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Review

Will "Tall Oaks from Little Acorns Grow"? White Oak (*Quercus alba*) Biology in the Anthropocene

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Abstract: *Quercus alba* L., also known as white oak, eastern white oak, or American white oak, is a quintessential North American species within the white oak section (*Quercus*) of the genus *Quercus*, subgenus *Quercus*. This species plays a vital role as a keystone species in eastern North American forests and plays a significant role in local and regional economies. As a long-lived woody perennial covering an extensive natural range, *Q. alba*'s biology is shaped by a myriad of adaptations accumulated throughout its natural history. Populations of *Q. alba* are crucial repositories of genetic, genomic, and evolutionary insights, capturing the essence of successful historical adaptations and ongoing responses to contemporary environmental challenges in the Anthropocene. This intersection offers an exceptional opportunity to integrate genomic knowledge with the discovery of climate-relevant traits, advancing tree improvement, forest ecology, and forest management strategies. This review provides a comprehensive examination of the current understanding of *Q. alba*'s biology, considering past, present, and future research perspectives. It encompasses aspects such as distribution, phylogeny, population structure, key adaptive traits to cyclical environmental conditions (including water use, reproduction, propagation, and growth), as well as the species' resilience to biotic and abiotic stressors. Additionally, this review highlights the state-of-the-art research resources available for the *Quercus* genus, including *Q. alba*, showcasing developments in genetics, genomics, biotechnology, and phenomics tools. This overview lays the groundwork for exploring and elucidating the principles of longevity in plants, positioning *Q. alba* as an emerging model tree species, ideally suited for investigating the biology of climate-relevant traits.

Keywords: *Quercus alba*; adaptations; environmental stress; Anthropocene; woody perennial; climate-relevant traits; research resources

1. Introduction

Oaks (*Quercus* spp.), as long-lived deciduous trees, are central to the biology of our planet, both as individual species and as members of complex ecosystems. Oaks underpin many regional and local economies worldwide and have been of great cultural significance for eons. Collectively, oak species contribute, either directly or indirectly, to human nutrition, medicines, energy, paper, construction materials, and ornamental landscape applications, and are socially and culturally significant, even in our advanced technology era [1]. Oaks are often dominant species within natural ecosystems, store significant amounts of sequestered carbon, provide ecosystem services such as water purification and oxygen production, and serve as keystone species that anchor complex multi-trophic communities [2]. These attributes derive in large part from the life history strategy of trees as long-living woody perennial plants, with the ability to adapt acutely and chronically to ever-changing environmental conditions [3,4]. Critically, the genomic evidence reveals that oaks have so far exhibited rapid adaptation to the changing climate of the Anthropocene [5], a chapter in history that is only just beginning.

1.1. Quercus alba L.

Quercus alba is the archetypic representative of the *Quercus* ('white oak') section of the oak genus *Quercus* (for phenotypic identifiers see Figure 1A), one of eight genera in the Fagaceae (beech) family. In eastern North America, one of the most important tree species to communities, regional economies, and industries, as well as being a keystone species of natural forest ecosystems [2]. The species accounts for the largest volume of oak lumber harvested from US forests, for use in flooring, furniture, construction, and the production of millions of barrels every year for the wine and spirits industry [6,7]. *Quercus alba* acorns serve as an important dietary component for many wild animal species, of prime importance after extirpation of the American chestnut (*Castanea dentata*).

Quercus alba has historically been a dominant canopy species in the central and eastern hardwood forests of North America from pre-European settlement times, providing important ecosystem services including habitat for a wide diversity of organisms, sequestering carbon, and filtering air and water [8–13] (Figure 1B). With the changing land-use patterns, *Q. alba* recruitment (growth into the forest canopy) declined during the 20th century with a concomitant decrease in white oak presence in North American forests (Figure 1C). Contrastingly, other oaks prospered during this period, leading to several important questions whose answers are critical to forecasting the future of the species, especially in rapidly changing climate scenarios. As posed by Abrams (2003 [8]), "Why did white oak, among all the upland oaks, dominate in the presettlement forest? What restricted the development of red oak in the presettlement forest on sites that it currently dominates? What role did anthropogenic factors play in the expansion of red oak and chestnut oak versus white oak? What ecophysiological limitations make white oak more susceptible than other oaks to the dramatic changes in land use over the past few hundred years?" Key to answering these questions is understanding the oak trait biology associated with competitive success in environmental niche adaptations. Thus, in *Q. alba* and other sympatric forest tree species, a more systematic, integrative understanding is needed; this would ideally encompass root/mycorrhizal biology, root/stem/leaf water transport, and vascular dynamics, as well as the physiological and genetic control of these traits and phenology, masting, and seedling regeneration in normal and abiotic/biotic stress conditions. Predicting the future competitive success of *Q. alba* in a rapidly changing climate (Figure 1D) will rely on understanding the degree of the plasticity of these traits and the reproductive, recruitment, and evolutionary constraints on long-lived perennial species.

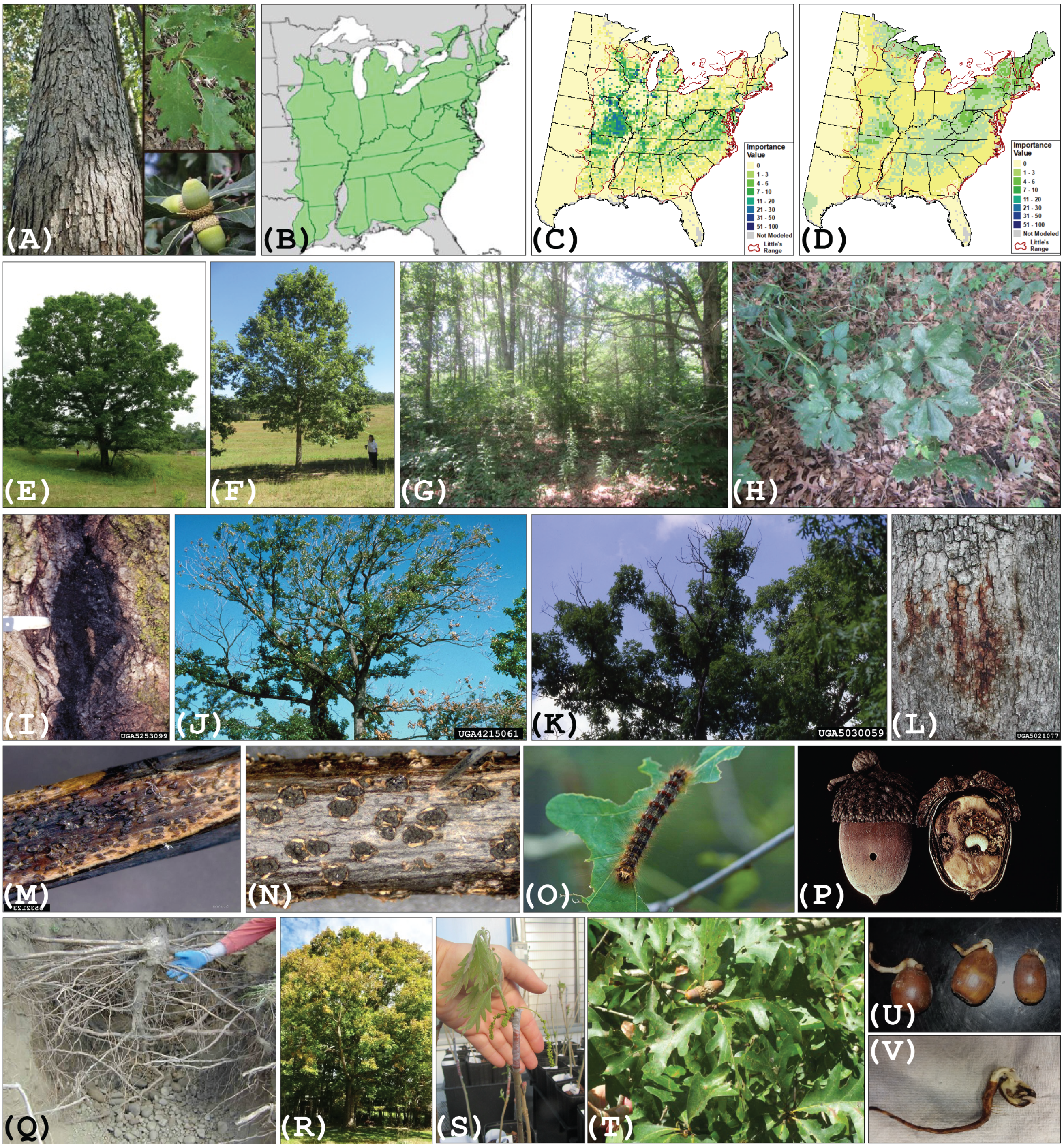

Figure 1. *Q. alba*, its range, and examples of healthy and disease/pest conditions. (**A**) *Q. alba* identifiers—bark, leaves, acorns; (**B**) Historical natural range of *Q. alba*; (**C**) Current Forest Inventory and Analysis; (**D**) Projected future habitat under harsh climate scenario; (**E**) Very old, healthy pasture tree; (**F**) Healthy seed orchard tree, Murphy NC; (**G**) White oak forest stand; (**H**) Natural regeneration; (**I**) *Phytophthora* root and crown rot; (**J**) Tree with oak wilt from *Bretziella fagacearum*; (**K**) Tree with oak decline; (**L**) Hypoxylon cankers; (**M**) Anthracnose (*Discula quercina*); (**N**) *Botryosphaeria* cankers; (**O**) *Lymantia dispar* (gypsy moth); (**P**) Acorn and nut weevils (Genus Curculio); (**Q**) Roots of 25-year-old oak tree showing taproot; (**R**) Masting *Q. alba* tree, Garrett County, MD, 2022; (**S**) Catkin on flowering *Q. alba* graft in the greenhouse; (**T**) Close-up of healthy branch with mature acorns; (**U**) Weevil exiting germinating acorn (long, healthy taproot, but the shoot is damaged and will not emerge); (**V**) Germinating acorns. Credits: (**A**) Laura DeWald; (**B**) The United States Geological Survey;

(**C**,**D**) USDA Forest Service https://www.fs.usda.gov/nrs/atlas/tree/802 (accessed on 30 November 2023); (**E**) John Carlson; (**F**–**H**) Laura DeWald; (**I**,**K**) Joseph OBrien, USDA Forest Service, https://www.bugwood.org/; (**J**) Fred Baker, Utah State University, https://www.bugwood.org/; (**L**) Pennsylvania Department of Conservation and Natural Resources—Forestry, https://www.bugwood.org/; (**M**,**N**) Bruce Watt, University of Maine, https://www.bugwood.org/; (**O**) John Ghent_Bugwood.org; (**P**) Louisiana State University, https://www.bugwood.org/; (**Q**) USDA Forest Service https://www.fs.usda.gov/; (**R**) William Buckel; (**S**–**V**) Laura DeWald.

1.2. Challenges for Oaks in the Anthropocene

Due to the continued rapid warming of the Earth during the Anthropocene, climate change is and will continue to impact the sustainability of global forest tree resources, both directly and indirectly [5]. Given sufficient time as regional climate conditions change, species may adapt to changing environments. However, rapid environmental changes pose major challenges to perennial species with very long generation times. This is particularly true for trees which can have long juvenility periods and cycles of flowering, seed production, and seed germination that are dependent on specific environmental conditions. Since adaptation relies on reproduction, the continued survival of long-lived species in their current locations is particularly uncertain. Indeed, direct impacts of recent global warming on tree reproduction are being reported in both fruit orchard and forest trees [14–19], and research is needed to understand the impact on perennials as climate change advances.

Considering the importance of oaks to ecosystems and the human endeavor, it is surprising how fragmented our climate-relevant knowledge of the biology of oak species is in comparison to that of economically important herbaceous species [20]. This is, in part, the result of long-lived perennial trees having been considered difficult models for the study of basic cellular, physiological, or genetic processes. Multiple reasons for this are apparent, but, particularly, the long sexual generation times and difficult asexual propagation methods are considered most inhibitory for basic research. This contrasts with annual crops and model plants where generation cycles can be months, not decades, providing well-controlled genetic materials for study. However, the realities of climate change, an ever-increasing population needing shelter and energy, and our emerging understanding of the crucial role that oak trees play in our environment have become compelling forces for important oak biology research across all levels, from cellular and whole-plant physiology, genetics, and genomics to forest ecology and species conservation. Rapidly advancing molecular technologies and large-scale, big data-driven approaches have generated powerful model systems for trees [21–24]. The study of oak biology provides new opportunities to delve deeper into the key features that define woody perennial plants and are shared among oaks and other hardwood forest trees [25].

The intent of this communication is to present an emerging picture of the current knowledge on *Q. alba* biology drawn from previous, ongoing, and future research perspectives as an example of a North American oak species that is critically important to regional/global economies and natural ecosystems. It is particularly timely as the sustainability of forests, including oak forests, are impacted by a rapidly changing environment. This overview aims to provide a foundation for defining and studying the emerging principles of long-lived perennial trees with a special emphasis on challenges posed to *Q. alba* in the Anthropocene, especially those related to the need for mitigation of climate change impacts and improvement of natural regeneration. For more detailed reviews of related phylogeny, diversity, ecology, and evolutionary studies on other *Quercus* species from the growing global community of oak researchers, readers are directed to other recent works such as [26,27].

2. Phylogeny and Distribution

Oaks (*Quercus* L., Fagaceae) are a large global genus of woody plants that dominate northern temperate deciduous forests [28]. Recent phylogenic divisions of the genus based on morphology and molecular genetics data divide the genus *Quercus* into two subgenera: subgenus *Cerris*, comprised of the three sections *Cyclobalanopsis*, *Cerris*, and *Ilex*; and subgenus *Quercus*, comprised of the five sections: *Lobatae* (red oaks), *Protobalanus* (intermediate oaks), *Ponticae* (California oaks), *Virentes* (live oaks), and *Quercus* (white oaks) [29,30] (Figure 2A). *Quercus* sect. *Quercus* includes 146 species distributed throughout North America, Central America, Western Eurasia, East Asia, and North Africa [31], of which 112 are found in North America (45 in the US and 67 in Mexico) [32,33]. Recent studies using genome sequencing technologies revealed that American oaks arose in North America and spread to the south, similar to pines [32–34] (Figure 2B). This dispersal pattern resulted in four major lineages. Species in the red and white oak sections radiated sympatrically and broadly across the north. Live oak and golden cup oak section species showed a much higher rate of parallel diversification, potentially driven by the more recent adaptation to milder niches in Mexico, based on climate and regional moisture gradients, relative to long-term diversifications [32,33] (Figure 2A).

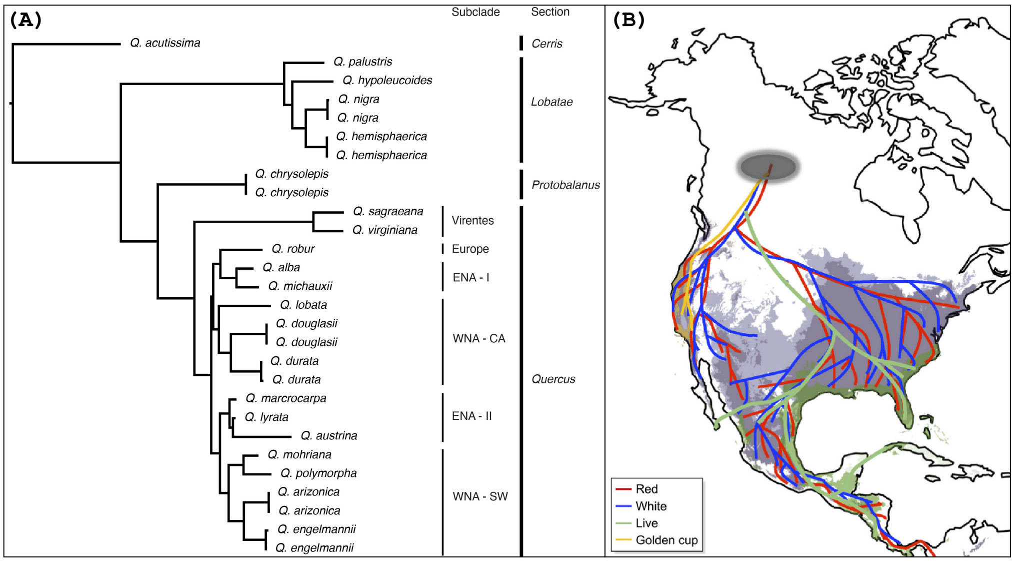

Figure 2. Phylogeny and speciation of clades in North American Oaks. (**A**) Phylogenetic tree of *Quercus*, focusing on species within the North American clade, from maximum likelihood analysis of RADseq data [31]; (**B**) Suggested migration routes from a common refugia pattern that can account for the sympatric parallel adaptive radiation of the four oak clades in North America [32,33].

North America has the greatest number of oak species (~240), encompassing the red, white, and intermediate sections of species and ranging from the east to west coast, from southern Canada through Mexico, and beyond to the Andes of Columbia [35]. Oaks populate a moisture gradient of environments, from the dry mesic conditions of the southwestern United States and Mexico, to the wet conditions in the southern limits of the northern boreal forest in northeastern US and southeastern Canada [35–38].

Quercus alba is one of the most widely distributed tree species in North America and grows throughout much of the eastern United States. Its historical distribution ranged from Maine to northern Florida, north through southern Ontario and Quebec, and west to Iowa, Kansas, Oklahoma, and Minnesota (Figure 1B) [37,39]. It is a relatively common as well as wide-spread species, but its abundance and ecological importance vary greatly with habitat factors across its range [2,32,40]. In addition to historical trends, recent declines in *Q. alba* oak populations within eastern forests from overharvesting, high grading, inconsistent regeneration, and poor regeneration are raising concerns [8,41] (Figure 1C). In addition, the range, abundance, and ecological importance of *Q. alba* is expected to shift as the climate changes [42] (Figure 1C,D).

3. White Oak Regeneration and Recruitment

A prominent factor affecting the eastern oak resources has been the ecological legacy of change in human disturbance patterns on the landscape. Prior to European settlement, the region's oak forests were maintained through periodic disturbances which included the use of fire by Native Americans [43,44]. The nature and intensity of post-European settlement disturbance combined with factors such as the demise of the America chestnut increased the prominence of oak on the landscape [44–46]. Since the mid-20th century, fire has been largely removed as a landscape-level disturbance [43], with the intensity and spatial magnitude of other human disturbance on the region's forests greatly increasing.

The demographic and distribution patterns of the eastern oak resources reflect the historical timeline of human use and successional responses of forest communities (Figure 1C,D). The contemporary age structure of the region's oak forests is skewed toward older age classes, with 60 to 70% of forests today between the ages of 40 and 100 years old and only 5 to 10% of oak forests being less than 10 years old [47,48] (Figure 1E,F). Near-term oak supplies are stable due to the large standing volumes in largely even-aged forests whose origin was facilitated by late 19th and early 20th century land-use and disturbance patterns. However, widespread recruitment failures throughout its geographic range have been reported by forest managers for many years [49]. Oaks in the canopy are being replaced by non-oak species [50,51] from forest successional dynamics that are influenced by the high levels of deer herbivory and a reduced frequency of low intensity fire which results in increased competition for light, water, and nutrients [44,50,52–56]. As overstory oaks are eliminated through natural mortality and harvesting, the inadequate recruitment of competitive *Q. alba* seedlings results in stand compositional shifts toward more shade-tolerant species such as red maple (*Acer rubrum* L.) and American beech (*Fagus grandifolia* Ehrh.) [37,57,58]. In these shaded conditions, the relatively poor competitiveness of *Q. alba* is due to slow above-ground juvenile growth and a preferential allocation of resources to the root system, combined with intermediate shade tolerance [34,57,59]. In recognition of the lack of *Q. alba* recruitment and large-scale species compositional shifts, efforts to conserve and restore oak ecosystems have been increasing (e.g., [51,60,61]). In addition to a variety of management approaches that are being tested and implemented (e.g., [52,62–65]), organizations such as the White Oak Initiative (www.whiteoakinitiative.org) have been created in order to support the sustainable growth of the *Q. alba* resources [66].

4. Climate Change and *Quercus alba* Biology: Direct Impacts

As sessile organisms, temperate trees have developmental and reproductive systems that are optimized for the annual cycle of changing environmental conditions. From studies of different plant species, these systems are sensitive to light/dark cycling, day/night temperatures, water availability, or a combination of the three. For a tree species in a particular climate zone, there are several key physiological systems adapted to the cyclic changing environmental conditions. These include but are not limited to: (1) tree water maintenance and transport systems; (2) juvenility and reproductive systems; (3) meristematic growth and development systems; and (4) abiotic and biotic cellular stress response systems. All these systems are composed of phenotypic traits that are critical for maintaining the species in its current environment. For *Q. alba*, as discussed above, of great interest are traits that maintain regeneration (flowering, pollination, seed development, and seedling survival and growth), enhance recruitment (drought and shade tolerance and sapling survival and growth) (Figure 1H), and tolerate or resist biotic (pathogens and pests) (Figure 1I–P) and abiotic stress.

Adaptation can be a long-term process depending on the phenotypic plasticity and genetic basis for any trait, especially for species with long generation times. Therefore, rapid climate change poses a significant threat to the continued presence of such species in their current environment. To predict the future success and distribution of oaks in the changing temperate forest zones with the objective of potentially assisting its future success, we must know: (1) Which adaptive traits were key to the oaks' success in their extant locations? (2) What is the degree and mechanism of phenotypic plasticity and/or genetic variation for these traits required by individuals or populations for adaptation? (3) What genes or molecular networks control the climate critical traits? (4) Which of these traits should be prioritized as targets for oak management, reforestation, and genetic improvement efforts in the future? The following are examples of oak traits likely to be important in their adaptive responses to rapid climate change.

4.1. Water Relations: Control of Root Growth in Oaks

Predicting the future success and distribution of *Q. alba* in North America relies heavily on our understanding of the physiology and genetics underlying this species' ability to adapt to the direct impacts of increased environmental warming. Although we have very limited knowledge of this in *Q. alba*, significant studies of drought tolerance and related traits, such as water-use efficiency in other models for annual and woody plant species [67–69], have provided research targets and foundational studies for deployment in the research on *Q. alba*. From the genetic perspective, several studies have revealed the sources of variation and candidate genes underlying drought tolerance and adaptation in European white oaks [70–74]. Unlike four other northeastern oaks studied by Reed and Kaye [75], *Q. alba* is responsive to rich soil composition and higher moisture levels, associated shale vs. sand bedrock. However, data and publications on the performance of *Q. alba* on different types of soil are scarce (for more information on site recommendations for *Q. alba*, refer to [76]). As *Q. alba* have a taproot architecture (Figure 1Q), presumably to enable deep soil water acquisition under drought conditions, studies focusing on the control of the development of this root form in woody plant species are particularly relevant.

Oaks exhibit both shallow and deep rooting systems, allowing them to access water at multiple depths in the soil profile during the annual cycles of rain and drought. They successfully compete with species possessing rooting systems more specialized for deep soil (e.g., maples and pines) [36]. The rooting architecture of oaks in concert with stem vascular organization (ring porous) and leaf structural features (thickness, stomatal size) enable oaks to exploit niches across regional and climatic zones greatly differing in hydrologic conditions [36,37], from mesic to xeric. Equally important, oaks survive and prosper in a broad range of different edaphic conditions and drought stress, due to the structural features of oak vascular tissues such as tyloses (vascular structures arising post-differentiation that limit the diffusion of liquids through the wood sample [77], deep rooting, and the ability to form and sustain mycorrhizal associations with a high diversity of fungi; for review, see [78]). *Quercus* species distributions provide excellent examples of how these anatomical traits and their associated physiological systems have enabled the species to become dominant in North American forests across a large range of environments (for a review of physiological characteristics, see [32,36,37,40,79]).

A recent review by Kościelniak et al. [80] lays out the current status of our understanding of taproot development and its control while highlighting several questions that need future study: "(1) how does organization and cellular signaling enable a taproot to grow and penetrate deep soil layers, (2) what internal factors enable taproots to grow rapidly and penetrate deep soil layers (Figure 1Q), and (3) how does soil water limitation induce the vertical growth of taproots (Figure 1Q). Aside from the unanswered questions above, how much does the genetic control of cell division explain the continued maintenance of root growth and apical dominance of taproot meristems?" As outlined by Kościelniak et al. [80], emerging concepts in the control of root growth come from studies of models such as *Arabidopsis* and other model tree species (e.g., *Populus* species). The control of root growth and architecture is related to phytohormone balance and pathway regulation, plant growth and development transcription factors, microRNAs, and signal transduction pathways. Additionally, emerging studies indicate that epigenetic factors likely also play a key role in the adaptive responses of trees to environmental change (for review, see [81,82]). In the case of epigenetics, work in *Populus* species on drought stress transcriptomic responses of clonally propagated material planted in differing geographic regions demonstrates specific DNA methylation patterning correlated with provenance and drought stress transcriptomic responses [82]. These types of studies linking local adaptation to epigenetic marks in reference to oak adaptation could unlock potential plasticity targets for the improvement of the species.

4.2. Reproduction

In European white oaks, Caignard et al. [83] presented evidence that increasing temperatures associated with climate change are responsible for an observed increased seed production in environments that are historically cooler and currently not impacted by water deficit. This contrasts to studies of other oak species in regions experiencing both temperature increase and water deficit, whereby tree growth and survival were negatively impacted by a warming climate [84]. Effects on other aspects of oak reproduction (e.g., masting) and the effects of other environmental changes (e.g., drought) need to be established before any meaningful modelling about the future habitat of deciduous oaks in the temperate forests. Current predictions suggest that oaks will expand northward with changing climate zones and retreat in warmer drought-prone areas. A recent limited provenance study of *Q. alba* performance suggests that white oaks from northern temperate locations, when challenged with more southerly climate conditions, do not perform as well as trees from more southern provenances, suggesting that there may be a fitness cost for *Q. alba* as the climate zones shift further northward [85]. Research into the fundamental genetics and physiology of oak species regeneration in response to environmental conditions are needed to predict outcomes and produce strategies in order to promote the continued presence and establishment of white oaks.

4.3. Pollination

Long-distance pollination is a well-established feature of the maintenance of genetic diversity within oak stands [86] (for review, see [7]). Multiple studies of isolated stands have revealed that long-distance pollen dispersal is evident and leads to the conclusion that the fragmentation of oak populations due to repurposed land use may not necessarily lead to local losses in genetic diversity [87–98]. However, other barriers may lead to loss of diversity or inbreeding, such as genetically determined fertilization incompatibilities and/or timing of flowering, which may play a significant role in determining the genetic architecture of oak forest stands, despite pollen dispersal [86]. Thus, climate change could lead to local maladaptation, due to incompatible phenology, making it difficult to predict future oak sustainability for species such as *Q. alba*, for which we know little regarding these traits and at what spatial scales these traits have adapted.

4.4. Flowering

Oaks are monoecious, with staminate and pistillate flowers on the same tree. Little is known of the physiology or genetics of the regulation of flowering in oaks. Contrastingly, there is a substantial body of growing knowledge about the molecular basis of flowering control in some model forest and fruit tree species (for recent review, see [99]). Both floral and leaf bud dormancy are initiated and controlled by key environmental factors such as light (day length), cold (chilling requirement), and stress (abiotic: heat, cold, osmotic; biotic: pathogens and pests). All of these will likely be significantly impacted by climate change. The establishment, maintenance, and release of dormancy are regulated by gene networks that respond to these different environmental cues, depending on the individual adaptation of a particular species or population. For example, *Prunus* fruit trees, such as peach (*P. persica*), establish, maintain, and release bud dormancy via pathways that are sensitive to temperature [100], while in *Populus* species, these steps are regulated more by day length [101] (reviewed by [102,103]). In general, these networks involve light response networks, temperature response networks, hormone pathways, cell cycle control, epigenetics, and others [99,100]. Genomics-based research on dormancy in the European pedunculate oak (*Q. robur*) has highlighted some of the gene networks evident in these previous fruit and forest tree studies, suggesting that oaks may utilize similar genetic control mechanisms as other tree species [104]. However, it is difficult to predict and improve the performance of *Q. alba* in terms of flowering traits (Figure 1S) without first obtaining substantial knowledge of the physiological, ecological, and genetic systems that underpin these traits in this species.

4.5. Masting

Masting is a population scale synchronous flowering event observed in certain tree species. However, as pointed out in a detailed review of the genetic control of masting [105], the manifestation of this event is dependent on the diversity in the flowering control mechanism among individual members of the species (diversity) and the coordinated response of these individuals within a population and year (synchrony). A resource-driven pollen limitation hypothesis was directly supported for two European oaks species, *Q. petrea* and *Q. robur* [106]. From studies of other perennial and annual plant species, the physiological and genetic control of masting could likely involve molecular networks controlling flowering and dormancy release [99,105,107]; abiotic and biotic stress response [108]; seed maturation, meristem growth, and developmental control [80,109]; root/shoot communication and sink-source physiology [110,111]; the epigenetic regulation of gene activity [112], and potentially others. Although not possible in the past, access to gene information in oaks is rapidly increasing (see Emerging tools and resources for oak biology and improvement, below) and the stage is ideally set to make significant progress in understanding the physiological and genetic underpinnings of this important climate critical trait in *Q. alba* (Figure 1R,T,U).

4.6. Seed Germination

In oaks, there are contrasting climate-related seedling germination strategies. In general, white oaks do not exhibit a stratification requirement and germinate in the fall, concomitant with acorn drop (Figure 1U), while red oak acorns overwinter and germinate the following spring during more favorable growing temperatures [113,114]. In some red oaks, this stratification requirement is not absolute as acorns will germinate without prior cold treatment (e.g., *Quercus pagoda* Raf. [115]); however, the germination efficiency increases substantially with cold treatment [113,115], leading to the conclusion that red oaks exhibit a physiological dormancy, rather than true dormancy (endodormancy) which is associated with cell cycle arrest and chill requirement for dormancy release. Unfortunately, we know very little about the genetics and physiology of this climate critical trait in oaks in contrast to what is known regarding annual crop and model species plants. In recent years, through studies of annual crop models, *Arabidopsis*, and a few woody perennial species (e.g., peach, poplar, and grape), major advances have been made in our understanding of the genetic and physiological underpinnings of seed and bud dormancy in plants. For reviews on seed germination, see [116], and for bud dormancy, [99]. However, much of our knowledge of seed dormancy and germination control comes from studies of plants with orthodox (annual) or typical seeds, such as *Arabidopsis*, whereby seeds mature concomitant with desiccation. This is not the case for recalcitrant or intermediate seed species, including oaks or other nut-producing species like chestnut, for which the desiccation of seeds after maturity significantly negatively impacts seed viability and germination [113,117].

The relationship between the chemistry, germination timing, and dispersal of acorns has been an area of interest for quite some time. An early study on germination in oaks [113] suggested that the fat content of acorns may be related to the germination control in red oak acorns and not the tannin content of the seed. Subsequent reports on northern red oak (*Quercus rubra*) and *Q. alba* germination and dispersal over the following decades were synthesized into a Differential Dispersal Hypothesis (DDH) [118], based on the characteristics of acorns reported to affect germination, feeding, and dispersal by animals.

The DDH summarized the primary features of *Q. alba* acorns affecting dispersal, such as low tannin and low-fat content, and early germination, predisposing *Q. alba* acorns to immediate and/or selective consumption (relative to northern red oak) in autumn, or embryo excision by squirrels prior to cashing. In northern red oak, acorns traits affecting dispersal included high tannin and high fat content, with delayed germination, associated with the selective caching of northern red oak acorns (relative to *Q. alba*) for later consumption during winter. Overall, the DDH predicted that northern red oak acorns would be selectively scatter-hoarded by animals across greater dispersal distances than *Q. alba*, especially smaller-seeded acorns, which jays could disperse over very long distances, primarily into open areas suitable for oak regeneration. More recently, studies in sawtooth white oak (*Q. aliena* var. *accuserata*) suggested that the acorn pericarp and cotyledons contain substances that inhibit germination, and that the removal of the pericarp and a portion of the cotyledon can increase germination efficiency [119]. The germination morphology of *Q. alba* seeds (the plumule separated from the cotyledons) (Figure 1U,V) promotes seedling establishment in case of pruning by rodents [120]. The comparison of red and white oak species acorns by maturity and germination demonstrates that transitions from maturation to germination show changes in cellular location and the metabolism of lipids, insoluble and soluble carbohydrates, and proteins (reviewed by [121]). Many features of the interaction of the genotype, phylogeny, ecotype, and physiology of seed germination remain to be clarified. For a more comprehensive history and detailed overview of ecology and biology research findings for oak seed dispersal, see [122]. Recent phylogenomic analyses have also highlighted the importance of seed structure and germination in the radiation of species, as well as introgression, within the Fagaceae family [123].

4.7. Seedling Growth Control

In oaks, some studies examine the effect of seed size on seed germination and seedling survival (for review see [124]). Among species, the question of seed size versus seed abundance for optimal species survival seems not to be an issue of a simple tradeoff but may also incorporate the longevity of the large-seeded species and the consequences of continued reproduction over extended time periods. Among and within species studies suggest that the larger seeds may have a significant advantage in germination and subsequent seedling recruitment [113,125–128]. Llanderal-Mendoza et al. [126] suggest that decreases in acorn size along latitudinal climatic differences in *Q. rugosa* in Mexico effect successful recruitment whereby the northward expansion of the species range has led to smaller-sized acorns with a reduction in germination and recruitment. Conclusions from this work were supported and further extended to other *Quercus* species in Mexico [127], whereby they demonstrated that, in a common garden experiment for seven red oak species and three white oak species, acorn fresh weight was positively correlated with germination efficiency, and acorn dry matter was driving this correlation. Furthermore, they demonstrated that nutritional storage compounds and not water content were responsible for this result. This size effect was consistent when compared between red and white oak species, as well as within red and white oak species. Finally, a recent study [128] demonstrated that large seed size was positively correlated with seed viability in *Q. robur* acorns collected from multiple sites in Croatia over a ten-year period.

Larger seedlings can improve the competitive status of oak regeneration relative to average-sized seedlings [34,52,129]. Extra-large seedlings [130–132] can be planted to enrich advanced natural regeneration and may be especially critical when harvesting occurs in years of poor mast production, which is a regular occurrence with *Q. alba* [133]. While these seedling size considerations are important, the genetic potential of the seedlings is also important for successful regeneration. Thus, the development of high-quality, well-performing *Q. alba* seedlings for artificial regeneration should be achievable through a combination of tree genetic improvement and good nursery and planting practices [132].

Unfortunately, it is difficult to predict how results from orthodox annual seed plants will translate to oaks and other nut-producing trees. However, we now have the genomic resources and materials in key oak species to bridge this knowledge gap. As stated in [134], "hardwood seed production, seed harvest, and seedling production must be approached as a coordinated system where all aspects from flower initiation to seed development, harvest, and storage to seedling production, transplanting and establishment are integrated. The best approach to insure predictable amounts of high-quality seeds and seedlings is to establish and manage seed orchards and use container production". However, sustained regenerative success in the forest in the long term will rely on an understanding of the genetic and environmental interplay on climate-relevant traits that underpin seed production, germination, and seedling establishment (Figure 1H,R–V). The contrasting strategies of flowering, seed maturation, seed germination, and seedling growth control between sympatric white and red oaks species is ideal for delimiting the genetic architecture of these climate-relevant traits and predicting the impact of climate change on their manifestation. This can lead to optimized management and tree improvement strategies incorporating genetic and physiological knowledge-based inputs.

5. Climate Change and *Quercus alba* Biology: Indirect Impacts

While the rapidly changing climate can directly impact tree growth and reproduction, it also indirectly impacts tree survival by altering the distributions of pests and pathogens, potentially leading to increased pest and pathogen pressure on native tree populations (for a review, see [135–137]). Oaks are susceptible to native and non-native pathogens (Table 1 and Figure 1I–P). Alone, many of these pests and pathogens are not necessarily lethal to the host; however, in concert with the plant stress imposed by a rapidly changing climate, these pathogens can significantly contribute to oak decline [138]. Therefore, the introduction of novel non-native pathogens or the climate-driven expansion of native pathogen ranges can be extremely detrimental to previously unexposed forest trees (for examples, see [139]). A case in point from a related Fagaceae species is the spread and subsequent impact on the American Chestnut of *Phytophthora cinnamomi* post its introduction to the eastern US [140,141]. This oomycete pathogen is hosted by over 5000 different plant species (for a review, see [142]) (see Figure 1I for *Phytophthora* root and crown rots in *Q. alba*) and is a major destructive pathogen of members of the Fagaceae. Its introduction into the southeastern US has created a major complication to the planned introduction of chestnut blight-resistant American chestnut from chestnut restoration programs. In oaks, its northward expansion with global warming is already impacting oaks and other forest trees as part of the oak decline syndrome in North America and Europe [143–145]. Another *Phytophthora* species, *P. ramorum*, is responsible for sudden oak death on California oaks (primarily *Quercus agrifolia*, coast live oak, in the red oak subgenus *Erythrobalanus*) and the related tanoak species *Notholithocarpus densiflorus* in the Fagaceae family, as well as other plant species in the western US. Its impact is predicted to mount with increased microclimate variability that is associated with climate change [146–148].

Many different diseases affect white oaks, including canker rots [149,150], oak anthracnose [151,152], leaf blisters [153], stem canker [154], oak wilt [155], oak decline [156], and stem decay [150] (Figure 1I–P for *Q. alba* images). Of all these diseases, oak decline and oak wilt are the two most devastating, with major impacts on oak survival and acorn production, resulting in altered forest structure and composition over time. Several additional diseases and insects that are rarely fatal can also impact acorn production and are expected to increase as climate change advances [157]. These relevant pathogens and pests are tabulated below (Table 1). For a more comprehensive discussion of each, see the Supplementary Materials (File S1) on diseases and pests of *Q. alba*.

Table 1. Pests and pathogens of *Quercus alba*.

Disease	Pathogen/Pest	Relevant Classification	Key Features	*Q. alba* Resistance?	References
Oak wilt	*Bretziella fagacearum* (Bretz) (Microascales: Certocystidaceae) (formerly *Ceratocystis fagacearum*)	Ascomycete fungus Necrotrophic	Vascular wilt, vectored through root grafts and sap-feeding beetles Scolytidae and Nitidulidae.	Somewhat resistant, exhibiting slower fungal growth.	[158–174]
Oak decline	*Agrilus bilineatus* Weber and *Armillaria mellea* [Vahl. Ex Fr.] and *Phytophthora cinnamomi*	Coleptylebran beetle and oomycete hemibiotroph interaction.	Caused by the interaction between severely stressed trees, secondary pests, such as the two-lined chestnut borer, and root diseases like armillaria root rot and ink disease.	Less susceptible than other North American oak species and less severe in young (less than 70 years) and heterogenous stands.	[175–181]
Hypoxylon cankers	*Hypoxylon atropunctatum* (Schw. ex Fr.) Cke	Ascomycete fungus Necrotrophic	Less pathogenic fungal species that frequently accompanies dieback.	Live healthy unstressed trees less susceptible.	[179]
Root and crown rot	*Phytophthora cinnamomi*	Oomycete hemibiotrophic	Extirpated American chestnut and a component of oak decline.	White oaks less effected by this pathogen?	[140–148,157]
Anthracnose	*Dendrostoma leiphaemia* Senan. and K.D. Hyde *(formerly Discula quercina* (Westend.) Arx Anamorph of Ascomycete *Apiognomonia quercina.*	Ascomycete fungus hemibiotrophic	One of the most damaging leaf and twig diseases, impacting reproduction and masting; widespread across North America.	Leaves are less susceptible as they age due to thicker protective cuticle; large range of the pathogen across a variety of climates suggests adaptation to distinct climates	[151,155,182]
Twig, branch and rots cankers	*Botryosphaeria spp. (including B. rhodina* [Berk. and Curt.] von Arx, *B. dothidea* [Moug. ex Fr.] Ces. and de Not., *B. obtusa* [Schw.] Shoemaker, and *B. quercum* [Sch.: Fr.] Saccardo) and *Botryodiplodia gallae* (Schw.) Petrak and Sydow	Ascomycete fungus necrotrophic/hemi biotrophic?	Can play role in oak decline syndrome.	Most susceptible under drought or cold stress.	[183]
Spongy moth (formally gypsy moth)	*Lymantia dispar*	Lepidopteran insect	A significant insect pest of *Q. alba* forests, usually in low numbers but occasionally surges surging to severe outbreaks.	*Q. alba* is preferred over the hundreds of tree species spongy moth caterpillars feed on.	[184–192]
Acorn weevil	*Curculio* and *Conotrachelus* spp.	Coleopteran insect	The major oak seed predator and a factor in the reduced regeneration in the eastern United States.	Unknown.	[193–196]

6. Emerging Tools and Resources for White Oak Biology Research and Genetic Improvement

6.1. Genomics/Genetics

The high diversity in adaptive traits and genes and the rapidly growing genomic resources for oaks make them a model clade for the integration of population, evolutionary, and ecological research, such as association mapping (Genome-wide Association Analyses, GWAS), landscape genetics, population epigenomics, paleogenomics, and phylogenomics studies. High density genetic linkage maps and Quantitative Trait Locus (QTL) studies are important tools for the detection of chromosomal regions associated with adaptive trait variation for the validation of causal associations in GWAS and of outlier loci between ecologically contrasting populations.

Due to the great ecological importance of oaks as keystone tree species across many northern hemisphere forest ecosystems, genomic resources and their applications in research have been increasing rapidly (as recently reviewed by [197,198]). This is particularly true for the white oak section, *Quercus* (sometimes referred to as subgenus *Leucobalanus*), for which sequence-based genetic markers, high density genetic linkage maps, QTLs, transcriptome resources, and whole genome assemblies are available for multiple species. Recently, the development of genomic, transcriptomic, and experimental resources for the genus *Quercus* and their applications of these resources to population genomic analyses were reviewed [199]. Here, we describe the genomics and genetics tools and resources available for white oaks. Table S1 (Supplementary Materials) summarizes the state-of-the-art genomic/genetic resources for white oak species.

Oak Genetic Maps and Genomes

Before whole genome sequencing efforts became commonplace, studies of oak genomes focused on determining the total nuclear content, the number of chromosomes, and the ploidy. The Plant DNA C-value database [200] contains details for DNA content studies across 29 oak species, which found a relatively small genome size of 0.5 to 1.22 C(pg), equivalent to a haploid genome content of 489 Mb to 1193 Mb [201–207]. Chromosome characterization in 22 of those species found 12 haploid chromosomes in a diploid state, unusually consistent for a species-rich genus [202–207].

Despite the laborious and expensive process of oak breeding, which must contend with long generation times, huge space requirements and irregular masting, pedigreed populations have been developed and leveraged in order to generate several genetic maps using a variety of marker types. The two largest and most dense are the composite genetic map for *Q. robur* and *Q. petraea* with 4261 SNP (Single Nucleotide Polymorphism) markers across 742 cM [208] and the framework genetic map for *Q. rubra* with 849 SNP markers across 652 cM [209]. The composite genetic map for *Q. robur* and *Q. petraea* was assembled from five full-sib mapping families from controlled intra- and interspecific crosses. The families were previously validated using multi-allelic microsatellite markers [210,211]. A high-density composite map could be assembled due to the high collinearity between the maps for the two species [208]. By contrast, the *Q. rubra* mapping population and genetic linkage map were developed using the paternity exclusion approach, in which full-sibs are identified with DNA markers from open-pollinated progeny families from a pair of neighboring trees.

The *Q. robur* and *Q. petraea* high-density composite map has been used to identify genomic regions associated with the adaptive traits and signatures of selection across species [212]. The evaluation of markers showing segregation distortion suggested that male gametophytic selection may be serving as a pre-zygotic reproductive barrier, at least partially, between the species [199]. The high collinearity between *Q. petraea* and *Q. robur* crosses [208] and *Q. rubra* (Northern red oak) genetic maps [209] enables the comparative mapping of adaptive traits and the identification of conserved genomic regions important in the environmental adaptation between oak sub-sections. Lower density genetic maps and full-sib families have also been generated for QTL analyses in European white oaks for a variety of traits including late flushing [213,214], bud burst timing [213,215], height growth [213], leaf morphology [213,216], water use efficiency [217], stomatal density [212], response to waterlogging [218], seed production and seed mass [219], and branching traits [220]. Applications for genetic maps in oak species have been more extensively reviewed [199]. The colocation of QTL for the timing of vegetative bud burst [221] between oak and chestnut (*Castanea sativa* Mill.) indicates that the genetic architecture of important adaptive traits may be conserved, even at the family level in the Fagaceae.

The high-density *Q. robur* and *Q. petraea* composite gene-based linkage map was also used to anchor and order scaffolds in the *Q. robur* genome assembly [222]. Subsequently, the high-density linkage map [208] was used to determine the number and location of quantitative trait loci (QTLs) underlying variation in resistance to *Erysiphe alphitoides* and *P. cinnamomi* infections along with QTLs for phenology and height growth, followed by the identification of candidate genes by reference to the genome assembly [223]. Likewise, the *Q. rubra* genetic linkage map was used to validate Hi-C chromosome-level scaffolding and to choose the orientation of the chromosomes in the recently reported reference genome assembly for *Q. rubra* [224].

Recent technological advances have simultaneously accelerated the production and the quality of sequenced reference genomes. The earliest oak genomes emerged as short read assemblies at the scaffold level for *Q. robur* [225], *Q. lobata* [226], and *Q. suber* [227]. Improvements to the *Q. robur* genome resulted in the first chromosome scale genome for oaks [222]. Currently, eleven *Quercus* species have high-quality, chromosome scale genomes, most of which are from the past year (Table 2). Two of these, *Q. robur* [228] and *Q. glauca* [229], provide haplotype resolved assemblies, i.e., a complete genomic sequence for both chromosomes, assembled independently from a diploid individual. Neither has a peer-reviewed citation but both are in public repositories. The early estimates of genome size, chromosome number, and ploidy have been borne out by the sequenced genomes to date, which range in size from 733 Mb to 926 Mb. Furthermore, no whole genome duplication events have been found since the ancient γ hexaploidization event shared by core eudicots [222,226,230–232].

The comparative analysis of the *Quercus* genomes has revealed some strongly conserved genome patterns. Oak species analyzed thus far have high genome heterozygosity, ranging from 0.5% in *Q. lobata* to 2.15% in *Q. variabilis* [222,230–233]. Despite this nucleotide level heterozygosity within species, the overall chromosome scale structure is highly conserved between species with one-to-one correspondence of the 12 chromosomes and no large rearrangements that would block hybridization. In contrast, large gene family expansions and contractions are still occurring through prevalent genome-wide tandem duplication blocks [222,230–233]. Plomion et al. [222] and Sork et al. [233] provided an in-depth analysis of this phenomenon and found that these blocks may have anywhere from a few to dozens of genes, and preferentially contain gene families that are characteristic of disease resistance, especially the NBS-type and RLK-type. Plomion et al. [222] estimated that *Q. robur* had twice the proportion of R genes to total genes in comparison to other plant species with sequenced genomes. This led to the hypothesis that R gene expansion contributes to the long lifespan and broad niche occupation of oaks in general [222,233]. Complicating this hypothesis, the R gene complement was found to be greatly reduced in *Q. mongolica*, with one third to one half as many genes in the major R gene families (NBS-type, RLP-type, and RLK-type) as in *Q. lobata* and *Q. robur*. Further clade-wide research in the R gene family expansion and contraction would be intriguing, particularly if assessed in terms of oak radiation, speciation, and adaptation.

Table 2. Currently available genomes for *Quercus* species.

Species	Subgenus	Section	Year	Genome Size (Mb)	Contig N50 (Mb)	Protein Coding Genes	Public Availability	References
Q. rubra	Quercus	Lobatae	2022	733	1.9	33,333	Phytozome v2.1	[224]
Q. lobata	Quercus	Quercus	2022	844	1	41,714	NCBI v3.2, accession GCA_001633185.5	[226,233]
Q. robur	Quercus	Quercus	2022	789 (H1); 762 (H2)	16 (H1); 1.6 (H2)	41,871	NCBI dhQueRobu3.1, accessions GCF_932294415.1 for main assembly (H1) and GCA_932294425.1 for alternate assembly (H2)	[228]
Q. glauca	Cerris	Cyclobalanopsis	2022	903 (NCBI); 865 (Hap1 FS); 896 (Hap2 FS)	7.6 (NCBI); 7.9 (Hap 1 FS); 7.3 (Hap 2 FS)	37,460 (H1); 38,312 (H2)	Genome haplotype 1 (Hap1) assembly only available at NCBI Accession GCA_023736055.1. Assembly and annotation available at figshare (FS; https://figshare.com/articles/dataset/High-quality_haplotype-resolved_genome_assemblies_of_ring-cup_oak/20448339/1 (accessed on 28 November 2023)). There is discrepancy between the Hap1 in NCBI and FigShare; NCBI appears to have more unplaced scaffolds available.	[229]
Q. gilva	Cerris	Cyclobalanopsis	2022	890	28.3	36,442	Genome from NCBI GCA_023621385.1; gene annotation from FigShare (https://doi.org/10.6084/m9.figshare.20411082.v3 (accessed on 28 November 2023))	[230]
Q. mongolica	Quercus	Quercus	2022	810	2.4	36,553	Genome from NCBI accession GCA_011696235.1; annotation from figshare (https://figshare.com/articles/dataset/A_chromosome-scale_genome_assembly_of_the_Mongolian_oak_Quercus_mongolica_/11888118/2 (accessed on 28 November 2023))	[231]
Q. variabilis	Cerris	Cerris	2022	796	26	32,466	China National GeneBank DataBase accession CNP0003390. No gene sequences available, annotation provided as gff3.	[232]
Q. dentata	Quercus	Quercus	2023	894	4.2	31,584	Genome from NCBI GCA_028216015.1, gene annotation from FigShare https://doi.org/10.6084/m9.figshare.21624159.v1 (accessed on 28 November 2023). Genome and annotation available from China National GeneBank Database accession GWHBRAD00000000	[234]

Table 2. *Cont.*

Species	Subgenus	Section	Year	Genome Size (Mb)	Contig N50 (Mb)	Protein Coding Genes	Public Availability	References
Q. acutissima	Cerris	Cerris	2022	756	1.4	31,490	Genome Warehouse in National Genomics Data Center accession GWHBGBO00000000	[235]
Q. ilex subsp. ballota	Cerris	Ilex	2023	842.2	3.3	39,443	Genome from NCBI GCA_032727855.1; no annotation publicly available.	[236]
Q. aquifolioides	Cerris	Ilex	2022	957	1.2	26,441	Genome from NCBI GCA_019022515.1, no annotation available. Sequence data deposited in the CNGB Sequence Archive (CNSA, https://db.cngb.org/cnsa/) of China National GeneBank DataBase (CNGBdb) repository, accession number CNP0003530, CNP0002992	[237]

As many of these papers emerged during 2022, almost all compare their genome to the few earlier chromosome-scale assemblies, *Q. robur* and *Q. lobata*. The plethora of oak genomes, with more to come, opens new avenues for broad comparative genomics and evolution research across the entire clade. One potential difficulty for researchers is finding and downloading genomes. The genomes we found are not available in any central location; indeed, we had to visit five different online resources to find and download the genome assemblies and annotations: NCBI Assembly (mirrored by ENA and DDBJ [238], figshare [239], Phytozome [240], CNCB-NGDC Genome Warehouse (National Genomics Data Center, China National Center for Bioinformation [241], and CNGBdb (China National GeneBank DataBase [242]. Annotations were not available for three of the genomes, and one had no gene sequences, only a gene structure file (gff3 format). This presents a major challenge to researchers. There is no central repository to identify and download genomes, and, further, there is no enforcement of shared file structure or file completeness. This problem is not restricted to oaks or to plants in general; it is an international, clade agnostic problem that must be addressed through community demand, unified and enforced submission requirements by funders and journals, data sharing between databases, and stable funding for biocuration at community databases, such as TreeGenes [243], that host and curate genomic resources.

Genomics research in oak is providing unprecedented new resolutions to studies of evolution, adaptation, and speciation. Oaks are famously a "worst case scenario for the biological species concept" [244], with many sympatric species maintaining species identity while also continuing to hybridize, forming a syngameon [245]. Lazic et al. [197] offer a comprehensive review of adaptive divergence research, highlighting the ongoing efforts to characterize the genomic signatures of this seeming contradiction. Previous studies on red oaks in North America and white oaks in both Europe and North America have reported that, while sympatric oak species each have a unique, detectable genetic identity, gene-flow occurs at relatively high rates (9–20%) between sympatric species pairs. In fact, it appears that related oaks hybridize wherever species ranges overlap (e.g., [246–249]), resulting in strong regional signals of introgression [250,251]. Hybrids are generally restricted to contact zones between species where local distributions overlap, which permits species to remain genetically and ecologically distinct [252,253]. Alleles may nevertheless introgress beyond the margins of contemporary species overlaps [212,254], leading to interspecific gene flow between species with different local adaptations. Furthermore, hybridization can be detected even beyond closely related sympatric oak species, i.e., between oak phylogenetic sections. Zhou et al. [230] detected significant gene flow among 41% of 12 species pairs tested between sections *Quercus* (white oaks) and *Ponticae* (California oaks). Kremer and Hipp [26] also found evidence of past introgression between *Quercus* and *Ponticae* sections, and more broadly across the Fagaceae family. This evidence of gene flow and subsequent genomic introgression suggests that it has contributed to adaptation in the past and may be a key resource for future adaptation in the face of climate change. Gaining further understanding of the adaptive divergence through hybridization and introgression could be invaluable to addressing climate change. As species range shifts, new opportunities for genome shuffling may be necessary for adaptation and long-term survival in new ecological niches [199].

Mechanisms underlying the maintenance of the identity of species amid gene flow within syngameons are also under investigation. In addition to pre-zygotic isolation mechanisms [242,254–256], postzygotic isolation also plays a role in the maintenance of species identity under most environmental conditions (e.g., [257,258]). Genome-wide genetic patterns differentiating oak species with different local adaptations have been detected as signatures of selection in the face of gene flow. Genome regions of high interspecific differentiation, surrounded by regions with low differentiation, distributed across nine of the twelve chromosomes, have been observed when *Q. robur* and *Q. petraea* were compared via genome scanning [199,259–263]. Gailing et al. [199] pointed out that such patterns have been predicted by models of early stages of ecological speciation amid gene flow and strong divergent selection [262–264], as is the case for the interfertile species *Q. robur* and *Q. petraea*. Furthermore, Gailing et al. [199] noted that levels of adaptive trait and gene introgression may be related to the differences in adaptations to environmental conditions, such as drought adaptation between the red oak species *Q. rubra* and *Q. ellipsoidalis* [248,265].

Considering the extensive work in genomics of white oak species presented in Table S1, and the sequencing efforts shown in Table 1, surprisingly little has been reported for *Q. alba*, arguably the most important white oak species of eastern North American forests. To address the paucity of genomics research in *Q. alba*, recent private/public partnerships (White Oak Genomics Working group, UKY; White Oak Genetics Improvement Initiative, UKY) are focusing on building *Q. alba* genetics/genomics research infrastructure, integrated with a *Q. alba* breeding and improvement program. This group has recently completed a high-quality, haplotype resolved genome sequence for *Q. alba* that will underpin much of the future white oak genetics/genomics and tree improvement research (Staton personal communication).

6.2. Genetics and Tree Improvement

Traditionally, tree improvement programs are preceded by one or more provenance trials established at common locations (i.e., common gardens), using seeds from multiple known origins (i.e., provenances or seed sources). Forest tree populations (e.g., provenances) adapt through natural selection, migration, and phenotypic plasticity in response to environmental conditions [266–272], and these mechanisms can be assessed in provenance trials planted at common locations. When such provenance tests include seed sources and planting locations representing different geographic or ecological zones, information can also be inferred regarding the performance and expected resilience of trees to future climates [273–277]. For example, the measurement of the timing of bud flushing in common garden experiments that includes sampling across latitudinal and elevational gradients provides an ideal opportunity to investigate the potential impact of climate change on the tested species [278]. Furthermore, such trials can also be designed in a nested provenance/progeny test configuration which facilitates the evaluation and selection of parent trees (backward selection) or high-performing offspring (forward selection) in order to advance tree improvement.

Tree genetic improvement for long-rotation hardwoods, including the oaks, remains less developed than that for shorter-rotation tree species [279], such as pines (*Pinus*) and poplars (*Populus*). Savill and Kanowski [280] described tree improvement strategies for European white oaks, and numerous studies have examined genetic variation patterns for some of these species (e.g., [281,282]). Most *Q. alba* genetic research has also focused on population structure [268,283,284], speciation and taxonomy delineation, or the quantification of variation for a variety of traits (e.g., [34,194,285–289]).

Quercus alba Tree Improvement

An assessment of early *Q. alba* tree improvement goals and activities in the US was summarized by Steiner [9], along with the prediction that few would ultimately be impactful without the deliberate steps to transfer genetic gains from seed orchards to operational plantations. This prediction was later substantiated in a review of forest genetics and tree improvement research in the US [289]. Provenance trials for *Q. alba* have been limited in scope and number, however, they have included only partial coverage of the natural range due to research objectives and practical limitations associated with the rarity of masting (wide-spread seed production) and lack of seed dormancy. Two examples are known—both sampling several provenances from multiple states [271,290,291], although representing relatively local (sub-regional) areas. The studies showed minor variation at the provenance level in the common garden plantings while demonstrating the potential for early selection (<10 years) on height growth.

The University of Tennessee Tree Improvement Program (http://treeimprovement.utk.edu/), established in 1959, includes the development of *Q. alba* seed orchards based on results from multiple progeny trials conducted at locations across Tennessee, US, some of which have progressed through 2–3 generations [290,292,293]. Most recently, the White Oak Genetics and Tree Improvement Program (WOGTIP) was initiated in 2019 in the Department of Forestry and Natural Resources at the University of Kentucky, in partnership with the USDA Forest Service, Southern Research Sation, in order to provide a sustainable supply of high-quality *Q. alba* seeds and seedlings to support the conservation, restoration, and management of *Q. alba* throughout the species range [294].

The WOGTIP is a collaborative project being conducted in three phases: (1) the collection of acorns and scions on a range-wide basis; (2) progeny testing at multiple sites across the range to identify parent trees that produce high-quality offspring; and (3) the development of seed orchards for acorn production and seedling deployment. The WOGTIP represents the only known effort to establish a range-wide provenance study of *Q. alba* [294]. The seed and scion collection effort has been highly successful due to the participation of volunteers from federal and state agencies, academic institutions, NGOs, woodland owners, and citizen volunteers. To date (2023), seeds have been collected from over 500 mother trees and a network of over 25 regional progeny tests have been planted. The scions collected from the mother trees are being grafted to create a clone bank; this will conserve genetic material for the establishment of seed orchards following parental selection, based on progeny performance in the nursery and field tests (Figure 1S).

In addition to the tree improvement specific objectives, the WOGTIP range-wide provenance test and regional progeny trials will provide research materials for the genetic assessment of important climate relevant traits, including stem growth rate, stem dieback, apical dominance, epicormic branching, crown architecture, spring and fall phenology, early flowering, and viable seed yield. The design of the studies will allow for quantitative genetic estimates of heritability, genetic correlations, and genotype–environment interaction, as well as genotype–phenotype–environment association analyses that can be used to develop seed source transfer tools for mitigating climate change. The provenance test and progeny trials will also provide a rich source of materials for studies of hybridization and introgression between *Q. alba* and other co-occurring white oaks across the range, including chinkapin, swamp white, chestnut, and/or post oak species for which the trial seedling leaf morphologies suggest are occurring in areas of the *Q. alba* range where other species overlaps occur.

6.3. Biotechnologies (Propagation, Tissue Culture, Transgenics)

6.3.1. Oak Propagation

The ability to vegetatively propagate individual genotypes is critical for establishing clonal seed orchards for tree improvement (Figure 1E) and for simplifying the interpretation of results from genetics, genomics, physiological, and other oak biology studies. In addition to the propagation of oaks from somatic embryos, there are several reports on the successful vegetative propagation of oak species using stem propagation from coppiced trees (reviews: [295–297]), in which hedge orchards could be used for clonal propagation, in addition to seed orchards (Figure 1E,S). Further development of rapid, inexpensive, genotype-neutral stem propagation techniques for *Q. alba* and other oak species are essential to the basic study of climate critical trait biology and for oak improvement programs and should be a priority for future research efforts with white oak.

6.3.2. Transgenic Oaks

Transgene technologies applied to forest trees have a dual purpose: (1) they enable the testing of candidate genes for traits critical as breeding targets, and (2) they provide a direct means to engineer traits in order to meet difficult-to-reach tree improvement goals, such as resistance to an introduced, invasive pathogen or pest. In the case of oaks, there have been several reports of success in the application of these technologies.

Successful *Agrobacterium tumefacians*-mediated transformation has been demonstrated in cork oak, *Q. suber*, by Alvarez et al. [298] and Sanchez et al. [299] with embryogenic cultures, and also by Alvarez et al. [300] with embryogenic masses containing the bar gene from *Streptomyces hygroscopicus*; similar results have been shown with *Q. robur* embryogenic tissues by Vidal et al. [301]. Subsequently, Mallon et al. [302] demonstrated the successful *A. tumefacians*-mediated transformation of *Q. robur* embryogenic tissue with a chestnut thaumatin-like protein gene, CsTL1, that had been shown to confer resistance to fungal pathogens in chestnuts [303]. In this report, they also demonstrated the subsequent regeneration of transgenic plants expressing the transgene. Similarly, Cano et al. [304] demonstrated the successful transformation and regeneration of Holm oak (*Q. ilex*) with the same CsTL1 gene from chestnuts. More recently, Serrazina et al. [305] demonstrated the successful *A. tumefacians*-mediated transformation of *Q. ilex* with the Ginkbilobin-2 homologous domain gene (Cast_Gnk2-like), which had previously been shown to exhibit antifungal activity [306]. The in vitro analysis of the transgenic plants demonstrated some resistance to the *P. cinnamomi* as judged by increased time post-inoculation to plant death of transgenic plants when compared to controls.

6.3.3. Transgenic *Quercus alba*

Progress has been made in the application of in vitro techniques for the propagation of *Q. alba* and other North American oaks which are notoriously difficult to propagate vegetatively. This prompted investigations into in vitro propagation. Sources and developmental stages of explant tissues were determined to be of primary importance in the successful initiation of somatic embryogenesis (SE) cultures for trees, including *Q. alba* [307–309], Merkle, pers. comm.). Highly productive *Q. alba* embryogenic cultures were obtained from immature seed explants. Somatic embryos were produced from the cultures and somatic seedlings were regenerated from them following a pre-germination cold treatment and culturing on basal WPM with activated charcoal in a lighted incubator. The somatic seedings continued growth following the transfer to ex vitro conditions (Figure 3; Merkle, unpublished). The establishment of prolific shoot cultures from forced shoots of six-to-seven-year-old trees was reported as an efficient means of micropropagation for *Q. alba*, *Q. bicolor*, and *Q. rubra*, albeit genotype-dependent [309]. This led to success, as reported by Corredoira et al. [310], in obtaining somatic embryogenesis and plant regeneration from shoot apices and leaf explants of shoot cultures derived from *Q. alba* trees. SE rates varied from 0 to 50%, depending on the explant source and genotype. These approaches using shoot explants represented a break-through in providing true clonal propagation of the donor genotype, thus avoiding genetic recombination at the seed embryo stage. It is expected that *Agrobacterium*-mediated transformation systems based on binary plant expression vectors and inducible gene constructs should be adaptable to *Q. alba* transformation, as successfully tested in chestnut [311], poplar [312], *Arabidopsis* [313], and other systems. The AlcR/alcA system exhibits little or no basal expression in plants and permits the rapid, reversible induction of transgene expression [312,314].

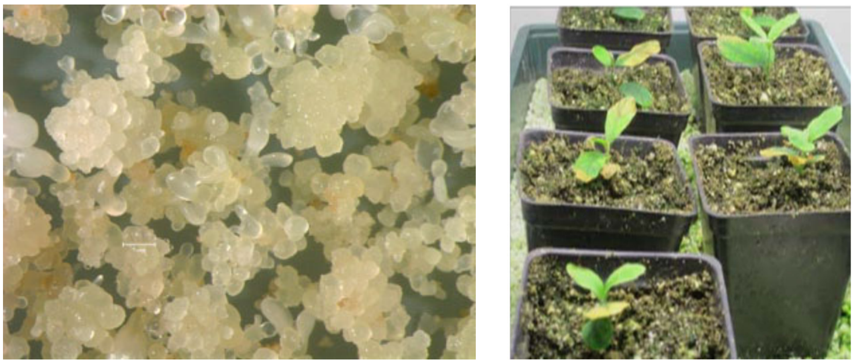

Figure 3. Embryogenic *Q. alba* culture (**left**) and *Q. alba* somatic seedlings (**right**). (courtesy S. Merkel).

6.4. Phenomics Field Scale Technologies for Oak Research

A critical need exists for determining the genomic/genetic underpinnings controlling phenotypic traits that affect key life-cycle processes of the oak forest, including regeneration, recruitment, and growth dynamics. Relying entirely on traditional common garden testing for phenotyping will extend tree improvement timelines by several decades. A field and forest-scale tree phenotyping platform would facilitate identifying and measuring key traits of white oaks in natural regeneration landscapes as well as planted field trials. This phenotypic information can then be integrated with existing and emerging genomics resources for white oak in order to track critical traits in white oak improvement programs, white oak forest management, and future reforestation initiatives.

Quadcopter drones offer an exceptional platform for conducting remote sensing over large plantations and forested areas with limited personnel. Drone-based sensors are already in widespread use for forest health monitoring and tree phenotyping [315,316]. The capabilities of these sensors and accompanying analyses characterize many aspects of tree physiology and above-ground anatomy. Individual tree segmentation and species identification are possible from both drone-based imagery and drone-based Light Detection and Ranging (LiDAR) [317–319]. Near-infrared (NIR), wide-infrared, and RGB sensors can be used to effectively measure tree water stress via various indices, such as the Normalized Difference Vegetation Index (NDVI) [320,321]. With the aid of machine-learning algorithms, both hyperspectral imagery and LiDAR accurately estimate tree height and Diameter at Breast Height (DBH) [321–323].

Several examples of studies focused specifically on the remote sensing of North American oak species have been published in the last few years. Mazis et al. [324] used hyperspectral imagery in a high-throughput plant phenotyping (HTPP) setting to assess biophysical traits and drought response in two white oak section species: swamp white oak, *Quercus bicolor*, and dwarf chestnut oak, *Quercus prinoides*. Using hyperspectral images, the study calculated 12 vegetation indices (VIs) and found that Vogelmann and Maccioni indices had the greatest potential for assessing oak seedling performance and health in drought conditions. These findings provide a ground-truthed method for rapid phenotyping that could be tested in white oak using drone-based hyperspectral sensors.

An additional study focused on oak wilt disease, which significantly threatens oak-dominated forests in the Eastern US. Sapes et al. [325] assessed the use of visible near-infrared (VNIR) and short-wave infrared (SWIR) in the detection of oak wilt and developed a stepwise approach to distinguish red oaks, *Q. rubra*, from other species in the canopy, and to also distinguish infected from uninfected red oaks. This study provides a framework for the future studies of oak wilt disease identification in white oaks. The combination of drone-based remote sensing, proximal hyperspectral sensing, and machine learning offers transformative potential in oak phenomics. These technologies enable efficient, large-scale phenotypic data collection, critical for elucidating genotype–phenotype relationships in a field progeny test or forest setting.

7. Conclusions and Perspectives

This review has taken a broad look into the research that has provided our current understanding of the biology of oaks, with a focus on *Q. alba*, from its natural history, phylogenetic placement, and ecological role as a keystone species, to the biotic and abiotic challenges facing the species. In addition, we have identified genomic, genetic, and biotechnology resources and tools that are providing new insights into the physiology of adaptive traits of *Q. alba* and a renewed potential for tree improvement to contribute to the performance metrics in forest management. Although species in the North American and Eurasian white oak clade have been the subject of research by silviculturists, forest ecologists and geneticists, and tree physiologists and pathologists for decades, an integration of the knowledge gained and tools developed across these disciplines is needed to develop the silvicultural practices required to assure the sustainability of *Q. alba* through improved regeneration and recruitment, increased resistance and tolerance to invasive pathogens and pests, and enhanced resilience to abiotic stress as induced by climate change.

If we are to answer yes to the title of our review, many small steps will be needed, adding to the knowledge base distilled here and leveraging the available technologies and resources discussed. To start, reliable regeneration and recruitment, no small thing, are necessary to provide the acorns that will develop into tall oaks. In the near-term given shortages in the smaller age classes of *Q. alba* and climate change mandates to mitigate and adapt, large numbers of seedlings will need to be planted across and within various sites and silvicultural prescriptions. Ensuring high-quality planting stock, both physiologically through nursery production and outplanting, and genetically though appropriate and improved seed sources, will be the first steps. The traits discussed here will need to be studied, managed, and improved in the *Q. alba* populations selected for future environments. The following challenges will need to be met in order to facilitate the study, management, and improvement of the traits required for the successful regeneration and recruitment and adaptation to climate change: (1) the development of forest-/field-scale phenomics platforms to link genes to traits; (2) the development of robust gene testing platforms and transformation technologies, (e.g., Crisper/CAS); (3) the development of efficient plant propagation protocols for germplasm preservation and experimental analyses; (4) the establishment of provenance/progeny trials for forest/field-scale analyses; (5) the development of methods to reduce the juvenility period, enabling rapid breeding and early seed production; (6) the development and production of genetically improved seed and high-quality seedlings for tree planting efforts; and (7) the development and broad-scale implementation of genetically informed, ecologically sound, and climate forward silvicultural practices for tree planting and early stand development.

Beyond *Q. alba* per se, we are in a period of climate crisis that is driving several mitigation approaches such as numerous broadscale worldwide tree planting initiatives [326–331]; however laudable these activities are, there is a danger of putting large numbers of trees on the landscape without any consideration of the longer-term consequences, including initial survival, competition control and early stand development, fire, and other environment risks. This potential "Band-Aid approach" can lead to even greater problems. The need for the large-scale reforestation of *Q. alba* and other forest tree species is a problem that requires solutions supported by experimental knowledge (e.g., as generated from the WOGTIP and working to overcome the challenges described above) integrated from multiple disciplines, including silviculture, soils, ecology, physiology, genetics, and climatology in order to ensure that these new forests continue to survive and produce tall trees, including oaks, in a future planetary environment that will be potentially quite different from the one today.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f15020269/s1, Table S1: An annotated listing of genetic and genomic resources for white oak species (genus *Quercus* subgenus *Quercus* section *Quercus*) is provided, with references [332–347], as supplemental Excel file "Table S1: White oak genomic/genetic resources". The supplemental file contains separate worksheets for Microsatellite (simple sequence repeat) DNA markers ('SSRs'), Single Nucleotide Polymorphism DNA markers ('SNPs'), Quantitative Trait Loci ('QTLs'), Expressed Sequence Tags ('ESTs'), nuclear genome assemblies ('nGenomes'), and chloroplast genome assemblies ('cpGenomes'). The spreadsheets are organized by species and by publication date, from earliest to latest. Additional information includes numbers of markers and sources of sequence data; Supplementary File S1: Pests and Diseases background information (References [122,152,158–175,177–196,348,349] are cited in File S1).

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