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Review / Revisión

Transcriptomics in oaks (Fagaceae; *Quercus*): A comprehensive review of advances, biases, and future directions

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Abstract

Oak species (*Quercus* genus) are highly diverse and pivotal in temperate forest ecosystems. Given their significant ecological and economic value, their management and conservation are crucial. In addition to their importance, oaks have emerged as non-classical models for integrating studies in genetics, ecology, and evolution, increasingly explored through modern "omics" approaches. The transcriptome encompasses the set of RNA molecules expressed in a cell or tissue under specific conditions, representing the active portion of the genome. Transcriptomics offers comprehensive insights into cellular regulatory systems and gene activity by investigating RNA profiles. Here, we present a comprehensive review of transcriptomics studies in oaks, analyzing 124 studies categorized into four primary research areas: (1) abiotic stress, (2) biotic interactions, (3) cork formation, and (4) somatic embryogenesis. These studies were conducted on 26 oak species, with *Q. robur*, *Q. suber*, *Q. ilex*, and *Q. petraea* being the most frequently studied. The Quercus *sensu stricto* section was the best-represented taxonomic group. Our analysis highlights significant geographic and species biases, with Mexican oak species—despite representing a biodiversity hotspot—notably absent from the literature. This underscores the urgent need for broader research efforts to include underrepresented species and regions, particularly given their evolutionary and ecological significance.

Keywords: *Quercus*, transcriptomics, gene expression, RNASeq.

Resumen

Las especies de encino (género *Quercus*) son muy diversas y fundamentales en los ecosistemas forestales templados. Debido a su importante valor ecológico y económico, su manejo y conservación son cruciales. Además de su importancia, los encinos se han convertido en modelos no clásicos para integrar estudios de genética, ecología y evolución, siendo explorados cada vez más mediante enfoques ómicos modernos. El transcriptoma engloba el conjunto de moléculas de ARN expresadas en una célula o tejido en condiciones específicas y representa la porción activa del genoma. La transcriptómica ofrece conocimientos completos sobre los sistemas reguladores celulares y la actividad genética mediante la investigación de perfiles de ARN. Aquí, presentamos una revisión exhaustiva de estudios transcriptómicos en encinos, analizando 124 estudios categorizados en cuatro áreas de investigación principales: (1) estrés abiótico, (2) interacciones bióticas, (3) formación de corcho y (4) embriogénesis somática. Estos estudios se realizaron en 26 especies de encinos, siendo *Q. robur*, *Q. suber*, *Q. ilex* y *Q. petraea* las más estudiadas. La sección Quercus *sensu stricto* fue el grupo taxonómico mejor representado. Nuestro análisis destaca importantes sesgos geográficos y de especie, con las especies de encino mexicano, a pesar de representar un punto crítico de biodiversidad, notablemente ausentes en la literatura. Esto subraya la urgente necesidad de ampliar los esfuerzos de investigación para incluir especies y regiones subrepresentadas, especialmente dada su importancia evolutiva y ecológica.

Palabras clave: *Quercus*, transcriptómica, expresión génica, RNASeq.

The term transcriptome was coined in 1996 by Charles Auffray (Piétu *et al*. 1999) and refers to the group of RNA molecules expressed in each cell or tissue at a particular time and condition, representing the transcribed portion of the genome (Morozova *et al.* 2009, Wolf 2013). In this context, transcriptomics is the study of all RNA-related aspects, providing an overview of the cell's genetic content and regulatory systems. Its usefulness lies in enabling fine-tuned analyses of gene expression patterns across different organisms in response to environmental changes (Yadav *et al.* 2018). Transcriptome studies commonly rely on EST (Expressed Sequence Tag)-based methods, SAGE (Serial Analysis of Gene Expression), hybridization-based microarrays, RT-qPCR (Real-Time Quantitative PCR), and RNA-Seq (RNA Sequencing) approaches. RNA-Seq, an untargeted technique also known as whole-transcriptome sequencing, is coupled with Next Generation Sequencing (NGS) and stands out as the most promising tool for studies of forest tree adaptation (Neale & Kremer 2011).

It allows for the assessment and quantification of differentially expressed genes under contrasting environmental conditions (Ekblom & Galindo 2011) and the detection of previously unidentified genes and splice variants (Wang *et al.* 2009). In addition, RNA-Seq enables dual transcriptome analyses of endogenous pathogenic organisms and their hosts, providing insights into pathogen action (Westermann *et al.* 2012, Liu *et al.* 2013, Hayden *et al.* 2014, Kovalchuk *et al.* 2019, Zamora-Ballesteros *et al.* 2021), as well as studies on symbiotic interactions, such as those involving fungal endophytes or ectomycorrhizas (Tarkka *et al.* 2013, Sebastiana *et al.* 2014, Tang *et al.* 2021). In recent years, the increasing availability and decreasing cost of NGS technologies have revolutionized the study of numerous aspects of genome function, leading to a rapid increase in the number of published tree genomes and a significant expansion of transcriptome studies.

Temperate forest ecosystems in the northern hemisphere represent 26 % of the world's forest cover and are mainly dominated by two families: Pinaceae (gymnosperms) and Fagaceae (angiosperms) (Keenan *et al.* 2015, Ritters *et al.* 2016). The Fagaceae family includes the genera *Castanea* (chestnuts), *Fagus* (beeches), and *Quercu*s (oaks), among others, with species recognized as keystone elements due to their essential role in maintaining biodiversity and providing forest resources such as biomass, wood products, fiber, and food, as well as serving as patrimonial and cultural resources (Kremer *et al.* 2012). Beyond their high ecological and economic relevance, the *Quercus* species are increasingly studied as non-classical models integrating genetics, ecology, and evolution, particularly by modern "omics" approaches such as genomics, transcriptomics, proteomics, and metabolomics (González-Martínez *et al.* 2006, Staszak & Pawlowski 2012, Petit *et al.* 2013).

Within the genus *Quercus*, approximately 469 species have been described (Cavender-Bares 2019, Wang *et al.* 2023c), with two regions standing out as hotspots of oak diversity: East Asia, with approximately 125 species, and Mexico, with 161 species. Notably, in Mexico, 109 of these species are endemic (Valencia-A 2004, Menitsky 2005, Nixon 2006). Oak species play key roles in ecosystem functioning by supporting biodiversity, sequestering carbon, and contributing to water and soil conservation. Their extensive root systems help prevent soil erosion, stabilize hillsides, and promote underground water storage, while leaf litter and decomposing trees fertilize soils, facilitating the growth and survival of other plant species (Wang *et al.* 2023c). For these reasons, oaks are considered among the most critical woody species in terms of diversity, ecological importance, dominance, and economic value, with research on them increasingly focusing on molecular approaches.

Despite this growing attention, only seven oak species currently have published whole-genome sequences: *Q. robur* L. (Plomion *et al.* 2016, 2018), *Q. lobata* Née (Sork *et al.* 2016, 2022), *Q. suber* L. (Ramos *et al.* 2018), *Q. acutissima* Carruth (Fu *et al*. 2022, Liu *et al*. 2022), *Q. mongolica* Fisch. Ex Ledeb. (Ai *et al*. 2022), *Q. ilex* L. (Rey *et al*. 2023), and *Q. variabilis* Blume (Wang *et al.* 2023a) (Table 1). Transcriptomes are a valuable genomic resource for studies in species for which genome sequences are not available, because they are smaller and less complex than genomes. Given this context, the present work aims to provide a comprehensive review of oak transcriptomics. To achieve this, a literature search of transcriptomics studies in oaks was conducted covering the period from 1996, when the term transcriptome was first introduced, to December 2024 (Figure 1). The Web of Science (www.webofscience.com) database was used with the following keywords: "gene expression analysis

and *Quercus*," "transcriptomics and *Quercus*," "transcriptomics and oaks," "transcriptome and *Quercus*," "differential gene expression analysis and *Quercus*," and "RNASeq analysis and *Quercus*." Reviews and opinion papers were excluded from the analysis.

Table 1. Assembly statistics of the whole-genome sequencing of *Quercus spp.*

Quercus spp	Section	Genome size (Mb)	Contig N50 (Mb)	Repetitive Sequences (%)	Protein-Coding Genes
Q. robur	*Quercus*	814.3	1.35	53.30	25,808
Q. lobata	*Quercus*	845.9	0.97	54.00	39,373
Q. suber	*Cerris*	953.3	0.81	11.96	33,658
Q. acutissima	*Cerris*	957.1	1.2	55.63	29,889
Q. mongolica	*Cerris*	809.8	2.64	53.75	36,553
Q. ilex	*Cerris*	842.2	3.3	53.00	39,443
Q. variabilis	*Cerris*	788.7	6.4	54.24	36,830

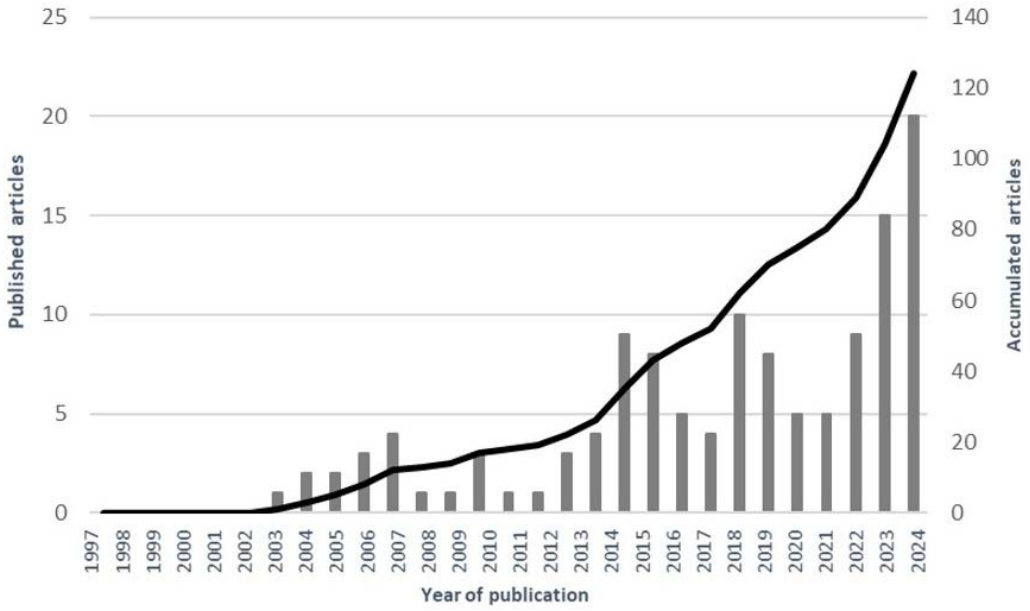

Figure 1. Transcriptomics studies of *Quercus spp.* published per year. Source: Author´s own elaboration.

Development of transcriptomics studies in oaks

Transcriptomics studies have been carried out on 26 oak species, with the Quercus *sensu stricto* section being the most represented group, alongside two studies focusing on hybrids (*Q. cerris* × *Q. suber* and *Q. ilex* × *Q. suber*) (Table 2). The most studied species to date are *Q. robur*, *Q. suber*, *Q. ilex*, and *Q. petraea* (Matt.) Liebl., followed by *Q. variabilis*, *Q. mongolica*, *Q. rubra* L., *Q. pubescens* Willd., and *Q. fabri* Hance. Most research efforts have concentrated on oak species distributed across Europe and Asia, with only eight studies addressing American oaks from the United States and Canada. Notably, Mexican oak species are completely absent from the current transcriptomic literature, despite the country's recognized role as a major center of oak diversity.

Table 2. Transcriptomics studies carried out on *Quercus* can be grouped into ten main thematic categories: 1) abiotic stress; 2) biotic interactions; 3) bud phenology; 4) somatic embryogenesis; 5) cork formation; 6) growth and development -including studies on acorn, flower, and root development; 7) methodology development- such as RNA extraction protocols, de novo transcriptome assembly, sequencing platform comparisons, candidate gene identification, and SSR marker development; 8) evolutionary processes -including divergent selection, introgression, and hybridization; 9) leaf coloration and senescence; and 10) fruit quality, particularly related to tannin content.

Quercus spp	**Section**	**Distribution**	**Study objective**	**Technique/Assay**	**Reference**
Q. aliena Blume	Quercus	Asia	Leaf senescense	RT-qPCR	Yang *et al.* 2022
			Somatic embryogenesis	RT-qPCR	Yang *et al.* 2024b
			Tannin evolution	RNA-Seq/RT-qPCR	Yang *et al.* 2024a
Q. acutissima Carruth	Cerris	Asia	Drought stress	RNA-Seq/RT-qPCR	Kim *et al.* 2024
			Acorn size	RT-qPCR	Byeon *et al*. 2024
Q. austrocochinchinensis Hickel & A. Camus	Cyclobalanopsis	Asia	De novo transcriptome assembly/Development of SSR markers	RNA-Seq	An *et al.* 2016
Q. berberidifolia Liebm.	Quercus	California	Hybridization and adaptive introgression	RNA seq	Oney-Birol *et al.* 2018
Q brantii Lindl.	Cerris	Asia	Oak decline	RNA-Seq	Safari *et al.* 2022
Q. cerris x suber hybrids			Cork formation	RT-qPCR	Meireles *et al.* 2018
Q. cornelius-mulleri Nixon *et* K.P.Steele	Quercus	California	Hybridization and adaptive introgression	RNA-Seq	Oney-Birol *et al.* 2018
Q. dentata Thunb	Quercus	Asia	Leaf color transition	RNA-Seq	Wang *et al.* 2023b
			Heavy metals stress	RT-qPCR	Zhang *et al.* 2023
			Tannin evolution	RNA-Seq/RT-qPCR	Yang *et al.* 2024a
Q. engelmanii Greene	Quercus	California	Hybridization and adaptive introgression	RNA-Seq	Oney-Birol *et al.* 2018
Q. fabri Hance	Quercus	Asia	Shoot branching	RNA-Seq/RT-qPCR	Xiong *et al.* 2023
			Tannin synthesis	qRT-PCR	Cai *et al.* 2024
			Tannin biosynthesis	RT-qPCR	Wu *et al.* 2024a
			Tannin biosynthesis	RNA-Seq/RT-qPCR	Wu *et al.* 2024b
Q. garryana Douglas ex Hook.	Quercus	North America	De novo transcriptome assembly/Divergent selection	RNA-Seq	Cokus *et al.* 2015

Quercus spp	**Section**	**Distribution**	**Study objective**	**Technique/Assay**	**Reference**
Q. ilex L.	Cerris	Europe	Heat stress	RACE-PCR	Fischbach *et al.* 2003
			De novo transcriptome assembly	RNA-Seq	Guerrero-Sánchez *et al.* 2017
			Cork formation	RNA-Seq	Boher *et al.* 2018
			Phytophtora cinnamomi infection	RT-qPCR	Gallardo *et al.* 2019
			Protocol optimization	RNA-Seq	López-Hidalgo *et al.* 2018
			Salt and ozone stress	RNA-Seq	Natali *et al.* 2018
			Drought stress	RT-qPCR	Rodríguez-Calcerrada *et al.* 2018
			Comparing illumina and Ion Torrent sequencing platforms	RNA-Seq	Guerrero-Sánchez *et al.* 2019
			Drought stress	RT-qPCR	Kotrade *et al.* 2019
			Drought stress	RNA-Seq	Madritsch *et al.* 2019
			Drought stress	RNA-Seq	Guerrero-Sánchez *et al.* 2021
			Phytophtora cinnamomi infection	qPCR	Morcillo *et al.* 2022
			Drought stress	RT-qPCR	Gori *et al.* 2023
			Cork formation	RNA-Seq/RT-qPCR	Armendariz *et al.* 2024
Q. ilex x suber hybrids			Cork formation	RNA-Seq/RT-qPCR	Armendariz *et al.* 2024
Q. infectoria G. Olivier	Cerris	Asia/Europe	De novo transcriptome assembly / Secondary metabolites medically important	RNA-Seq	Joudaki *et al.* 2023
Q. kerrii Craib.	Cyclobalanopsis	Asia	De novo transcriptome assembly / Development of SSR markers	RNA-Seq	An *et al.* 2016
Q. liaotungensis Koidz.	Quercus	Asia	Divergent selection	RNA-Seq	Sun *et al.* 2018
			Drought stress	RNA-Seq	Wang & Qin 2021

Quercus spp	**Section**	**Distribution**	**Study objective**	**Technique/Assay**	**Reference**
Q. lobata Née	Quercus	California	Divergent selection	RNA-Seq	Cokus *et al.* 2015
			Drought stress	RNA-Seq	Gugger *et al.* 2017
			Drought stress	RNA-Seq	Mead *et al.* 2019
Q. macrocarpa Micchx.	Quercus	North America	Water transport	RT-qPCR	Voicu *et al.* 2009
Q. mongolica Fisch. ex Ledeb.	Quercus	Asia	Divergent selection	RNA-Seq	Sun *et al.* 2018
			Response to different cultivation practices	RNA-seq	Jiang *et al.* 2022
			Abiotic stress (cold, salt, drought, light and heavy metals)	RT-qPCR	Zhan *et al.* 2022
			Growth/development/local adaptation	RNA-Seq/RT-qPCR	Li *et al.* 2023
			Abiotic stress (cold, salt, drought, light)	RT-qPCR	Zhan *et al.* 2023
			Light stress	RNA-Seq/RT-qPCR	Li *et al.* 2024
			Leaf color	RNA-Seq/RT-qPCR	Yuan *et al.* 2024
Q. palustris Münchh.	Lobatae	North America	Drought stress	RNA-Seq/RT-qPCR	Kim *et al.* 2024
Q. petraea (Matt.) Liebl.	Quercus	Europe	Flooding	RACE-PCR /RT-PCR	Folzer *et al.* 2005
			Osmotic stress	Substractive hybridization/qPCR	Porth *et al.* 2005
			Bud development	SSH (suppression subtractive hybridization) libraries Macroarray / RT-PCR	Derory *et al.* 2006
			Flooding	Norther blot hybridization	Folzer *et al.* 2006
			Osmotic stress	EST	Porth *et al.* 2006
			EST catalogue of candidate genes	Sanger sequencing (Sanger EST) / pyrosequencing	Ueno *et al.* 2010

Quercus spp	**Section**	**Distribution**	**Study objective**	**Technique/Assay**	**Reference**
			Waterlogging	RT-qPCR	Le Provost *et al.* 2012
			Bud dormancy	RNA-Seq	Lesur *et al.* 2015
			Waterlogging	RT-qPCR	Rasheed-Depardieu *et al.* 2015
			Waterlogging	RNA-Seq	Le Provost *et al.* 2016
			Drought stress	RNA-Seq/RT-qPCR	Le Provost *et al.* 2022b
			Waterlogging/Drought stress	RNA-Seq/RT-qPCR	Le Provost *et al.* 2022a
			Bud phenology	RNA-Seq/RT-qPCR	Le Provost *et al.* 2023
Q. pubescens Willd.	Quercus	Europe	De novo transcriptome assembly	RNA-Seq	Torre *et al.* 2014
			Drought stress	RT-qPCR	Kotrade *et al.* 2019
			Drought stress	RNA-Seq	Madritsch *et al.* 2019
			Drought stress	RNA-Seq	Mevy *et al.* 2020
Q. robur L.	Quercus	Europe	Embryo development	Northern blot	Sunderlíková & Wilhelm *et al.* 2002
			Maturation process	Northern blot	Gil *et al.* 2003
			Pre-mycorrhizal interactions / *Piloderma croceum*	Northern hybridization /RT-qPCR	Krüger *et al.* 2004
			Pre-mycorrhizal interactions / *Piloderma croceum*	RT-qPCR	Frettinger *et al.* 2006
			Pre-mycorrhizal interactions / *Piloderma croceum*	RT-qPCR	Frettinger *et al.* 2007
			Osmotic stress	Substractive hybridization/qPCR	Porth *et al.* 2005
			Osmotic stress	EST	Porth *et al.* 2006
			Seed response to water stress	In situ hybridization	Sunderlíková *et al.* 2009a
			Embryogenesis /seed development	Northern blot / In situ hybridization	Sunderlíková *et al.* 2009b
			EST catalogue of candidate genes	Sanger sequencing (Sanger EST) and pyrosequencing	Ueno *et al.* 2010

Quercus spp	Section	Distribution	Study objective	Technique/Assay	Reference
			Waterlogging	RT-qPCR	Le Provost *et al.* 2012
			Drought stress	Microarrays	Spieß *et al.* 2012
			Oak pest *Tortrix Viridiana*	RNA-Seq	Kersten *et al.* 2013
			Ectomycorrhizal interaction / *Piloderma croceum*	RNA-Seq	Tarkka *et al.* 2013
			Ectomycorrhizal interaction / *Piloderma croceum* /	RNA-Seq	Herrmann *et al.* 2015
			Ectomycorrhiza formation / mycorrhiza helper bacteria *Streptomyces sp.*	RNA-Seq/RT-qPCR	Kurth *et al.* 2015
			Bud dormancy	RNA-Seq	Lesur *et al.* 2015
			Resistance / tolerence to fungi diseases	RT-qPCR	Mallón *et al.* 2014
			Waterlogging	RT-qPCR	Rasheed-Depardieu *et al.* 2015
			Waterlogging	RNA-Seq	Le Provost *et al.* 2016
			Plant- parasitic nematode	RNA-Seq	Maboreke *et al.* 2016
			Root herbivory (*Melolontha hippocastani*)	RT-qPCR	Creyaufmüller *et al.* 2018
			Ectomycorrhizal interaction (*Piloderma croceum*)	RNA-Seq	Graf *et al.* 2019
			Drought stress	RT-qPCR	Kotrade *et al.* 2019
			Drought stress	RNA-Seq	Madritsch *et al.* 2019
			Ectomycorrhizal and orchid mycorrhizal interaction	RNA-Seq/RT-qPCR	Bouffaud *et al.* 2020
			Drought stress	RT-qPCR	Trudic *et al.* 2021
			Root growth	RNA-Seq/RT-qPCR	Koscielniak *et al.* 2022
			Waterlogging and drought stress	RNA-Seq/RT-qPCR	Le Provost *et al.* 2022
			Hervibore defense	RT-qPCR	Fernández *et al.* 2024
			Root growth	RNA-Seq/RT-qPCR	Koscielniak *et al.* 2024

Quercus spp	**Section**	**Distribution**	**Study objective**	**Technique/Assay**	**Reference**
			Stress response	RT-qPCR	*et al.* 2024
Q. rubra L.	Lobatae	North America	Nickel resistance	RT-qPCR	Makela *et al.* 2016
			Nickel resistance	RT-qPCR	Djeukam & Nkongolo 2018
			Nickel resistance	RT-qPCR	Djeukam *et al.* 2019
			Ozone stress	RNAseq	Soltani *et al.* 2020
			PFK gen family evolution	RT-qPCR	Kim *et al.* 2023
			Drought stress	RT-qPCR	Lim *et al.* 2024
Q. shumardii Buckley	Lobatae	North America	Leaf coloration	RNA-Seq/RT-qPCR	Dong *et al.* 2020
Q. suber L.	Cerris	Europe	Oxidative stress	In situ hybridization	Mir *et al.* 2004
			Phytophtora cinnamomi infection	RACE-PCR	Coelho *et al.* 2006
			Cork formation	Microarreys/ RT-PCR	Soler *et al.* 2007
			Cork formation	RT-PCR	Soler *et al.* 2008
			Temperature stress	RT-qPCR	Chaves *et al.* 2011
			Reference genes selection for RT-qPCR	RT-qPCR	Marum *et al.* 2012
			Cork formation	RT-qPCR	Almeida *et al.* 2013a
			Drought and heat stress	RT-qPCR	Almeida *et al.* 2013b
			Heat stress	RT-qPCR	Correia *et al.* 2014
			Phytophtora cinnamomi infection	cDNA-AFLP, RT-qPCR	Ebadzad & Cravador 2014
			EST catalogue of candidate genes	EST Sequencing	Pereira-Leal *et al.* 2014
			Male and female flower development	Pyrosequencing/ RT-qPCR	Rocheta *et al.* 2014
			Ectomycorrhizal interaction	Pyrosequencing / RT-qPCR	Sebastiana *et al.* 2014
			Cork formation	RT-qPCR	Teixeira *et al.* 2014, 2018

Quercus spp	Section	Distribution	Study objective	Technique/Assay	Reference
			RNA extraction protocol	RT-qPCR	Carvalho *et al.* 2015
			Acorn development	RNA-Seq	Miguel *et al.* 2015
			Somatic embryogenesis	RT-PCR	Pérez *et al.* 2015
			Drought stress	RNA-Seq	Magalhães *et al.* 2016
			Male and female flower development	RT-qPCR	Sobral & Costa 2017
			Somatic embryogenesis	RNA-Seq	Capote *et al.* 2019
			Cork formation	RNA-Seq	Boher *et al.* 2018
			Bud sprouting	RNA-Seq	Usié *et al.* 2017
			Male and female flower development	RT-qPCR	Sobral *et al.* 2020
			Cork formation	RNA-Seq/RT-qPCR	Fernández-Piñán *et al.* 2021
			Salt stress	RT-qPCR	Dias *et al.* 2022
			RNA extraction protocol	RNA-Seq	Costa-Pires *et al.* 2023
			Somatic embyogenesis	RT-qPCR	Carneros *et al.* 2023
			Cork formation	RNA-Seq/RT-qPCR	Armendariz *et al.* 2024
			Cork formation	RNA-Seq/RT-qPCR	Lopes *et al.* 2024
Q. variabilis Blume	Cerris	Asia	Seed desiccation sensitivity	RNA-Seq/RT-qPCR	Li *et al.* 2021
			Cork formation	RNA-Seq	Chang *et al.* 2023
			Tannin biosynthesis	RNA-Seq/RT-qPCR	Yang *et al.* 2023
			Root development	RNA-Seq/RT-qPCR	Dou *et al.* 2024
			Heavy metals stress	RNA-Seq/RT-qPCR	Tan *et al.* 2024
			Seed dormancy	RT-qPCR	Wang *et al.* 2024a
			Tannin biosynthesis	Dual luciferase assay	Wang *et al.* 2024b

Quercus spp	**Section**	**Distribution**	**Study objective**	**Technique/Assay**	**Reference**
			Tannin evolution	RNA-Seq/RT-qPCR	Yang *et al.* 2024b
Q. wutaishanica Mayr.	Quercus	Asia	Drought stress	RT-qPCR	Zhao *et al.* 2024

The body of research reviewed can be grouped into ten main thematic categories (Table 2) but given the growing interest in understanding how oaks will respond to the ongoing global climate challenges, their economic relevance, and conservation-oriented forest strategies, the following sections summarize recent transcriptomic advances in key categories such as cork formation, abiotic stress, biotic interactions, and somatic embryogenesis.

Abiotic stress. Abiotic stress is an unfavorable environmental condition affecting many aspects of tree physiology and metabolism and can negatively impact tree growth, development, and distribution. It is considered the main threat to the survival of the most critical forest ecosystem worldwide, as current change patterns indicate likely increases in the severity and frequency of extreme weather events such as extreme temperatures or drought (Harfouche *et al.* 2014, Méndez-Espinoza & Vallejo Reyna 2019). Drought is an important abiotic stressor that affects plant growth and survival, with profound ecological and economic consequences (Lim *et al.* 2024), and from a molecular level has been well investigated in plants with short growth cycles such as *Arabidopsis thaliana* or *Oryza sativa* (Shinozaki & Yamaguchi-Shinozaki 2007) (Figure 2). Transcriptomic studies on abiotic stress in oaks have primarily focused on drought response and most research has concentrated on a few European and Asian species (Figure 3).

Abscisic acid (ABA) is a key phytohormone that confers abiotic stress tolerance, well studied in *Arabidopsis*, rice and other plants (Zhu 2002). It is known that under drought stress ABA-mediated stomatal closure reduces water loss by decreasing transpiration rate. Furthermore, ABA gradually increases hydraulic conductivity and stimulates root cell elongation, enabling plants recovery from water-limited conditions (Muhammad Aslam *et al.* 2022). Expression levels of several ABA synthesis genes are up-regulated by drought stress and their regulation is known to be controlled by major transcriptions factors (TFs) families such as bZIP, MYB, MYC, NAC, ERF and DREB/CBF. Few of these TFs have been identified in *Q. liaotungensis* Koidz. leaf transcriptome (Wang & Qin 2021); ERF have been identified in *Q. acutissima* and in *Q. palustris* Münchh. (Kim *et al.* 2024). Moreover, the expression levels of MYB108 were investigated among various tissues (stem, leaf, flower, acorn), and different levels of drought stress in *Q. wutaishanica* Mayr. with the highest level of expression found in leaves (Zhao *et al.* 2024).

A possible involvement of ABA response to drought stress was indicated by the ABA-responsive expression of the basic helix-loop-helix (bHLH30) gene in *Q. ilex*, and through the activation of ABA/auxin-mediated gene expression (RD22, WAT1) and NAC transcription factors in *Q. robur* (Madritsch *et al.* 2019). Genes of bHLH family were also studied among different tissues (leaves, stems, and roots) of *Q. mongolica* being characterized and categorized (Zhan *et al.* 2023). AREB genes are transcription factors that respond to ABA and were identified as upregulated in *Q. lobata* (Mead *et al.* 2019).

Besides, in *Q. suber*, an analysis of root transcriptome under drought stress revealed induction of the core ABA signaling pathway involving PP2C-SnRK2-ABF components as a mechanism of drought tolerance (Magalhães *et al.* 2016). Glyceraldehyde-3-phosphate dehydrogenase (GAPDH) is a key enzyme in glycolysis. Studies of GAPDH genes in *Populus deltoides* (Lim *et al.* 2025) and *Q. rubra* (Lim *et al.* 2024) exhibit varied expression patterns suggesting their potential role in drought tolerance.

In response to drought, plants often increase the overall concentration of soluble sugars (glucose, fructose, and sucrose) in various tissues playing a key role in osmotic potential adjustments (Dong *et al.* 2023). It has been reported that, in *Q. ilex*, starch reserves are reduced to release soluble sugars as a response to drought stress (Rodríguez-Calcerrada *et al.* 2017, 2021). This is supported by starch consumption, resulting from the upregulation of the β-amylase gene BAM3, along with the downregulation of glucose (GPT1) and sucrose (SUC27) transport genes reported by

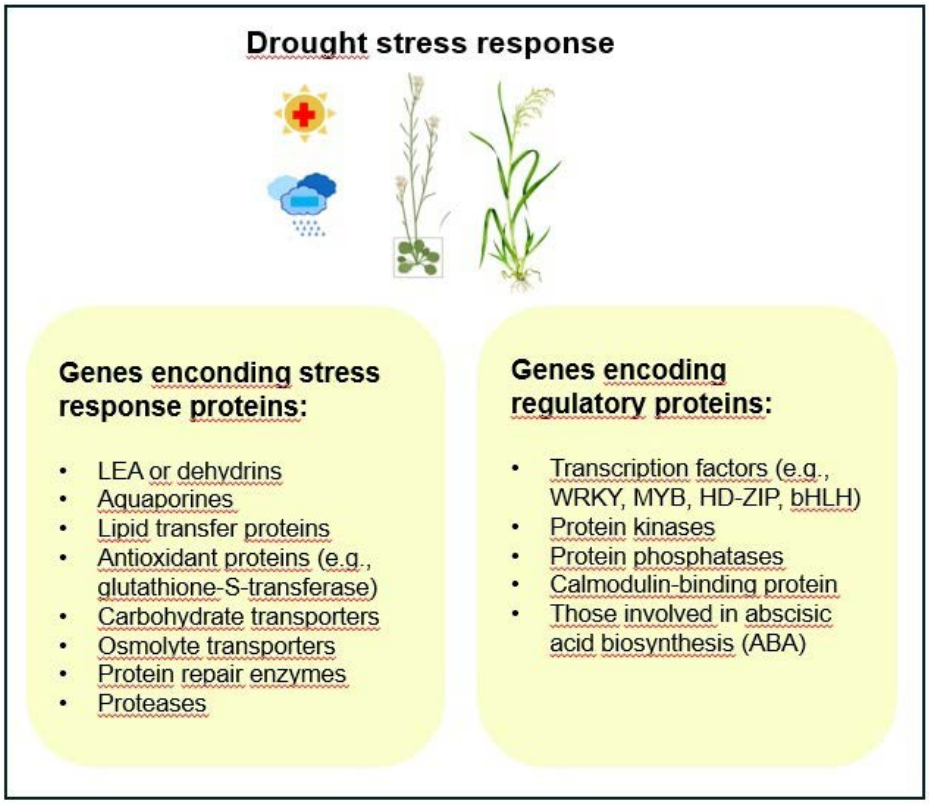

Figure 2. Main genes involved in drought stress response. Source: Gugger *et al*. 2017.

Gori *et al.* (2023). Similarly, it was evidenced that soluble sugars content significantly increased in *Q. acutissima* y *Q. palustris* seedlings subjected to drought stress treatment. In *Q. palustris* the expression of genes related to starch-degrading enzymes (alpha-amylase-like LOC112024135 and LOC112024130, beta-amylase 1 LOC112017453), increased during drought and decreased upon rewatering (Kim *et al.* 2024).

Candidate genes refer to a specific gene that has been hypothesized to be associated with a specific trait or condition. The expression patterns of classical candidate genes, potentially involved in oak drought tolerance (GASA, GLOBULIN, GST, LEA, RD22, XET2) were studied in leaf samples of *Q. robur* taken from individuals grown in nature (Trudic *et al.* 2021). Furthermore, as a result from comparative transcriptomic analysis, novel candidate references genes involved in drought stress response have been identified in *Q. mongolica* (Zhan *et al.* 2022), *Q. liaotungensis* (Wang & Qin 2021), *Q. ilex* (Kotrade *et al.* 2019, Guerrero-Sánchez *et al.* 2021), *Q. robur* and *Q. pubescens* (Kotrade *et al.* 2019).

Finally, oaks are known to display a broad range of adaptive variation for drought tolerance among species (Tyler *et al.* 2006) and among populations within species (Roussel *et al.* 2009). Drought responses, at a molecular level, can vary depending on the genetic background of the individuals, which may be related to local adaptation. In recent studies, *Q. lobata* (endemic to California), grown in different regions, was reported to exhibit differential gene expression depending on its region of origin in response to drought (Gugger *et al.* 2017, Mead *et al.* 2019).

Biotic interactions. Interactions between plants and various microorganisms (bacteria, fungi, viruses), can range from mutualistic, where both the plant and microbe benefit, to pathogenic, where the microbe causes harm to the plant. Understanding these relationships is important, as they can significantly impact plant health, growth, and productivity (Li 2023).

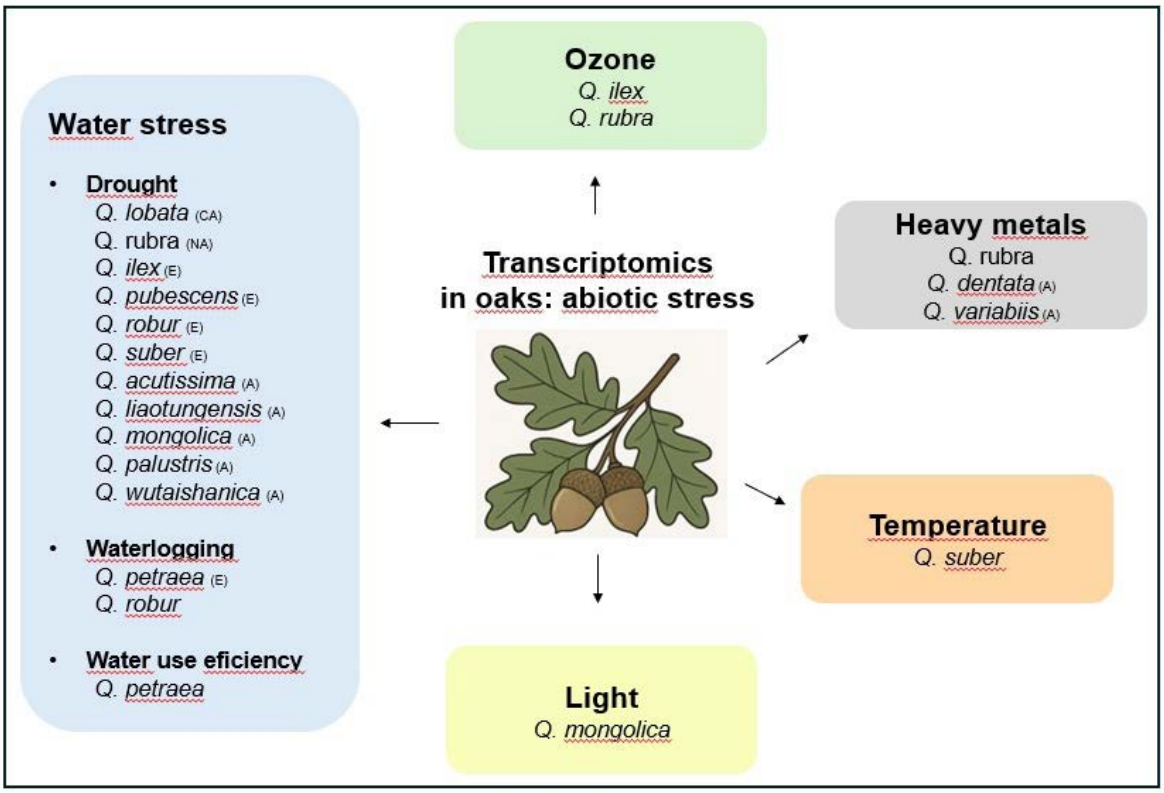

Figure 3. Abiotic stress studied in oaks using transcriptomics. Oak species from North America (NA), Europe (E), Asia (A), and endemic to California (CA). Source: Author´s own elaboration.

Ectomycorrhizal symbiosis is crucial for the life and health of trees in temperate and boreal forests. It plays a key role in nutrient cycling and the functioning of the forest ecosystem as the fungal partners promote the acquisition of water and nutrients from the soils. Trees with ectomycorrhizal root tips are more tolerant to environmental stresses, like drought, and biotic stresses, such as root pathogens (Sebastiana *et al.* 2014). Ectomicorrhizal colonization in *Q. suber* and in *Q. robur* resulted in extensive cell wall modifications, evidenced by the upregulation of genes that encodes endoglucanases, cellulose synthase, polygalacturonase and xyloglucan endotransglucosylase hydrolase; and the up-regulated expression transcription factors involved in responses to abiotic stress, such as MYB, WRKY, BAK 1, LRR-RLK FLS2-like, NORK, DMI1, among others, that constitute potential targets for the recognition events between the root cells and ectomycorrhiza fungi (Sebastiana *et al.* 2014, Kurth *et al.* 2015, Bouffaud *et al.* 2020). Genes involved in auxin and jasmonic acid pathways, which are known to be important in formation of ectomycorrhiza in pine and poplar (Laurans *et al.* 2001, Plett *et al.* 2014), were identified in *Q. robur* roots (Bouffaud *et al.* 2020).

As mentioned above, not all plant-microbe interactions are beneficial. *Phytophtora cinnamomi* is an oomycete that devastates forest species worldwide, causing significant ecological and economic impacts (Fernandes *et al.* 2024). This pathogen affects numerous oak species (*i.e., Q. brantii* Lindl., *Q. elliptica* Née, *Q. ilex*, *Q. laurifolia* Michx. *Q. magnoliifolia* Née, *Q. petraea*, *Q. robur*, *Q. salicifolia* Née, *Q. suber*, *Q. variabilis*, among others) causing their massive death, known as oak decline (Alvarado-Rosales *et al.* 2008, Morcillo *et al.* 2022, Saiz-Fernández *et al.* 2022). Jasmonic acid (JA) is a key signaling phytohormone involved in plant defense against insects and pathogens, and it is the main precursor of methyl jasmonate (MeJA) (Ho *et al.* 2020). Recently, exogenous application of MeJA to plant *in vitro* cultures has come out as a novel technique for inducing hyperaccumulation of secondary metabolites, and it has been demonstrated that this elicitor activates antioxidant enzymes and upregulates the expression of defense-related genes (Ho *et al.* 2018, 2020). It is known that in *Q. ilex* MeJA acts as an induced resistance stimulus against *P. cinnamomi* infection (Morcillo *et al.* 2022).

Tannins are secondary metabolites that are defensive against pathogen infection and herbivory attack (Gallardo *et al.* 2019). Studies on chestnuts (*Castanea crenata*) have shown that this tree responds to *P. cinnamomi* infection activating genes involved in the phenylpropanoid (which includes tannin biosynthesis) and jasmonic acid pathways (Fernandes *et al.* 2024). However, there is evidence that in *Q. ilex* the oomycete infection inhibits the expression of some genes related to tannin biosynthesis and jasmonic acid pathway contributing to its susceptibility (Gallardo *et al.* 2019, Morcillo *et al*. 2022). Loop-helix proteins (bHLH) is a family of transcription factors that have an important role in jasmonate signalling. Members of this family have been identified in *Q. brantii* affected trees (Safari *et al.* 2022).

Furthermore, genes that encode cinnamyl alcohol dehydrogenase2 (CAD2) and a thaumatin-like protein (TLP) were identified in *Q. suber* roots infected with *P. cinnamomi* (Ebadzad & Cravador 2014). TLP is suggested to be candidate resistance gene for *P. cinnamomi* in chesnut (*C. sativa*) (Fernandes *et al.* 2024); and in rice, CAD2 has been shown to be involved in developmental lignification and defense responses to stresses like bacterial infection (Park *et al.* 2018).

Cork formation. Cork (phellem) is a protective tissue formed by suberized cells, creating a thick layer covering the stem, branches, and roots. It protects against drought, solar irradiation, pathogens, and fires (Teixeira *et al.* 2014). It originates from a specific meristematic layer called phellogen, which grows continuously and homogeneously, producing multiple layers of radially aligned cells that accumulate into annual cork rings. The phellogen possesses self-regeneration properties after damage or peeling of the cork layer, without causing apparent injury to the tree. This ability allows successive cork debarking from the same tree at periodic intervals and sustainable cork production throughout the tree's life, which is the basis for a unique industry in the world (Teixeira *et al.* 2014). Cork is mainly supplied by two oak species, *Q. suber* in the Mediterranean region and *Q. variabilis* in East Asia (Leite *et al.* 2020).

There are many studies on the physical structure, chemical composition, thickness, and molecular mechanisms of cork in *Q. suber* which has a long history of breeding and cultivation (Teixeira *et al*. 2014, 2018). However, only a few studies have focused on cork in *Q. variabilis.* There is an interesting study about the cork's seasonal growth transcriptome in *Q. suber.* The study evidence that cell proliferation and cell differentiation is enriched at the beginning of the cork growth (April), while metabolic processes such as the biosynthesis of suberin, lignin, triterpenes, and soluble aromatic compounds are predominant during maximum and advanced cork growth (June and July), and that abiotic stress signaling is a constant factor (Fernández-Piñán *et al.* 2021), in fact, cork formation and stress are related (Teixeira *et al*. 2014).

Regulatory genes are highly induced at the beginning of cork growing season. Plant hormones such as auxins and brassinosteroids play an important role in the regulation of vascular cambium activities. In this context, two putative orthologs genes PIN3, an auxin transporter, and DWF1, a brassinosteroid biosynthetic enzyme were upregulated in *Q. suber* (Boher *et al.* 2018). WOX is another gene with important regulatory activities during cork formation that has been identified in *Q. suber* (Boher *et al.* 2018, Lopes *et al.* 2020, Armendariz *et al.* 2024).

A comparative transcriptomic analysis of good- and bad-quality cork, in *Q. suber*, showed that transcripts that belong to the families of AP2-EREBP, WRKY, histone, MADS C2H2, bHLH, and transcription factors of the families AP2/EREBP, bZIP/HD-ZIP, and MYB, and several classes of zinc finger domains, have been implicated in plant stress responses and have been mainly expressed in bad quality cork tissues, while the upregulation of heat-shock proteins (HSPs) was only observed in good quality cork tissues (Teixeira *et al*. 2014, 2018). Furthermore, genes codifying for the thaumatin-like protein (TLP) and chitinase (CLP) were highly expressed in *Q. suber* cork formation being both associated with defense signaling pathways (Meireles *et al.* 2018).

The thickness of cork is a key characteristic in determining its value (Teixeira *et al*. 2014). The suberin content determines cork qualities, such as thickness, permeability and elasticity (Chang *et al.* 2023). It is known that members of transcription factor families such as HD-ZIP III, WRKY, NAC, GRAS and MYB are key in phellem cells differentiation and, also play key roles in suberin biosynthesis in *Q. suber* and in *Q. variabilis* (Teixeira *et al*. 2014, Boher *et al.* 2018, Chang *et al.* 2023, Lopes *et al.* 2024).

Some studies revealed that gene families such as CYP86A1 (cytochrome p450 86A1), GPAT (glycerol-3-phosphate acyltransferase), KCS (3-ketoacyl-CoA synthase), and ABCG (ABC transporter G family) encode important enzymes involved in the suberin biosynthesis in the root and seed coat of *Arabidopsis thaliana* and in the periderm of *Solanum tuberosum* (Serra *et al*. 2009, Yadav *et al*. 2014). Also, GPAT family have been involved in suberin biosynthesis in poplar (Rains *et al.* 2018). These genes have been expressed in cork of *Q.* suber (Teixeira *et al*. 2014, 2018, Meireles *et al.* 2018, Lopes *et al.* 2020, Armendariz *et al.* 2024) and *Q. variabilis* (Chang *et al.* 2023). Transcripts related with fatty acid biosynthetic pathway, including fatty acyl-CoA reductase (FAR), long-chain acyl-CoA synthetase (LACS), have been identified and associated with the suberin pathway in *Q. suber* (Lopes *et al.* 2020).

MicroRNAs (miRNAs) are an essential class of small non-coding RNAs in plants that regulate gene expression at the post transcriptional level; this regulation is crucial for various plant processes, including development and stress responses (Bartel 2004, Liu & Vance 2010, Sunkar 2010). In *Q. suber*, miRNAs specifically involved in regulating phellogen functioning and phellem differentiation have been identified, with the most abundant being miR167, miR165/166, miR396, miR159, miR168, and miR390 (Chaves *et al.* 2014, Lopes *et al.* 2024). Phytohormones, particularly auxins, are major regulators of cambial activity during secondary growth, miR167 and miR390 are involved in the regulation of auxin signaling pathways in *Arabidopsis* (Wu *et al.* 2006, Marin *et al*. 2010). Furthermore, it has been shown that their activity increased significantly during active growth in poplar' cambium (Ding *et al.* 2014).

Somatic Embryogenesis (SE). SE is an important technique for the vegetative propagation of trees, that consists in the developmental in vitro process in which embryos are produced from somatic cells (Hazubska-Przybył *et al.* 2022). Traditional genetic breeding programs have significant limitations in forest trees due to their long reproductive cycles and the difficulty of seed conservation and vegetative reproduction (Carneros *et al.* 2023). Nowadays, SE is considered the most appropriate *in vitro* regeneration system and has become a useful biotechnological tool for plant breeding, propagation, and conservation strategies in forest tree species, like spruces, pines and oaks (Hazubska-Przybył *et al.* 2022, Carneros *et al*. 2023). SE has been applied in multiple oak species such as *Q. alba* L., *Q. ilex*, *Q. robur*, *Q. rubra*, and *Q. suber* (Yang *et al.* 2024b). However, transcriptomic research in this area remains limited to a few species like *Q. aliena* Blume and *Q. suber* pointing to a gap in applying SE-focused transcriptomics across the genus.

Somatic embryos follow similar developmental patterns as zygotic ones. Embryo development and maturation needs the coordinated action of several signaling pathways integrating genetic, epigenetic, and hormonal regulation (Capote *et al.* 2019). There is evidence that auxin (AUX) and abscisic acid (ABA) are the most common regulators in plant SE (Yang *et al*. 2024b). In *Picea abies* and *Abies alba*, it has been hypothesized that AUX at the proliferation and early developmental stages of SE is crucial for embryos to develop to the maturation phase (Carneros *et al.* 2023). YUC4 and ARF5 are key genes involved in the AUX biosynthesis and plant development and which activation have been detected in developmental stages of *Q. suber* SE (Capote *et al.* 2019, Carneros *et al.* 2023).

On the other hand, genes involved in the ABA pathway, have been identified during development and maturation of *Q. suber* somatic embryos, such as NCED3, HUB1, HUB2, AUR3, HDA6, HDA19, PICKLE, and VAL1 genes. Homolog sequences of these genes have been also identified in *Arabidopsis thaliana*, *Populus trichocarpa*, and *Castanea sativa* (Pérez *et al.* 2015). Exogenous ABA application has been shown to enhance SE in species such as *Pseudotsuga menziesii* (Walther *et al.* 2022). In *Q. aliena*, it was evidenced that the expression of LEC2 and CALS11, genes involved in the SE process, are affected by exogenous ABA signals (Yang *et al.* 2024b).

Bias and perspectives in oaks transcriptomics

Forest degradation, fragmentation, and anthropogenic pressures, such as overexploitation, fires, and land-use changes, are major drivers of increased tree mortality and deforestation worldwide (Grantham *et al.* 2020). Furthermore, adverse abiotic and biotic factors significantly hinder forest conservation efforts by limiting tree growth and development, and, depending on their severity and duration, can ultimately lead to tree mortality (Wardlaw *et al.* 2015). Climate change, particularly rising temperatures and the increasing frequency of extreme events like droughts, further

exacerbates these challenges, altering forest structure, dynamics, and ecosystem services (Petritan *et al.* 2021). In this review, we identified that the primary application of transcriptomics studies in oaks is to unravel the molecular mechanisms underlying responses to abiotic stress, especially drought.

To our knowledge, along with contributions from Kremer *et al.* (2012), Escandón *et al.* (2021), and Maldonado-Alconada *et al.* (2022), this is among the few reviews synthesizing molecular research on the *Quercus* genus. RNA-Seq technologies have revolutionized our understanding of transcriptomes by enabling a comprehensive analysis of gene expression patterns, alternative splicing events, and regulatory networks (Kukurba & Montgomery 2015). These advances, along with the availability of reference genomes, facilitate functional genomics, comparative studies, and the identification of candidate genes related to adaptive traits (Escandón *et al.* 2021). However, significant geographic and taxonomic biases remain. To date, only seven *Quercus* species have fully sequenced reference genomes, mainly from Europe, Asia, and North America. Notably, no Mexican oak species have been included in transcriptomic studies despite Mexico being a major center of oak diversity (Valencia 2004, Cavender-Bares *et al.* 2015).

Given Mexico's complex geological history and position at the intersection of the Nearctic and Neotropical regions (Mastretta-Yanes *et al.* 2015), its oak species present unique evolutionary and ecological research opportunities. Developing reference genomes for Mexican oaks would enable more inclusive and comparative genomic and transcriptomic studies, aiding in exploring adaptation processes and informing conservation strategies. Additionally, despite advancements in genomic approaches for certain Mexican species (*Q. rugosa* Née, *Q. macdougallii* Martínez, *Q. castanea* Née, *Q. laeta* Liebm.) (Martins *et al.* 2018, Pacheco-Cruz 2019, Lara-De La Cruz 2021, Morales-Saldaña 2023), transcriptomic information remains limited or nonexistent. Bridging this knowledge gap is essential for understanding the molecular foundations of stress tolerance and resilience in these highly diverse and ecologically significant species. Besides, recent studies on pinus and poplar, have emphasized the importance of integrating data from multiple omics layers —such as transcriptomics, proteomics, and metabolomics—to gain a holistic comprehension and understand complex biological processes (*e.g.*, abiotic and biotic stress, adaptive mechanisms, plant growth) (Escandón *et al.* 2024, Gallois *et al.* 2025), but to date, there are few multi-omics studies in oak species (López-Hidalgo *et al.* 2018, Maldonado-Alconada *et al.* 2022, Xiong *et al.* 2025).

Final considerations

As demonstrated in this review, transcriptomic research in the *Quercus* genus has primarily focused on stress responses, underscoring the urgent need to understand how oak species cope with the environmental challenges of the Anthropocene. However, the number of studied species remains limited, mainly due to the lack of well-annotated oak genomes. Consequently, many transcriptomic analyses still rely heavily on homology with model species such as *Arabidopsis thaliana*, *Oryza sativa*, or *Populus trichocarpa*. Expanding the number of available *Quercus* species reference genomes will be crucial for enabling species-specific insights and leveraging the full potential of transcriptomic technologies. Our analysis also revealed notable geographic biases. Most studies concentrated on European and Asian oaks, while American oaks—especially those from Mexico—remain largely unstudied. Given that East Asia and Mexico are recognized as centers of oak diversification, this represents a significant gap in current research efforts.

We hope this review synthesizes current knowledge while also highlighting underexplored opportunities. We emphasize the importance of including Mexican oak species in future transcriptomic studies to fully capture this remarkable genus's evolutionary, ecological, and functional diversity.

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