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Review

Molecular Traits for Adaptation to Drought and Salt Stress in Birch, Oak and Poplar Species

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Abstract: *Betula* spp., *Quercus* spp., and *Populus* spp. are the most promising deciduous woody plants in forestry. However, these species were found to be sensitive to climate change that can badly affect their plantations. Thus, a deep understanding of genetic mechanisms of adaptation to adverse environmental conditions plays an important role in preventing the reduction of deciduous forest area. This mini review describes the stress responses of *Betula* spp., *Quercus* spp., and *Populus* spp. to drought and salt stresses. The overall stress response of the reviewed tree species includes ROS scavenging, ABA- and JA-mediated signaling pathways, and antioxidant and chaperone activities. Short-term drought promotes accumulation of proline, indicating the osmotic stress response. In turn, long-term drought stress activates the DNA repair and chromatin remodeling systems aimed at adapting and gene protecting. Furthermore, alternative pathways of carbohydrate production are used under nutrient deficiencies. It should be noted that stomatal movement control and cell wall remodeling are always observed during drought. In turn, the main response to salt stress includes the maintenance of ion homeostasis and the accumulation of osmoprotectant, as well as cell wall remodeling due to the biosynthesis of cellulotic and non-cellulotic cell wall compounds. It should be noted that the described species demonstrate similar molecular traits for adaptation to drought and salt stress, which may be due to their common habitats.

Keywords: abiotic stress; birch; deciduous woody plants; differential gene expression; oak; poplar; transcriptome; trees

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1. Introduction

Deciduous woody plants are economically valuable tree species with a high potential for plantation forestry, covering large areas in the Eurasian continent. However, due to global climate change, including an increase in average annual temperature [1] and sea level rise [2], as well as low rates of reforestation after active felling, the areas under deciduous forests are declining every year. With respect to forest tree species such as birches, oaks, and poplars, the resistance to adverse environmental conditions is of particular importance.

Responses of deciduous woody plants to abiotic stress may depend both on the intensity of stress factors, such as drought [3–5], soil salinity [6,7], and tree species composition [8,9]. Abiotic stresses induce rapid tissue release of various reactive oxygen species (ROS), such as hydrogen peroxide (H_2O_2) and superoxide anion (O^{2-}) [10], which negatively affect the structural integrity of the cell wall, carbohydrate metabolism, biosynthesis and folding of proteins, etc. In addition, there are changes in formation of roots [11,12], leaves [13], and wood [14], as well as in the susceptibility to pathogens and insects [15,16]. Thus, plants have developed a wide range of molecular mechanisms to support their growth and development, thereby reducing the cost of adaption to stress conditions, in particular, stomatal movement control to avoid water and electrolyte leakage and penetration of pathogens [17,18], accumulation of osmoprotectants [19,20], biosynthesis of cell wall compounds [21–23] and antioxidants [24,25], specific DNA loci associated with phenotypic traits important for drought tolerance [26], as well as stress memory systems based on epigenetic regulation [27].

A deeper understanding of these mechanisms has been made possible by advances in differential gene expression analysis using next generation sequencing that has greatly enhanced our current knowledge of the stress response of deciduous woody plants. Several recent reviews described physiological and molecular responses of woody plants to abiotic stress, but generally, without focusing on particular important species (e.g., [28–31]).

Birch (*Betula* spp.), oak (*Quercus* spp.), and poplar (*Populus* spp.) are among the most promising species for plantation forestry. Birches are most numerous in the boreal zone of Northern Europe [32]. Due to the increased cold tolerance and the ability to grow on poor soil, the birch habitat extends up to Central Siberia and has a higher altitude limit. In turn, oaks are widespread throughout most of Europe, stretching from the northern regions of Scotland to southern Turkey, as well as continental Russia as far as the Urals [33]. Oak's taproots penetrate deep into the soil, giving them structural wind resistance and tolerance to moderate drought. Poplar is cosmopolitan and grows in Europe, Asia, North America, and East Africa [34]. Obviously, these species use different ecological strategies. Therefore, suggesting that they also have different traits for adaption to stress, this mini review is focused on a detailed description of common approaches and unique features of the response to drought and salt stresses of these species.

2. Dominant Abiotic Stresses Affecting Deciduous Woody Plants

Drought, as a major abiotic stress, significantly affects woody plants. Long-term water deprivation increases the ROS content in cells and the rate of electrolyte leakage, which can lead to cell wall destruction. In turn, soil salinity depends on the concentration of salts dissolved in irrigation water. Na^+, K^+, and Ca^{2+} ions are often found in soil–water extracts. High soil salinity significantly affects the soil structure and microbiome, which can lead to a decrease in the diversity of plants and forest plantations [35,36].

The effects of these stresses are quite similar including ion misbalance and water deprivation. Therefore, understanding the mechanisms of drought and salt tolerance in birch, oak, and poplar is urgently needed, especially given climate change, which causes more frequent and dramatic droughts in temperate and boreal forests.

2.1. Drought Stress

Deciduous woody plants are characterized by a rapid early response to drought stress. In particular, the drought response of *Betula platyphylla* under short-term drought stress includes a high induction of genes associated with the abiotic stress response and ROS scavenging [37]. Here, the most abundant drought-induced transcription factor (TF) genes belong to the myeloblastosis oncogene (MYB) and the ethylene responsive factor (ERF). In particular, the drought tolerance of birch increases through the increase in the expression level of *BpERF2* and *BpMYB102* genes, belonging to these TFs families. There is evidence that the level of ERF2 gene expression can be up-regulated in tomato roots under low iron stress [38] or be involved in calcium signaling in postharvest apples [39]. In turn,

in *B. platyphylla* cells, the *BpERF2* gene regulates numerous genes of late embryogenesis abundant (LEA) proteins (LEA1, LEA8, LEA-D29, dehydrin-2), heat shock proteins (HSP) (Hsp18.5, Hsp23.6, Hsp26.5), and the SOD5 and RPD1 genes. Up-regulation of these genes provides for a decrease in ROS and malondialdehyde (MDA) content, as well as that in electrolyte leakage [37]. It should be noted that the LEA genes have a number of different *cis*-elements in the promoters [40]. Some of these elements are associated with the plant response to drought, low temperature, and high soil salinity, as well as hormones (abscisic acid (ABA), auxin, gibberellins (GAs), and salicylic acid (SA)), the content of which increases in plant cells under stress conditions. Thus, the up-regulation of LEA genes is a representative plant response to abiotic stress. In particular, dehydrins belonging to the LEA subfamily indirectly ensure the adaptation of model plants to adverse environmental conditions, affecting the architecture of the deep root system [41]. The interaction between the amphipathic α-helix of LEA1 and the fatty acid tails ensures the stabilization of the cell membrane [42]. Thus, the *BpERF2* gene in *B. platyphylla* cells is responsible for the primary drought stress response, including ROS scavenging, the response to abiotic stress, and structural cell wall integrity.

Similar to the *BpERF2* gene, the *BpMYB102* gene induces the expression of LEA1, Hsp16.9, Hsp18.5, and SOD5, regulating the abiotic stress response and ROS scavenging [37]. In addition, ROS scavenging in *B. platyphylla* cells can be performed not only with SOD5, but also with catalase (CAT) and peroxidase (POD). Their activities can be regulated by the transcription activator PTI5 in tomato [43], whose expression was also induced by *BpMYB102* gene in *B. platyphylla* [37]. According to [43], overexpression of the PTI5 gene in *Solanum lycopersicum* can also provide for increased resistance to pathogens. Based on the fact that bacterial influence can mediate drought tolerance [44], the PTI5-mediated pathogen response can be part of the drought response in *B. platyphylla* cells.

Overexpression of the *BpMYB102* gene in *B. platyphylla* also induced the expression of gibberellin-20-oxidase (GA20ox) [37], which plays an important role in the final stage of GAs biosynthesis [45]. There is evidence that water deficiency reduces the level of bioactive GAs produced with GA20ox in tomato [46]. Inhibition of GA20ox in *S. lycopersicum* contributes to a decrease in the water-loss rate due to a decrease in the size of plants [46], whose growth is also partly controlled by GAs [47]. Based on this, we can assume that, in addition to improving ROS scavenging, *MYB102* also supports birch growth under drought conditions by inducing of GA20ox gene expression [37]. Moreover, the up-regulation of the GA20ox gene by *BpMYB102* enhances the primary drought response due to the GAs' biosynthesis, which affects the promoters of LEA genes in *Salvia miltiorrhiza* [40].

Interestingly, in [37], 4-coumarate-CoA ligase 10 (4CL10), which plays an important role in the synthesis of lignin and flavonoids [48], was significantly down-regulated in *B. platyphylla* cells overexpressing *BpMYB102* [37]. These results demonstrate that inhibition of the *Bp4CL10* gene by the *BpMYB102* gene induced under drought stress conditions increases the drought tolerance of *B. platyphylla*. However, several studies have shown that suppression of the 4CL10 gene in poplar [49] and overexpression of *OsMYB102* gene from *Oryza sativa* in transgenic *Arabidopsis* [50] can lead to increased drought susceptibility due to secondary cell wall malformations and suppression of ABA biosynthesis, respectively. Thus, the role of MYB102 in structural integrity of *B. platyphylla* cells is still ambiguous and requires a more detailed study. In summary, the drought response in *B. platyphylla* includes enhanced chaperone activity, ROS scavenging, and pathogen response.

The drought response of different *Quercus* spp. can vary significantly and includes the up-regulation of the genes associated with hormone pathways, osmoprotection, photosynthesis, and cell wall remodeling [5]. In cells of the most drought susceptible oak *Quercus robur*, the drought tolerance increased through induction of chaperone activity (LEAs and HSPs), which is also inherent in *B. platyphylla* [37]. Secondary cell wall remodeling in *Q. robur* cells can be associated with up-regulated WAT1, since members of the WAT family were found to be involved in auxin- and SA-mediated lignin biosynthesis [51–53]. At the same time, the content of cellulotic and non-cellulotic cell wall compounds can be

decreased by down-regulation of sugar transporters SWEET1 and GFT1. Overexpression of the SWEET1 gene in poplar cells increases the xylem area and contributes to the enrichment of the secondary cell wall with cellulose [54]. In turn, a decrease in the expression of the GDP-L-fucose transporter GFT1, which is ubiquitously expressed in *Arabidopsis*, is accompanied by a decrease in the content of pectin and xyloglucan in the cell wall, which leads to developmental anomalies such as morphological defects and growth inhibition [55]. Thus, it can be assumed that the rigidity of the cell wall of *Q. robur* cells decreases under drought stress, which can lead to an increase in its permeability and facilitation of nutrient and water transport.

As the amount of water in the soil decreases, osmotic stress goes up. Osmotic stress response in *Q. robur* cells is represented through the up-regulation of various sugar synthetases (SPS4) and transporters (MSSP2, GPT2) [5]. The mechanism of osmoprotection, described in [56], assumes the biosynthesis of sucrose as an intermediate of starch biosynthesis in the amyloplasts of *Arabidopsis thaliana* cells. Solís-Guzmán et al. [56] have found that the accumulation of starch in these organelles increases their density and sedimentation capacity. These features allow amyloplasts to function as statoliths and affect root development. In addition, Cai et al. [57] demonstrated that overexpression of sucrose transporters in transgenic *Arabidopsis* lines leads to significant increase in drought tolerance.

It should be noted that the high susceptibility of *Q. robur* to drought may be manifested through the up-regulation of genes of the DREB2A-interacting protein 1 (DRIP1) and NAC72 [5]. The product of the DRIP1 gene in *Arabidopsis* as a negative regulator mediates the proteolysis of DREB2A [58,59], which regulates the drought-responsive genes involved in root development and ROS scavenging [60]. In turn, Wu et al. [61] found that in *Poncirus trifoliata* transgenic lines, overexpressed NAC72 recognizes and binds to the CACG motif in the arginine decarboxylase (ADC) gene promoter, down-regulating ADC expression. ADC is associated with the accumulation of putrescine in response to abiotic stress, and a decrease in its activity may lead to a decrease in ROS scavenging. Thus, activity of DRIP1 and NAC72 can lead to ROS accumulation in *Q. robur* cells, which mediates its sensitivity to drought.

The drought tolerance of *Q. pubescens* is higher than that of *Q. robur*, even though it is also a deciduous oak [5]. Here, the drought response included hormone biosynthesis by up-regulation of lipoxygenase (LOX3.1) and allene oxide synthase 1 (AOS1). Members of the LOX and AOS families are ubiquitous in various plants and are involved in JA biosynthesis [10,62,63]. In particular, in transgenic leaves of *Arabidopsis*, overexpression of LOX3 and LOX4 promotes the biosynthesis of JA precursors in response to mechanical damage [62]. In *O. sativa* cells, AOS2 activity increased in response to fungal pathogens [63]. It should be noted that, according to [64], LOXs can be involved in a wide range of stress responses due to *cis*-elements in the LOX gene promoters associated with hormones (ABA, SA, GAs, ethylene, and auxin) and abiotic stresses (drought, low temperature, mechanical damage). As in *Q. robur* [5] and *B. platyphylla* [37], many differentially expressed genes (DEGs) in *Q. pubescens* are associated with chaperone activity (ERD8/HSP80/HSP90.2, HSP83/HSP90.1), indicating the rapid early response to drought and temperature. In addition, the response to temperature changes can be improved by up-regulation of the heat stress TF HSFA4. In transgenic *Arabidopsis* cells, overexpression of the HSFA4 gene increases the basal thermotolerance due to interaction with promoters of heat stress response (HSP, ZAT, WRKY families) and ROS scavenging (ascorbate peroxidase 2) genes under high temperature, increasing their expression level [65].

Compared to *Q. robur*, where the secondary cell wall thickness was regulated by auxin-mediated gene expression (WAT1) [5], in *Q. pubescens*, the cell wall strengthening can be regulated due to the lignin incorporation mediated by the up-regulated DEGs of phenylalanine ammonia lyase (PAL), 4-coumarate-CoA ligase (4CL), and caffeic acid 3-O-methyltransferase (COMT) [66]. It should be noted that overexpression of the *FuPAL1* gene from *Fritillaria unibracteata* in transgenic *Arabidopsis* leads to activation of the biosynthesis of both lignin and SA via the phenylpropanoid pathway [67]. Thus, acti-

vation of genes of the phenylpropanoid pathway in *Q. pubescence* indicates a response to both drought and pathogens. Long-term drought stress provokes significant changes in carbohydrate metabolism in *Q. pubescens* cells [4]. The most down-regulated DEGs are associated with biosynthesis of raffinose oligosaccharides through the activity of the inositol-3-α-galactosyltransferase. Raffinose family oligosaccharides (RFO) and their precursor galactinol play an important role in the drought and cold tolerances of plants. The study [68] demonstrated high contents of raffinose and galactinol accumulated in *Arabidopsis* cells treated with drought, high salinity, and cold. Inhibition of the raffinose synthase gene (*ZmRAFS*) in *Zea mays* results in an increase in electrolyte leakage and leaf damage under drought stress [69]. The suppression of inositol-3-α-galactosyltransferase leads to a decrease in the RFO content, which indicates that this stress-response pathway is not preferable for *Q. pubescens*.

Severe drought results in pyruvate accumulation in *Q. pubescens* cells due to an increase in the lyase activity, mainly by 4-hydroxy-4-methyl-2-oxoglutarate aldolase (HMG) activity [4]. Shen et al. [70] suggested that pyruvate induced stomatal closure in *A. thaliana*. This pathway, although less efficient than ABA, may still be an alternative way to control the stomatal aperture. At the same time, accumulation of metabolites such as oxalic acid, malate, and isocitrate indicates an alternative pathway to glucose production under drought conditions [4].

Among the revealed DEGs in *Q. pubescens* cells, up-regulated genes of ferrochelatase (FC) and thiol-dependent ubiquitin-specific protease (UBP) are also of interest [4]. Overexpression of FC genes in model cells of *Hordeum vulgare* induces genes associated with ROS scavenging, reducing oxidative damage [71]. In addition, transgenic plants demonstrated high photosynthetic activity, which was reflected in a significantly higher chlorophyll content compared to the wild type. In turn, in *A. thaliana*, FC gene expression increases under salt stress, which is reflected in improved root development, reduced electrolyte leakage, and proline accumulation [72]. The loss of FC function leads to impaired seed germination. At the same time, UBPs are involved in drought and salt tolerance, ABA signaling, and plant nutrient deficiency response, as well as plant immunity regulation [73]. In particular, Lim et al. [74] demonstrated that UBP12 positively regulates the drought response in *Nicotiana benthamiana*. Suppression of the *NbUBP12* gene leads to a significantly wilted phenotype and high content of MDA in leaves in response to drought treatment. Moreover, a delayed fluorescence measurement showed a decrease in the content of chlorophyll, indicating a delay in photosynthetic activity. In addition, UBP promotes drought tolerance through ABA-mediated stomatal closure. This feature can be indirectly reflected through a change in leaf surface temperature due to a decrease in evaporative cooling. On the other hand, DEGs associated with the tryptophan metabolic process, auxin efflux, chromatin methylation, ROS-mediated apoptosis, and transmembrane phosphate ion transporter activity in *Q. pubescens* were suppressed [4].

Thus, the drought stress response of *Q. pubescens* cells includes the maintenance of the structural integrity of the cell wall through lignin accumulation, activation of the SA- and JA-mediated stress response, temperature response, changes in carbohydrate storage metabolism, improvement in photosynthetic activity, ROS scavenging, osmoprotection, salt stress response, and control of stomatal movement by ABA-dependent and ABA-independent pathways.

The evergreen holm oak *Q. ilex* has the highest drought tolerance of the mentioned oak species. Drought-stressed seedlings have a large number of gene products associated with stress response, including those exhibiting antioxidant, protease, and chaperone activities [3], also inherent in both *B. platyphylla* [37] and *Quercus* spp. [5]. In addition, since high temperatures lead to drought, pathways of temperature acclimatization are activated in *Q. ilex* cells through the up-regulation of caseinolytic peptidase B (ClpB1, ClpB3) and small heat-shock protein Hsp22. Panzade et al. [75] found that a rapid increase in the expression level of the *ZnJClpB 1-C* gene (*Ziziphus nummularia*) in transgenic *Nicotiana tobaccum* cv. 'Benthamiana' under heat stress indicates protection against protein denaturation. The pho-

tosynthetic activity increases, which is reflected in high chlorophyll content in transgenic cells. In addition, a decrease in MDA content indicates an increase in the expression level of genes associated with ROS scavenging. In turn, the study [76] showed that thermosoluble small Hsp22 [77] is part of the heat memory in *A. thaliana* cells. Methylation of histones that bind the Hsp22 gene is regulated by specific conserved demethylases, suppression of which leads to a decrease in survival rates. These results suggest that Hsp22 is involved in both thermotolerance and epigenetic heat acclimatization in *Q. ilex* [3].

The molecular consequences of drought, in particular heat memory, can significantly affect the growth and development of a plant after stress, when energy and metabolic requirements differ from those under stress. Metalloprotease FtsH6, which is up-regulated in *Q. ilex* cells [3], resets thermomemory in *A. thaliana* via degradation of HSP21 to maximize post-stress growth [78].

In turn, under long-term drought stress, *Q. ilex* drought tolerance is represented through biosynthesis of cell wall compounds, such as xyloglucan (β-1,2-xylosyltransferase (XYLT)) and lignin (COMT) [5], which is also observed for *Q. pubescens* [5] and epigenetic regulation. Protein chromatin remodeling 35 (DRD1), which is up-regulated in *Q. ilex* under drought, is involved in RNA-mediated epigenetic modification of the genome in rice and *Arabidopsis* [79]. Antioxidant activity was enhanced by induction of JA biosynthesis and ABA signaling (AOS3, cullin-1 (CUL1)). It should be noted that CUL1 is a scaffold protein for assembling the cullin-RING E3 ubiquitin ligase (CRL) complex [80], which is associated with DNA repair; ABA signaling under drought and osmotic stress conditions, including ABA-mediated stomatal closure; as well as auxin signaling in responses to temperature stress and nutrient deficiencies [81]. In addition, as mentioned above, members of the AOS family may be involved in the response to fungal pathogens [63].

Up-regulated NADH kinase 3 (NADK3) in *Q. ilex* cells is involved in the oxidative stress response [5]. Chai et al. [82] showed that suppression of NADK3 in *Arabidopsis* cells leads to hypersensitivity to oxidative and osmotic stress and delayed seed germination. In addition, as in *Q. pubescens* [4], cell wall remodeling is also part of the drought stress response in *Q. ilex*, represented through the up-regulation of cellulose synthase-like protein E6 (CSLE6), arabinosyltransferase (ARAD1), wall-associated receptor kinase (WAK1, WAK5), and expansin-A1 (ExPA1). CSLE6 is involved in cellulose biosynthesis. In *Elymus sibiricus*, CSLE6 had a high expression level during the tillering period, as well as under salt, heat, and osmotic stresses [83]. In turn, ARAD1 is involved in the biosynthesis of arabinans, which modulate the flexibility of plant cell walls. Verhertbruggen et al. [84] demonstrated that arabinan-deficient mutants of *A. thaliana* have a reduced content of pectic arabinans, which leads to a change in mechanical damage response. Thus, the biosynthesis of cellulotic and non-cellulotic compounds in *Q. ilex* cells is an important part of the drought stress response, in contrast to *Q. robur*, where these processes are inhibited by down-regulation of sugar transporter genes [5].

There is evidence that members of the WAK family, by binding to pectin in the cell wall, play an important role in the growth and development of *Arabidopsis* leaves [85]. In addition, the study [86] showed that expression of WAK genes is also induced in *Arabidopsis* cells treated with bile acid deoxycholate, which is used to protect plants from pathogens. As WAKs, expansin proteins are not involved in the biosynthesis of cell wall compounds. Their main function is to regulate cell wall permeability, which ensures its plasticity to protect against mechanical and osmotic stresses [87]. In particular, Narayan et al. [88] found that in *Saccharum* spp. the expression level of the ExPA1 gene gradually increases during the drought stress, which may maintain cell wall flexibility under long-term water deprivation. It should also be noted that the metabolic activity in *Q. ilex* cells is suppressed due to down-regulation of genes associated with photosynthesis [3].

Obviously, the effectiveness of the drought tolerance strategy of *Q. ilex* is ensured not only by ROS scavenging, epigenetic regulation, and antioxidant activity, but also by enhanced cell wall remodeling, represented by the biosynthesis of various cell wall

compounds providing both structural integrity and flexibility for efficient water and nutrient transport.

To compare the drought response of *Quercus* spp., the main results of the respective studies are summarized in Table 1.

Table 1. Initial conditions and main results of differential expression analysis for *Quercus* spp. under drought stress.

Species	***Q. robur***	***Q. pubescens***	***Q. pubescens***	***Q. pubescens***	***Q. ilex***	***Q. ilex***	***Q. ilex***
Plant age	9-year-old	9-year-old	100-year-old	100-year-old	6-month-old	6-month-old	9-year-old
Drought stress conditions	>10% soil moisture	>10% soil moisture	11% soil moisture	20% soil moisture	44 °C, relative humidity 40%	44 °C, relative humidity 40%	>10% soil moisture
Exposure time, day	124	124	1460	1460	17	24	124
Number of DEGs	415	79	31	11	872	1084	222
Up-regulated DEGs	132	48	5	2	312	308	112
Down-regulated DEGs	283	31	18	7	560	776	110
Up-regulated TF families	MYB, NAC	ERF, bHLH	n/a	n/a	ZHD	ZHD	n/a
Down-regulated TF families	WRKY, MYB	n/a	n/a	n/a	WRKY, ATH, NAC, MYB, AZF	WRKY, ATH, NAC, MYB, AZF	n/a
Biological processes	Response to stimulus; Response to stress; Multi-organism process	Response to stress; Small molecule metabolic process; Multi-organism process	Response to fructose; Response to glucose; Response to sucrose	Stabilization of membrane potential; Cellular potassium ion homeostasis; Protein oligomerization	Response to stimulus; Response to chemical; RNA metabolic process; Response to abiotic stimulus	Cellular process; Metabolic process; Organic substance metabolic process	Response to stimulus; Response to stress; Cell communication
Cellular component	Nucleus; Integral component of membrane; Plasma membrane	Nucleus; Integral component of membrane; Plasma membrane	n/a	n/a	Cellular component; Cell; Cell part	Cellular component; Cell; Cell part	Nucleus; Integral component of membrane; Plasma membrane
Molecular function	ATP binding; Metal ion binding; RNA binding	ATP binding; Metal ion binding; RNA binding	Ribonuclease inhibitor activity; Ferrohelatase activity; Oxaloacetate decarboxylase activity	Leak channel activity; Potassium ion leak channel activity; Narrow pore channel activity	Transcription factor activity; Core RNA polymerase binding; Plastid sigma factor activity	Molecular function; Binding; Catalytic activity	ATP binding; Metal ion binding; RNA binding
Reference	[5]	[5]	[4]	[4]	[3]	[3]	[5]

The *Quercus* spp. example shows that the number of DEGs depends on both the time of drought exposure and the age of the sample. The older the sample and the longer the exposure time, the smaller number of DEGs can be identified. Gene Ontology (GO) classification analysis showed that in biological processes (BP) categories of genes involved in response to stress, defense response, response to biotic and abiotic stimulus, chemical compounds, metabolic process, and signal transduction were enriched for all mentioned *Quercus* spp., which reflects through the high chaperone activity [3,5], ROS scavenging [5], and activation of JA and ABA signaling [4]. Compared to *B. platyphylla* [37], in *Quercus* spp. the costs of maintaining the structural integrity of cells under drought stress are significantly higher, which reflects the high enrichment of the genes involved in biosynthesis of cellular parts and their components, membrane compounds, and membrane integral components, as well as parts of the cytoplasm, cytosol, mitochondrion, nucleus, plasma membrane, and plasmodesma. In the molecular function (MF), the categories of genes associated with RNA/DNA binding, ATP binding, DNA binding-transcription factor activity, and metal ion binding were significantly enriched. Nucleotide binding activity predominates, indicating both the DNA-binding activity of TF and the processes of epigenetic regulation and DNA repair. In turn, the enriched category "metal ion binding" may indicate, in particular, changes in the photosynthetic system, which is reflected through the up-regulation of DEGs associated with this process.

Thus, the rapid response of *Betula* spp. and *Quercus* spp. to drought includes chaperone activity, ROS scavenging, activation of various signaling pathways (JA, ethylene), and stomatal movement control. During stress development, genes associated with cell wall remodeling, antioxidant activity, and DNA modification are up-regulated. Finally, the late response involves activation of alternative carbohydrate production pathways under nutrient deficiencies.

2.2. PEG-Mediated Osmotic Stress

A laboratory experiment to discover the effect of drought on deciduous woody plants can be quite lengthy. PEG-mediated osmotic stress as a simulation of drought conditions is widely used to reduce the experiment duration. In particular, in three-month-old seedlings of *B. platyphylla*, the greatest number of genes was activated in the first four hours of PEG-mediated osmotic stress, revealing the most significant changes in the expression level of genes associated with the biosynthesis and metabolic process of JA and the water-deficiency response [89]. Using the gene regulatory network, it was found that at this stage TFs ERF017, AGL61, WRKY6, and ERF2 played essential roles in the regulation of expression of the most structural genes. As was mentioned above, ERF2 is an important TF for *B. platyphylla* and regulates the primary drought response, including the enhancement of chaperone activity and ROS scavenging [37]. In turn, ERF017, by binding to promoters, directly regulates the expression of genes associated with the biosynthesis of monolignols in *Miscanthus* × *giganteus* [90], which can ensure the structural integrity of the cell wall under abiotic stress. In addition, Hou et al. [91] proposed to use ERF017 as a biomarker to detect Pb stress in *Lycopersicon esculentum* roots, since its expression level correlates negatively with Pb treatment. AGL61 is associated with the early development of seeds of *Ricinus communis* [92] and flowers of *Dryopteris fragrans* [93], while in the *R. communis* seedlings, its activity is regulated by methylation [92]. Up-regulation of AGL61 in *B. platyphylla* indicates the effect of the PEG-mediated osmotic stress on the reproductive system. At the same time, the required level of intensity of the primary osmotic response is maintained by the up-regulated WRKY6. In *Gossypium hirsutum* and transgenic *Arabidopsis*, this TF acts as a negative regulator of ABA-mediated stomatal movement [94]. Overexpression of WRKY6 increases sensitivity to drought and salt stress, which affects root development and seed germination.

The highest expression level in *B. platyphylla* was observed for the homeobox-leucine zipper protein HB7 belonging to the HD-Zip family [37]. In *A. thaliana*, HB7 is activated by moderate water and osmotic stress and causes stomatal closure [95]. Members of this TF family play an important role in responses to various abiotic stresses, which makes them interesting research objects [96]. In particular, the role of the *BpHOX2* gene in the PEG-mediated drought response was discovered by Tan et al. [97]. Osmotic tolerance is represented here by electrolytes and water-leakage rate reduction and the low content of MDA and H_2O_2 in transgenic seedlings. It should be noted that the content of proline, which plays an important role in osmoprotection, was also increased, which can be explained by the *BpHOX2* induction of the genes *BpP5CS1* and *BpP5CS2* [97]. Suppression of the *P5CS* genes in transgenic *A. thaliana* leads to an increase in the sensitivity to salt stress and to a decrease in proline content [98]. Among the expressed DEGs-TFs, ERF114, WRKY29, and TGA5 should be noted as the genes with the highest expression bias [97]. In [99], ERF114 in *A. thaliana* is involved in pathogen response by induction of resistance to the PevD1-induced disease that causes cell wall damage [100] through regulating lignin and salicylic acid (SA) accumulation. In addition, there is evidence that overexpression of ERF114 could be involved in the auxin signaling pathway in response to mechanical damage [101]. In turn, up-regulation of WRKY29 in the *BpHOX2* transgenic *B. platyphylla* may lead to an increase in susceptibility to PEG-mediated osmotic stress. Hezema et al. [102] demonstrated that in apple rootstocks under hard osmotic stress WRKY29 acts as a negative regulator of ABA-mediated stomatal closure, which can lead to water leakage. Thus, the WRKY29 gene is down-regulated under osmotic stress in apple rootstocks.

Finally, TGA5 in *B. platyphylla* may contribute to ROS scavenging. The study [103] showed that in *Arabidopsis* TGA5 is involved in the response to UV-B stress by increasing the expression of the genes of peroxide-scavenging enzymes, such as members of the glutathione-S-transferase family. In turn, suppression of the TGA genes in *Arabidopsis* leads to an increase in the H_2O_2 content [103].

Thus, the drought and the PEG-mediated osmotic stress in *B. platyphylla* induced the expression of many genes of the ROS scavenging enzymes and their TFs, activation of water deprivation and mechanical damage responses, and cell wall protection. In addition, it can be assumed that there is a system for the formation of an adequate stress response, which implies a balance between tolerance and susceptibility by controlling of ABA-mediated stomatal movement [97,102].

To compare the drought and PEG-mediated osmotic responses of *B. platyphylla*, the main results of the respective studies are summarized in Table 2.

Table 2. Initial conditions and main results of differential expression analysis in the three-month-old seedlings of *B. platyphylla* under drought and PEG-mediated osmotic stress.

Species	***B. platyphylla***	***B. platyphylla***	***B. platyphylla BpHOX2***
Abiotic stress	20% PEG6000	Drought	9% PEG6000
Exposure time, h	2, 4, 6, 9	120	360
Number of DEGs	6291, 6843, 4186, 5639	2917	1453
Up-regulated DEGs	n/a	1127	866
Down-regulated DEGs	n/a	1790	587
Up-regulated TF families	ERF, NAC, MADS-box, WRKY	MYB, ERF, NAC, WRKY	MYB, ERF, NAC, WRKY, bHLH
Biological processes	JA biosynthesis; JA metabolic process; Response to oxidative stress; Response to JA	Oxidation-reduction process; Defense response to fungus; Protein phosphorylation; Regulation of transcription	Cellular process; Metabolic process; Response to stimulus; Biological regulation
Cellular component	n/a	Integral component of membrane; Membrane; Nucleus	Cell part; Organelle; Organelle part; Membrane
Molecular function	n/a	Metal ion binding; Heme binding	Catalytic activity; Binding; Transporter activity
Reference	[89]	[37]	[97]

As noted above, the largest amount of DEG was identified during the early drought response. Over time, this number is significantly reduced. Up-regulation of the TFs of ERF, NAC, and WRKY families was observed in *B. platyphylla* under various drought treatments. Under short-term drought stress, the highest expression level was observed for TFs of the ERF family. This is reflected in the enrichment of the genes involved in response to hormones, in particular to ethylene (biological processes). However, during the long-term drought, the greatest bias in the expression level was observed for TFs of the MYB family, members of which play an important role in antioxidant activity and hormone signaling transduction. GO classification showed that in the BP, the categories of genes involved in the hormone signal transduction (JA, ABA, and ethylene), responses of oxidative and osmotic stresses, water deprivation response, and stomatal movement regulation were highly enriched during the early drought response. In turn, the genes involved in metabolic processes, immune response, and developmental processes were enriched during the long-term drought and PEG-mediated osmotic stresses. In the cellular component (CC), the

expression level of the genes associated with the biosynthesis of the membrane components increased under long-term drought stress. In turn, during long-term PEG-mediated osmotic stress, the categories of both membrane and internal cell compartments were highly enriched. Finally, compared to long-term drought stress, long-term PEG-mediated osmotic stress showed an increase in catalytic, transport, transcriptional, and signal transduction activity. These differences in stress response can be explained by both the time of exposure and the type of stress.

Another osmotic response has been observed in *Populus ussuriensis* [104]. In BP, the genes involved in transcription, transcription regulation, and mRNA processing were enriched, which was also observed for *B. platyphylla* under drought stress (Table 2) [37]. In turn, the enriched categories of CC (nucleus, cytoplasm, integral component of membrane, cytosol, plasma membrane, chloroplast) and MF (ATP binding, metal ion binding, DNA binding) for *P. ussuriensis* were the same as for *Quercus* spp. (Table 1) and *B. platyphylla* under drought stress (Table 2). It should be noted that the GO categories for *B. platyphylla* under PEG-mediated osmotic stress and *P. ussuriensis* under drought stress differ. Based on these results, it can be assumed that the main traits of drought response of *Betula* spp., *Quercus* spp., and *Populus* spp. are quite similar.

The ABA response to PEG-mediated osmotic stress in *P. ussuriensis* is suppressed through the up-regulation of protein phosphotase 2C (PP2C) [104]. Noh et al. [105] showed that a high expression of the PP2CA gene, enhanced by overexpression of bZIP4, leads to a significant decrease of the ABA response in *Arabidopsis*. At the same time, degradation of the ABA receptor PYL4, which negatively regulates PP2C and is down-regulated in *P. ussuriensis* under osmotic stress [104], leads to ABA hypersensitivity in *Arabidopsis* [106]. Overexpression of *BpPP2C* in *B. platyphylla* under salt stress leads to damage of electron transport chains and, as a result, the high content of ROS and MDA [107]. Thus, this manner of suppression of ABA signaling in *P. ussuriensis* may negatively affect the rate of water leakage under osmotic stress.

Early response of *P. ussuriensis* to drought is manifested in intensive antioxidant and chaperone activities [104], typical of both birches [37,89] and oaks [4,5]. In particular, it manifests through the up-regulation of NAC35, which in *Scutellaria baicalensis* Georgi is involved in the biosynthesis of anthocyanins [108]. On the other hand, suppression of the NAC35 gene in wheat leads to an increase in the resistance to the wheat leaf rust pathogen [109].

Among the up-regulated TFs, we should also note WRKY33, MYB58, zinc finger protein ZAT11, and HB7. Shen et al. [110] found that WRKY33 is an important TF that regulates the development of *Arabidopsis* roots under nutrient deficiency. Knockout mutants demonstrated the inhibition of primary root growth under phosphate deficiency, as well as increased iron accumulation. As WRKY33, MYB58 is also involved in the iron deficiency response, expression of which is induced in *Arabidopsis* under by Fe deficit conditions [111]. Overexpression of MYB58 leads to an enhanced growth of primary and lateral roots, as well as to an increase in chlorophyll content. Wang et al. [111] discovered that under Fe deficiency, MYB58 directly binds to the promoter of MATE43, which is responsible for drug and toxin transport, is involved in iron homeostasis, and prevents Fe ion leakage. In turn, the expression of the ZAT11 gene in *A. thaliana*, as WRKY33 and MYB58, also positively correlates with primary root growth but reduces the tolerance to Ni^{2+} [112], which means that this TF cannot protect against the toxic effect of ROS induced by heavy metal ions. It can be assumed that in *P. ussuriensis*, ZAT11 is involved in root development but does not improve the response to oxidative stress induced by PEG-mediated osmotic stress.

As was mentioned above, HB7, up-regulated in *B. platyphylla* under drought stress [37], in *A. thaliana* is involved in a water-deficiency response, regulating the stomatal aperture [95]. In addition, HB7 in *Populus* spp. plays an important role in the development of vascular tissues, especially in the xylem, which transports water and nutrients from roots to stems and leaves [113]. HB7 suppression results in a reduction in leaf size and height of transgenic poplars. However, overexpression of HB7 causes serious phenotypic

changes and overdifferentiation of the xylem, which is expressed, in particular, in the development of needle-shaped leaves. Therefore, HB7 is not a suitable target gene for increasing tolerance to abiotic stresses.

PEG-mediated osmotic stress induces a premature senescence in *P. ussuriensis*, which is manifested through the up-regulation of WRKY75 [104]. In particular, Xu et al. [114] demonstrated that WRKY75 is involved in ethylen-mediated petal senescence of *Dianthus caryophyllus*. It should be noted that homologous protein WRKY45 in *Arabidopsis* also regulates senescence by direct-binding W-box elements in the promoters of the SAG (Senescence Associated Genes) family members [115]. In turn, *Arabidopsis* WRKY75 binds to the W-box in the promoters of the Golden-2-like protein family members and, thus, regulates both ABA-mediated leaf senescence and seed germination [116]. Finally, overexpression of WRKY75 in *Populus deltoides* × *Populus euramericana* leads to an increase in the content of H_2O_2, the oxidative activity of which can provoke premature senescence [117]. Thus, WRKY75 may be a useful target gene for the construction of transgenic poplar trees with osmotic and senescence tolerance.

It should be noted that the activation of genes from the phenylpropanoid pathway (trans-cinnamate 4-monooxygenase (C4H), cinnamyl alcohol dehydrogenase (CAD), cinnamoyl CoA reductase (CCR), and PAL) in *P. ussuriensis* indicates cell wall remodeling [104], which is also observed in *Q. pubescens* under drought stress [5]. Thus, compared to the birch and oak, the poplar strategy of early response to drought includes intensive cell wall remodeling, high antioxidant activity, iron homeostasis, and active control of tissue development.

2.3. Salt Stress

The response to long-term salt exposure (greater than 24 h) in hybrid poplar *Populus simonii* × *Populus nigra* is manifested mainly through the up-regulation of genes of ethylene-responsive ERF15, indole-3-acetic acid-amido synthetase (GH3), MYB308, and ERF76 [7,118,119]. The study [120] showed that ERF15 plays an important role in the herbivore resistance of *S. lycopersicum*. It was found that expression of the LOX, AOS, and allene oxide cyclase (AOC) genes involved in JA biosynthesis [10,62,63] is increased in *S. lycopersicum* leaves in response to the attack of *Helicoverpa armigera*. The promoters of LOX and AOC genes contain ERF-binding elements, with which ERF15 directly interacts. Suppression of the ERF15 gene leads to a decrease in the JA content and the expression of LOX and AOC genes. It should be noted that LOX and AOS genes are also up-regulated in *Q. pubescence* under drought stress [5].

In turn, tissue-specific auxin-responsive genes of the GH3 family are involved in various biological processes in plants, since the promoters of these genes contain many *cis*-elements, including phytohormone-dependent ones and those associated with development, growth, and stress response [121]. This feature makes GH3 a promising object for creating highly stress-tolerant transgenic trees. In particular, Zou et al. [122] showed that during the first hours of exposure to ABA and methyl jasmonate (MetJA), the number of GH3 transcripts in *Saccharum spontaneum* cells rapidly increases, indicating an intense early stress response. At the same time, overexpression of *ScGH3-1* gene increases the sensitivity of transgenic *Nicotiana benthamiana* to *Fusarium solani* var. *coeruleum* pathogens.

Yao et al. [123] found that ERF76 binds *cis*-elements in the promoters of a number of genes, in particular, genes of protective proteins (LEA, HSP, SOD, and POD), various oxidases and oxygenases, genes associated with the response to pathogens and cold, as well as genes of the NAC family, which are widely up-regulated in *P. simonii* × *P. nigra* under salt response [7]. Overexpressed ERF76 in *P. simonii* × *P. nigra* increases the primary root length, stomatal aperture, and the number of stomata on the leaf surface, and also improves ROS scavenging. Differential expression analysis showed that DEGs associated with stress response, namely POD, SOD, GST, and LEA, were up-regulated in poplar hybrid [119]. Along with the ROS scavenging and antioxidant activity, overexpression of the ERF76 gene in transgenic *N. tobacum* promotes the proline accumulation under salt stress [124]. These results indicate an extreme involvement of ERF76 in the salt response of *P. simonii* × *P. nigra*,

making them a promising target for the development of salt-tolerant poplars. As mentioned above, iron homeostasis is an important process for *P. ussuriensis* under PEG-mediated osmotic stress, which is promoted by up-regulation of MYB58 [104]. Here, MYB308 also performs this function [118], since, according to Fun et al. [125], MYB308 mediates the iron homeostasis in citrus species Zhique by direct binding of the promoter of the HA6 gene, which promotes root H^+ efflux and iron uptake.

Thus, the response to salt stress in *P. simonii* × *P. nigra* implies an enhancement of JA biosynthesis and JA response, activation of genes associated with the primary stress response, iron homeostasis, and the response to pathogens. It should be noted that *Betula* spp. and *Quercus* spp. exhibit similar rapid stress response by up-regulation of protective genes (LEA, HSP, SOD etc.) [5,37].

As mentioned above, in *P. simonii* × *P. nigra* under salt stress, induction of TF genes from the NAC family predominates [7]. Among these TFs, we can note NAC4, NAC42, NAC17, NAC2, and NAC72 with the highest expression bias [7,118]. In [126], it was discovered that NAC4 gene expression in *A. thaliana* was induced by salt treatment. Suppression of this gene leads to a decrease in salt sensitivity, which is reflected in a significant decrease in primary root growth. On the other hand, NAC42 plays an important role in fruit ripening of *Musa acuminata* by directly binding to promoters of genes associated with ROS scavenging, chaperone activity, and post-translational modification [127]. Overexpression of the *MaNAC42* gene in transgenic *Arabidopsis* reduces the rate of leaf senescence, which is reflected in a low rate of electrolyte leakage, maintenance of cell membrane integrity, and a decrease in the expression level of the senescence marker genes SAG12 and SAG13. In turn, Jung et al. [128] demonstrated that the NAC17 expression in *O. sativa* shoots is significantly increased in response to drought and salt stress. Overexpression of the *OsNAC17* gene increases the drought tolerance in rice seedlings at the reproductive and vegetative stages, while the survival rates of knockout mutants is dramatically low. Differential expression analysis showed that in transgenic plants with improved NAC17 expression, genes associated with phenylpropanoid pathway were up-regulated, indicating enhanced lignin biosynthesis [128]. Finally, overexpression of the *SlNAC2* gene from *S. lycopersicum* in transgenic *A. thaliana* under salt stress increases survival rates and improves antioxidant activity, which is reflected in a decrease in ROS and MDA content due to the activation of genes associated with glutathione biosynthesis and a decrease in the water leakage rate [129]. On the other hand, proline biosynthesis is reduced compared to the wild type. In turn, van Beek et al. [130] found that in *SlNAC2* transgenic *N. tobaccum* cv. Samsun under long-term drought stress, the content of MDA in leaves was similar between wild-type and transgenic plants, while the proline content was significantly higher, suggesting that NAC2 gene expression may depend either on type of stress or on exposure time.

It should be noted that the expression of the gene of the equilibrative nucleoside transporter (ENT) in *P. simonii* × *P. nigra* cells is down-regulated [7]. Transport of nucleosides and analogs across the cell membrane is an important process associated with an alternative pathway for nucleotide synthesis under adverse environmental conditions [131]. For instance, *Arabidopsis* knockout mutants exhibit a resistance to cytotoxic 5-fluorouridine [132], suggesting that the nucleoside uptake may be depressed under salt stress in *P. simonii* × *P. nigra*.

Thus, these results indicate that up-regulation of genes from the NAC family in the poplar hybrid *P. simonii* × *P. nigra* in response to salt stress leads to the activation of genes associated with salt response, cell wall remodeling, and premature senescence.

Another poplar hybrid, *Populus davidiana* × *Populus bolleana*, under salt stress demonstrated sequential development of the stress response depending on the time of salt exposure supported by the TF regulatory network, which includes TFs from 26 different families (mainly ERF, MYB, WRKY, and NAC) [6]. Among these TFs, WRKY30 and MYB4 are of main interest, since these genes have the highest expression change during the first three hours of stress.

The study [63] showed that the number of WRKY30 transcripts in *O. sativa* moderately increased in response to hormone exposure (JA and SA) and treatment with pathogens. Overexpression of this TF in transgenic *O. sativa* results in increased resistance to *Magnaporthe grisea* [63]. In addition, WRKY30 regulates the expression of the LOX and AOS genes involved in JA biosynthesis. Thus, WRKY30 in *P. davidiana* × *P. bolleana* may be involved in the pathogen response, as well as in the JA response, and mediates its biosynthesis. It should be noted that a similar intense JA response mediated by ERF15 was observed in *P. simonii* × *P. nigra* [7]. In turn, Zuo et al. [133] showed that WRKY30 mediates the resistance to cucumber mosaic virus (CMV) in *Arabidopsis*. Knockout mutants demonstrated a decrease in the activity of photoprotective mechanisms after CMV treatment. On the other hand, overexpression of WRKY30 in *Arabidopsis* leads to an enhancement in antioxidant activity, including the SOD, whose activity increased in the first 12 h in *P. davidiana* × *P. bolleana* under salt stress [6].

The study [134] notes that *BpMYB4* from *B. platyphylla* is homologous to *EgMYB1* from *Eucalyptus robusta* Smith, which is involved in the reduction of secondary cell wall thickness in transgenic *Arabidopsis* and poplars by inhibiting genes associated with lignin biosynthesis [135]. It should be noted that overexpression of *BpMYB4* in transgenic *Arabidopsis* also negatively affects lignin accumulation, but it contributes to an increase in the cellulose content. Using these properties of MYB4, Paolo et al. [136] proposed a promising transgenic *Cynara cardunculus* var. *altilis*, in which the overexpression of *AtMYB4* from *A. thaliana* provides a high growth rate of seedlings in the exponential phase and, due to the low content of phenolic compounds, increases the efficiency of biomass processing. The positive effect of *BpMYB4* on stress tolerance of *B. platyphylla* is also expressed as an increase in proline content and a decrease in ROS content, which indicates the osmotic stress response [134]. As in *P. ussuriensis* under PEG-mediated stress [104] and in *P. simonii* × *P. nigra* under salt stress [118], TFs of the MYB family play an important role in iron homeostasis in *P. davidiana* × *P. bolleana* under salt stress [6]. In particular, *MhR2R3-MYB4* transgenic *Arabidopsis* demonstrated improved growth, increased iron and chlorophyll contents, and intense ROS scavenging under iron deficiency [137].

Thus, poplar hybrids *P. davidiana* × *P. bolleana* and *P. simonii* × *P. nigra* demonstrate similar early salt stress responses, including intense JA biosynthesis and JA-mediated pathogen response, antioxidant activity, iron deficiency response, proline accumulation, and ROS scavenging [6,7]. It should be noted that such an intense salt response in *P. simonii* × *P. nigra* persists for more than 24 h, which indicates a salt tolerance higher than in *P. davidiana* × *P. bolleana*. In addition, unlike *P. simonii* × *P. nigra*, the structural integrity of the cell wall in *P. davidiana* × *P. bolleana* is maintained by the biosynthesis of cellulose rather than lignin.

Long-term salt treatment (greater than 24 h) apparently contributed to the onset of premature senescence in *P. davidiana* × *P. bolleana* and, as a result, up-regulation of such TFs as the cytokinin response factor 6 (CRF6) [6]. There is evidence that overexpression of CRF6 in transgenic *Arabidopsis* leads to an accelerated transition to reproductive development [138]. In addition, it was found that CRF6 transcription is induced by heat, salt, and peroxide stresses.

It should be noted that after 24 h of a salt exposure, only 29 DEGs of TFs were identified in the *P. davidiana* × *P. bolleana* cells [6], among which the down-regulation of bZIP4 is of interest. According to Ma et al. [139], *ZmbZIP4* overexpression increases *Z. mays* resistance to abiotic stress by enhancing the expression of genes associated with ABA synthesis. At the same time, overexpression of bZIP4 in *Arabidopsis* also enhances the expression of genes encoding the protein phosphatases ABI1, ABI2, and PP2CA, which suppress the ABA responsiveness [105]. Based on these results, it can be assumed that *P. davidiana* × *P. bolleana* cells have a balanced response to salt stress, which includes the reduction of ABA biosynthesis with a simultaneous increase in the ABA sensitivity through the down-regulation of bZIP4.

Thus, unlike the intense early salt stress response, including many genes and processes, long-term salt stress in *P. davidiana* × *P. bolleana* causes premature senescence and "fine tuning" of ABA response.

It should be noted that the described results were obtained for hybrid poplars subjected to a single exposure to a high salt concentration. The response to repeated salt stress can vary due to adaptive processes. In particular, Liu et al. [140] proposed the salt adaptation of poplar hybrid *Populus alba* × *Populus glandulosa*, including short-term salt pretreatment followed by three days of recovery. Seedlings treated with a high-salt solution without adaptation demonstrated the pronounced salt stress phenotype and the longer lag in recovery compared to adapted seedlings. The DEGs-TFs of the MYB, NAC, ERF, bHLH, and WRKY families were identified in both high-salt-treated and adapted plants. However, for adapted seedlings, the DEGs-TFs of the SOS, ARF, GRAS, BES1, and various zinc finger protein (C2H2, C3H) families were also identified. These results suggest that, in the long term, adaptation of hybrid poplars to salt stress may include the ion homeostasis control [141], hormone signaling (auxins [142], gibberellins [143], and brassinosteroids [144]), and epigenetic regulation through DNA modification [145].

To compare the salt response of poplar hybrids, the main results of the respective studies are summarized in Table 3.

Table 3. The initial conditions and main results of differential expression analysis for poplar hybrids *Populus* spp. under salt stress.

Species	***P. simonii* × *P. nigra***	***P. simonii* × *P. nigra***	***P. davidiana* × *P. bolleana***	***P. alba* × *P. glandulosa***
Object	1-month-old twig seedlings	1-month-old seedlings	40-day-old seedling	Adapted 2-month-old seedlings
Abiotic stress	150 mM NaCl	150 mM NaCl	200 mM NaCl	200 mM NaCl
Exposure time, h	36	24	3, 6, 12, 24, 48	1, 3, 6, 12
Tissue	Roots, stems, leaves	Leaves	Roots	Apex to 4th internode
Number of DEGs	2819, 1951, 8175	n/a	1417, 525, 280, 1015, 309	179, 4863, 872, 2100
Up-regulated DEGs	1228, 908, 5215	n/a	929, 317, 163, 915, 204	127, 2356, 528, 1198
Down-regulated DEGs	1591, 1043, 2960	n/a	488, 208, 117, 100, 105	52, 2507, 344, 902
Up-regulated TF families	HD-Zip, bHLH, ERF, bZIP, MYB	WRKY, NAC, MYB, bHLH, ERF, bZIP, C2H2	ERF, WRKY, MYB, NAC, bHLH	GRAS, bZIP, MYB, AP2, GATA, WRKY
Down-regulated TF families	TCP, HD-Zip, MYB	MYB, bHLH, NAC, C2H2, bZIP, WRKY, ERF	bZIP, CO-like, GRAS	AP2, GRAS, MADS-box, NAC, GATA, bZIP
Biological processes	Plant development; Stress responses; Metabolism process; Hormone signaling	n/a	Cellular process; Metabolic process; Response to stimulus; Biological regulation	Cellular process; Organic substance; Cellular metabolic process; Metabolic process
Cellular component	n/a	n/a	Cell part; Cell; Organelle; Membrane	Cell; Cell part; Intracellular; Intracellular part
Molecular function	n/a	n/a	Catalytic activity; Binding; Transcription regulator activity; Transporter activity	Binding; Catalytic activity; Organic cyclic compound binding; Heterocyclic compound binding
Reference	[7]	[118]	[6]	[140]

As for *Quercus* spp. and *Betula* spp. (Tables 1 and 2), the relationship between the age of the samples, the stress exposure time, and the number of identified DEGs for *Populus* spp. are also observed. This is clearly seen when comparing the results of differential expression analysis for poplar hybrids *P. simonii* × *P. nigra* and *P. davidiana* × *P. bolleana* after long-term salt stress (greater than 24 h). In turn, the maximum amount of DEGs was achieved during the early response to salt stress, which can be observed in *P. davidiana* × *P. bolleana* and *P. alba* × *P. glandulosa* hybrids after three hours. The same result was also observed

for *B. platyphylla* under drought stress conditions (Table 2). It should be noted that in adapted seedlings of *P. alba* × *P. glandulosa*, the reaction to salt stress was much more intense. As it can be seen, during the first three hours of salt stress, the amount of DEGs increases significantly and then sharply goes down. For non-adapted poplar seedlings of *P. davidiana* × *P. bolleana*, this decline continues for the next 20 h, while for adapted *P. alba* × *P. glandulosa*, this period is reduced to nine hours. All mentioned poplar hybrids revealed many common up-regulated TFs belonging to the MYB, bZIP, bHLH, WRKY, and ERF families. This result is evident due to the fact that members of these TF families are involved in the plant response to abiotic stress. For poplar hybrids, common BP categories of genes involved in cellular process, stimulus response, metabolic process, and developmental process were enriched, which differs from the results for *P. ussuriensis* under PEG-mediated osmotic stress, where enriched genes associated with transcription predominated [104]. This indicates a relationship between stress response and type of stress in *Populus* spp.

According to Shao et al. [146], the main processes ensuring the tolerance to salt stress in *Betula halophila* are associated with K^+, Na^+, and Ca^{2+} ion homeostasis, synthesis of osmoprotectants (proline and polyols), antioxidant activity (peroxidase, ascorbate oxidase, flavonoid-3′,5′-hydroxylase), hormone regulation (ABA signaling pathway), activation of TFs (WRKY, ERF, and AHL), and chaperone activity. This is reflected in the enrichment of genes from the MF categories (binding, catalytic activity, transport activity), which is also observed for poplar hybrids (Table 3).

In turn, *Q. ilex* demonstrates a slightly different salt stress response [147]. In BP, the genes involved in the metabolic process, biosynthetic process, and cellular process were enriched, which was also observed for *Q. ilex* under long-term drought stress (Table 1). The enriched MF category "nucleotide binding" *Q. ilex* under salt stress is similar to *Quercus* spp. under drought (Table 1). In turn, the enriched category "catalytic activity" was also observed for *B. halophila* [146] and *Populus* spp. under salt stress (Table 3). Interestingly, the "membrane" in CC for *Q. ilex* under salt stress dominates, which indicates an enhanced mechanism for maintaining the structural integrity of the cell wall.

As for *B. halophila* [146] and poplar hybrids [6,7,140], the overexpression of TF genes belonging to the ABA-dependent (MYB, NAC, WRKY) and ABA-independent (ABI, ERF) signaling pathways was observed. Antioxidant activity and ROS scavenging in *Q. ilex* under salt stress, represented through the up-regulation of genes associated with JA and SA response [148,149], are also characteristic of poplar hybrids [7] and *Q. pubescence* under drought [5]. On the other hand, structural cell wall integrity is maintained by up-regulated endo-1,4-beta-xylanase. Hu et al. [150] noted that the *Z. mays* knockout mutant exhibits dwarfing and leaf wilt as a result of water transport disruption. This mutation changes the structure of the mutant's cell wall, resulting in growth retardation. Decreased xylan deposition results in reduced secondary cell wall thickness and increased sensitivity to drought, heat, and salt stress. Finally, since ABA can induce protein kinases [151], up-regulated DEGs associated with phosphorylation provide a rapid stress response through post-translational modifications [152].

Thus, as with drought, the salt stress response of deciduous woody plants includes antioxidant activity, cell wall remodeling, phytohormone signaling, and ROS scavenging. At the same time, the activation of an MYB-mediated iron deficiency response was observed.

3. Main Aspects of Adaptation to Drought and Salt Stress in *Betula* spp., *Quercus* spp., and *Populus* spp.

The results of this research analysis indicate that the response of deciduous woody plants to various abiotic stresses includes both regular activities and specific responses (Table S1). The identified genes can be promising candidates for gene editing and targeted selection [153].

Based on Table S1, the main responses to drought and salt stresses of birches, oaks, and poplars were identified (Figure 1).

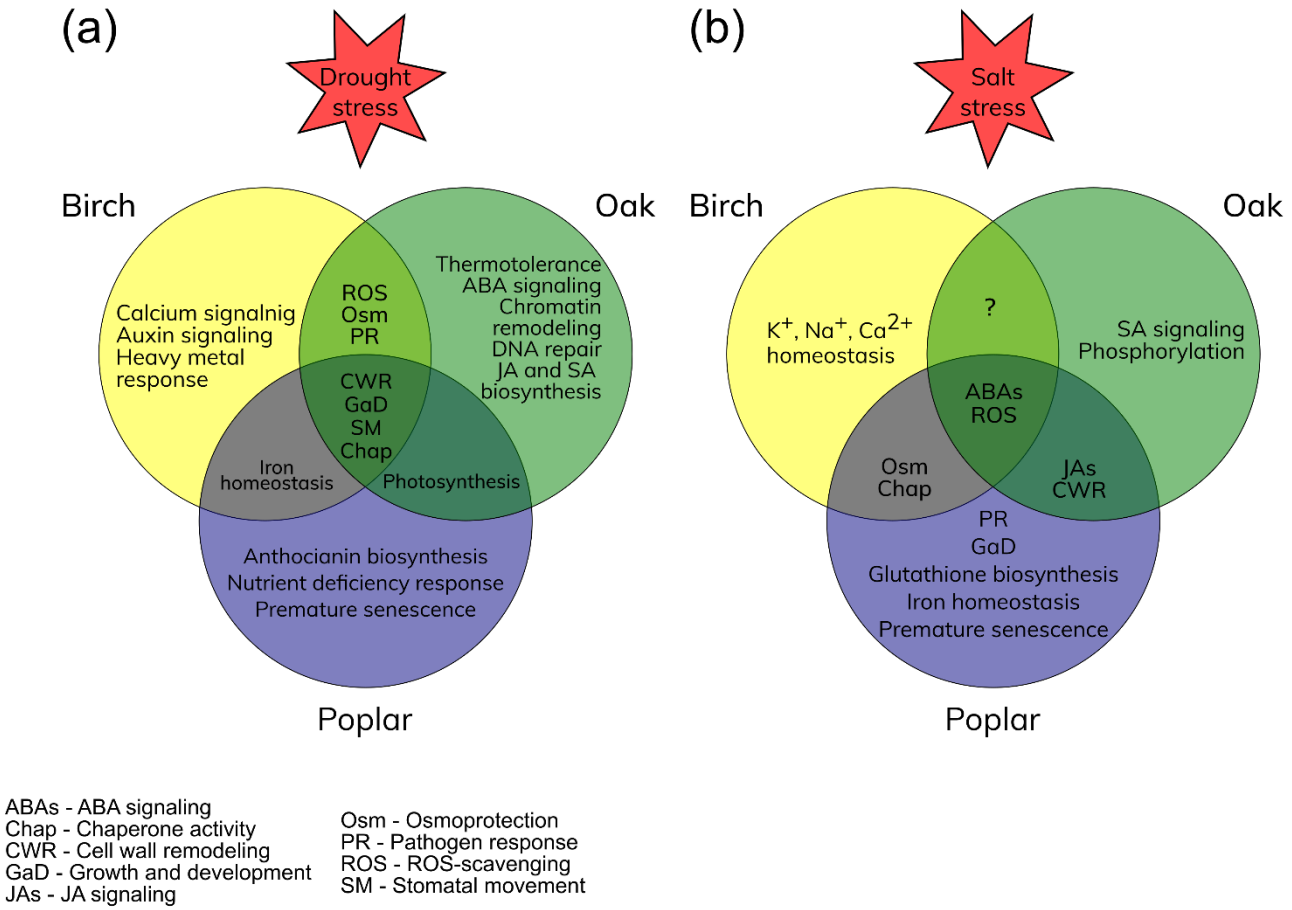

Figure 1. Main responses of birches, oaks, and poplars to drought (**a**) and salt (**b**) stress conditions. Overlapping circle parts represent the common stress responses.

During the early response of *Betula* spp. to drought, the TFs of the ERF, NAC, WRKY, and AGL families associated with the prevention of water leakage were significantly up-regulated. Drought protection included mainly the control of stomatal movement and the osmotic stress response (Figure 1a). The biosynthesis and metabolism of JA, as well as signaling pathways with its participation, were also activated, which indicates the control of plant growth and development. It should be noted that ABA-mediated stomatal movement may be suppressed here in favor of an alternative pathway. Further exposure to drought, accompanied by ROS accumulation and impaired protein folding, promotes the induction of genes associated with chaperone activity (LEAs and HSP) and ROS scavenging through up-regulation of TFs of MYB and ERF families and the transcriptional activators of the PTI family. Long-term drought mediates the accumulation of proline and lignin in birch cells through the up-regulation of the TFs of the HOX and ERF families (Table S1).

Compared to birch, oak's early reaction to drought is more pronounced, which is expressed in an increase in thermal tolerance and activation of JA and SA signaling pathways. (Figure 1a). Intensive cell wall remodeling, represented by monosaccharide polymerization and cellulose and lignin biosynthesis, was observed during long-term drought stress. During this drought period, ROS scavenging systems and antioxidant biosynthesis became significantly more active. Up-regulation of the genes associated with chromatin remodeling indicates formation of stress memory based on epigenetic regulation. It should be noted that DNA repair activity was also detected, which indicates that the long-term drought stress may affect the gene integrity in oak's cells.

Poplar's response to drought includes antioxidant activity, represented by anthocyanin biosynthesis, and a response to nutrient deficiency. It should be noted that the photosyn-

thetic system is improved due to iron homeostasis, which makes poplars related to birches and oaks (Figure 1a). The ABA-mediated stomatal movement here can be suppressed by protein phosphatase activity (Table S1). In addition, TFs of the MYB, WRKY, and ZFP families were involved in root growth and tissue development to prevent water leakage (Table S1). It should be noted that drought-mediated premature senescence in poplar cells (Figure 1a) was manifested through the activation of DEGs associated with tissue senescence and accumulation of hydrogen peroxide (Table S1).

Under short-term salt stress in birch cells, with the leakage of water and electrolytes, the systems for maintaining ion homeostasis and the biosynthesis of osmoprotectants (proline and polyols) are activated (Figure 1b). The response to oxidative stress is represented by ROS scavenging (peroxidase, ascorbate oxidase, and flavonoid 3′,5′-hydroxylase). Stomatal movement here can be mediated through the ABA signaling pathway. The complex response to abiotic stress was regulated by the activation of TFs of the WRKY, ERF, ZIP, and AHL families. At the same time, the processes of development, reproduction, and growth are suppressed.

As with birch, oak's response to salt stress also includes ROS scavenging and ABA signaling (Figure 1b). However, in this case, phytohormone signaling pathways (JA and SA) and TFs (MYB, NAC, WRKY, ABI, and ERF families) were significantly more activated (Figure 1b). It should be noted that common processes of the response to salt stress only between birch and oak have not been identified (Figure 1b). However, this does not indicate their absence. Research in this area should be continued.

In turn, the reaction of poplar to salt stress includes many common processes with birch and oak, such as osmoprotection, chaperone activity, and cell wall remodeling (Figure 1b). In addition, the early salt stress response also includes control of root growth and development, glutathione biosynthesis, and activation of genes associated with the response to pathogens. At the same time, up-regulation of some TFs of the MYB family associated with tolerance to iron deficiency may indicate adaptation of the photosynthetic system to salt stress (Figure 1b, Table S1).

We should also note several TFs, the action mechanism of which is of interest. In particular, the responses of *B. platyphylla* to drought and PEG-mediated osmotic stress are very similar, when ERF2 plays a crucial role [37,89], involving in the chaperone activity, cell wall remodeling, and ROS scavenging. In both cases, ABA-mediated stomatal movement is suppressed by either negative regulation [89] or a decrease in ABA biosynthesis [37]. On the other hand, according to Yao et al. [7,124], ERF76 is also involved in primary salt stress response in poplar hybrid *P. simonii* × *P. nigra*, directly regulating activity of LEA, HSP, SOD, and POD and stomatal aperture. Given these results, it would be promising to investigate functions of these TFs and the mechanisms of their actions in tandem with other deciduous woody plants.

The same research can be carried out for WRKY6 and WRKY29. According to Jia et al. [89], WRKY6 performs the negative regulation of ABA-mediated stomatal movement in *B. platyphylla* under 20% PEG6000 treatment during 9 h. In turn, WRKY29 was also up-regulated in *B. platyphylla* under milder osmotic stress conditions (9% PEG6000), over 25 days [97]. Therefore, the mechanisms of separate and cooperative actions of WRKY6 and WRKY29 should be investigated in detail.

The bZIP4-PP2C-system mediating suppression of ABA signaling [105] was identified in *P. ussuriensis* under PEG-mediated osmotic stress [104] and in *B. platyphylla* under salt stress [107]. Silencing this pathway can lead to increased sensitivity to ABA and, consequently, increased stress tolerance.

Finally, interestingly, NAC72 and HB7, which are involved in a drought response in *Q. robur* [5] and *B. platyphylla* [37], stomatal movement in *A. thaliana* [95], and osmotic stress in *Populus* spp. [113], were also up-regulated in *P. simonii* × *P. nigra* under salt stress [7]. This feature makes these genes a promising object of research in the field of response to abiotic stresses in deciduous woody plants.

Thus, according to the above, it can be assumed that the species *Betula* spp., *Quercus* spp., and *Populus* spp., although phylogenetically relatively distant from each other, may demonstrate similar molecular traits for adaptation to drought and salt stress. This feature can be explained both by sympatry [32,33] and by the overlap of their habitats [32–34].

4. Conclusions

Finally, we can conclude that the results of current research review indicate that the mechanism of adaptation to abiotic stresses in deciduous woody plants include many interrelated processes that may depend both on the type of stress and the time of its exposure, and on the area of growth and the local biodiversity. Differential expression analysis is a powerful tool for establishing the nuances of these responses, despite its inability to reveal post-translational modifications, which may play a crucial role in the functionality of the considered gene products. Nonetheless, the next step in the application of transcriptomic analysis in this area may be the determination of a time-dependent expression profile that demonstrates the features of early, intermediate, and long-term tissue-specific responses to stress in deciduous woody plants.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f14010007/s1, Table S1: List of differentially expressed genes (DEGs) identified in *Betula* spp., *Quercus* spp., and *Populus* spp. under drought, PEG-mediated osmotic stress, and salt stress.

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