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Breeding and Conservation of Pedunculate Oak (*Quercus robur* L.) Genetic Resources in Serbia and Croatia: Recent Advances and Future Challenges

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ABSTRACT

Pedunculate oak (*Quercus robur* L.) natural populations in Serbia and Croatia represent the southern (rear-edge) distribution limit of the species, having high conservation and management values, not only at the national levels, but also at the European scale. Despite their relevance, these forests are under growing pressure from habitat alteration, biotic and abiotic threats and climate change. To address these issues and enhance the conservation and sustainable use of *Q. robur* genetic resources, multiple research initiatives have been carried out in Serbia and Croatia aiming to: i) assess genetic diversity and genetic structure of populations grown *in situ* and *ex situ*, ii) evaluate the growth performances of provenances/populations/half-sib families in the field experiments, and iii) assess the species' adaptive potential and drought response mechanisms through the leaf functional traits and gene expression analyses. In the present paper we attempted to systematically summarize the literature sources on the aforementioned topics and review the current knowledge on genetic resources of *Q. robur* in Serbia and Croatia, emphasizing scientific actions that can be implemented to strengthen breeding and conservation programmes for *Q. robur*, particularly through coordinated, cross-border efforts between Serbia and Croatia.

Keywords: genetic diversity; stress physiology; functional traits; adaptive potential; progeny trials; ectomycorrhizal fungi

INTRODUCTION

Pedunculate oak (*Quercus robur* L.) is a widespread native tree species in Europe, spanning from the northern Iberian Peninsula, southern Italy, the Balkan Peninsula and Turkey through central and western Europe to southern Scandinavia (Eaton et al. 2016). In Serbia and Croatia, *Q. robur* primarily occurs in lowlands and along major rivers, such as the Sava and Danube (and the Drava and Kupa in Croatia), forming extensive floodplain forest complexes that play a crucial ecological and economic role by supporting biodiversity, providing valuable timber and delivering key ecosystem services (Kesić et al. 2021, Popović et al. 2023). For example, Jokanović et al. (2022) found that three mixed stands of *Q. robur*, *Fraxinus angustifolia* and *Carpinus betulus* in the region of Gornji Srem, Serbia hosted 139 medical herbs, belonging to 43 families. Likewise, *Q. robur* from the cross-border region of Serbia and Croatia is characterized by exceptional physical and mechanical properties, which makes it highly market-demanded throughout Europe, resulted in an increased market value of the wood. Based on the timber price lists of the public company Hrvatske šume Ltd. (Croatia) and the Public Enterprise Vojvodinašume (Serbia) the prices of the veneer logs F-I (i.e. highest-quality log class) amount to 840 and 770 EUR·m^{-3} before VAT, respectively (Hrvatske

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šume Ltd. 2025, JP Vojvodinašume 2025), although there is evidence where average selling prices exceed 1,000 EUR·m^{-3} in the case of public tenders (Landekić et al. 2024).

Despite their high ecological and economic value, *Q. robur* forests in Serbia and Croatia are becoming increasingly vulnerable due to the combined effects of habitat modification, biological threats and changing climatic conditions, reflecting broader trends observed across Europe (Thomas et al. 2002, Degen et al. 2021, Macháčová et al. 2022, Tkaczyk 2023, Dyderski et al. 2025, Hung et al. 2025). Nowadays, the natural watering regimes of both groundwater and surface waters in the *Q. robur* forests in Serbia and Croatia are highly disturbed by human activities, such as the construction of embankments, the drainage of marshes and forest areas, the construction of road infrastructure, etc. (Prpić and Anić 2000, Nikolić Jokanović et al. 2020, Nikolić Jokanović et al. 2024). In addition, *Q. robur* in Serbia and Croatia has been shown to be frequently exposed to severe infestations and infections by both native and non-native pests and diseases (Zorić et al. 2023, Hoch et al. 2024, Zlatković et al. 2024, Kranjec Orlović et al. 2025). Of particular concern, however, is the growing evidence of acute oak decline in both countries, which is considered a consequence of the synergistic effects of abiotic and biotic stressors (Zlatković et al. 2018). A clear example of this phenomenon is observed in the Mura-Drava-Danube Biosphere Reserve (MDD BR), where *Q. robur* is initially exposed to abiotic stress factors that reduce tree vitality (Kostić et al. 2021a, 2021b), thereby increasing susceptibility to biotic stressors, including pests and pathogens such as *Diplodia seriata*, the *Tubakia dryina/dryinoides* species complex and *Didymella macrostoma* (Zlatković et al. 2018, Zlatković et al. 2024). Lastly, climate change scenarios indicate that *Q. robur* may face a significant decline in suitable habitat range in Serbia and Croatia, as the consequence of increased frequency and extent of drought periods, further intensified by heat wave events and a reduction in precipitation in Southeast Europe (IPCC 2007).

Stojanović et al. (2014) reported that significant change of *Q. robur* bioclimatic niche is expected before the end of this century according to A2 scenario, assuming that this species will be also one of the most endangered tree species in Serbia due to the extreme change of its habitat. Similarly, by modelling ecological niches and improving the understanding of the relationships between *Q. robur* and ecological elements, in particular climate, Ugarković et al. (2016) forecasted that the natural habitat of this species will be altered and reduced in Croatia, making it one of the most vulnerable tree species to such conditions (Matić 2000). In contrast, recent study of Miletić et al. (2021) failed to provide evidence about climate change impact on the occurrence of *Q. robur*, *Q. cerris* and *Fraxinus angustifolia* using EQ (Ellenberg Quotient Index) and FAI (Forest Aridity Index) under RCP 4.5 and RCP 8.5 scenarios, probably as a consequence of model design which is predominantly based on bioclimatic variables, neglecting the influence of others relevant environmental parameters, such as soil characteristics (Walthert and Meier 2017). Namely, the existence of riparian forests, including *Q. robur* forest communities, is strongly controlled by hydrological conditions and specific water regimes that are often omitted in environmental data sets. Indeed, studying spatial distribution patterns of several native riparian tree species in Mura-Drava-Danube Biosphere Reserve (MDD BR) using bioclimatic continent-wide model and a regional model based on climate, soil and river data for central to south-eastern Europe, Sallmannshofer et al. (2021) reported primacy of edaphic (soil) predictors over bioclimatic variables, whereas hydrological (river) features exhibited a roughly equivalent degree of explanatory power. Nevertheless, considering the entire area of MDD BR, the authors concluded that certain foundation tree species, including *Q. robur* are expected to substantially suffer from changing climate conditions. However, it is encouraging that a recent study, integrating dendroecological indicators with species distribution model predictions, has found that this tree species does not seem to be severely impacted by climate change as previously anticipated, even in areas where its range is expected to contract, such as Southern Europe (Popa et al. 2025).

The occurrence of *Q. robur* natural populations in Serbia and Croatia at the southern (rear-edge) limit of the species' distribution range implies particularly high conservation and management value, not only at the national level, but also at the European scale (Kesić et al. 2021, Popović et al. 2023). Rear-edge populations are often exposed to marginal environmental conditions and therefore tend to harbor unique, locally adapted genetic variation shaped by long-term exposure to warmer and drier climates (Fady et al. 2016). As such, these populations represent an irreplaceable reservoir of genetic diversity that is crucial to safeguard the species' gene pool and ensure its sustainable application in future breeding and conservation initiatives. Their susceptibility to climate change and other stressors highlights the need for targeted conservation actions and coordinated, science-based management, particularly in transboundary forest systems shared by the two countries.

This study was prompted by the severe climate-related disturbances, specifically the extreme storm events during July 2023, that heavily impacted *Q. robur* forests across both Croatia and Serbia. According to the data of the Hrvatske šume Ltd. almost 4 million m^3 of timber was damaged in Croatia, of which the most was *Q. robur* (app. 1.9 million m^3) (Đuka et al. 2025). The greatest damage occurred in the Vinkovci Forest Administration in eastern Croatia, where approximately 2.7 million m^3 of timber was affected, including about 1.8 million m^3 of *Q. robur* from the Spačva basin, covering an area of roughly 16,600 ha (Đuka et al. 2025). In Serbia, according to data provided by the Public Enterprise Vojvodinašume damage on pure and mixed *Q. robur* forests were recorded on approximately 6,485 ha, with a total of 231,525 m^3 of timber impacted. Of this amount, 127,965 m^3 was recorded in the Bosut basin, where *Q. robur* accounted for about 70% of the total damage. This is particularly important given that it is the largest complex of *Q. robur* forests in Serbia (i.e. Ravni Srem region) (Rađević et al. 2020).

The scale of the damage led to a joint initiative by Serbian and Croatian scientific (Institute of Lowland Forestry and

Environment and Croatian Forest Research Institute) and forestry institutions (PE Vojvodinašume and Hrvatske šume Ltd.), resulting in a collaborative IPA Interreg Croatia-Serbia project: "Strengthening cross-border capacity for better climate resilience of forest ecosystems by advanced assessment, testing and demonstrating solutions for ecosystem restoration (REBIOFORESTS)", which is focused on revitalization of the forests of the Spačva-Bosut basin to preserve biodiversity and enhancing cross-border capacity for improved resilience of forest ecosystems to climate change. To support the project implementation, this paper aims to systematically review the scientific literature on recent advances in understanding: i) *Q. robur* genetic diversity and population structure in Serbia and Croatia, ii) the growing performances of its populations/provenance/families across the field experiments in two countries, and iii) the effects of major stressors (biotic, abiotic and their interactions) on the species' physiological responses and overall adaptive potential. This regionally focused review complements a recent Europe-wide synthesis of marker- and genomics-based research on *Q. robur*, which linked evidence on genetic diversity and adaptive potential to operational conservation strategies (Trudić et al. 2026). Based on the information obtained, we attempted to identify existing knowledge gaps and outline key directions for future research to support conservation of the species genetic resources and the development of breeding programmes in the transboundary region.

GENETIC DIVERSITY ASSESSMENT OF *QUERCUS ROBUR* L. IN SERBIA AND CROATIA

Multiple studies emphasize high genetic diversity in Serbian and Croatian *Q. robur* populations using DNA nuclear microsatellites (nSSRs). Kesić et al. (2021) observed high genetic diversity in terms of observed and expected heterozygosity (Ho=0.595; He=0.769) between natural *Q. robur* populations in Serbia, as well as low differentiation among the populations, as reflected by low values of fixation index (F_{st}=0.032; p>0.05). Similarly, the study conducted across 17 Croatian populations cultivated in progeny trial demonstrated high nuclear genetic diversity (He=0.760) with low interpopulation differentiation (F_{st}=0.013) (Popović et al. 2023). Trudić et al. (2021a) observed very low differentiation between two neighboring subpopulations in Serbia (F_{st}=0.003). The same study also reported mean values of Ho=0.779 and He=0.794 across the 12 microsatellite loci. An analysis of molecular variance (AMOVA) analysis for the partitioning of microsatellite diversity among and within these populations confirmed high intra-population diversity (>98%) and a small, but significant inter-population differentiation. Lastly, high genetic diversity was also observed between clonal seed orchards (CSO) in Croatia (Ho=0.619; He=0.741) (Katičić Bogdan et al. 2018). In contrast to the previous results, obtained across natural populations, F_{st} values recorded here showed lack of significant differentiation between CSOs which is also confirmed by AMOVA analysis (99.96% of diversity was harbored within CSO).

A comprehensive locus-wise comparison of genetic diversity in *Q. robur* populations across Europe has already been provided by Katičić Bogdan et al. (2018) and Trudić et al. (2021a), we therefore target only the shared loci between the Serbian and Croatian studies to evaluate their comparative polymorphism levels and genetic diversity patterns. The results demonstrated that loci QrZAG31/QrZAG30 showed the highest He values (He>0.9) across these studies (Morić 2016, Katičić Bogdan et al. 2018, Kesić et al. 2021). In contrast, the nuclear microsatellite QrZAG96, which is linked to a Quantitative Trait Locus (QTL) associated with petiole length in oaks and can discriminate between *Q. petraea* and *Q. robur* (Saintagne et al. 2004), displayed the lowest value of He in all studies; i.e. He=0.404 (Kesić et al. 2021), He=0.422 (Morić 2016), He=0.381 (Trudić et al. 2021a) and He=0.288 (Katičić Bogdan et al. 2018).

All the studies consistently highlight QrZAG87 as one of the most genetically diverse loci in Serbian and Croatian *Q. robur* populations/CSOs. Namely, Morić (2016), Katičić Bogdan et al. (2018), and Kesić et al. (2021), evidenced high expected heterozygosity at this locus (He=0.882, He=0.871 and He=0.874, respectively). In addition, Trudić et al. (2021a) reported exceptionally high diversity at QrZAG87 (Ho=0.916; He=0.909), placing the studied population among the most genetically diverse in Europe. Considering that this microsatellite locus is linked to genomic regions controlling the timing of bud burst in *Q. robur*, its high diversity likely reflects the sampling approach, which included both early-flushing (var. *praecox*) and late-flushing (var. *tardissima* and var. *tardiflora*) genotypes, thereby capturing allelic variation associated with adaptive phenological traits (Scotti-Saintagne et al. 2004).

Besides nSSRs, Katičić Bogdan et al. (2018) and Popović et al. (2023) also used chloroplast microsatellites (cpSSRs) to study intra- and inter-population/CSO genetic variability and differentiation, thereby shedding light on the species' potential recolonization history and the impact of human-mediated seed movement on existing genetic patterns in Croatia. Both authors found high diversity of chloroplast haplotype in *Q. robur* in Croatia (28 and 66 distinct haplotypes, respectively), reflecting historical post-glacial migration and the coexistence of different maternal lineages. Moreover, significant haplotypic differentiation among populations/orchards shows cpSSR markers capture maternal lineage structure, even when nSSRs show little differentiation.

Moreover, Temunović et al. (2020) investigated genetic diversity based on single-nucleotide polymorphisms (SNPs) across 19 floodplain populations of *Q. robur* in Croatia, focusing on polymorphisms within 117 candidate genes, to understand how genetic variation was shaped under the influence of climatic factors associated with water availability. Despite weak overall genetic differentiation among populations (F_{st}=0.013; p<0.001), the authors reported high among-population genetic connectivity implying extensive gene flow or shared ancestry. In addition, many significant genotype-environment associations between SNP allele frequencies and water-related climatic variables were observed. Namely, a total of 61

associations involving 37 SNPs from 35 candidate genes were associated with at least one environmental variable, predominantly those related to water availability and its seasonal variation, highlighting potentially adaptive genetic variation in Croatian oak populations (Temunović et al. 2020). At a broader geographical scale, Jansen et al. (2026) analyzed 1,500 individuals from 56 populations across Central and Southeastern Europe and identified three nuclear genetic clusters, with genetic diversity increasing towards the southeast. Southeastern populations showed high regional allelic richness and many private alleles and chloroplast haplotypes, while shared chloroplast lineages across the contact zone between the two subspecies were consistent with gene flow.

In addition to molecular markers, the variability of *in situ* populations in Serbia and Croatia has been extensively examined through analyses of leaf functional traits. The most comprehensive overview of intra- and inter-population variation in leaf morphometric traits across the Western Balkan countries (Bosnia and Herzegovina, Croatia, Montenegro and Serbia) was provided by Ballian et al. (2010), who investigated the variability of 14 morphological traits in 65 populations. The authors observed significant differences both between populations and among individuals within populations, with intrapopulation variability being statistically more pronounced than interpopulation variability. Similarly, more recent research of Kesić et al. (2026) has generally confirmed the predominance of intrapopulation variability in leaf morphology among 11 *Q. robur* populations from Serbia and Bosnia and Herzegovina, while multivariate analyses revealed clear geographic structuring between populations. The distinct morphological position of the Lukavica and Ugljevik populations from Bosnia and Herzegovina was particularly notable, as both were clearly differentiated from the remaining populations and were subsequently identified as priority candidates for conservation of *Q. robur* genetic resources.

Comparable evidence of among-population phenotypic and functional differentiation has also been reported by Batos et al. (2010, 2017) who detected population-level variation in leaf morphological and anatomical characteristics, while Kesić (2022) reported differences in leaf micro- and macronutrient composition among populations from northern Serbia. Similarly, Ivanković et al. (2011) identified variation in acorn size among seed stands in Croatia. Taken together, these studies indicate that the differentiation observed among populations is not restricted to molecular markers but is also expressed in morphological, anatomical and physiological traits, although the underlying contribution of genetic versus environmental effects may differ among traits and studies.

EVALUATION OF *QUERCUS ROBUR* L. PERFORMANCES IN THE FIELD EXPERIMENTS

Considering the effectiveness of provenance trials, where populations of different geographical origins are analyzed under uniform climatic conditions (Bischoff et al. 2010, Kapeller et al. 2013), considerable effort over the last two decades have been directed towards evaluating *Q. robur* populations to identify and select populations with desirable traits for growth and adaptability and conservation, particularly important under climate change (Bogdan et al. 2017).

Monitoring of *Q. robur* provenance performance in Croatia began in the mid-1980s, with the establishment of the first nursery trial at the Croatian Forest Research Institute, comprising 11 Croatian provenances and one Serbian provenance. This was followed by the establishment of two provenance trials in Gajno and Slavir, which included four additional provenances, bringing the total to 16 (Gračan et al. 1991, Gračan 1993, Gračan and Perić 1993). By assessing the height and survival rate, this preliminary study identified Spačva provenances as superior to others in both trials and highlighted the importance of early selection and identification of productive seed sources that are suitable for cultivation in different forest regions. Three decades later, the study of Đodan et al. (2024) confirms preliminary results of Perić (2001) and reveals significant differences in growth parameters between provenances and trial sites, with some provenances showing opposite performances in two plots (i.e. Velika Gorica), thus highlighting the importance of evidence-based provenance selection for future reforestation programmes. The subsequent long-term assessment by Đodan et al. (2026a) further reinforced the importance of site-dependent provenance performance, while providing evidence of both temporal consistency and changes in provenance ranking. At Gajno, significant differences among provenances were detected, with Velika Gorica consistently among the best-performing provenances in terms of tree volume, whereas Motovun showed the lowest values during most of the assessment period. In contrast, at Slavir, provenance differences were not statistically significant, although Guševac consistently exhibited the highest mean tree volume and Velika Gorica the lowest. Notably, the comparison between the two trials revealed significantly higher productivity at Slavir and a significant site by provenance interaction, demonstrating that the relative performance of individual provenances can change substantially depending on the environmental conditions of the trial site. Collectively, these long-term observations demonstrate that provenance selection for the restoration and sustainable management of *Q. robur* forests should account not only for overall growth potential, but also for provenance-specific responses to local environmental conditions and the stability of performance across contrasting sites. Furthermore, a study of morphological research of leaf shape in the Gajno provenance trial revealed the linkage between observed provenances depended on microsite condition rather than their origin, highlighting the importance of determining the compatibility of microsites rather than when it comes to the seed distribution (Franjić et al. 2000). Indeed, studying leaf morphological and anatomical traits in six provenances cultivated in two provenance trials (Koška and Vrbanja), Škvorc et al. (2018) found that the greatest differences in the analyzed traits were between the trial plots, with

strong reaction of seedlings to drought conditions at the Koška experimental site (e.g. thicker lower epidermis and palisade parenchyma, lower leaf dry mass, and a higher specific leaf area).

Additional provenance-related studies were directed towards the assessment of the adaptive genetic variability and differentiation in populations. For instance, by estimating the survival rate and height of provenances originating from Croatia and Austria for over two consecutive years characterized by low precipitation, the main findings showed that those provenances from the southeastern part of the pedunculate oak's distribution range revealed outstandingly high mean survival rates, reflecting their adaptability to a relatively long period of water deficit (Bogdan et al. 2017). These results are of high practical importance in forest management, conservation, and climate adaptation strategies in Croatia by helping practitioners to identify drought-resilient populations for reforestation (Popović et al. 2023, Nosenko et al. 2025). Further results of the study showed considerable genetic variation among populations in assessed traits, reflecting the influence of natural selection driven by differences in the moisture availability of the habitats from which the populations originated, further evidencing an ecotypic pattern of quantitative genetic differentiation (Bogdan et al. 2017).

Besides provenance trials, in the last few decades the evaluation of the genetic potential, specifically the genetic trend of traits, heritability and genetic gain for height and diameter growth of this species has been evaluated in open-pollinated progeny trial tests, established with the aim to enhance genetic quality and periodicity of fructifying (Kajba et al. 2011), an issue even more intensified under predicted climate changes. The results of this study indicated high individual genetic variability in progeny trials Vukojevački Šikar and Čazma, and suggested that high additive variability in terms of heights could result from considerable variability for flushing traits and from ecotypic differentiation in their original population, as a significant co-dependence was found between height and flushing phenology. Additional research conducted in an open-pollinated progeny test, by analyzing the quantitative traits further, provided evidence related to the high intra-population variability, coupled with the lack of significant differentiation between populations in part of its distributional range in Croatia (Bogdan et al. 2004). Comparable results were reported by Ivanković et al. (2011), who examined the height growth of one-year-old seedlings grown from seeds collected across *Q. robur* stands in Croatia. Lastly, Popović et al. (2024) reported a significant maternal effect on seedlings morphometrical (i.e. stem and root) traits, as well as the strong relationship between root and aboveground biomass suggesting the possibility of identification and selection of reproductive material with a well-developed habitus that may contribute to enhanced regeneration of pedunculate oak forests.

Another question that has emerged over the past several years in Croatia concerns the periodical fructification and acorn yields of the species, which has led to the initiation of two research projects funded by the Croatian Science Foundation, namely: „Conservation of genetic resources of forest trees in light of climate changes (ConForClim IP-2013-11-8131)" and „Dynamic of fructification and conservation of genetic resources of pedunculate oak (*Quercus robur* L.) and european beech (*Fagus sylvatica* L.) in light of climate changes (CropForClim IP-2018-01-8189)" (Gavranović Markić et al. 2022a). Namely, with the aim to address the questions related to how individual trees and oak populations allocate resources for acorn production, in terms of the yield size and the quality, results of ten continuous years have been summarized (from 2009 to 2018) from 119 *Q. robur* forest seed stands throughout Croatia (Gavranović Markić et al. 2022b). On the observed timescale, acorn productivity was found to be highly variable, with four years (2010, 2011, 2015, and 2017) proving to be superior to the others, characterized by a higher quantity of collected seeds. The study further evidenced the high interdependence between seed size and seed moisture content with seed viability of this taxon. This study, along with many others (Vieitez et al. 2012, Abbot et al. 2024) implied that poor and irregular acorn yield recorded during the past several years has made the natural regeneration of *Q. robur* challenging, highlighting artificial regeneration as an important silvicultural intervention for the sustainability of the future forests (Rađević et al. 2020). Moreover, it is crucial source for nursery production for both artificial regeneration and restoration activities (Đodan and Perić 2022, Đodan et al. 2023, 2026b).

DROUGHT STRESS PHYSIOLOGY OF *QUERCUS ROBUR* L.

Taking into consideration that the decrease in water availability has been recognized as one of main triggering factors of *Q. robur* decline (Stojanović et al. 2015, Kostić et al. 2021a, 2021b), understanding how this species reacts to drought stress under the ongoing climate change has been one of the initial phases towards the selection of drought-tolerant genotypes and populations (Kesić et al. 2023). To address this issue, leaf gas exchange of an oak population originating from Morović, Serbia was monitored in a semi-controlled greenhouse experiment to evaluate the effects of prolonged summer drought on their diurnal patterns (Bojović et al. 2017a). This study presented evidence-based information regarding the negative effects of permanent water deficit condition on the physiological parameters related to the process of photosynthesis in *Q. robur* leaves, with different changing trends in their diurnal dynamics. In detail, well-watered seedlings exhibited a typical double peaked diurnal pattern of net photosynthesis (A), transpiration rate (E) and stomatal conductance (g_s) with a clear midday inhibition, opposed to seedlings subjected to water withholding condition, with atypical double peaked pattern of A and single peaked curve of E and g_s. Moreover, to quantify the potential of *Q. robur* populations to overcome the challenges imposed by predicted climate-change pressures, drought-induced stress was evaluated in two selected populations from Serbia, namely from

Morović and Fruška Gora, based on foliar gas-exchange parameters and recovery capacity, providing evidence of population-based differences in leaf gas-exchange responses and indicating differences in drought tolerance among populations (Bojović et al. 2017b).

In addition to drought, carbon assimilation of *Quercus* species, in particular *Q. robur* and *Q. cerris*, was evaluated under high-temperature stress, as another consequence of climate change that poses a threat to forest ecosystems, including oak habitats (Horak et al. 2019). The findings demonstrated that down-regulation of carbon assimilation under acute high-temperature stress is primarily attributable to stomatal regulation, whereas under prolonged stress, inhibition of photosynthesis is limited by the biochemical capacity of the leaf. Furthermore, this study highlighted the importance of evaluating specific physiological responses to high-temperature stress for understanding the vulnerability of oak forest populations, selecting and recommending resistant genotypes capable of persisting under such conditions, enhancing reforestation initiatives and providing strategies for the conservation of existing gene pools under high-temperature events accompanied by drought events.

Apart from understanding the effects of drought by providing detailed insights into the mechanisms of drought-stress responses, a vital objective for those tasked with securing the resilience of oak forests was addressed to evaluate the adaptation potential of this species, as their long-term survival depends on their capacity to cope with the changing environment (Chown et al. 2010, Somero 2010, Berry et al. 2013). When it comes to the effect of drought on plant metabolic functions, in addition to its severity, a relatively under-researched question is whether the timing of drought is an equally critical factor. In this sense, particular attention in Croatia has been given to the influence of water scarcity on leaf phenology in *Q. robur* forest complexes and provenance trials (Čehulić et al. 2019), as phenological shifts have been evidenced to be closely associated with the susceptibility of various tree species to late spring and early autumn frosts (Morin and Chuine 2014, Dantec et al. 2015, Vitasse et al. 2019). To improve our understanding of the underlying mechanism related to how drought induces changes in leaf phenology and spring frost susceptibility in *Q. robur*, one-year-old seedlings from nine provenances were subjected to simulated drought followed by a recovery cycle lasting for the two following years, during which both spring and autumn leaf phenology were tested (Čehulić et al. 2019). The findings of this study highlighted the adverse effects of water scarcity, reflected in delayed autumn leaves' senescence and a carry-over effect on budburst date. In more detail, the mean bud burst dates were found to be shifted in the reverse direction in the two examined years, depending on the differences in the timing of water scarcity perception. What the results of this study practically imply is that when an oak seedling perceives water scarcity during the initial phase of the growing season, a postponed bud burst date in the spring following year might be expected. On the other hand, if an oak seedling senses water limitation during the end of the growing season, bud burst phase will likely shift towards an earlier date in the following spring. Moreover, this study evidenced that summer drought increased frost susceptibility in *Q. robur* seedlings, most likely resulting from the shifts in spring leaf phenology. Regarding the influence of water limitation on leaf senescence, the study highlighted that delayed senescence may increase the vulnerability of *Q. robur* to early autumn frosts. Likewise, to address this question, Bačurin et al. (2025) subjected the seedlings of *Q. robur* to water withholding at different periods while monitoring height growth, spring flushing, autumn leaf senescence and carbon assimilation. The main outcome of this research provided evidence that the timing of drought strongly influences growth and phenology, with late-spring and summer droughts being negatively associated with height growth and delaying autumn senescence, thereby limiting recovery, whereas mid-spring drought allowed for compensatory biomass accumulation (Bačurin et al. 2025). From a practical perspective, these findings highlight the importance of considering phenological plasticity when developing adaptation strategies for *Q. robur* under increasing abiotic pressure. Furthermore, recent evidence that rootstock can contribute to intra-clonal variation in budburst suggests that rootstock-scion combinations may represent an additional, although still insufficiently explored, avenue for manipulating spring phenology and enhancing stress avoidance in *Q. robur* (Bačurin et al. 2026).

In order to address the question how the selected species react to drought concerning adaptation potential more precisely, a detailed estimation of 24 parameters, categorized into biometrical traits, leaf anatomy and chlorophyll fluorescence parameters was performed in Serbia (Vaštag et al. 2020). In response to naturally occurring severe drought stress, half-sib lines endured drought stress differently with an array of morphological, physiological and biochemical adaptations. The evaluated biometrical traits (seedling height, root length, root to shoot ratio of dry mass and specific leaf area), leaf stomatal traits (stomatal density, stomata guard cell length and width, stomatal aperture length and width) and leaf structural traits (adaxial epidermis thickness, palisade parenchyma thickness, spongy parenchyma thickness, lamina thickness) resulted as suitable indicators for screening *Q. robur* half-sib lines for drought tolerance (Vaštag et al. 2020).

Given the previously proven effectiveness of biochemical attributes as adaptability descriptors in the light of forthcoming climate change (Popović et al. 2013, Stojnić et al. 2016, Kebert et al. 2022a), a significant contribution during recent years was made toward the definition of biochemical tests which might promote future efforts of genetic monitoring of *Q. robur*. To contribute to this aim, Trudić et al. (2023) studied the potential of oxidative stress parameters for screening of genotypes characterized with different health conditions and belonging to different phenological varieties of this species (early flushing - var. *praecox*, and late flushing - var. *tardissima*). Surprisingly, although no differences were observed among the individual characterized by different health statuses, four of the seven antioxidant parameters, namely, total phenolic compounds content (TPC), total flavonoids content (TFC), NO radical scavenger activities and Ferric Reducing Antioxidant Power essay (FRAP) clearly distinguished sampled trees belonging to var. *praecox* and var. *tardissima*. These results align with the previous findings of Trudić et al. (2021b), who demonstrated

distinct expression patterns in relative gene expression (i.e. genes related to genotypes response to abiotic stress) levels between var. *praecox* (3 genes upregulated) and var. *tardissima* (8 genes upregulated).

A more recent challenge involves identifying methods to enhance the intrinsic water-use efficiency of *Q. robur* through tree breeding programs. Because this trait serves as a foundational component of plant drought adaptation, targeting it represents a viable strategy for improving overall drought tolerance (Blum 2009, Gago et al. 2014). To improve our understanding of inter-relationships among intrinsic water-use efficiency (WUE_i) and physiological, biometrical and morpho-anatomical trait responses aligned with improved drought tolerance, multivariate statistical approach was applied, pointing out that stomatal density and leaf dry mass per unit leaf area could be targeted by breeders to enhance the drought-tolerance in genotypes of this species (Stojnić et al. 2019). This observation highlighted that under drought stress of mild intensity WUE_i resulted from the plants' structural adjustment in response to environmental change. This observation was recently supported by Škvorc et al. (2026), who demonstrated that the adaptation of *Q. robur* provenances to drier habitats is more closely associated with structural than physiological traits. Provenances originating from drier habitats exhibited lower specific leaf area and differed in their acclimation to repeated drought, showing a stronger reduction in stomatal density and a smaller increase in leaf dry matter content compared with provenances from more humid areas.

BIOTIC AND COMBINED STRESSORS EFFECT ON *QUERCUS ROBUR* L. SEEDLINGS

Even though abiotic factors have been considered as the primary causes of oak decline, a complex interaction was evidenced between climatic parameters as predisposition factors and various biotic stressors, highlighting the multifaceted nature of oak decline phenomenon and the potential effects of biotic agents, as well (Sonesson and Drobyshev 2010, Macháčová et al. 2022, Kowsari and Karimi 2023). In case of biotic factors, considerable progress has been made during recent years in the understanding of how oak powdery mildew (*Erysiphe alphitoides* (Griffon and Maubl.) U. Braun and S. Takam.), as one of the most important foliar diseases, affects leaf photosynthetic characteristics of *Q. robur* seedlings. Alterations in physiological activity were quantified in highly infected seedlings, i.e. when coverage of epiphytic mycelia visually reached more than 75% of the surface of leaves and pointed to the reduction of foliage photosynthetic activity and effectiveness of fast kinetics of chlorophyll *a* fluorescence parameters in the detection and monitoring of severe biotic stress condition (Vaštag et al. 2019). Considering the effects of this pathogen on net CO_2 assimilation rate, a major consequence was observed in young seedlings depending upon the severity of the infestation, particularly disturbed under the highest degree of leaf infestation (>75%) (Pap et al. 2014). Given that concentration in photosynthetic pigments and leaf dry matter resulted as sensitive indicators of biotic adversity, a recommendation was made to incorporate them in future studies dealing with the performance of plants under fungal infection. Further investigations in regard to oak powdery mildew, revealed the effectiveness of slow fluorescence kinetics as well, in particular the coefficient of non-photochemical fluorescence quenching and the Stern-Volmer type nonphotochemical fluorescence quenching parameters, as the fastest deployed protective mechanism of *Q. robur* seedlings under moderate (50% of leaf coverage by epiphytic mycelia) and severe (75% of leaf coverage by epiphytic mycelia) stress condition (Vaštag et al. 2022). In addition, the adverse effects of this biotic agent were evident on leaf stomatal traits as well, as under stress conditions the pathogen signaling system was triggering the initiation of decrease of stomata guard cell width in parallel with the increase of stomatal density, all of which progressed in time and was dictated by the severity of the infection. Further initiatives in the field of biotic stress responses of *Q. robur* aimed to deepen our knowledge of plant-pest interactions, particularly the effects of *Corythucha arcuata* (Say, 1832) infestation on the physiological responses of this species (Nikolić et al. 2019). The findings revealed that infestation by *C. arcuata* significantly affected biochemical properties, namely the concentrations of photosynthetic pigments and the activities of the antioxidant enzymes catalase and ascorbate peroxidase, along with physiological properties, including photosynthesis, transpiration and stomatal conductance, thus informing adaptive management practices aimed at preserving oak forests endangered by *C. arcuata*.

Since drought stress has been acknowledged to enhance the susceptibility of trees to biotic stress imposed by herbivores and pathogens (Cohen et al. 2023, Netherer et al. 2024), over the recent years growing interest within the scientific community was showed toward the understanding of the processes and mechanisms of concurrent stress responses in *Q. robur*, which might help in mitigating the potential adverse effects of these factors under future climatic conditions. To address the knowledge gap related to physiological mechanisms of combined stress responses in *Q. robur* Pilipović et al. (2020) examined the specific consequences of water deficit for plant interactions with herbivore attack of gypsy moth (*Lymantria dispar* L.). The results of the study showed the individual and synergic adverse effects of water scarcity and herbivore attack on carbon and nitrogen metabolic processes of *Q. robur* families, resulting in a dominantly non-stomatal limitation to CO_2 assimilation rate. Followed by the well-watered condition, the observed families showed different physiological responses, while general observation indicated that the recovery of stressed plants should take longer than the investigated period of 7 days. Overall, Pilipović et al. (2020) accentuated the need of breeding for climate change resilience and the importance of physiological parameters in the selection of progenies and provenances of *Q. robur* resistant toward biotic and abiotic stressors. An additional study investigated the complex interactions among plants, insects and pathogens, focusing on the effects of a root pathogen *Phytophthora plurivora* on a leaf-eating insect *L. dispar* hosted by two

provenances of *Q. robur* (Sombor and Belgrade) under enhanced CO_2 concentrations (Milanović et al. 2020). The results supported the hypothesis that rising atmospheric CO_2 levels are likely to modify existing interactions among *P. plurivora*, *Q. robur* and *L. dispar*, indicating that changing climatic conditions can substantially influence these three-way interactions. Specifically, under a pessimistic climate-change scenario predicting atmospheric CO_2 concentrations of up to 900-1000 ppm by the end of the 21st century, *L. dispar* larvae feeding on leaves of *P. plurivora*-infected *Q. robur* seedlings showed significantly diminished performance compared with larvae feeding on non-infected seedlings. Furthermore, the results demonstrated a pronounced effect of plant provenance on both herbivore and tree performance, suggesting potential for enhancing forest resilience to climate change through targeted breeding strategy.

USE OF MYCORRHIZAL FUNGI IN IMPROVING TOLERANCE OF *QUERCUS ROBUR* L. SEEDLINGS TO BIOTIC AND ABIOTIC STRESS

The use of mycorrhizal fungi in forest practice is important for improving the tolerance of *Q. robur* seedlings to both biotic and abiotic stress, particularly during the critical establishment phase. Mycorrhizal associations enhance water and nutrient uptake, improve water-use efficiency, and support seedling growth under drought and nutrient-poor conditions (Milović et al. 2022). In addition, mycorrhizae can increase resistance towards biotic stressors, while contributing to the recovery of soil biological functions in disturbed or degraded forest sites, such as sites affected by storms (i.e. Spačva-Bosut basin), where natural mycorrhizal networks are often disrupted (Milović et al. 2023). Consequently, mycorrhizal inoculation can increase seedling growth and survival during regeneration phase, thereby supporting successful restoration of *Q. robur* forests.

In this context, the project "Development of Climate-Smart Forestry (CSF) concept in the Republic of Serbia through mycorrhizal modulation of polyamine metabolism in pedunculate oak (*Quercus robur* L.) trees (MYCOCLIMART)", funded by the Science Fund of the Republic of Serbia, has proposed an innovative approach which consisted of priming this tree species with ectomycorrhizal fungi (ECM) in order to alleviate biotic and abiotic stress and produce bioprotective properties. To prove whether artificial inoculation with ECM possess the effectiveness upon biochemical and physiological stress response in *Q. robur*, in particular toward drought, heat wave and infection by oak powdery mildew, Institute of Lowland Forestry and Environment have launched a series of pioneering studies that have helped in understanding the underlying plant defence mechanisms in three-way interactions among plants and biotic/abiotic adversities and ECM (Kebert et al. 2022b, 2022c, 2023).

The beneficial and bioprotective effects of ECM which were evidenced with respect to the mitigation of biotic stress caused by powdery mildew (*E. alphitoides*), observed in amplification of the main polyamines, proline, non-protein thiols in parallel with relatively stable physiological parameters, phenolics and antioxidant capacity (Kebert et al. 2022b). Concerning the heat stress experiment, ECM inoculation increased proline and total phenolic content, as well as ferric reducing antioxidant power (FRAP), radical-scavenging capacity against 2,2′-azinobis(3-ethylbenzothiazoline-6-sulfonic acid) (ABTS), non-protein thiol levels, and lipid peroxidation, while glycine betaine and flavonoid levels declined. Further advantages of ECM were observed on physiological process as well, through increase of net assimilation rate and water transport efficiency (Kebert et al. 2022c). Regarding drought stress, the results evidenced the beneficial interactions of ECM with seedlings of *Q. robur* in alleviating abiotic stress response, through significant alternations at the physiological and biochemical level, particularly in amplification of proline and the Abscisic acid (ABA) response (Kebert et al. 2023). The beneficial effects of ECM (especially *Scleroderma citrinum*) were evidenced in modulating osmolytes, polyamines and the priming effect by enchanting specific plant hormones resulted in overall increased tolerance of *Q. robur* seedlings toward water scarcity.

FUTURE CHALLENGES AND STRATEGIC APPROACH

Supplementary Material S1 provides a structured, comparative synthesis of research domains investigated in *Q. robur* populations in Serbia and Croatia, explicitly mapping the availability of genetic, phenotypic, physiological and functional datasets across the two countries. For each research parameter, the table identifies whether empirical evidence exists in Serbia and Croatia and links this coverage to a clearly defined interdisciplinary benefit and a testable future research hypothesis. This approach highlights not only areas of convergence between the two national research trajectories, but also critical asymmetries, such as the absence of chloroplast haplotype assessments and SNP – environment association analyses in Serbian populations, or the limited physiological and transcriptomic coverage in Croatia. By explicitly coupling each parameter with a forward-looking hypothesis, the table functions as a diagnostic and hypothesis-generating framework rather than a descriptive inventory. It thereby underpins the rationale for coordinated cross-border research and provides a transparent justification for the integrative roadmap proposed in Supplementary Material S2.

Supplementary Material S2 translates the parameter-level evidence and research gaps identified in Supplementary Material S1 into a time-structured, action-oriented strategic roadmap for the period 2027-2036. The table is organized along three consecutive phases: gap closure and standardization (2027-2030), integration and modelling (2030-2033) and deployment and application (2033-2036) and explicitly aligns each research domain with the corresponding criteria for Dynamic Conservation Units (DCUs) as defined by the European Forest Genetic Resources Programme (EUFORGEN) (Lefèvre et al. 2020). For each domain, the roadmap specifies concrete scientific actions, their expected analytical integration and their ultimate application in conservation, breeding, monitoring

and policy contexts. In doing so, the table operationalizes the link between molecular and physiological research and applied forest genetic resource management, demonstrating how neutral diversity, adaptive genetic variation, phenotypic plasticity and functional resilience jointly inform DCU designation, monitoring and long-term viability under climate change. The roadmap thus serves as a bridge between empirical research and implementation, ensuring that conservation units are supported by reproducible genetic evidence, validated adaptive indicators and harmonized cross-border governance mechanisms.

Also, this sub-chapter highlights key future challenges with great potential to advance long-term conservation and genetic improvement of *Q. robur* in the cross-border region. Here, we will not address activities related to establishment of *in situ* and *ex situ* objects (i.e. seed stands and seed orchards), nor the nursery production of *Q. robur* reproductive material and reforestation initiatives, as these activities were not the topic of the literature review either. We will, instead, focus on the research activities designed to potentially improve breeding and conservation programs in both countries, with the focus on those that can be implemented by joint efforts in cross-border region of Serbia and Croatia (i.e. Spačva-Bosut basin). These actions are also numbered in Supplementary Material S1 to complement the strategic framework of this comprehensive, integrated review. They are presented in the table column "Appropriate strategic action", enabling each research hypothesis and interdisciplinary benefit to be linked directly to the corresponding recommended conservation and/or management action/project:

1. Implementation of joint genetic monitoring programme in the transboundary region, following the protocol of Sever et al. (2020), which is developed within LIFE project: "Life for European Forest Genetic Monitoring System (LIFEGENMON)" (reference: LIFE13 ENV/SI/000148). Such activity can provide multiple benefits to both forestry science and practice, such as: i) monitoring the state and changes of neutral and adaptive genetic variation of *Q. robur* genetic resources through time, ii) establishing an early-warning system to evaluate the species response to management measures and environmental pressures, iii) at the European scale, the established plots may be integrated into a regional genetic monitoring scheme implemented in Slovenia, Germany and Greece, as part of the aforementioned project, thereby forming a north-south transect of research plots spanning across a climatic gradient from Central to Southern Europe.
2. Establish a joint cross-border Serbia-Croatia geospatial-genetic monitoring programme for *Q. robur* that systematically integrates high-resolution geospatial sensing and data driven technological outputs (i.e. Unmanned Aerial Vehicle (UAV) derived multispectral indices, Sentinel-2 drought/stress indicators, LiDAR-derived canopy and structure metrics) with existing genetic information and provenance trial data to identify, prioritise and dynamically manage climate-resilient seed stands and breeding populations (Trudić et al. 2024, 2025). The basis for such an initiative could be provided by the project "Enhancing Forest Monitoring of BEECH Forests in South-East Europe (FORBEECH)," funded by the European Union through the FORWARDS project (Horizon Europe Project No. 101084481), which is designed to conduct parallel terrestrial and airborne measurements using Internet of Things (IoT) technology, hyperspectral imaging and LiDAR scanning. Although this project is focused on European beech (*Fagus sylvatica* L.), it could generate valuable outputs and methodological approaches that could also be applied to *Q. robur* ecosystems.
3. Development of research and monitoring network, based on novel IoT technologies, able to automatically generate data of trees growth and physiological status in a near real-time. Such an initiative could build on the outcomes of the project: "Enhancing forest monitoring of OAK forests in South-East Europe (OAKS)" funded by the European Union through FORWARDS (Horizon Europe Project No. 101084481) grants, which sought to strengthen existing intensive monitoring of *Q. robur* across Slovenia, Croatia and Serbia conducted in the framework of the "International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests)". Extending this network with additional pilot plots would allow intensive spatio-temporal observation of tree physiology across a wide environmental gradient, enabling a better understanding of seasonal and diurnal patterns of stem radius increment and their relationships with environmental conditions, including drought-related responses to water deficits.
4. Incorporating epigenetic analyses, particularly DNA methylation, can complement current genetic approaches by revealing adaptive variation not captured by neutral markers and by helping identify provenances, populations and half-sib families with enhanced stress resilience for conservation prioritization (Bräutigam et al. 2013). In breeding programmes, epigenetic information may improve early selection efficiency and support the identification of superior reproductive material (Lebedev et al. 2020).
5. Genome wide association studies (GWAS) for identifying genes and alleles associated with key adaptive traits (Tibbs Cortes et al. 2021). By pinpointing the genetic determinants of these traits, GWAS would facilitate targeted breeding programmes and strengthen efforts to enhance the species' capacity to withstand climatic stressors. Complementing this, high resolution population genomics could provide a robust basis for conservation planning, whereas functional genomics can further deepen this understanding by elucidating the molecular mechanisms underlying traits, such as water-use efficiency.

6. Considering the limitations of classical phenotyping, such as low throughput, labor intensity, subjectivity, destructive measurements and restricted temporal and spatial resolution (Lebedev et al. 2020), High-Throughput Phenotyping (HTP) can be implemented as an alternative approach to overcome these constraints by enabling rapid, objective, non-destructive and repeatable measurements across large numbers of plants and spatial scales with high temporal resolution. Namely, HTP would represent an efficient approach for enhancing knowledge of *Q. robur* plants functioning, while also supporting improvements in forest reproductive material nursery production and the monitoring of forest stand conditions (Vugdelija et al. 2025). A further advantage of this approach lies in the multi-scale applicability of HTP, which can be deployed using ground-based platforms, satellite remote sensing, or UAVs, depending on the spatial scale and resolution required (from single plants to forest stands).
7. Comparative studies of *Q. robur* in parallel to additional temperate *Quercus* species cultivated in Serbia and Croatia, including *Q. frainetto*, *Q. petraea* and *Q. cerris*, may provide valuable perspectives by revealing species-specific adaptive mechanisms that complement intraspecific resilience strategies and can thus be incorporated into future conservation and breeding programmes.
8. Establish a formal research partnership with INRAE's tree-genomics groups to integrate genomic datasets from Serbian and Croatian *Q. robur* populations into QUERCUS PORTAL (https://quercusportal.pierroton.inrae.fr/) and conduct joint bioinformatic analyses targeting the Balkan refugial gene pool. This cooperation would enable high-resolution comparative genomics, genome-wide scans of adaptive variation, and gene-network modelling under drought, heat, pathogens and other stressors. Integrating these insights with field-based phenotypic and silvicultural data would directly strengthen the scientific basis for conservation planning, dynamic gene-conservation units, and the development of cost-effective and accelerated Breeding-without-Breeding strategies, thereby accelerating the establishment of climate-resilient reproductive material and operational breeding programmes for *Q. robur* in both countries.
9. In light of recent findings by Popa et al. (2025), which identified weaknesses in current species distribution models for assessing range shift scenarios of *Q. robur*, the development of future predictive models which combine genomic, transcriptomic, phenotypic and environmental datasets, should be considered for the entire Balkan region to more reliably forecast this species response to climate change.

Author Contributions

SS and BT conceptualized the study; BT, EV and SS wrote the original draft of the manuscript; SO, SP, JM and MĐ reviewed and edited the manuscript. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest

The authors declare no conflict of interest.

Supplementary Materials

Supplementary Material S1. Research parameters in Quercus robur, with country attribution, interdisciplinary benefits and future research hypotheses.

Supplementary Material S2. Integrated Serbia-Croatia strategic roadmap for Quercus robur (2027-2036) research and conservation aligned with EUFORGEN Dynamic Conservation Unit (DCU) criteria.

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