Oaks as Beacons of Hope for Threatened Mixed Forests in Central Europe

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INTRODUCTION

Climate change has a severe impact on forest ecosystems (Seidl et al., 2017). Adaptation of trees to the rapidly changing regional climate is hampered by their longevity and late reproductive age. Therefore, the increases in frequency, duration and intensity of drought episodes, heat waves and heavy rainfall events (Spinoni et al., 2018; Hari et al., 2020) threaten many tree species of European forests. As a result, environmentally stressed trees will become vulnerable to pronounced damage from herbivorous insects and pathogens. Thus, the damage caused by insects increases the vulnerability of forests to fungal infections and secondary pests (Meyer et al., 2015), and conversely, fungal infections can promote the development of herbivores (Eberl et al., 2020). Both together then contribute to the higher overall vulnerability of forests.

With regional shifts in weather conditions and climate zones in Europe, complex combinations of abiotic and biotic stresses will likely occur. The quick succession of abiotic and biotic stresses can further worsen forest damage. A quantification of the vulnerability of European forests to windthrows (40% of losses), fires (34%), and insect outbreaks (26%) during the period 1979–2018 revealed that about 33.4 billion tons of forest biomass were seriously affected by these disturbances (Forzieri et al., 2021). There is a clear trend toward higher overall forest vulnerability driven by a warming-induced reduction in plant defenses against insect outbreaks, especially at high latitudes.

If forests fail to adapt to climate changes, there will be manifold consequences for the ecosystem function and services, productivity, biodiversity, and negative feedbacks to climate (Ammer, 2019).

IMPORTANCE OF EUROPEAN OAKS AND HISTORY OF OAK DECLINE

The two predominant oak species in Central Europe, English oak (*Quercus robur* L.) and sessile oak (*Q. petraea* Matt.) are two of about 50 tree species growing in European forests. Together their share of about 10% of the stands makes oaks the second most common deciduous tree species in Europe after beech (Bolte et al., 2007; BMEL., 2014). Among tree species native to Europe, oaks have the highest species diversity at all trophic levels. More than a thousand animal species (including insects, birds, small mammals) live on and with oaks (ProQuercus). Economically, oak wood has a special importance due to its high strength and resistance. It is used as construction timber, as well as processed into barrels, railroad sleepers, furniture, parquet, and veneers.

In Central Europe, frequent insect outbreaks are believed to be one of the causes of the oak decline observed in the last century (Gasow, 1925; Thomas et al., 2002; Denman and Webber, 2009). The first important oak dieback was observed already in 1911–1920 and later in the 1980s; oaks of all age groups died at a rate of 2–5 trees per hectare and per year due to insect defoliation often co-occurring with drought events (Hartmann and Blank, 1992; Denman and Webber, 2009).

The decline of European oaks can be explained by changing climatic conditions and their consequences like heavy rains, local floods, and pests (Keča et al., 2016). Root pathogens from the genus *Phytophthora* DeBary especially benefit from wet soils following heavy rain events. *Phytophthora* threats have been observed in oaks in North America and Europe since the 1990s with various impact on different species (Sturrock et al., 2011). For *Q. robur*, soil acidity was recognized as the main factor for enhanced susceptibility to *Phytophthora* infections (Jönsson et al., 2003).

A decline in growth rate was observed in the second or third year after drought events when comparing tree-ring series in *Q. robur* and *Q. petraea* stems at three different sites (Perkins et al., 2018). Being a ring-porous tree species, oaks are most likely categorized as anisohydric species which strive to regulate stomatal conductance to keep photosynthetic processes alive, even during drought periods. However, anisohydric traits may lead to a longer drought memory due to high investments to sustain photosynthetic activity, thus leading to a hangover of drought effects (Perkins et al., 2018).

Even more herbivorous insect species from Southern and Eastern Europe will likely migrate into central European forests (Sturrock et al., 2011; Pureswaran et al., 2018), as it has been observed for the oak processionary moth *Thaumetopoea processionea* L. (Bolte et al., 2009). Owing to climate change, also native species, such as the oak splendor beetle *Agrilus biguttatus* Fabr., increase their infestation ability and are predicted to cause more serious damage (Bolte et al., 2009; Sanders et al., 2013).

ADVANTAGES OF EUROPEAN OAKS (*QUERCUS* SPP.)

Temperature increase during the last decades caused changes in the abundance of broadleaved species in European forests, e.g., beech (*Fagus sylvatica* L.) forests have declined in several regions of Central Europe (Denmark: Huang et al., 2017; Germany: Dulamsuren et al., 2017; Austria: Corcobado et al., 2020). This decline of beech is only marginally caused by outbreaks of insects. This is not unexpected because compared to oaks, beech suffers only from a low number of insect pests as e.g., the splendor beetle *Agrilus viridis* L. (Bolte et al., 2009). A major threat for beeches are *Phytophthora* infections which are observed since the 1930s. In combination with drought periods and heatwaves since 2003, the beech decline has increased dramatically in comparison with oak (Corcobado et al., 2020).

A study covering 50 years of phenological data showed that oak and beech follow different phenological strategies with oaks having the better adaptation capacity to climate change due to a higher phenological plasticity (Wenden et al., 2019). Furthermore, oaks have the possibility to maintain their hydraulic status during dry summers due to their extensive root system reaching deep soil layers (Zapater et al., 2011; Scharnweber et al., 2013). Beech reacts with phenological maladaptation to changes in temperature and water regime, slightly compensated by within-population genetic diversity (Frank et al., 2017). Beech is threatened especially in its warmer distribution areas with potential reduction of its vitality (Wenden et al., 2019). Under future climate projection, 10–16% growth rate decline is predicted for *F. sylvatica* by 2100, while an increase of 12% growth rate is expected for *Q. robur* (Huang et al., 2017). Therefore, in climatically warmer areas, where beech is likely to reach its limits (Kramer et al., 2010), oak may prevail over beech because it is already adapted to the warmer climate (Delb, 2012; Cuervo-Alarcon et al., 2021). In more northern regions, on the other hand, a successful strategy should be to support oak and beech to maintain resilient mixed forests that help mitigate the effects of climate change because an adequate species mix can even lead to increased productivity (Pretzsch et al., 2013).
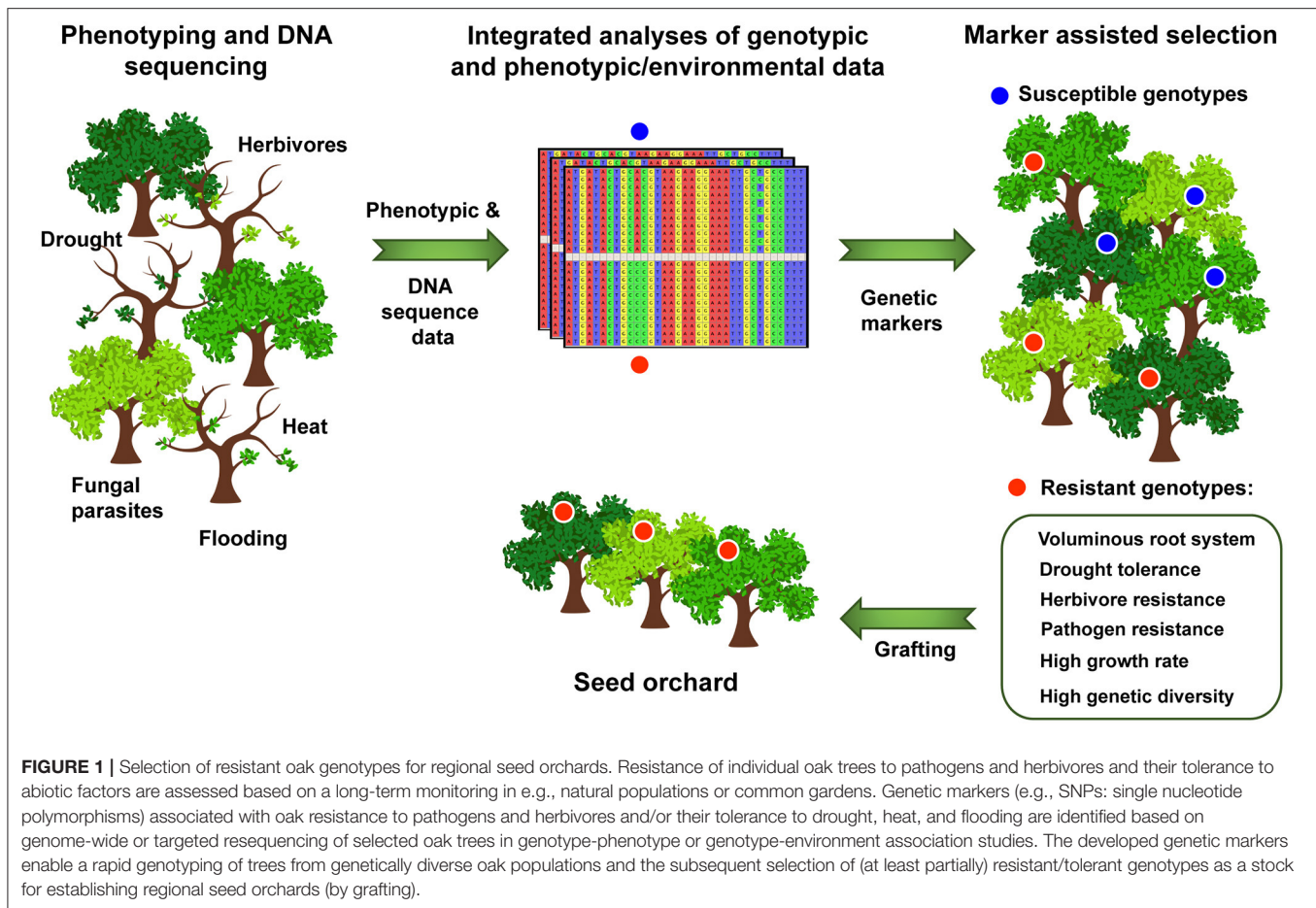
Increasing spring temperatures enhance seed production and dispersal in temperate oaks (Caignard et al., 2017). A higher reproduction success of temperate oaks is associated with improved fitness. Furthermore, the extension of the growing season leads to an increase in vegetative growth of *Q. petraea* and *Q. robur* (Saxe et al., 2001; Caignard et al., 2017). So, both higher seed production and vegetative growth seem possible in temperate oaks during climate change. A comparative analysis of genetic diversity in adult and offspring generations in beech and oak populations coexisting in a naturally established old-growth forest stand, revealed that adult generations of both species exhibited high levels of genetic diversity (He: 0.657 for beech; 0.821 for oak; depending on the sets of selected genetic markers) (Sandurska et al., 2017).

The high genetic diversity of oaks and beeches will facilitate adaptation to climate change. In addition, there is the adaptive potential in oaks resulting from introgression (hybridization of e.g., *Q. petraea* and *Q. robur* in overlapping habitats; Kremer and Hipp, 2020). It is increasingly recognized that hybrids play an important role in evolutionary processes. Thus, natural or man-made oak hybrids together with successful oak breeding programs and grafting of superior individuals may lead to novel traits that give oak decisive advantages in evolutionary processes, facilitating gene flow.

Due to massive anthropogenic activities in the past, natural regeneration of European tree species is mostly developed from remaining local stocks (Bradshaw, 2004). In our opinion, this may result in lower genetic diversity for naturally regenerating tree species as beech compared to bred and out-planted tree species as temperate oaks.

GENOMICS AND MOLECULAR MARKERS OF CLIMATE-CHANGE RELEVANT TRAITS

In oaks, phenotypic traits of particular importance include among others drought tolerance, resistance to insects and

FIGURE 1 | Selection of resistant oak genotypes for regional seed orchards. Resistance of individual oak trees to pathogens and herbivores and their tolerance to abiotic factors are assessed based on a long-term monitoring in e.g., natural populations or common gardens. Genetic markers (e.g., SNPs: single nucleotide polymorphisms) associated with oak resistance to pathogens and herbivores and/or their tolerance to drought, heat, and flooding are identified based on genome-wide or targeted resequencing of selected oak trees in genotype-phenotype or genotype-environment association studies. The developed genetic markers enable a rapid genotyping of trees from genetically diverse oak populations and the subsequent selection of (at least partially) resistant/tolerant genotypes as a stock for establishing regional seed orchards (by grafting).

pathogens, and growth-related traits. These traits are expected to be influenced multi-factorially and inherited poly-genetically. The increasing availability of reference genomes for different oak species is the prerequisite to identify the underlying genes/genomic loci and develop diagnostic genetic markers for breeding programs (Badenes et al., 2016). First success is shown, for example, in the quantitative trait loci (QTL) study which identified two regions associated with *Erysiphe alphitoides* infection in the *Q. robur* genome (Bartholomé et al., 2020).

In addition to QTL studies, genome-wide association studies (GWAS) in natural populations, common gardens, or other experimental settings (e.g., McKown et al., 2018) provide new insights (**Figure 1**). Challenging in these studies is the lack of efficient methods for tree phenotyping (Dungey et al., 2018) and the modeling of complex genomic traits. Multi-trait GWAS approaches, as applied to *Populus trichocarpa* (Chhetri et al., 2019), may help to uncover potentially pleiotropic effects of individual genes in *Quercus*, especially when analyzing climate-relevant traits.

Analyzing genome-wide associations between single nucleotide polymorphisms and environmental/climate variables may be the key to identify adaptive genetic markers in *Quercus* (**Figure 1**). Alternatively, genomic selection approaches may help identifying genotypes with the climate change-relevant

traits and their genotypic plasticity. Using a large-scale common garden experiment in combination with genome sequencing and calculation of genomic estimated breeding values, Browne et al. (2019) identified several *Q. lobata* genotypes that grow relatively fast under higher temperatures. These genotypes, which are presumably pre-adapted to future climates, were proposed by the authors to serve as seed sources for assisted gene flow programs.

An alternative approach is developing molecular markers for important traits in the genus *Quercus* based on transcriptome, proteome, and metabolome data. Examples include omics studies on signaling pathways induced in *Q. robur* by herbivory (e.g., Ghirardo et al., 2012; Kersten et al., 2013), which play a central role in plant defense against herbivorous insects (summarized in Erb and Reymond, 2019). Another example is cross-species comparative transcriptomics analysis of *Q. robur, Q. pubescens,* and the evergreen *Q. ilex* L. to reveal drought-related molecular patterns (Madritsch et al., 2019).

Once developed, molecular markers can be used to identify and select (at least partially) resistant/tolerant oak ecotypes/genotypes using marker-assisted selection (**Figure 1**). Among several modern strategies (Cortés et al., 2020), the use of molecular markers is one of the most promising

strategies to evaluate and breed oak adaptation to changing climatic conditions.

CONCLUSIONS

We need to prepare our forests for the impending climate change consequences through silvicultural and breeding measures to mitigate forest vulnerability. Ecosystems should increment genotypes that are characterized by an increased tolerance to various biotic and abiotic stresses. Overall, complex consideration of tree tolerance to different stressors is crucial for assessing their adaptive capacity to climate change.

Particularly in the more northern European forests, supporting oaks and beeches will help maintain resilient mixed forests to mitigate climate change effects on forest ecosystems. The asynchrony of drought responses between these tree species could stabilize productivity in forests where both species occur (Rubio-Cuadrado et al., 2018). *Q. robur*, *Q. petraea*, and related hybrids may play a crucial role in helping forests adapting to climate change. Therefore, silvicultural approaches for the climate-smart forestry should take advantage of these climate-stable properties of oaks by establishing the required light regime for this species to increase its proportion in European forests (Perkins et al., 2018). Future development and application of genetic markers will aid in assessing the

adaptability and resilience of planted oak material in the face of the proposed shifts of the climate zones and in selecting material that can withstand the multiple challenges of climate change for the forest of the future.

AUTHOR CONTRIBUTIONS

HS and BK wrote the first draft of the manuscript. TN developed and designed the figure. All authors developed the concept, structure of the manuscript, accomplished, checked the first version, and read and approved the submitted version.

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