNA and 3 rRNA genes [57] (Bi et al. 2019). The mitogenome of *Q. suber* is presented by three distinguished linear contigs including one large contig with 442,094 bp and two smaller contigs of 52,064 bp and 37,700 bp, respectively [60] (Usié et al. 2023). It contains a total of 66 genes, including

40 protein-coding, 23 tRNA, and 3 rRNA. The mitogenome of *Q. robur* is the shortest and presented by a single linear contig, but it is not verified and annotated yet. However, studies indicate that the mitochondrial genome of *Q. robur* might have considerable variation in its structural organization, contributing to genetic diversity across oak populations. Both genomes chloroplast and mitochondrial are maternally inherited in *Q. robur* [51] (Dumolin et al. 1995).

Studies of the mitochondrial markers help understanding evolutionary relationships, population differentiation, and adaptation strategies in plant species [61] (Grosser et al. 2023). Studies of *Q. robur* populations based on the mitochondrial markers are insufficient, while they can provide valuable population genetic data. However, because oak mitochondrial genomes undergo complex rearrangements and are highly repetitive, further efforts on sequencing and assembly of the *Q. robur* mitogenome are necessary for detailed insights into its genetic and evolutionary roles. This mitochondrial genome complexity is not unique to oaks; many tree species exhibit similarly large and complex mitochondrial genomes, which challenge sequencing and interpretation but are crucial for insights into plant genetics and adaptation strategies [62–66] (Mosca et al. 2019; Putintseva et al. 2020; Feng et al. 2023; Wang et al. 2024; Wu et al. 2024).

5. Genetic Variation and Population Structure of *Q. robur*

The genetic variation and population structure of *Q. robur* have been extensively studied due to its importance in forest ecosystems and its wide distribution across Europe. Studies highlights significant genetic diversity within populations, with studies showing high intra-population diversity (up to 98.5% of the total genetic variability), suggesting a robust capacity for adaptation within local populations [67–70] (Mullagulov et al. 2008; Popović et al. 2023; Semerikova et al. 2023; Degen et al. 2022). For instance, analysis of allozyme polymorphism in isolated populations on the eastern border of *Q. robur* showed that of the total variability of the two populations, 94.6% was represented by the intrapopulation component, while interpopulation variability was only 3.4% [67] (Mullagulov et al. 2008). Later, it was confirmed by SNP markers: analysis of 327 nuclear SNPs in 97 populations on the eastern part of *Q. robur* distribution range showed that of the total variability, 92.8% was represented by the intrapopulation component, while interpopulation variability was only 7.2% [70] (Degen et al. 2022). The total mean value of observed heterozygosity for the 12 allozyme loci was 0.229 and 0.161 in the *Q. robur* populations in Central and Eastern Europe, respectively [71] (Gömöry et al. 2001). In Croatia, a study on peripheral populations revealed that these oaks have high levels of nuclear and chloroplast genetic variation, with 66 unique chloroplast haplotypes detected across populations, a likely result of historical recolonization events and gene flow among populations. However, despite this diversity, inter-population differentiation remains relatively low, attributed to ongoing gene flow and hybridization with *Q. petraea*, which further enriches genetic diversity within mixed oak forests [72] (Degen et al. 2021).

Analysis of genetic polymorphism of oak populations growing in Russia using random amplified polymorphic DNA (RAPD) markers revealed that the total genetic variation varied from 0.202 in Voronezh populations to 0.245 in Great (Velikij) Novgorod, which corresponded to the estimates for populations of this species from Central and Western Europe [73] (Yakovlev and Kleinschmidt, 2002). These populations showed low interpopulation differentiation ($G_{ST} = 0.098$) and relatively high; gene flow ($N_e m = 4.61$). The proportion of among-population variation accounted for 7% of the total variation; more than 93% of the total variation was explained by individual and intrapopulation variation [73] (Yakovlev and Kleinschmidt, 2002). Similarly, the ISSR (Inter Simple Sequence Repeat) markers and allozyme loci showed that the lowest polymorphism was found for the Trans-Ural oak groves [74] (Gabitova et al. 2015). High polymorphism of populations was shown for geographically marginal stands, comparable to or exceeding the diversity of ISSR fragments in the oak grove in the Ufa forestry (65.6%). For some populations, maximum DNA polymorphism was identified, exceeding 80% [74] (Gabitova et al. 2015). Studies of different biotope affiliation of stands from ravine and floodplain oak groves in the south of Russia based on the analysis of the structure of 5 ISSR primers showed that their genetic differences were statistically significant, in particular, heterozygosity was lower in ravine oak groves [75] (Chokheli et al. 2018).

The genetic study of several populations and groups of *Q. robur* in Bosnia and Herzegovina using four nuclear microsatellite markers confirmed a higher heterozygosity in these populations compared to the populations of *Q. robur* in Western Europe [76] (Ballian et al. 2010). The authors explained it by the proximity of the studied populations to their glacial refuges. This may be a reason for their higher resistance and endurance compared to the populations of Western and Central Europe.

Despite the strong reduction and fragmentation of *Q. robur* forests over the last several centuries and comparatively small sizes of present stands in Eastern Europe a high within population variation but relatively low differentiation between populations have been also observed in the seven *Q. robur* populations located in the basins of the Volga River and its two main tributaries, Kama and Belaya based on the nuclear SNPs genotyped using double digest restriction site associated DNA sequencing (ddRADseq) [77] (Degen et al. 2021). The large number and age diversity of local populations, as well as the complexity of migration routes of common oak from Pleistocene refugia and secondary Holocene shelters may be the cause of this phenomenon. However, population differentiation and heterogeneity were statistically significant and should be taken into account in seed zoning and reforestation.

The study of 17 Croatian *Q. robur* populations representing southern range peripheral populations using 10 nuclear and 9 chloroplast SSRs also found high within population variation for both sets of markers, and relatively low between population differentiation for nuclear, but high for chloroplast markers [68] (Popović et al. 2023). Isolation by distance explained 19.6% of haplotypic chloroplast differentiation. Analysis of within and between lineages showed that original recolonization patterns of nuclear diversity were subsequently erased by gene flow.

Meanwhile, the population structure and differentiation of *Q. robur* is clearly observed at the large scale [69,70,76] (Semerikova et al. 2023; Degen et al. 2022; Ballian et al. 2010). A clear spatial trend was observed in the estimates of genetic diversity and differentiation of Italian *Q. robur* populations [78,79] (Avanzi et al. 2023; Di Pietro et al. 2024).

Q. robur populations are also affected by isolation-by-distance effects, contributing to some genetic differentiation among populations. For instance, studies show that approximately 19.6% of genetic differentiation can be explained by geographic distance between populations [68] (Popović et al. 2023). Additionally, genetic markers, such as simple sequence repeats (SSRs), have been used to assess genetic structure, revealing variations in allelic diversity that reflect both local adaptations and historical dispersal patterns [80] (Neophytou et al. 2010). Understanding these patterns is essential for conservation, especially as peripheral populations face heightened selection pressures from climate change, which could affect their genetic resilience and adaptive potential.

The effect of past environmental changes on the demography and genetic diversity of natural populations was investigated across seven main widely distributed and ecologically contrasting phylogenetically distant European tree species, including *Q. petraea* using comparative population genomic analyses and demographic inferences based on concerted sampling of 164 populations across their natural ranges [81] (Milesi et al. 2024). For all seven species studied, the effective population size (N_e) either grew or remained constant across numerous glacial cycles, extending as far back as 15 million years in the most extreme cases. The extensive genealogy of *Q. petraea* and its relatively high N_e is likely due to long generation times and also result from ongoing hybridization with other abundant, closely related white oak species, including *Q. robur*. Interestingly, despite the significant environmental changes brought about by the Pleistocene glacial cycles and substantial shifts in geographic ranges, the genetic diversity of dominant forest tree species has remained largely unaffected. Altogether, these results indicate that forest trees have been able to retain their evolutionary potential over very long periods of time despite strong environmental changes.

Mining genome-wide DNA sequences enabled the discovery of a subset of 38 SNPs that are near-diagnostic markers for species assignment in four European white oaks (10 for *Q. petraea*, 7 for *Q. pubescens*, 9 for *Q. pyrenaica*, and 12 for *Q. robur*, respectively) despite their low interspecific differentiation [82] (Kremer et al. 2024). These near-diagnostic markers, which are nearly species-specific, are almost completely fixed in one species and absent in the other three. They offer an

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efficient, reliable molecular tool for identifying *Q. petraea*, *Q. robur*, *Q. pubescens*, and *Q. pyrenaica*, making them suitable for routine use in species identification, taxonomic classification, and applications in forest research and management.

In total, 31.9 Millions SNPs were detected using whole-genome sequence data from pools of individuals of four species (*Q. robur*, *Q. petraea*, *Q. pyrenaica* and *Q. pubescens*) resequenced at 400X coverage [45] (Quercus PORTAL). In addition, 30 Millions SNPs were detected using whole-genome sequence data from 18 *Q. petraea* populations resequenced at >100X coverage.

These findings underscore the importance of studying and conserving genetic diversity in *Q. robur* populations to enhance forest resilience and adaptability under environmental changes. They provide crucial insights for forest management and conservation strategies, especially for maintaining genetic resources in fragmented or climate-sensitive regions.

5.1. Introgressive Hybridization

Early studies of introgressive hybridization between *Q. robur* and *Q. petraea* using chloroplast, mitochondrial and nuclear (allozymes and SSRs) markers are reviewed in [54] (Blanc-Jolivet & Liesebach, 2015). Large-scale genetic study of *Q. robur* using 1970 *Q. robur* trees from 197 locations in 13 European countries and 1763 putative *Q. petraea* trees genotyped with the same 381 polymorphic markers (356 nuclear SNPs, 3 nuclear InDels, 17 chloroplast SNPs, and 5 mitochondrial SNPs) a strong spatial pattern was found for both organelle and nuclear markers with a highly significant autocorrelation up to a range of 1250 km [72] (Degen et al. 2021). However, the differentiation at the nuclear gene markers was much lower compared to the organelle gene markers. There are two main genetic clusters were found. The western gene pool was significantly influenced by introgression from *Q. petraea* in the past. In Germany, a contact zone for *Q. robur* with varying levels of introgression was identified, likely due to differing historical introgression levels in glacial refugia or during postglacial recolonization. The primary postglacial recolonization routes moved from south to north and south to northwest in Western and Central Europe, while eastern haplotypes spread from east to west across Central Europe. In contrast, pollen-mediated gene flow and introgression from *Q. petraea* significantly altered the large-scale nuclear gene structure, showing a pronounced west-to-east pattern. Asymmetric nature of interspecific hybridization between *Q. robur*s and *Q. petraea* was observed in mixed stands in southern Lithuania using SSR and RAPD markers [83] (Jurkšienė et al. 2020).

Introgressive hybridization of *Q. robur* with other oak species, notable with sessile oak (*Q. petraea*) may be an important source of new alleles for adaptation in rapidly changing environments, perhaps even more important than constant variation [84] (Leroy et al. 2020). Hybridization and adaptive introgression seem to be major drivers of ecological success of oaks [85,86] (Leroy et al. 2020; Cannon & Petit 2020). Similar conclusions have been done for two closely related and introgressing spruce species (*Picea abies* and *P. sibirica*) [87,88] (Karunarathne et al. 2024; Zhou et al. 2024). It is important to note that, based on analyses of historical and recent gene flow events between *Q. petraea* and *Q. robur* using two independent methods—diffusion approximation to the joint frequency spectrum and approximate Bayesian computation (ABC)—and 3,524 randomly distributed SNPs across the genome, these species evolved in isolation for most of their history. They only recently entered secondary contact, likely due to the latest phase of postglacial warming [89] (Leroy et al., 2017). Research indicates that substantial genetic differentiation existed before this secondary contact, allowing for the development of barriers to gene flow. Consequently, the genomes of modern European white oaks exhibit a mosaic structure, containing both genes that have crossed species boundaries and genes resistant to gene flow.

It is interesting that for two oak species, *Q. acutissima* and *Q. variabilis*, it was determined that the introgressed genomic adaptation signatures were predominantly localized in regions with suppressed recombination rates [90] (Fu *et al.* 2022). Introgression likely promotes adaptation in these oak populations by introducing allelic variations in cis-regulatory elements, particularly through the insertion of transposable elements, thereby altering the regulation of stress-related genes. These results open new avenues for studying mechanisms of hybridization-mediated adaptation in sympatric species.

6. Epigenetic Variation of *Q. robur*

Oak species were quite actively studied for the epigenetic variation in general and in response for environmental stimuli [91–95] (Correia et al. 2013; Sork et al. 2019; Escandón et al. 2021; Silva et al. 2020; Labella-Ortega 2024). Epigenetic variation plays a vital role in the adaptability of oaks to diverse and changing environments [91,93] (Correia et al. 2013; Escandón et al. 2021). Through epigenetics mechanisms such as DNA methylation, histone modification, and small RNA regulation, oaks can adjust gene expression and fine-tune their physiological and developmental processes in response to stress without altering their genetic code. These epigenetic changes not only aid in immediate acclimatization but can also be inherited, providing future generations with a pre-existing ability to cope with environmental challenges.

DNA methylation is the most studied epigenetic process in the tree species. Most early studies of DNA methylation were done for the Californian oaks. Three populations of valley oak (*Q. lobata*) have been studied to assess whether methylation could be involved in response to the environment using reduced-representation bisulfite sequencing (RRBS). They found significant differentiation among populations at single-methylation variants of the CpG context, which was much higher than differentiation found in the underlying DNA sequence at single-nucleotide polymorphisms (SNPs) [92,96] (Sork et al. 2019; Gugger et al. 2016). It was defined by patterns of genetic and epigenetic differentiations that indicate local adaptation of the oak genome. Methylation polymorphisms of the CpG context plays more important role in local adaptation, while CHG context methylation looks to be less important targets for natural selection, either directly or through linkage to regions under selection [97] (Platt et al. 2015). These findings are consistent with the notion that the environmental conditions of different locations are responsible for different patterns of methylation and created high levels of epigenetic differentiation among these populations [92] (Sork et al. 2019).

Epigenetic regulation of gene activity in plants is shaped by their evolutionary background, developmental strategies, and lifestyle. This initial exploration into the epigenetic chromatin landscape of the long-lived oak species *Quercus robur* has revealed some unique characteristics when compared to other angiosperms, showing more similarities to long-lived gymnosperms such as *Pinus* and *Picea* [98] (Fuchs et al., 2008). *Q. robur* displays distinctive traits in both genome structure and its epigenetic landscape, setting it apart from other plant species. Ongoing studies of its genome and epigenome are anticipated to shed new light on the interactions between sequence composition, chromatin organization during interphase, epigenetic markers, and the functional aspects of this unique plant genome [99] (Vičić et al. 2013).

Characterization of chromatin in cyclin cells of *Q. robur* revealed that DNA methylation was not restricted to constitutive heterochromatin but was associated with both euchromatic and heterochromatic domains. Multiple chromatin modification showed dispersed distribution along chromatin. While H3K9ac (i.e. gene activating mark) exhibited typical euchromatin-specific distribution, the H3K9me1 and H3K27me2, both heterochromatin-associated marks (i.e. gene repressive marks), were not restricted to chromocenters, but showed additional dispersed distribution within euchromatin. It has been suggested that intermediate heterochromatin, containing both silencing and activation marks, is heritably maintained in plants, providing a particular epigenetic flexibility and contributing to epigenetic defense mechanisms [94] (Vičić et al. 2013).

Analysis of transcriptome, methylome and small RNA data for two oak species with contrasting levels of drought tolerance (*Q. robur* and *Q. petraea*), under control and drought stress conditions revealed high differences between species, consistent with species-specific response to drought stress [100] (Rubio et al. 2023). After investigation of the methylation dynamics under the moderate drought conditions, in total, there was less differentially methylated regions (DMRs) in *Q. robur* with very low overlap of common DMRs between species. The highest difference was found in CHH context, considering higher importance of CHH methylation for adaptive responses.

Similarly, small RNAs populations were different between species and the number of common sRNAs under drought stress were visibly reduced in *Q. robur*. It is considered that *Q. robur* deployed different molecular mechanisms in response to drought stress, consistent with the greater sensitivity to drought of this species. An integrative approach of the three datasets revealed genomic co-locations of potential importance for forest three adaptation to drought stress [100] (Rubio et al. 2023).

Q. robur displays a high degree of phenotypic plasticity, which allows it to thrive in diverse environments ranging from wetlands to dry forest stands. This adaptability is partially driven by epigenetic changes that regulate genes involved in stress tolerance, growth regulation, and metabolic adjustments. As shown above, the epigenetic marks can change in response to environmental stressors like drought or high temperatures, enabling oaks to adjust physiological processes such as stomatal regulation, water use efficiency, and leaf morphology.

A strategy for studying epigenetic diversity in natural populations of *Q. petraea*, as a concept oak species, is outlined in [101] (Lesur et al. 2024). However, for oaks and other forest tree species, information on the importance of epigenetics in their response to the environment is sparse because their longevity and other life-history traits make experimental approaches difficult. Nevertheless, because of this longevity and wide ecological ranges, epigenetic processes may be as important, or even more important, than genetic processes in shaping responses to rapidly changing environments.

7. Transcriptome and Gene Expression of *Q. robur*

With the development of NGS and RNA sequencing, the accumulation of gene expression data has accelerated significantly. For example, Lesur et al. 2015 [102] created a complete gene expression catalog for oak based on the functional annotation of 91,000 unique transcriptome contigs (transcripts or unigenes) of *Q. robur* and *Q. petraea*. Transcriptome analysis showed that most of the transcriptome is common to all tissues, but tissue-specific transcripts were also identified [102] (Lesur et al. 2015). Transcriptome analysis in oak bud tissues showed that gene expression patterns in dormant and swelling buds are different. In the buds entering dormancy, genes associated with resistance to cold stress and water deficit are overexpressed, while in swelling buds, genes associated with cell division and development are overexpressed [102,103] (Lesur et al. 2015; Derory et al. 2006). This analysis provided important information about oak genome evolution and regulation of genes related to vegetative bud phenology, an important adaptive trait in trees. This resource contributes to the annotation of the oak genome sequence and will help link genotypes to adaptive traits. Annotated transcriptomes derived from different tissues under a variety of treatments are listed for ten oak species, including *Q. robur* in Table 1 in [18] (Gailing et al. 2021). The RNA sequencing data on roots of oak trees were integrated into a single comprehensive database, named OakRootRNADB that contains information on both coding and noncoding RNAs [104] (Kóscielniak et al. 2022). The sequences in the database also provide information on transcription factors, transcriptional regulators and chromatin regulators, as well as a prediction of the cellular localization of a transcript.

8. Phenotypic Variation and Plasticity of *Q. robur*

Tree phenotype is a product of its genotype and the interaction of genotype with the environment. The latter represent phenotypic plasticity and arises in response to changes in growing conditions and is manifested in changes in growth, shoot length, phenology shift, the ratio of male and female shoots in monoecious trees and other reactions to the environment. *Q. robur*, a species with broad continental distribution range, demonstrated high phenotypic plasticity of the adaptive traits suggesting that this species has a great potential to adapt to environmental changes that may occur from global warming and indicating good perspectives for oak gene conservation and tree breeding [105–107] (Baliuckas and Pliura, 2003; Hautsalo et al. 2015; George et al. 2020).

When studying variability in tree species, three groups of traits are studied as the main ones: structural (morphological), reflecting the structural features of the shape and size of organs and their parts; physiological, characterizing the features of physiological and biochemical processes; biochemical and molecular genetic changes at the genome level.

Intraspecific variation of *Q. robur*, represented by numerous phenological, ecological and morphological forms, varieties, etc., is the basis for the search, conservation and rational use of its genetic potential. According to the type of crowns, the following biotypes are distinguished in *Q. robur* [108] (Kaplina, 2019): 1) spreading type (P-type) - developed crown with powerful lower branches; 2) umbrella-shaped type (Z-type) - crown without lower branches lost in the process of competition; 3) narrow-crown type (U-type) - a small crown, usually formed by underdeveloped secondary branches that replaced the primary crown.

Semerikov and Glotov [109] used numeric morphological traits of oak leaves and generative organs – fruit stalk, cupule, acorns – to characterize oak variability, which allowed them to identify six population groups in the Caucasus and five population groups of *Q. robur* in the Volga and Cis-Urals regions.

Gneusheva et al. [110] showed the informativeness of relative values of the shape and size of leaf blades of *Q. robur* to establish the intraspecific taxonomic rank of its populations and their geographical and ecological fragments.

Seeds of *Q. robur* have significant variation in morphometric parameters. Morphological forms of acorns are distinguished as large-fruited and small-fruited forms of acorns. According to their shape, they are divided as 1) cylindrical, 2) teardrop-shaped, 3) conical, 4) elliptical, oblong, 5) barrel-shaped, and 6) round [111] (Kryukova, Shirnin, 2016). However, the shape coefficient of acorns is not associated with shape diversity [112] (Storozhenko et al. 2020). It is noted that acorns of saline oak groves are characterized by poor survival rate and low growth of the first-year seedlings in height. According to [113] (Chernodubov 2018), the highest germination of *Q. robur* acorns was noted for small forms (90%), the germination percentage for medium-sized acorns was 82%, large ones - 78%.

Acorn yield is characterized by significant interannual variations. *Q. robur* belongs to the species in which the number of acorns is determined not by the number of emerged flowers, but by the number of remained pollinated flowers and mature acorns, which determines the yield of the year (masting year) [114] (McClory et al. 2024). The study presents clear evidence of maternal choice during acorn development in *Q. robur*, demonstrating the positive effects of pollen supplementation. It also confirms that *Q. robur* exhibits masting behavior in fruit maturation; at this site, the occurrence of a mast year is determined by the abortion of pollinated flowers and immature acorns, rather than by the quantity of flowers produced. Taking into account the periodicity and variability of flowering and pollen production in the oaks, as well as the fact that not all trees of the same species in a population produce good quality pollen, it is necessary to preserve the viability of pollen by storing it under certain conditions for targeted acorn production and breeding, since this allows to have a good yield [115] (Batos, 2012). Moreover, it is important to note that the patterns of spatial, temporal and individual variability of *Q. robur* pollen grain viability is under the influence of climatic factors, which are showing compelling changing trends from year to year [116] (Batos, Miljković, 2017).

9. Phenology of *Q. robur*

Phenological analyses in populations of *Q. robur* (phenophase of leaf unfolding, flowering and leaf fall, duration of vegetation) revealed more significant differences between trees and populations than between years of study. The same phenological form was also noted in individual trees within populations, which indicates their supposed common origin. Based on this, it can be concluded that the differences between populations are due to high intraspecific variability, i.e. the phenological form of the population (phenoform). The onset of the phenophase is largely under genetic control, and this is important for the classification of source material in the process of forest tree breeding [115] (Batos, 2012). The phenomenon of polycyclism is also characteristic of oak - the ability to begin growth several times during the same growing season. Polycyclism of *Q. robur* also includes a rare phenomenon such as summer flowering [115] (Batos, 2012).

There are different varieties (forms) of *Q. robur*: "early" and "late". The early (*Q. robur* L. f. praecox Czern.) and late (*Q. robur* L. f. *tardiflora* Czern.) phenological forms were first described by E. F. Zyablovsky in 1804 and V. M. Chernyaev in 1858 [117] (Silchenko, 2012). In addition to these extreme forms, medium and winter-leafed forms are also sometimes distinguished. In the north-eastern part of the *Q. robur* range, the bud burst phenological varieties are practically absent, but varieties differed by the terms of autumn lead fall were clearly distinguished [118] (Danilov et al. 1975). The difference between the two bud burst forms or varieties in growing degree units (at the base temperature of 5 °C) is more than 15 °C according to [119] (Efimov, 1975) and up to 35 °C according to [120] (En′kova, 1976). The difference in the time of leafing onset between the early and late forms ranges from 2 to 4 weeks [121–124] (Puchałka et al. 2015; Slepykh, 2016; Wesołowski et al. 2008; Orlović et al. 2008). As shown by studies of the genetic determination of phenological forms in oak, these forms separated due to a mismatch in their flowering periods [125,126] (Batos et al. 2012; Utkina et al. 2017). Thus, the gene flow between them is limited [122] (Slepykh, 2016), and their genetic differences are confirmed by molecular studies [127,128] (Pirko et al. 2018; Ueno et al. 2021).

According to the phenological structure of the population, most trees maintain the same tendency from year to year, i.e. they remain in the same phenological group (designated as "early", "middle" and "late") or change it by one phenological level, which indicates a genetic influence on the manifestation of this trait. Since these populations are located in similar environmental conditions, the differences between them can be considered as a consequence of intraspecific variability of *Q. robur* and the genetic structure of the population [129] (Batos et al. 2014). The phenological forms within the species *Q. robur* differ in the timing of leafing. Significant differences in vegetation timing requirements were found between the three flowering phase phenoforms, early, intermediate and late [130] (Andrić et al. 2018).

In the forests of Lekenik and Otok in Croatia, local environmental factors influenced the timing and duration of *Q. robur* phenophases, contributing to variability in its morphological and physiological traits [131] (Tikvić et al., 2006). Variations in the start and end of flowering phases were influenced by both genetic makeup and environmental effects. Specifically, the onset of leaf phenophase development in *Q. robur* showed a notable difference of 42 days between early and late leaf-developing phenotypes, although no such differences were observed in reproductive phenophases. The timing of early and late leaf flushing in *Q. robur* was primarily determined by genetic factors, with environmental factors playing a lesser role.

Studies of oak phenoforms under similar soil and moisture conditions revealed no consistent association between leafing time and factors such as tree age, size, or stand position, suggesting that phenological variation may be genetically driven [132] (Chokheli et al., 2016). Comparative research on the long-term dynamics of growth and leaf phenology, xylogenesis in the two phenological forms, and their responses to meteorological factors show an absence of uniform climatic response. Instead, individual patterns in leaf and xylem development point to substantial genetic variability [133–137] (Puchałka et al., 2016, 2017; Kitin, 1992; Kostić et al., 2021; Koval & Kostyashkin, 2015).

Significant differences in leaf phenology and xylogenesis timing were found among individual trees in [134] (Puchałka et al. 2017). The smallest differences in wood formation between trees were observed at the beginning of the vegetation period, when the first earlywood vessels were detected (9 days). High seasonal variability in the number of cambial cell layers was observed. Differences in the timing of cambial activity cessation and xylogenesis amounted up to a month. Oak tree ring width and the size and number of early wood vessels may not be sensitive indicators of early spring temperature and spring defoliation; the lack of a relationship between leaf phenophases and xylogenesis, as well as phenological variability, may be the reasons for the lack of a clear climate model observed in [134] (Puchałka et al. 2017).

The phenological forms are particularly noteworthy due to their differing responses to growth conditions, extreme climatic factors, and pest outbreaks. Most researchers observe that late-forming trees have a shorter growing season, are not affected by spring frosts, grow faster, produce higher-quality wood, and are more resistant to oak forest pests, including powdery mildew (*Erysiphe alphitoides*), *phytophthora*, lace bug (*Corythucha arcuata*), and various species of gall wasps (genus *Cynips*) [115,126,136,138] (Batos 2012; Utkina et al. 2017; Kostić et al. 2021; Bobinac et al. 2012).

The crown height of the early form is 15–20% higher than that of the late one [139,140] (Levlev 1970; Lukyanets 1979). In late-forming stands, there are usually more trees with valuable economic traits [140] (Lukyanets 1979), the so-called “plus trees” [141,142] (Shitov 1986; Shutyaev 1998).

Although young trees of the early form grow faster [137,140] (Koval, Kostyashkin, 2015; Lukyanets 1979), the growth energy of the late phenological form increases with age [138,143] (Bobinac et al. 2012; Kobranov 1925).

Local growth conditions affect the growth rate of both phenological forms [121,142] (Puchałka et al., 2015; Shutyaev, 1998), but air temperatures have the most significant impact on leafing [119,144] (Efimov, 2012; Pukacka, 2006). In addition to growth energy and leafing timing, morphological differences are also observed: the late form typically has straight, fully woody trunks and high, raised crowns, while the early form has wide, spreading crowns and curved trunks [126,145] (Utkina, Rubtsov, 2017; Antin et al., 2013). In humid soils with frost risks, the late form has an advantage over the early form. In drier conditions, the early form is less affected by spring frosts and outperforms the late form in growth rate. It is believed to better utilize favorable spring moisture conditions but is more susceptible to defoliation from late frosts and insects. Its earlier start to the growing season allows it to begin growth before summer droughts set in [123,133,146] (Wesołowski, Rowiński, 2008; Puchałka et al., 2016; Rubtsov, Utkina, 2008). In contrast, the late form avoids the spring defoliation risk from frost and insects, with its growth more concentrated in the summer due to a delayed start of the growing season, making it more vulnerable to summer droughts. As a result, it tends to occur in more humid soils [136,146,147] (Kostić et al., 2021; Rubtsov, Utkina, 2008; Vikhrov, 1954). Understanding the biological and ecological traits of these phenological forms is crucial from a silvicultural standpoint, as selecting the wrong oak phenological form for specific moisture conditions can lead to forest management failures and oak stand decline [115,146] (Batos 2012; Rubtsov, Utkina 2008). Individual variability in the onset of individual phenophases or their duration influence the degree of plant resistance to herbivores and pathogens. *Q. robur* with an earlier onset of leaf fall are more susceptible to defoliators, since there is synchronization between the phenophase and the defoliator development cycle [123,148,149] (Wesołowski & Rowiński, 2008; van Asch & Visser 2007; Wagenhoff et al. 2013).

Early and late phenological forms of *Q. robur* were studied on healthy oak trees in permanent sample plots in wet, dry, and very dry oak stands grown on different soil types in Shipov Forest, Voronezh Region, Russia using dendroclimatic analysis [150] (Milenin et al. 2023). The late phenological form trees showed higher radial growth rates on wet sites than the early phenological forms, which annual radial growth was less stable and more variable compared with the late phenological forms. For both phenoforms, the key factors influencing radial growth are composite indicators that reflect the balance between temperature and moisture, such as Selyaninov's hydrothermal coefficient and Lang's rain factor. Generally, the periods of minimal radial growth occurred simultaneously on both dry and wet sites, while maximum growth periods were linked to years with high water availability [150] (Milenin et al. 2023).

10. Phylogenetics and Phylogeography of *Q. robur*

Based on 9,549 conserved orthologous sequences a simplified phylogenic tree places oaks in the group of Fabids (Eurosids I) between peach and poplar genomes (Fig. 3 in [102] (Lesur et al. 2015). *Quercus* is a species-rich genus with a mostly northern hemisphere distribution of around 435 species divided into two subgenera (*Quercus* or "white oaks" and *Cerris* or "red or black oaks") and eight sections: five in subgenus *Quercus* - *Quercus* (white oaks in North America and Eurasia), *Mesobalanus* (Central and Eastern European), *Ponticae* (mainly in Western Asian), *Protobalanus* (golden oaks in the southwestern United States and northern Mexico), *Virentes* (live oaks common in the southeastern U.S.), and three in subgenus *Cerris* - *Cerris* (Turkey oaks mostly in Eurasia), *Ilex* (Holly oaks in the Mediterranean), *Lobatae* (red oaks in primarily distributed in North America) [151–153] (Denk et al. 2017; Hipp et al. 2018, 2020). It was shown based on genetic data that oaks have tighter macrosynteny with and are more closely related to chestnuts than to beeches [154] (Kremer et al. 2012).

Genetic data on 260 oak species have shown for the first time how these species have varied across the continents of the Northern Hemisphere and that their rates of diversification have increased in response to migration to new habitats [153] (Hipp et al. 2020). The oak gene phylogenies are highly reticulate and reflect histories of introgression, lineage sorting and divergence [153] (Hipp et al. 2020). Fossil data and restriction-site associated DNA sequencing (RAD-seq) for 632 individuals representing nearly 250 oak species were used in [153] (Hipp et al. 2020) to infer a time-calibrated phylogeny of the world's oaks and to investigate global patterns of oak diversity and test the hypothesis that there are regions of the oak genome that are informative about phylogeny. Oak lineages have diversified across different geographic regions, followed by ecological divergence within those regions, in both the Americas and Eurasia. Approximately 60% of oak diversity can be traced to four clades that underwent increases in net diversification, likely driven by climatic changes or ecological opportunities. While the phylogeny is strongly supported, it contrasts with significant genomic heterogeneity in phylogenetic signals and introgression. Oaks are phylogenomic mosaics, and their diversity may actually be influenced by the gene flow that shapes the oak genome. Oaks of Eurasia point to the important role of ecological and morphological convergence among unrelated oaks. The phylogeny of the Eurasian white oaks represented by 23 of the estimated 25 white oaks in the Roburoid clade of section *Quercus*, including *Q. robur*, has been addressed in detail with the strongest sampling of white oak species up to date. They concluded a northern temperate clade. The increase in diversification rate in the Roburoids with divergence within clades and geographic regions is in agreement with their ecological diversity, ranging from lowland swamp to Mediterranean scrub, and from mesic lowland forests to subalpine timberline. The European Roburoids are not readily diagnosable morphologically, and the morphological and ecological convergence among clades has led to taxonomic confusion. This study demonstrates that across the genus, ecological diversification within clades has shaped diversification and that there is no a single genome part that can discriminate all the oak species [153] (Hipp et al. 2020). A dated phylogeny of oaks shows high diversification rates since the Pliocene in sections *Quercus* and *Lobatae* [153] (Hipp et al. 2020).

The geographic distribution throughout Europe of each of 32 chloroplast DNA variants belonging to eight white oak species sampled from 2613 populations including pedunculated oak is presented in [155] (Petit et al. 2002). These distributions, together with the available palynological information, inferred colonization routes out of the glacial period refugia. In western Europe, movements out of the Iberian and Italian Peninsulas are particularly evident. Separate refugia were also found in the eastern Balkans, while the western part of the peninsula showed similarities with Italy. These movements, which likely involved the exchange of haplotypes between refugia during the current interglacial period and possibly during earlier glacial cycles, suggest that phylogenetically divergent haplotypes often followed similar colonization routes, somewhat limiting the phylogeographic structure. Geographic disjunctions in the current distribution of haplotypes are also apparent, likely caused by rapid climatic shifts at the end of the glacial period (notably the Younger Dryas cold phase), which led to range contractions following an earlier warm period when oak first expanded from its primary refugia. This cold phase was followed by another expansion period at the start of the Holocene, which in some cases involved 'secondary' refugia. These short climate oscillations likely caused a partial reshuffling of haplotype distribution. The data also suggest early associations between haplotypes and oak species, although extensive introgression among species has largely obscured this pattern. This implies that colonization routes may have initially been shaped by the ecological traits of the species hosting each chloroplast variant. For instance, it suggests that two oak species in the north of the Iberian Peninsula (*Q. petraea* and *Q. pubescens*) are recent post-glacial immigrants. When considered together, the conclusions drawn from molecular data and fossil pollen data regarding the location of glacial refugia and colonization routes appear to be largely compatible and complementary [155] (Petit et al. 2002).

Genomic data on early and recent oak evolution reveal evolutionary mechanisms that allowed oaks to colonize the Northern Hemisphere [156] (Kremer & Hipp, 2020). It suggested that Roburoid oaks arose as a result of migration of the oaks in the North American section *Alba* into Eurasia and introgressive hybridization with European species of the section *Pontica*.

Geographic structure of chloroplast DNA variation studied in 42 populations of Q. robur in the European part of Russia, Belarus, Poland, Ukraine, the Urals, and the Caucasus demonstrates sharp differences between western and eastern populations [52] (Semerikova et al. 2021. The authors concluded that this outcome is due to postglacial colonization by both species from distinct, long-isolated refugia, some of which were located in the eastern part of the studied areas. In the Urals, the differentiation of oak between the southern regions (Ural River and Belaya River basins) and the more northern areas (Ufa River basin and the Middle Urals) can likely be attributed to different historical colonization patterns of these regions by oak [52] (Semerikova et al. 2021).

Genetic differentiation was studied in 41 populations (755 trees) of *Q. robur* and six populations (109 trees) of *Q. petraea* in North Eastern Europe, the Balkans, the Crimea, and the Caucasus using 14 nuclear microsatellite loci (nSSR) and compared with the previously obtained chloroplast DNA data [69] (Semerikova et al. 2023). A low level of nuclear DNA introgression of *Q. petraea* in *Q. robur* was revealed. No significant influence of *Q. petraea* on the geographic structure of *Q. robur* diversity was found. High differentiation in nuclear markers between populations of *Q. robur* from different geographical regions and within the Caucasus was obtained. The largest difference was observed between Caucasian populations and the populations of North Eastern Europe. In the northern part of Eastern Europe, a weak trend from east to west was observed based on nuclear markers, in contrast to the chloroplast DNA data, which revealed a sharp distinction between the populations in the eastern Russian Plain and Urals and those in the western regions due to the absence of shared haplotypes. Populations in the southeastern Balkans differed from those in Northeastern Europe, and the ABC estimate of divergence time (910 generations) significantly exceeded the age of the Last Glacial Maximum, ruling out the involvement of the southeastern Balkans in the recolonization of Eastern Europe after the last glaciation. In the Caucasus, the structure of nuclear DNA generally aligned with the phylogeography of chloroplast DNA and morphological data. There was a clear differentiation between western and eastern Caucasian populations based on nuclear markers. A mix of the Balkan and West Caucasian clusters was identified, which, along with chloroplast DNA data, suggests their origin from multiple migration events. This group of populations contained only West Caucasian and Crimean endemic chloroplast haplotypes, without Balkan haplotypes, indicating gene introgression from the Balkan cluster into the Crimean and West Caucasian populations via pollen flow, without seed transfer [69] (Semerikova et al. 2023).

11. Response of *Q. robur* to Environmental Factors in Dendroecological and Dendrochronological Studies

Response and adaptation to environmental factors, identification and cataloguing of genes of adaptive significance remains an important step in understanding the evolutionary responses of *Q. robur* to selection pressures. The key factors implicated in oak decline and effective management of declining oaks include drought, pests and pathogens, but extreme frost, waterlogging, soil properties, land management, nitrogen pollution, heavy metal pollution, genetic predisposition and mycorrhizal changes could also be involved in decline [157] (Gosling et al. 2024). The amount that each main stressor contributes towards these declines and the ‘tipping points’ are discussed below and likely to differ between decline events, sites and even individual trees.

11.1. Drought

In the experiment with scions grafted and vegetatively propagated from 40 pedunculate oaks older than 80 years from natural stands in the Republic of Croatia moderate drought stress significantly reduced net photosynthetic rate, stem diameter increment and height growth increment, but acorn mass was not affected [158] (Sever et al. 2022). Comparison of drought and nitrogen deficiency factors showed that moderate drought is a more dominant stress factor for photosynthesis and growth of *Q. robur*, but not for acorn development. Acorn mass decreased in both wet and dry years under suboptimal nitrogen nutrition [158] (Sever et al. 2022).

It was demonstrated in another experiment that droughts increased the accumulation of osmolytes, such as proline and glycine betaine, as well as higher polyamines (spermidine and spermine) levels and decreased putrescine levels in *Q. robur* seedlings [159] (Kebert et al. 2023). This study demonstrated also beneficial function of the ectomycorrhizal fungi, in particular *Scleroderma citrinum*, in reducing the effects of drought stress in pedunculate oak.

The response of oak trees to drought depends on its physiological status and phenological form. The most significant differences in the relative expression levels of candidate genes associated with drought tolerance were observed during the flowering period between phenoforms and between senescent and vital trees [160] (Trudić et al. 2021). Three genes *wrky53*, *rd22* and *sag21* showed upregulated expression pattern in senescent physiological groups, indicating their possible role in the coping mechanisms of oak in stressed environment.

Overall, *Q. robur* is considered a very drought-tolerant species and a relatively major beneficiary of climate change among broadleaf species [161] (Bose et al. 2021).

11.2. Waterlogging

The radial growth of *Q. robur* depends on precipitation at the beginning of the growing season, and from late spring until the end of the growing season it increasingly depends on the groundwater level. [162] (Basu et al. 2024a). These authors also revealed that radial growth during the *Q. robur* vegetation period depends on various water sources: in spring, growth is mainly driven by precipitation, while in summer and autumn, groundwater levels play a more critical role [163] (Basu et al., 2024b). Overall, this study highlights the considerable threat that both groundwater changes and the increasing frequency of drought events pose to floodplain forests. The oak's dependence on water bodies and the proximity of groundwater increases their photosynthetic activity, with the lowest photosynthesis values being determined in the area furthest from the water source [164] (Kesic et al. 2023).

The *Q. robur* adapts to waterlogged soil by changing the anatomical features of the wood - a general increase in the number of vessels and the width of the annual ring [165] (Resente et al. 2024). The *Q. robur* has the ability to quickly regenerate the root system after waterlogging (or flooding), which allows it to survive in hydromorphic soils. It is assumed that the *Q. robur* is able to preserve its carbohydrate reserves until the growing conditions become more favorable [166] (Gérard 2008).

Resistance to waterlogging in *Q. robur* is determined by molecular mechanisms of formation of a radial barrier against oxygen loss in the roots, similar to species resistant to waterlogging due to increased biosynthesis of suberin [167] (Le Provost et al. 2016).

11.3. Geographic Origin and Cultures, and Provenance Tests

The large area of natural growth of *Q. robur* indicates its wide ecological amplitude. Its populations adapt to a variety of different microhabitats, promoting inter- and intra-population variability. A study of biomass accumulation depending on environmental conditions and origin showed a greater influence of genetic characteristics of populations, although leaf parameters are more dependent on micro-environments of growth [168] (Peric et al. 2006).

The mother trees origin affects the morphological characteristics of *Q. robur* seedlings [169] (Popović et al. 2024). A high degree of variation has been observed for root collar diameter, height, weight of aboveground part, root weight, Roller's sturdiness coefficient and seedlings quality index. The high degree of correlation was observed between root weight and aboveground part weight, between root weight and aboveground part weight. Provenance trial and common garden experiments in in Belgium and Denmark demonstrated that the environment of origin influenced the bud phenology of seedlings, and this provenance effect was dependent on the seedlings' growing environment. Furthermore, the results suggested that the impact of warming may vary between provenances, and that the environmental history of previous generations is likely to affect the response of tree seedlings [170] (Dewan et al. 2021).

Variability of oak is often associated with the frequency of interspecific hybridization, which occurs as a result of the absence of a phenological barrier during the flowering period between *Q. robur* and *Q. petraea*. Locality and climatic conditions have a dominant effect on plant growth and development, i.e. on nutrition and absorption of nutrients. The observed variability in plant adaptability is manifested in changes in the size and weight of leaves, the number of stomata, and may be a consequence of species adaptation [115] (Batos 2012).

There is significant variation in the physiological response of *Q. robur* trees of different origins to heat stress, and selection of offspring from origins with a more pronounced adaptive response is possible [171] (Cuza, 2023). Populations of *Q. robur* with similar morphological and physiological characteristics could be combined into groups in accordance with the ecological zoning of vegetation in Bosnia and Herzegovina; it was suggested that it is possible to use reproductive material within these groups of regions for reforestation and, with additional study, an exchange between certain regions is also possible [172] **(**Ballian et al. 2017). Genetic analysis is currently used to select the origins with the best production potential; by selecting the best origins of *Q. robur* and propagating them, it is possible to achieve a significant increase in the height and thickness of the plants, i.e. the yield of wood pulp [173] (Ballian and Hodžić 2022).

11.4. Climate Change, Temperature and Precipitation

Predictive models show that climate change will negatively affect the ecological niche of *Q. robur* in the future. For example, in Croatia, the model predicts an increase in the minimum temperature in the coldest month and the maximum temperature in the warmest month, as well as a decrease in precipitation in both the driest and wettest months [174] (Ugarković et al. 2016). Climate change is seen as a leading factor in oak decline in southern Sweden according to a simple model linking climatic variation, site-level condition, and the risk or proportion of trees affected by the decline [175] (Sonesson & Drobyshev, 2010).

Poor winter hardiness is thought to limit oak cultivation in northern latitudes and set a limit to the northward expansion of *Q. robur*, but high intra-population variability offers opportunities for the development of more frost-resistant genotypes [176] (Repo et al. 2022). It is interesting that the results of a study of oak regeneration in Sweden showed a lack of latitudinal association with oak regeneration, in contrast to the assumption of decline towards the range margin [177] (Franzén et al. 2024). Contrary to the hypothesis that oak regeneration would decrease at the range margin, these results did not support this notion. This suggests the possibility of a future northward expansion of oak populations. The study also found a positive correlation between oak regeneration and stand age, while higher nitrogen and ground moisture levels were inversely related to regeneration. The age-dependent positive effect on recruitment implies that species recruitment dynamics within forests may be influenced by age-related factors in the tree community, with important implications for forestry and conservation management. Notably, the successful natural regeneration of the introduced *Q. rubra* highlights its adaptation to the Swedish climate and forests. This study represents the first large-scale analysis of oak regeneration across multiple oak species in Sweden [177] (Franzén et al. 2024).

The spring bud break phase of *Q. robur* depends on both genetic characteristics (phenoform) and climatic factors. It was demonstrated that for all three studied flushing groups (early, intermediate and late flushing groups, respectively) insolation and the day of year were statistically significant predictors for growing degree days (GDD) [130] (Andrić et al. 2018). Insolation was demonstrated to be the primary factor with the largest influence on the GDD values. GDD model was univariate for the early ($GDD_{early} = -27.651 + 0.539 \times$ insolation) and intermediate ($GDD_{inter} = -48.084 + 0.690 \times$ insolation) flushing groups and the multivariate model ($GDD_{late} = -237.839 + 0.559 \times$ insolation $+ 2.479 \times$ day of year) for the late flushing group. To break dormancy, chilling needs to fall within the range of ± 40 chilling units. If the values are outside this range, the trees will require significantly higher forcing temperatures [124] (Andrić et al. 2018).

The study by Firmat et al. [178] (Firmat et al. 2017) showed that leaf phenology traits depend primarily on the plastic variability exhibited by a tree during its life. Both spring and autumn (bud break and senescence, respectively) phenological periods were involved in local adaptation, but bud break was likely the trait most susceptible to climate change-induced selection.

The increase in spring temperatures observed over the last decade significantly increases the reproductive capacity (formation of acorns) of temperate oaks; with warming, not only the number but also the mass of acorns increases [179,180] (Caignard et al. 2017; Hanley et al. 2019). While the amount of precipitation does not significantly affect the formation of acorns [179] (Caignard et al. 2017).

In general, there is an increase in *Q. petraea* and *Q. robur* vegetative and reproductive growth in recent decades in central Europe. Along with rising temperatures, higher carbon dioxide levels in the atmosphere may also enhance tree growth in certain species, while increased nitrogen (N) deposition has been shown to boost forest growth and carbon sequestration in Europe. Thus, global warming may promote the proliferation of oak in temperate ecosystems [179] (Caignard et al. 2017).

11.5. Climate Response in Genetic and Dendrochronological Studies

The tree-ring chronology obtained for 20 trees of *Q. robur* growing in Donetsk Region (the steppe zone in Eastern Europe) is strongly correlated with local spring and summer precipitation, and local temperatures in April, June, and July. Dynamic correlation analysis indicates that the relationships between oak growth and late winter and early spring temperatures, and between oak growth and February and August precipitation have changed over the past 80 years. These data suggest that warming has led to both advances in oak phenology and changes in early spring climatic conditions [181] (Netsvetov et al. 2017).

The greatest influence on the radial growth of *Q. robur* in western and north–eastern Poland was exerted by spring precipitation in the year preceding the formation of the annual ring, and the temperatures of the previous and current springs, when the trees formed the growth [182] (Kalisty, 2022). The response of forest stands to climatic factors depends on their age. In young forest stands, a contradictory response was observed, in contrast to older ones.

A study of the climatic response in *Q. robur* populations in the Southern Urals showed that the response to monthly temperatures in radial increment was more pronounced in the mountain stands, while it was absent in the Bashkir Cis-Urals [183] (Ianbaev et al. 2023). On the contrary, in the latter part of the region, trees were more sensitive to precipitation. In some cases, the considered climatic factors had opposite effects on different stands. Precipitation in winter (December and January), May and summer (June and July) were especially important for the radial increment of the species. In the mountain stands, significant negative correlations were observed between this parameter and the air temperature of October of the previous year, March, April, May and July of the current year. Thus, the climatic response of English oak has regional features and depends on the biological characteristics of the analyzed individuals/populations (age, origin).

Rellstab et al. [184] used a pooled amplicon sequencing of 94 genes in 71 populations of *Q. petraea, Q. pubescens* and *Q. robur* in Switzerland to genotype ~3500 SNPs and associate their variation with abiotic factors related to local topography, historical climate and soil characteristics. They also tried to predict the fate of these species under the scenario of climate change. They identified several SNPs and genes likely involved in local adaptation and pinpointed the environmental factors that may be driving this process. They then integrated the allele frequency data of these candidate SNPs with current and future climate data to assess the potential adaptability of the oak populations and species under projected climate change. In total, they found 545 significant abiotic factors-SNP associations for 181 SNPs in 68 genes in *Q. robur*. In *Q. robur*, in this order, humidity, number of precipitation days in summer, annual precipitation, continentality, mean annual temperature, index for average summer drought and clay content were the factors most often associated with SNPs. In average, populations of *Q. robur* were modelled to experience the smallest increase in mean annual temperature. Risk of nonadaptedness (RONA) to future mean annual temperature and site water balance (precipitation minus evapotranspiration) was modelled, and for both environmental factors, the general linear mixed model revealed that RONA to the projected future climate varied significantly among species and populations within species. While *Q. robur* populations were predicted to be the most adaptable to changes in mean annual temperature, they were the least well-adapted to future changes in site water balance. As a result, *Q. robur*, typically found in warm, moist habitats, exhibited the lowest RONA to increased temperature and the highest RONA to reduced water availability in the future [184] (Rellstab et al. 2016).

Notably, the plants' response to global change can be rapid, even in long-lived species, like *Q. petraea*, which is a very close relative to *Q. robur* and displayed a genome-wide response to the Little Ice Age (~1650 AD) despite its ~50-year generation time [185] (Saleh et al. 2022). Although *Q. petraea* is predicted to maintain its climatic niche at the northeastern cooler boundary, it is expected to produce wood at a slower rate due to the anticipated warmer climate in central Europe, with more frequent heatwaves and summer droughts [186] (Puchałka et al. 2024).

Meanwhile, it seems that *Q. robur* has a significant adaptive potential to withstand the climatic stresses and adapt to climate change, although, perhaps, with some help via assisted migration [13,187,188] Schroeder et al. 2021; Hlásny et al. 2014; Bussotti et al. 2015). For instance, the genetic diversity of 720 candidate genes associated with bud burst in *Q. robur* individuals sampled from 6 provenances in the provenance/family common garden trial of *Q. robur* established in Forest District Mogilica in north-western Poland and representing eight forest seed stands in Poland was explored using the sequence capture technique [189] (Meger et al. 2024). In total, 18,799 SNPs were genotyped in 720 candidate genes in 87 trees of *Q. robur* originated from 6 provenances. Using landscape genomic approaches, 8 F_{ST} outliers were identified and 781 unique SNPs in 389 genes associated and correlated with geography, climate, and phenotypic variables (individual/family spring and autumn phenology, family diameter at breast height (DBH), height, and survival) that are potentially involved in local adaptation. Then, vulnerable areas of the *Q. robur* distribution in Poland that are at risk from climate change were identified using a nonlinear multivariate model, Gradient Forests. The *Q. robur* populations in the eastern part of the analyzed geographical region are the most sensitive to climate change. Use of genomic resources and approaches to assess adaptive potential, divergence and introgression in oaks is nicely reviewed in [190] (Lazic et al. 2021).

12. Factors of Resilience to Environmental Factors in Oaks and Their Longevity

An important feature of *Quercus* species that contributes to their stability and distribution is the presence of climatypes. Using North American oaks as an example, it has been shown that species are differentiated within lines by sets of functional traits that show correlated evolution and adaptation to contrasting habitats [191] (Cavender-Bares and Reich, 2012). Climatypes have multidirectional indicators associated with resistance to various factors. For example, areas with frequent and severe fires are characterized by oaks with a high ability to grow shoots from rhizomes and increased bark thickness [192] (Cavender-Bares, 2019). The altitudinal gradient also affects physiological and morphological features [193,194] (Sean 2011; Bresson et al. 2011). Thus, depending on the conditions of the territory, it is necessary to select the most suitable climate types. Recent studies on the drought resistance of *Quercus* species, including *Q. robur*, have shown that their resilience to drought stress involves a balance between mechanisms to prevent water deficiency and the ability to quickly restore water levels after stress. For example, research highlights that during drought, oaks exhibit reduced stomatal conductance and a decrease in water potential, which limits water loss from leaves and maintains internal hydration. Additionally, upon rehydration, physiological processes such as photosynthesis and enzyme activity rapidly return to normal, helping the plant recover efficiently. This combination of minimizing water loss and promoting rapid water uptake upon rehydration is essential for oaks to survive in fluctuating moisture environments [195–197] (Chai et al. 2015; Kaproth et al. 2023; Liu et al. 2024). Oak species respond to drought through increased antioxidant enzyme activity and osmotic solute accumulation, which help mitigate oxidative stress and maintain cell turgor under low water conditions [198,199] (Xiong et al. 2022; Tikhomirova et al. 2023). These adaptations underscore how *Quercus* species balance both moisture retention in leaves and recovery to maintain growth and survival in dry conditions.

Lifespan probably correlates with resistance to stress and adverse environmental factors. Thus, forest communities whose framework consists of long-lived trees are apparently more resistant and adaptive to adverse external factors. Research in various fields of forest science reveals features that may be associated with a long lifespan of trees. It was theorized that the “chemostat effect” model observed in bacterial colonies that persist for several generations and accumulate neutral mutations is applicable to long-lived woody plants [200] (Klekowski, 1988). The extent of mutational load in populations of long-lived plants depends on the origin and accumulation of mutations. If mutation rate is measured as mutations per cell division, per growing season, or another similar biological time unit, the overall frequency of mutant cells will rise as the plant ages (the aforementioned "chemostat effect"). Thus a 20-year-old tree should have a lower mutation frequency in its sex cells than a 200-year-old tree of the same species. Based on the fact that apical meristems undergo about five divisions of initials during the growing season, Klekowski suggested that approximately 5% of the initials would be mutant in 100-year-old trees, 10% - in 200-year-old trees and so on; tree branches are considered as stem cell lines [200] (Klekowski, 1988). During iterative branching, the number of branches grows exponentially, while the number of cell divisions rises linearly [201] (Burian et al., 2016). Additionally, computational modeling demonstrates that the arrangement of stem cells and the positioning of axillary meristems help distribute somatic mutations across the main shoot, preventing their fixation and promoting genetic diversity. These features slow down "Muller's ratchet" (accumulate deleterious mutations in an irreversible manner) and thereby extend lifespan.

This theory of accumulation of somatic mutations was confirmed for the genus *Quercus* by Plomion et al. 2018 [49]. The emergence of new gene variations is associated with meiotic mutations that occur during sexual reproduction. Somatic mutations that arise in apical meristems and can be transmitted to generative tissues and offspring were also found in oak, therefore somatic mutations along with meiosis can increase the genetic diversity of long-lived trees [49] (Plomion et al. 2018), which may also indicate the contribution of mutational load to adaptation, in particular with regard to protection against new pests and pathogens. The accumulation of somatic mutations in resistance genes was shown also for another long-lived tree - *Eucalyptus* [202] (Padovan et al. 2013).

Moreover, increased lifespan largely depends on the immunity of trees to infectious organisms. Based on the analysis of the *O. robur* genome, Plomion et al. 2018 [49] showed that disease resistance genes have multiple tandem duplicates, thus increasing the number of copies of an important gene aimed at preventing damage caused by pathogens, and therefore the resistance of the organism as a whole. It is assumed that the immune system makes a significant contribution to the survival of long-lived plants for several centuries and leads to adaptive plasticity [49,203] (Plomion et al. 2018; Tobias, Guest, 2014). According to [203] (Tobias, Guest, 2014), tree defense and longevity are based on a three genomic approaches: 1) gene numbers, 2) genomic architecture, and 3) mutation loads accumulated over long lifespans. The genomic architecture is expressed in the clustering of genes and their repetition, a high number of transposable elements. Mainly the genes of the metabolic pathway and R-resistance genes are clustered.

Such long-lived sessile organisms as trees must persist in the face of a wide range of abiotic and biotic threats throughout their lifespan. A consequence of the long lifespan of trees is the accumulation of somatic mutations during mitotic divisions of stem cells present in shoot apical meristems. Empirical approaches and modeling have shown that intra-organism genetic heterogeneity provides advantages in the fight against short-lived pests and pathogens due to the combination of intra-organism phenotypes. In the oak example, we see the accumulation and transmission of somatic mutations and the expansion of tree disease resistance gene families [49] (Plomion *et al.* 2018). However, for old-growth trees, low levels of mutations in meristems were shown. Schmid-Siegert et al. [204] sequenced the genome of two terminal branches from a 234-year-old *Q. robur* tree and identified several fixed somatic single-nucleotide variants. These variants could be traced through nested sectors of younger branches, revealing a sequential pattern. Their findings suggest that the stem cells of shoot meristems in trees are effectively shielded from the accumulation of mutations. They found that oaks protect their bud meristems from ultraviolet radiation with multilayered leaf-like structures, potentially reducing the likelihood of ultraviolet mutagenesis [204] (Schmid-Siegert et al. 2017). This can contribute into maintenance of tree health and explain the lifespan that can reach several hundred years, up to almost half a century in *Q. robur* [205] (Biondi et al. 2023). Thus, long-lived trees, such as *Q. robur*, have mechanisms for both protection against somatic mutations and fixing the emerging "useful" mutations to combat pathogens. Different genetic mechanisms of aging in trees are reviewed also in [206–210] (Popov et al. 2022; Batalova & Krutovsky 2023; Cui et al. 2024; Liu et al. 2024; Volkava & Riha 2024).

Ianbaev et al. 2022 [211] suggest that maintaining a high level of genetic variability in *Q. robur* populations is also the basis for their resistance to environmental factors in the context of global climate change. The authors suggest that this may be due to the efficiency of genetically realized pollen flow, including between remote stands. Based on 412 SNPs, high intrapopulation genetic variability was shown in *Q. robur* populations in the Republic of Bashkortostan (Russia) growing in significantly different rainfall regimes and amounts, mainly by months of the growing season [211] (Ianbaev et al. 2022). Thus, it is important to note the need to maintain high genetic diversity in *Q. robur* populations, which is necessary for adaptation to changing environmental conditions, through maintaining effective gene flow between remote stands, including through the creation of green belts and promoting long distance gene exchange via assisted migration.

13. Plus Trees and Main Breeding Traits of *Q. robur*

Traditional breeding of *Q. robur* was carried out by selection of stands (origins, plus stands, etc.), individual selection (selection by progeny) and crossing or hybridization [212,213] (Kajba et al. 2011; Fedorkov 2019]. Breeding is carried out in two directions toward economically valuable traits and adaptation to changing climatic parameters. In order to obtain maximum productivity of valuable timber, selection markers are focused on morphological traits of the trunk, physical and mechanical properties of wood. In addition, selection of origins based on the progeny with a properly formed habitus is possible, which is based on the identified correlation between root mass and aboveground part mass and the heritability of this relationship. This feature may facilitate the selection of suitable reproductive material sources for restoring *Q. robur* forests within a particular region of distribution [169] (Popović et al. 2024). For maintaining populations and preventing degradation of oak forests, selection is aimed at choosing maternal populations that show adaptive growth in changing conditions, and in which collection of standard seed material is possible. Forest tree breeding and silviculture of *Q. robur* need to take into account large genetic multiplicities, to manage *in situ* maintenance of numerous and sufficiently large, locally adapted stands [214] (Herzog 1996).

In order to obtain maximum productivity of valuable timber, selection markers are focused on morphological features of the trunk, physical and mechanical properties of the wood. In addition, selection of origins by progeny with a correctly formed habitus is possible, which is based on the identified correlation between the mass of the root and the mass of the above-ground part and the heritability of this relationship. This feature may facilitate the selection of suitable reproductive material sources for regenerating *Q. robur* forests within particular region of distribution [169] (Popović et al. 2024).

Kostrikin et al. 2021 [215] developed criteria for selection of plus stands. For an ideal variety of forest tree species, including *Q. robur*, it is proposed to use the following main parameters: productivity, variability, genetic determination, wood characteristics. They suggest classifying stands as "plus stands" if their forest density is between 0.7 and 0.9, more than 35% of the trees have commercial-quality wood, and the plot contains at least one plus tree per two hectares. It is noted that under the externally outstanding phenotype there are hidden quality features of the different value, with their variation from the lowest (wood density) to the highest (sapwood width) level [216] (Shirnin & Kryukova, 2015). Thus, it is impossible to limit oneself exclusively to phenotypic parameters; it is necessary to supplement the characteristics of plus trees with features of macro- and microstructure, indicators of physical and mechanical properties. In Japan, England, Sweden, Bulgaria and the USA, breeding is also based on wood density characteristics.

The success of selection activities depends on the comprehensiveness of the approach to selection and determination of the leading group of traits, as well as the assessment of heritability [212] (Kajba et al. 2011). The most valuable for selection are plus trees. The following can act as "plus trees":

- trees-phenomena;
- trees-veterans;
- record-breaking best in technical and economic terms and at the same time highly viable;
- fast-growing;

- straight-trunked;
- knot-free;
- possessing the best wood qualities;
- undamaged by rot, harmful insects, frost and other factors.

Plus trees represent a valuable state breeding resource for the improvement and reproduction of forests and their use in protective afforestation [217,218] (Tsarev et al. 2021; Suhorukih & Biganova 2023). Using the example of the Krasnoye Forestry of the Vorontsovsky timber industry enterprise of the Voronezh Region in the Shipovaya oak grove (Russia), where the largest number of plus trees was found, criteria for the assessment and selection of plus oak stands have been developed for the purpose of harvesting selectively improved seeds [215] (Kostrikin et al. 2021).

Breeding and forestry programs are generally aimed at preserving oak stands. The current stage of forest management development should include measures both for selecting the best trees and for preserving genetic diversity. It is also recommended to establish permanent observation plots in oak populations in order to monitor the development and inheritance of quantitative traits that are controlled by multiple genes. A strategic plan for conservation of *Q. robur* populations (*in situ* and *ex situ*) will ensure the survival of the species under the ongoing climatic changes. [219] (Trudić et al. 2021). Recommendations for future *Q. robur* breeding and conservation programs should include the setup of experiments that will focus on genetic, phenological, chemical and morphometric analysis of *Q. robur* in natural conditions, greenhouses and *in vitro* culture [220,221] (Stojnić et al. 2014: Fedorkov 2024).

Finally, it is important to highlight that genomic selection shows significant promise for oaks, as it can match or even exceed the effectiveness of phenotypic selection for traits related to growth and wood quality. Genomic selection accelerates genetic improvement by increasing selection intensity, drastically reducing the generation interval, and enhancing the accuracy of estimated breeding values, thus boosting genetic gain per unit time [222–224] (Lebedev et al. 2020; Grattapaglia, 2022; Sharma et al. 2024).

14. Conclusions

The data of population genetics, genomics, phylogenetics, phylogeography, phenology, dendroecology and dendrochronology presented in this review are important for determining the adaptive and evolutionary processes that contribute to the survival and distribution of *Q. robur* under a changing climate. We assume that the conservation and adaptation of *Q. robur* depends to a large extent on the accumulation of large reserves of genetic variability within populations, high phenotypic plasticity, the ability to quickly migrate and introgressive hybridization, which contributes to adaptive introgression and facilitates migration. However, there are concerns regarding *Q. robur*'s adaptive response to current selection pressures. Some studies indicate that *Q. robur* may experience a gradual decline in certain regions, particularly in mixed stands with *Q. petraea*. This aligns with the differing demographic trends observed between the two species, suggesting that *Q. petraea* may have a competitive edge under certain environmental conditions. [225] (Alexandre et al. 2020). However, fluctuations of selection and a rapid evolutionary response of oak populations to climatic transitions in the past suggest that similar trends may be at work now [225] (Caignard et al. 2024) and European oaks may survive and thrive in the changing environment with some adaptive management assistance.

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