Improving Flooding Tolerance of Crop Plants

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Abstract: A major problem of climate change is the increasing duration and frequency of heavy rainfall events. This leads to soil flooding that negatively affects plant growth, eventually leading to death of plants if the flooding persists for several days. Most crop plants are very sensitive to flooding, and dramatic yield losses occur due to flooding each year. This review summarizes recent progress and approaches to enhance crop resistance to flooding. Most experiments have been done on maize, barley, and soybean. Work on other crops such as wheat and rape has only started. The most promising traits that might enhance crop flooding tolerance are anatomical adaptations such as aerenchyma formation, the formation of a barrier against radial oxygen loss, and the growth of adventitious roots. Metabolic adaptations might be able to improve waterlogging tolerance as well, but more studies are needed in this direction. Reasonable approaches for future studies are quantitative trait locus (QTL) analyses or genome-wide association (GWA) studies in combination with specific tolerance traits that can be easily assessed. The usage of flooding-tolerant relatives or ancestral cultivars of the crop of interest in these experiments might enhance the chances of finding useful tolerance traits to be used in breeding.

Keywords: hypoxia; waterlogging; submergence; flooding; maize; soybean; barley; aerenchyma

1. Introduction

In times of changing climate, agriculture faces increasing problems with extreme weather events leading to considerable yield losses. In combination with a growing population and higher food demand, this presents a challenge to scientists and breeders to maintain the current food supply. Certainly, more effort is required to develop stress-resistant crops and improve agricultural practices in order to cope with these problems.

Plants are, due to their sessile nature, exposed to all changes in abiotic and biotic factors occurring at their habitat. Water availability, for example, is always problematic and can change from periods of drought to periods of flooding after a heavy rainfall. Plants can adapt to changing environmental conditions, but this comes at the cost of reduced growth and reproduction. If stress duration or severity exceeds the plant's ability to adapt, it will eventually die.

Most crop plants are rather sensitive to stresses since they were selected for high yield. In order to improve crop plant resistance to stresses, and to improve their productivity and survival, two research strategies are required. First, mechanisms of tolerance against stresses have to be understood. This requires analyses at the molecular level (transcriptomics, proteomics, metabolomics) in order not only to get to know adaptive mechanisms but also to understand their activation and regulation. The best approach for these analyses is the usage of a stress-resistant plant species closely related or even ancestral to the crop of interest, that potentially has lost some adaptational responses.

Second, due to the long history of breeding all over the world, a huge number of cultivars has become available for many crop plants. These breeding processes often focused on high yield and food quality, concomitant with a loss of genetic diversity and stress resistance. However, older cultivars

with low productivity might still contain tolerance loci for a certain stress condition that could be transferred to modern, highly productive cultivars. Strategies to achieve this goal are (1) screening of a wide range of cultivars under a specific stress condition; (2) selection of cultivars with low and high resistance; (3) understanding the physiological basis for resistance, i.e., the tolerance trait; and (4) the genetic analysis of those cultivars by quantitative trait locus (QTL) analysis and other molecular methods in order to find the genetic locus that underlies the tolerance trait. If a genetic locus has been discovered and characterized, it subsequently can be transferred into modern varieties using marker-assisted breeding technology to achieve stress-tolerant cultivars.

In this review, the current progress in crop resistance to flooding will be presented. First, overall plant responses and survival strategies under flooding conditions will be summarized. Then, breeding approaches in different temperate crops will be presented. The focus of this article will be on temperate plants, rather than rice and other tropical crops like cotton or sorghum. Flooding research on rice and its flooding-tolerance traits has been reviewed and discussed in several publications previously [1–5].

2. Plant Responses to Flooding

Besides the low availability of water leading to drought stress, plants can also be affected by too much water. Flooding primarily restricts gas diffusion between the plant and its surroundings due to physical properties (e.g., [6–8]). Oxygen as well as CO_2 cannot be easily exchanged via stomata and cell walls under water. This leads to a lack of oxygen inside flooded plant parts, and mainly limits heterotrophic energy production in mitochondria. Furthermore, low CO_2 availability in flooded leaves restricts photosynthesis. Therefore, flooding causes an energy crisis within plant cells.

Flooding events can be classified by two versions, (1) waterlogging, where only the root system inside the soil is affected; and (2) submergence, where also parts or the whole shoot are under water [9]. In flooded plant parts without ongoing photosynthesis, the oxygen concentration quickly declines and leads to hypoxic conditions (e.g., [10,11]).

Several plant species have developed mechanisms to cope with flooding stress, which enable them even to grow and reproduce in wet soil or under water. But also non-wetland plants can survive flooding, at least for a short period of time. Survival strategies can be divided into two major forms, (1) avoidance of oxygen deficiency within plant tissues; and (2) adaptation to oxygen deficiency. These strategies are described below.

2.1. Avoidance of Oxygen Deficiency by Morphological Modifications

The first strategy, the avoidance of oxygen deficiency inside the flooded plant parts, mainly involves anatomical and morphological modifications that improve gas exchange with the surroundings [8,12]. These modifications are largely mediated by the gaseous plant hormone ethylene that naturally accumulates in flooded plant parts [13].

One of the most prominent modifications is the increase of intercellular gas spaces, the so-called aerenchyma formation, to improve gas transport and distribution inside submerged plant tissues. Aerenchyma can develop in the root cortex as well as in stems and leaves. They are inducible by flooding conditions in several non-wetland species (e.g., wheat, maize [14,15]), or constitutive in many wetland species (e.g., rice, *Zea nicaraguensis* H.H.Iltis and B.F. Benz 2000 [12,15]). The formation of shoot-born adventitious roots has been observed in some plant species under water, for example in rice [16,17] and *Solanum dulcamara* L. [18,19]. Those roots also contain large aerenchyma. In order to restrict gas loss through the root surface, many roots of wetland plants also develop a barrier against radial oxygen loss (ROL) surrounding the aerenchyma-containing tissue (e.g., rice [20,21]; *Z. nicaraguensis* [12,22]).

When the whole plant is under water, some plants have developed the ability to move their leaves up in order to reach the water surface and to restore contact to air. This is achieved by hyponastic growth, meaning the change of the leaf angle to a more upright position, which can be observed in non-wetland (e.g., *Arabidopsis thaliana* (L.) Heynh. [10]) as well as in wetland plants species (e.g., *Rumex*

palustris Sm. [23]). Some plant species can go one step further and enhance the shoot growth under water to get their leaves out of the water. This so-called "escape strategy" can be achieved either by growth acceleration in petioles (e.g., *Rumex palustris* Sm. [24,25]; *Ranunculus sceleratus* L. [26]), or by enhanced growth of stems (e.g., rice [27,28]).

2.2. Adaptation to Oxygen Deficiency by Metabolic Modifications

If a plant species is not able to induce morphological modifications, or if water levels are too high to be outgrown, they have to cope with restricted gas exchange, mainly with low-oxygen concentrations. This adaptation involves metabolic modifications (summarized in [7,29]). A first response of plant cells under oxygen deficiency is the induction of fermentation. Since the mitochondrial ATP production is limited by oxygen availability, plants are dependent on glycolytic ATP production. During glycolysis, NADH accumulates and needs to be re-oxidized to NAD in order to maintain the glycolytic process. This is done by lactic acid fermentation, but mainly by ethanolic fermentation via alcohol dehydrogenase and pyruvate decarboxylase.

The higher transcription of genes encoding fermentative enzymes under oxygen deficiency is largely regulated by a group of oxygen-labile transcription factors, group VII of the ethylene-response factor family (groupVII-ERFs). The Arabidopsis groupVII-ERFs AtRAP2.2, AtRAP2.12, and AtRAP2.3 are constitutively expressed, but the proteins are degraded under normoxia by the Arg-branch of the N-end rule pathway. Under hypoxia, they can accumulate and act as transcriptional activators for example for genes encoding fermentative enzymes, but also for other metabolic and regulatory proteins [30–32].

While all plant species analyzed so far are able to induce fermentative enzymes under oxygen deficiency, the availability of carbohydrates and the efficiency to cope with lower energy production (2 Mol ATP per Mol glucose in glycolysis versus 30–36 Mol ATP per Mol glucose in mitochondrial respiration) restrict plant productivity and survival. Sensitive plant species often die from energy deficiency due to exhaustion of fermentable substrates, before the flooding period ends.

However, certain plant species and organs can consume large amounts of carbohydrates from sources such as starch that are otherwise difficult to access under oxygen deficiency. This is achieved by specific amylases and manipulation of the regulatory pathways (e.g., rice coleoptiles [33,34]; *Potamogeton pectinatus* (L.) Böerner tubers [35]). This high carbohydrate availability enables the strong elongation growth in plants exerting the "escape strategy". Other species, among them certain cultivars of rice, restrict metabolism and growth under water and apply the so-called "quiescence strategy", which enables them to survive for longer times with restricted carbohydrate supply. Some plant species might also make use of alternative energy pathways (e.g., the utilization of pyrophosphate instead of ATP for phosphorylation), but this has still not been fully explored [36–38].

2.3. Tolerance Traits for Flooding Survival and Their Usage in Breeding

The overview presented above of adaptational mechanisms employed by plants in response to flooding conditions makes it obvious that there is not only one mechanism or trait of tolerance in a tolerant plant. Hence, the contribution of individual metabolic pathways and morphological modifications to overall flooding tolerance has to be deciphered. This knowledge should enable scientists to focus on specific adaptational mechanisms, and to discover the underlying genetic basis for tolerance traits, which subsequently can be used for breeders in order to improve a crop's tolerance to flooding.

The most prominent example of successful agronomical application of knowledge on a flooding-tolerance trait and its transfer to crops comes from rice. Although this crop is naturally flooding-tolerant, most rice cultivars cannot survive more than one week of complete submergence [39]. Cultivars with the "quiescence strategy" can survive deep floods for up to 14 days, by restricting growth and carbohydrate consumption. On the other hand, deepwater-rice can outgrow a flood within a short time, using the "escape strategy", and thus restores contact to air, enabling long-term

survival [27,28]. For both traits, QTL analyses and subsequent molecular investigations have revealed the underlying genes. In both cases transcription factors related to groupVII-ERFs have been made responsible for either restriction of growth under water (SUB1A-1 [39,40]), or for enhanced growth (SNORKEL1/2 [28]). However, only the first genetic trait, the ability to induce quiescence, has been successfully used for crop improvement [5,41], because the second strategy has negative effects on crop stability once the floods recede.

In the next sections, we discuss what progress has been made in improving the flooding tolerance of major temperate crops, and what strategies are currently being applied in research. Among temperate crops, several species have been used for tolerance screenings and QTL analyses. Among the cereals, maize, wheat, and barley are well studied, and some data exist on the pasture grass *Lolium perenne* L. Hardly any data exist on other cereals such as oat and rye (Table 1). Among dicot plants, soybean and rape have been used in several studies, while others like potato or sugar beet have been seldom analyzed. Here, the model species *Arabidopsis thaliana* (L.) Heynh. is the best studied dicot plant with a wealth of expression and metabolic data, and an extended analysis comparing ecotype performances under submergence [11]. However, even here, the underlying mechanisms and genes responsible for tolerance are only now starting to emerge [42–44].

Table 1. Overview over crop species referred to in this review article.

Species	Cultivar Differences in Flooding Tolerance	Quantitative Trait Loci (QTL) Associated with Flooding Tolerance	Genome Sequence	-Omics Data on Flooding/Low-Oxygen Response
Monocots				
Zea mays	yes	yes (Table 2)	[45,46]	available
Triticum aestivum	yes	yes	[47]	not available
Hordeum vulgare	yes	yes (Table 3)	[48]	not available
Avena sativa	unknown	no	not available	not available
Secale cereale	unknown	no	[49]	not available
Lolium perenne	yes	yes	[50]	not available
Dicots				
Glycine max	yes	yes (Table 4)	[51]	available
Brassica napus	yes	yes	[52]	available
Helianthus annuus	unknown	no	[53]	not available
Beta vulgaris	unknown	no	[54]	not available
Solanum tuberosum	unknown	no	[55]	not available

3. Waterlogging Tolerance of Maize and Teosinte

The field crop maize (*Zea mays* L.) is not only a major human food source, but can also be used for animal feed as well as bioethanol production. However, it is relatively flooding-sensitive. Interestingly, maize has several close relatives with higher flooding tolerance, among them the teosinte species *Z. nicaraguensis*, *Z. luxurians*, and *Z. mays* ssp. *huehuetenangensis*. These species have been employed in the past as a basis to improve flooding tolerance of maize, similarly as a huge panel of maize cultivars, as described in detail below.

3.1. Morphological Adaptations of Teosinte as Tolerance Traits

The flooding tolerance of teosinte species has been largely associated with morphological modifications, namely the growth of adventitious roots, the formation of aerenchyma under non-flooded conditions as well as the establishment of a barrier against ROL [22,56,57]. Even under non-waterlogged conditions, *Z. nicaraguensis* and *Z. luxurians* are able to form large aerenchyma in the root cortex. These mechanisms improve aeration of flooded roots and thus enhance waterlogging tolerance [22,56,58]. Multiple QTL analyses revealed several loci associated with the constitutive

aerenchyma formation ([59–62], summarized in [63], see also Table 2). Similar studies have been done with another maize relative, *Z. luxurians* [64]. However, the gene(s) that are responsible for constitutive aerenchyma formation have not yet been identified.

Table 2. Overview over promising QTLs to improve flooding tolerance of maize (*Zea mays* L.).

Crossed Cultivars	Treatment	Trait for Tolerance	QTL	Position (Chr, cM)	Reference
Leaf traits					
Z. mays cv. F1649 × cv. H84	14 days waterlogging with starch solution	Leaf chlorosis	1.03-4	Chr 1	[68]
Z. nicaraguensis CIMMYT 13,451 × *Z. mays* Mi29	16 days waterlogging with starch solution	Leaf chlorosis	Qft-rd4.07-4.11	Chr 4	[69]
Z. mays cv. Mo18W × B73	48 h submergence	Leaf senescence	Subtol6	Chr 6 (162 Mb)	[70]
Adventitious root formation					
Z. mays ssp. *huehuetenangensis* × *Z. mays* B64	14 days waterlogging	Adventitious root formation	Qarf8.05 Qarf8.03 Qarf5.03	Chr 8 Chr 8 Chr 5	[66]
Z. mays cv. Na4 × B64	14 days waterlogging	Adventitious root formation	Qarf8.05	Chr 8	[71]
Z. mays ssp. *huehuetenangensis* × *Z. mays* Mi29	14 days waterlogging	Adventitious root formation	Qarf8.05 Qarf5.03	Chr 8 Chr 5	[67]
Z. nicaraguensis CIMMYT 13,451 × *Z. mays* Mi29	14 days waterlogging	Adventitious root formation	Qarf3.04 Qarf8.03	Chr 3 Chr 8	[67]
Constitutive aerenchyma formation					
Z. nicaraguensis CIMMYT 13,451 × *Z. mays* B64	none	Constitutive aerenchyma formation	Qaer1.07 Qaer1.02-3 Qaer5.09 Qaer8.06-7	Chr 1, 144 Chr 1, 35 Chr 5, 138 Chr 8, 97-101	[59]
Z. nicaraguensis CIMMYT 13,451 × *Z. mays* Mi29	none	Constitutive aerenchyma formation	Qaer1.06 Qaer1.11 Qaer5.09n	Chr 1 Chr 1 Chr 5	[60]
Z. nicaraguensis CIMMYT 13,451 × *Z. mays* Mi29	none	Constitutive aerenchyma formation	Qaer1.05-6 Qaer8.05	Chr 1, 45 Chr 8, 0	[61]
Z. luxurians × *Z. mays* B73	none	Constitutive aerenchyma formation	Qaer2.06 Qaer5.05-6	Chr 2, 88 Chr 5, 96	[64]
Formation of a barrier against radial oxygen loss (ROL)					
Z. nicaraguensis CIMMYT 13,451 × *Z. mays* Mi29	14 days stagnant nutrient solution	ROL formation		Chr 3	[65]

The formation of a barrier against ROL has been observed in *Z. nicaraguensis* under stagnant conditions (i.e., hypoxic nutrient solution), but not in *Z. mays* [22]. Even though maize can form aerenchyma under waterlogging, and therefore transport oxygen-rich air into the roots, root tips usually remain hypoxic. This is due to leaking of oxygen to the outside medium along the whole root. This radial oxygen loss is prevented in teosinte species by a tight barrier in the outer root layers. A locus on chromosome 3 of teosinte was involved in this formation and was sufficient to facilitate barrier formation in maize [65], but more studies need to be done to reveal the responsible gene.

Another close relative, *Z. mays* ssp. *huehuetenangensis*, has a larger potential to form adventitious roots than *Z. mays* cultivars [66,67] (see also Table 2). A QTL analysis suggested loci on chromosomes 4, 5, and 8, but the underlying gene(s) have not been identified yet. Also in *Z. nicaraguensis*, QTLs associated with adventitious root formation have been discovered on chromosomes 3 and 8 [67].

These studies suggest that there is a potential to improve maize flooding tolerance by manipulating its anatomical and morphological responses. It is now important to transfer more of these traits from teosinte into elite maize cultivars in order to improve their flooding tolerance, without negatively affecting yield and food quality. However, it remains to be elucidated, which and how many genes are required for this approach.

3.2. QTL Analyses of Maize Cultivars with Contrasting Flooding Tolerance

Several studies have compared waterlogging or submergence tolerance of different maize cultivars, for example of Chinese origin [72,73], tropic cultivars [74–76], or of a wide range of lines [70]. Thereby, analyses have either focused on metabolic changes, or on anatomical differences associated with tolerance.

Many of these experiments have been complemented with subsequent QTL analyses. For example, Mano et al. [71] determined QTLs associated with adventitious root formation between cultivars B64 and Na4 on chromosomes 3, 7, and 8, the latter potentially linked to a locus identified previously during a species comparison between maize and teosinte ([66], Table 2). Another QTL on chromosome 1 from the tolerant inbred line F1649 compared to sensitive H84 was associated with waterlogging tolerance under reducing conditions that often occur in flooded soils [68]. A cross between the tolerant cultivar HZ32 and the intolerant cultivar K12 [72] identified several gene loci associated with waterlogging tolerance [77–79]. Another cross of the tolerant HZ32 with sensitive Mo17 suggested the gene Cyp51 (of the Cytochrome P450 family) as a potential hypoxia tolerance gene [80]. Among tropical cultivars, tolerant CAWL-46-3-1 was compared to the sensitive line CML311-2-1-3, which again revealed several QTLs [81]. All of these QTLs await further characterization and a link to specific tolerance traits.

Growing knowledge of the molecular response of maize and teosinte to flooding might help during the identification of responsible genes for sensitivity and tolerance traits. The transcriptomic response of maize has been studied under several circumstances and with different goals. Laser microdissection in combination with microarray analysis has been used on root sections to study aerenchyma formation mechanisms [82,83], which could be used in future to improve elite cultivars, in combination with QTL analyses and the comparisons to teosinte as described above.

A comparative study of four maize cultivars with contrasting tolerance (Mo18W & M162W as tolerant and B97 & B73 as sensitive lines) analyzed the transcriptional response to submergence [70]. A major QTL on chromosome 6 was associated with submergence tolerance, Subtol6, but the underlying gene remains to be characterized. Another RNAseq analysis of several tropical maize lines with contrasting waterlogging tolerance also revealed many candidate genes that might be associated with flooding tolerance [76], among them one gene, GRMZM2G055704, that lies in a region on chromosome 1 that had been previously identified by other screens [78].

A comparison of the tolerant maize cultivar HKI1105 and the sensitive cultivar V372 under waterlogging observed the differential expression of many genes [84]. Subsequently, Arora et al. [85] studied the root transcriptional response under waterlogging of this tolerant cultivar and found metabolism-associated genes as well as genes related to aerenchyma formation that could be important for tolerance. Especially cell-wall-related genes could be important for maize tolerance [86], which is again associated with anatomical properties rather than with metabolic adaptations. Another set of cultivars, sensitive Mo17 and tolerant Hz32, was also studied at the transcript level [87–89]. In these experiments, many differentially expressed genes were observed, yet no gene was clearly associable with tolerance.

In summary, so far no gene or gene variant has been verified to be important for maize waterlogging tolerance. The complex regulatory network and multiple responses in morphology as well as metabolism make it unlikely to find the one gene that determines tolerance. Recent progress in sequencing technologies might help to speed up this process. Rather than laborious crosses between two genotypes with contrasting tolerance and subsequent screening of the progeny, information of many genotypes can be included into one analysis. For such genome-wide association studies

(GWAS), tolerance traits are correlated with single nucleotid polymorphisms (SNPs). This approach requires knowledge on the genomic sequence of the species (for an overview, see Table 1) as well as genotype-specific sequence information. This technique is now also used in order to improve waterlogging tolerance of maize [76,90].

4. Waterlogging Tolerance of Barley and Other Hordeum Species

Another major cereal for human food production is barley (*Hordeum vulgare* L.), used for brewery and animal feed. Barley is more flooding-sensitive than other cereals [91]. As maize, barley has flooding-tolerant relatives such as *H. marinum* and *H. spontaneum*, which have been utilized in studying flooding-tolerance mechanisms.

Several screens for waterlogging tolerance have been performed, for example with large cultivar collections [92,93] at the germination stage. However, smaller screens at later developmental stages might be more effective and practicable [91,94]. In such screens, scientists analyzed selections of Chinese cultivars [95,96], Australian cultivars [91], Nordic cultivars [97], or selections from bigger collections [98]. Thereby, screening methods and parameters observed differed considerably, leading to very different results.

Subsequent QTL analyses have been performed, but in many cases the association with a specific tolerance trait is still missing, making it hard to functionally study them. From the Nordic cultivars, several major QTLs were revealed by different crosses [99], but the underlying mechanisms or genes have not yet been identified. After the screening of the Chinese cultivars [95,96,100], several crosses were performed to do QTL analyses for tolerance traits. Crosses were done between tolerant TX9425 and sensitive Franklin [94], or with sensitive Naso Nijo [96]. Another QTL analysis was done between tolerant Yerong and sensitive Franklin [94,101,102]. Next, the tolerant line YYXT was used for a cross with the cultivar Franklin [103]. These studies revealed several major and minor QTLs that might be used in breeding (for an overview, see Table 3). Three examples that went further and focused on specific tolerance traits are described below.

Table 3. Promising QTLs from barley (*Hordeum vulgare*) and related species associated with waterlogging tolerance.

Tolerant Cultivar	Treatment	Parameters Analyzed	Name of QTL	Location of QTL (Chr, cM)	References
Hordeum vulgare L.					
cv. Yerong	9 weeks waterlogging	Survival rate	QWL.YeFr.4H QWL.YeFr.2H.2	4H, 108–117 2H, 113–118	[101]
cv. Yerong	7 days waterlogging	Aerenchyma formation		4H, 80.95–99.08	[104]
cv. YYXT	9 weeks waterlogging	Survival rate	QWl.YyFr.2H QWl.YyFr.3H QWl.YyFr.4H QWl.YyFr.6H	2H, 76.1 3H, 5.2 4H, 121.1 6H, 78.4	[103]
cv. YYXT	21 days stagnant solution	Root porosity		4H, 116	[105]
cv. Psaknon	18 days waterlogging	Chlorophyll fluorescence (ΦPSII)	QY1 QY2	6H, 114 7H, 59	[99]
cv. TX9425	2 days stagnant	Root membrane potential	QMP.TxNn.2H	2H, 8.85	[106]
H. spontaneum					
cv. TAM407227	7 days waterlogging	Aerenchyma formation	AER.4H	4H, 98.8	[107]

4.1. Morphological Adaptations in Hordeum Genotypes

Waterlogging tolerance of *H. marinum* is mediated by anatomical properties, namely high root porosity of adventitious roots as well as a barrier against ROL [108,109]. A study on 35 Hordeum species and genotypes revealed strong variation in the ability to anatomically adapt to waterlogging, by formation of aerenchyma or a barrier against ROL [110]. However, so far *H. marinum* has not been used in breeding processes to improve barley flooding tolerance, probably due to significant genetic variation between both species [110].

Also in some *H. vulgare* cultivar screens, scientists focused on anatomical differences between accessions. A cross between tolerant YYXT and sensitive Franklin was analyzed in respect of aerenchyma formation in adventitious roots leading to higher root porosity and therefore better survival [111]. The first study, still focusing on overall waterlogging tolerance, revealed four major QTLs [103], while a subsequent analysis exposed a major QTL on chromosome 4H associated with root porosity [105]. This QTL was confirmed again in another cross between tolerant Yerong and sensitive Franklin [104]. Moreover, in a cross between sensitive Franklin and tolerant *H. spontaneum*, this QTL was discovered besides several others [107]. Fine mapping narrowed down a region of 58 genes that are candidates underlying this waterlogging-tolerance trait [112]. Further studies are required to identify the responsible gene.

4.2. Root Ion Transport as a Tolerance Trait

Another comparison between two barley varieties focused on differences in root ion transport, namely the function of K^+ channels [113]. Root K^+ content was negatively affected under waterlogging in the sensitive variety Naso Nijo, but remained stable in the tolerant variety TX9425. Uptake of ions required for growth and metabolism is energy-dependent, and an energy deficiency under oxygen deficiency should negatively influence ion uptake processes [114]. Recently, a higher K^+ loss through the membrane under oxygen deficiency was associated with lower viability of the root cells [115]. A subsequent QTL analysis of a cross between the two cultivars revealed a major QTL on chromosome 2H underlying this tolerance trait [106]. However, it is currently not clear which gene is responsible for this trait, and whether proton pumps or K^+ channels are involved in the observed tolerance.

Although QTL analyses of barley under waterlogging have been extensively done, hardly anything is known on the transcriptional response to waterlogging as well as on proteomic and metabolomic changes. Very recently, proteomic changes under waterlogging were studied in different tolerant and sensitive barley cultivars, revealing more protection against ROS and higher fermentation capacity in the tolerant varieties [116]. More work is needed here in order to understand and interpret flooding responses in barley.

5. Analysis of Waterlogging Tolerance in Wheat

Wheat is one of the major cereals in Europe, and it is rather waterlogging-sensitive (e.g., [117]). Since wheat is a hexaploid species, the genetic analysis of this cereal is difficult. Furthermore, spring and winter wheat cultivars are available, making this species even more complex.

5.1. Variation in Wheat Waterlogging Tolerance

A number of waterlogging tolerance screens has been performed over many years. For example, van Ginkel et al. [118] tested 1344 lines of spring wheat from the Mexican CIMMYT (Centro Internacional de Mejoramiento de Maiz y Trigo) germplasm collection. A subsequent study re-analyzed six of them and included more lines, confirming the high waterlogging tolerance of the cultivar Ducula [119]. Some of these lines were further examined by crossing tolerant and sensitive lines, and suggested at least four genes to be involved in the tolerance mechanism(s) [120]. One mechanism could be the higher root porosity in waterlogged roots of tolerant lines [121]. This observation was also made

during a screen of Australian cultivars [122]. Additionally, a small analysis of only three lines revealed the importance of adventitious (seminal) roots and their porosity for waterlogging survival [117].

A screen of 34 winter wheat cultivars not only considered flooding, but also winter hardiness [123]. On a smaller scale, Huang et al. [124] identified Bayles as a sensitive and Savannah as a tolerant genotype out of six winter wheat cultivars. The usage of UK cultivars, however, did not result in superior genotypes [125]. Other screens tested further winter wheat cultivars, with different physiological parameters analyzed (e.g., mineral content [126], grain yield [127], root length [128,129]).

After identification of cultivars with different flooding tolerance, subsequent physiological studies tried to link the tolerance with certain morphological or metabolic traits. In one analysis, Savannah was more tolerant than Bayles partially due to higher root porosity [130]. A recent evaluation of Norwegian genotypes identified tolerant ones that showed specific root traits (e.g., stele and aerenchyma area) in comparison to sensitive cultivars [131,132]. Another experiment demonstrated that the tolerant cultivar Jackson was more tolerant than Coker 9835 probably because of a lower respiration rate [133]. Recently, the same cultivar Jackson was compared to sensitive Frument, and several metabolic differences were reported in leaves between both cultivars, but no clear tolerance mechanism has been found yet [134]. Another experimental set-up also considered different temperatures during a rather artificial anoxia treatment, demonstrating that genotypic differences were more pronounced at higher temperatures, but also here a single tolerance trait was not discovered [135].

Scientists have started to reveal underlying genes responsible for waterlogging tolerance by QTL analyses. A cross between two winter wheat cultivars, USG3209 and Jaypee, exposed two major QTLs on chromosomes 1B and 6D, to be used in further experiments [136]. The implication of the synthetic genotype W7984 together with the cultivated genotype Opata85 described 32 QTLs associated with waterlogging tolerance, which need to be studied further [137]. Another QTL analysis between SHWL1 and Chuanmai 32 discovered ten QTLs [138].

However, these diverse screens with different genotypes and at different locations also revealed a low reproducibility of tolerant and sensitive cultivars, as summarized in Setter et al. [139], pointing to multiple tolerance mechanisms that could be superior at one site, but not at other locations [91]. This could also be the reason for the lack of confirmed QTLs associated with waterlogging tolerance from different studies. The best strategy to continue would be the selection of one specific tolerance trait and its genetic analysis, as has already been done for barley varieties (see above).

5.2. Can Related Species be Used to Improve Wheat Waterlogging Tolerance?

So far, the classical QTL approach has not revealed single tolerance genes or loci in wheat. A different interesting approach was developed in Australia: An amphiploid from wheat with the tolerant grass *H. marinum* was created in order to produce flooding-tolerant wheat cultivars [140]. This approach resulted in some lines with a stronger barrier against ROL [141]. However, those lines show lower growth and grain yield, and are therefore not yet suitable for agriculture. So far, this morphological trait could not be transferred to wheat by use of disomic chromosome addition lines [142]. More analyses are required in order to be successful with this approach.

Potentially, also in wheat there are more flooding-tolerant relatives such as *Triticum macha* L. or *T. dicoccum* cv. Pontus [143], or *T. spelta* [144] that could be used in improving flooding tolerance of wheat. The latter species was included in a QTL analysis that revealed several loci associated with flooding tolerance at the germination state, among them five that were related to enhanced coleoptile growth [145]. However, this developmental stage does not necessarily help in improving waterlogging tolerance in the field.

Despite the wealth of greenhouse and field trials, there is not much progress yet in understanding wheat molecular responses to waterlogging, or in improving its waterlogging tolerance. Studies at the transcriptomic, proteomic, and metabolomic level are required to first understand the reason for the sensitivity of wheat cultivars in order to use this as a base for breeding. Probably the most promising direction would be the introduction of morphological changes that could be transferred from

related species. Recent experiments have begun to understand how aerenchyma formation in wheat is regulated [146,147], but also knowledge from other grass species such as rice, maize, and barley should be used.

6. Flooding Tolerance of Ryegrass

One of the most important pasture grasses, *Lolium perenne* L., is often grown on soils not suitable for cereals, for example due to poor drainage. Therefore, it is also a target species to improve its waterlogging tolerance.

One comparison of two genotypes, Aurora6 and Nth African6, together with two F1 lines, was done after four weeks of waterlogging, and Aurora6 was more tolerant than the other genotypes [148]. This cross was subsequently used for a QTL analysis, and 37 loci were identified that were associated with waterlogging tolerance [149]. Another four varieties were studied after one week of waterlogging [150]. Here, antioxidant activity was correlated with waterlogging tolerance. However, more work needs to be done to find loci or genes that are associated with *Lolium perenne* L. waterlogging tolerance.

Another set of studies analyzed the submergence tolerance of 94 to 99 genotypes. In one publication, the behavior of the genotypes was evaluated after seven days of submergence and seven days of recovery, and differential responses of genotypes were observed, ranging from sensitive cultivars to tolerant cultivars with either the quiescence or the escape strategy [151]. This study is an exciting start point for further experiments. In another study, submergence tolerance was correlated with simple sequence repeat (SSR) markers across all genotypes [152]. Finally, a targeted approach was used, and candidate genes were selected from previous physiological experiments and analyzed for SNPs to be related to submergence tolerance [153]. However, verification of these candidate genes is still required.

In summary, work on *Lolium perenne* L. waterlogging and submergence tolerance has only just started. More cultivar screens and QTL analyses are needed, preferentially with specific traits in morphology and metabolism. Furthermore, little is known on the molecular response of ryegrass to waterlogging and submergence, and transcriptomic as well as metabolomic studies need to be done in order to build a basis for breeders and scientists.

7. Soybean Tolerance under Waterlogging

Soybean is a very important crop that can be used as protein-rich food for humans, but is mostly utilized as animal feed. As most other crop species, it is very waterlogging sensitive. In some regions of the world, for example in the mid-south of the US or in Asia, it is grown in rotation with rice on fields that are often flood-prone [154,155]. An improvement of its waterlogging tolerance is therefore of great importance.

Soybean plants are of special importance for food production since they are able to fix nitrogen from air in their nodules with the help of rhizobia, and can facilitate soil enrichment with organic nitrogen compounds. Although nitrogenase is sensitive to oxygen and is therefore protected inside the bacteroids in the nodules, the nitrogen fixation process is very energy-demanding. Therefore, nitrogen fixation quickly stops after waterlogging of soybean roots and nodules, even before roots become fully hypoxic [156].

7.1. Screening for Waterlogging Tolerance in the US and Asia

A first screen on 84 Northern soybean cultivars revealed great variation in waterlogging tolerance [157]. Using one selected tolerant cultivar, Archer, two recombinant inbred line (RIL) populations were created with the sensitive northern cultivars Noir 1 and Minsoy. These were used in a QTL analysis, which exposed one major locus, Sat_064, located on chromosome 18, to be involved in the tolerance [158]. This locus was crossed into two southern genotypes to create near isogenic lines (NILs), but their waterlogging tolerance could not be related to the presence or absence of this

locus [154]. Therefore, further analyses tried to identify other QTLs related to waterlogging tolerance in Archer in RILs emerging from crosses with two southern soybean cultivars, A5403 and P9641. These efforts revealed at least five more markers, for example on chromosomes 5 and 13, pointing to several genes involved in stress tolerance [159,160] (see also Table 4). Further crosses of these genotypes produced some RILs and NILs with improved waterlogging tolerance [161], but no distinct gene has yet been associated with the waterlogging tolerance of the cultivar Archer.

Another line combination was used to study flooding tolerance and resistance to the pathogen *Phytophthora sojae*, namely the susceptible elite cultivar S99-2281 and the tolerant exotic cultivar PI 408105A [162]. This analysis identified four QTLs associated with flooding tolerance on chromosomes 11 and 13, of which one overlapped with a QTL for resistance to *Phytophthora sojae* (see also Table 4). Subsequently, physiological features between these two lines were compared that might underlay differences in tolerance [163–166]. Multiple differences were observed between the two genotypes studied, for example in respect to adventitious root and aerenchyma formation (more in the tolerant genotype), gene expression of SUB1-like transcription factors, as well as abscisic acid networks. However, the major contributing factor remains to be determined. Interestingly, differences in adventitious root formation were also observed between Vietnamese genotypes with contrasting tolerance [167], hinting at an importance of morphological traits, as also seen for cereals (see above). Crosses of the susceptible line S99-2281 and another tolerant line, PI 561271, revealed two more QTLs on chromosomes 3 and 10 [160,168] (see also Table 4). The QTL at chromosome 3 was narrowed down to a region of 23 genes, and research is ongoing to identify the responsible tolerance gene [168].

Marker-assisted selection was used to transfer those QTLs into high-yield cultivars, resulting in three new flooding-tolerant germplasm lines for application in breeding programs [160]. Still, further screens with up to 722 cultivars are ongoing, in order to further improve und understand soybean waterlogging tolerance [169,170].

Also in Asia, soybean is increasingly grown on rice paddy fields. Therefore, also Japanese soybean cultivars were used for tolerance screens. A cross between the tolerant cultivar Misuzudaizu and the sensitive cultivar Moshidou Gong 503 was evaluated for waterlogging tolerance of young soybean plants, revealing several QTLs [155]. Other screens were performed with 92 Japanese cultivars [171], 400 Korean cultivars [172], 21 Vietnamese cultivars [173], and 16 Indonesian cultivars [174], or mixtures of different origin [175,176].

Table 4. QTLs associated with waterlogging tolerance in soybean (*Glycine max* (L.) Merr.).

Crossed Cultivars	Treatment	Parameters Analyzed	Name of QTL	Location of QTL	References
cv. Archer × northers lines	14 days waterlogging	Plant growth, seed yield	Gm18	Chr 18, Sat_064	[158]
cv. Archer × southern lines	14 days waterlogging	Damages and survival	Gm5 Gm13	Chr 5, Satt385 Chr 13, Satt269	[159,160]
cv. Misuzudaizu × cv. Moshidou Gong 503	21 days waterlogging	Seed yield	ft1	Chr 6, Satt100	[155]
cv. S99-2281 × cv. PI 408105A	14 days waterlogging	Damages and survival	FTS11 FTS13	Chr 11 Chr 13	[162]
cv. S99-2281 × cv. PI 561271	4–6 days waterlogging	Damages and survival	qWT_Gm03 qWT_Gm10	Chr 3 Chr 10	[160,168]
cv. Iyodaizu × cv. Tachinagaha	7 days 0.1% stagnant agar solution	Root traits	Qhti-12-2	Chr 12, Satt052-Satt302	[177]

In all of those screens, differences in waterlogging tolerance were observed, but physiological and genetic factors underlying these tolerance differences could be studied further only in a few cases. For example, the tolerant Japanese variety Iyodaizu was used for a QTL analysis with sensitive Tachinagaha. Scientists identified 11 QTLs, of which a QTL region on chromosome 12 was most promising, as shown also with NILs [177]. Next, as for other species, soybean seed germination is likewise oxygen dependent. Therefore, seed germination was also studied in several Asian cultivars, revealing four QTLs related to a high germination rate under water [178].

Recently, GWAS have emerged as another strategy to identify genomic loci associated with waterlogging tolerance, and has been used to study another legume, *Phaseolus vulgaris* L. (e.g., [179,180]). These experiments discovered an interesting overlap between *Phaseolus vulgaris* L. flooding tolerance loci with soybean QTLs [179], namely with Sat_064 [158] and Satt187 [178]. Furthermore, Soybean (*agronomy-328455*) has also a close relative that is more waterlogging-tolerant, namely *G. sojae*, which could be included in breeding programs for higher tolerance [160].

7.2. Physiological and Molecular Responses of Soybean to Waterlogging

During one screen of soybean cultivars, scientists discovered spongy white roots in the cultivar Manokin, pointing to an aerenchyma-like structure, but this was not observed in the most tolerant cultivar Delsoy 4710 [181]. Such secondary aerenchyma around roots, stems, and nodules, emerging from phellem, has been observed before in waterlogged soybean, and might improve aeration of the flooded tissues [182,183]. In contrast to several grasses, soybean develops only small primary aerenchyma in its root cortex [184]. Whether secondary aerenchyma formation or their extension is generally related to waterlogging tolerance, remains to be studied. Some experiments suggest that morphological parameters such as adventitious root formation or root porosity might be associated with higher tolerance also in soybean [163,164,167].

The molecular response of soybean to flooding has been well studied already, especially at the proteome level, using different organs, developmental stages, and treatment conditions (summarized in [185]). In one study, several tolerant and sensitive Asian lines, classified at the seedling stage, were analyzed at the proteome level [175]. These experiments revealed multiple differences in protein expression among genotypes but no obvious trend, pointing to multiple tolerance factors.

Also the transcriptional response has been studied in several experiments, providing a rich base for future functional analyses. For example, the response of leaves to seven days of waterlogging treatment of the roots was explored by RNAseq, showing a negative impact of root stress on leaf photosynthesis [186]. Also roots were investigated directly after root hypoxia [187,188]. The same group also developed a flooding-tolerant soybean mutant, by gamma-irradiation [189] which was compared to wildtype soybean. This study revealed many genes that were differentially expressed between both genotypes [190], but a subsequent analysis of candidate genes responsible for tolerance is required, as well as the identification of the mutation.

8. Waterlogging Tolerance of *Brassica napus* L. and Relatives

Rape (*Brassica napus* L.) is an important oil crop and can also be used as animal feed. It has a complex genetic structure since it is an allotetraploid species that originated from the two diploid species *B. rapa* and *B. oleracea*. Despite its rather recent origin, a wide range of cultivars exists ranging from winter to spring types, but also semi-winter types can be found for example in China (e.g., [191]). Rape is very sensitive to waterlogging, even if compared to other Brassica species [192]. This is at least in part due to its inability to form aerenchyma [193], similar to its parent *B. rapa* [194].

8.1. Chinese Semi-Winter Rape Cultivars Show Contrasting Waterlogging Tolerance

So far, most data available for rape waterlogging tolerance come from Chinese semi-winter cultivars. The interest in flooding tolerance of Chinese cultivars is due to the fact that rape in China is often used as a rotation crop on rice paddy fields, and therefore it is often affected by waterlogging.

A comparison of 18 cultivars, with different seed coat color, tested germination ability after 24 h of submergence. Interestingly, yellow-colored cultivars were mainly sensitive to submergence at the seed stage, including GH01, and dark-colored cultivars were mainly tolerant, including Zhongshuang 9 and 10 [195]. These cultivars also came up in other screens for waterlogging tolerance [196]. Further screens with more Chinese lines were performed at later developmental stages [197–199], confirmed previous tolerant lines (Zhongshuang 9 and 10), and identified further lines to be tolerant (Xiangyou 13, Huayouza 9, Ningyou 12) and sensitive (Yuhuang 1, Zhongyouza 3, Zhongshuang 8).

A subsequent genetic analysis suggested two genes to be involved in waterlogging tolerance of Zhongshuang 9, but no QTL has been described yet underlying this tolerance [200]. A cross between six cultivars differing in waterlogging tolerance revealed additive and non-additive effects pointing to several genes or alleles involved, with Zhongshuang 9 being the most potent cultivar [201]. An independent group used a double haploid population between two lines different from the ones mentioned above with high and low waterlogging and drought tolerance [202]. They identified at least 11 QTL for waterlogging tolerance, suggesting a complex regulation also in this species.

An attempt to associate waterlogging tolerance with physiological traits suggested the importance of the antioxidant system [196]. Other analyses observed a difference in nitrate metabolism between two Chinese cultivars under waterlogging [203]. Furthermore, a correlation of low ethanolic fermentation and higher waterlogging tolerance was described [204].

So far, there is little knowledge on the molecular response of rape to waterlogging or submergence, making it hard to find a basis to select candidate genes in the QTL regions. A first attempt to solve this problem was done on two Chinese cultivars with contrasting waterlogging tolerance, GH01 and Zhongshuang 9 [205,206]. The transcriptional response of roots to 12 h of waterlogging was studied by use of RNAseq, and many genes responded to the stress treatment, mainly similar in both genotypes. However, there were some differences between the two cultivars, possibly related to the plant hormone abscisic acid, but this has to be explored further. Unfortunately, these two lines have not yet been subjected to a full QTL analysis. Another transcriptomic study focused on shoot responses after 36 and 72 h of waterlogging, revealing downregulation of photosynthesis [207], as was also shown for soybean [186].

8.2. Can Relatives of Brassica napus Help to Enhance Its Flooding Tolerance?

The genus Brassica contains, among other species, the diploid species *B. rapa*, *B. nigra*, and *B. oleracea*, and the allotretraploid species *B. juncea*, *B. napus*, and *B. carinata*, which often contain multiple subspecies and cultivars (e.g., [208]). Little is known on waterlogging tolerance of other Brassica species, besides one study that described *B. juncea* and *B. carinata* as more waterlogging tolerant than rape [192]. A direct comparison of rape with diploid Brassica species under waterlogging would be most helpful.

So far, some other diploid Brassica species have been studied on their own, revealing also cultivar differences in flooding tolerance. An analysis with two populations of *B. rapa* with different waterlogging tolerance suggested the importance of carbohydrate supply to roots as a potential parameter for tolerance [209]. Second, *B. oleracea* was studied at the seed stage. As reported for other species above, seed germination of Brassica species is particularly strongly dependent on oxygen. A QTL analysis between two *B. oleracea* cultivars, a sensitive Chinese cultivar (A12DHd) and a more tolerant calabrese cultivar (GDDH33), revealed three QTLs that are associated with germination ability under low-oxygen concentrations [210], but associated genes have not yet been identified.

The relative high relatedness of rape to the well-studied model Brassicaceae *Arabidopsis thaliana* (L.) Heynh. might be another way to use existing knowledge in improving rape waterlogging tolerance. First ecotype screens on Arabidopsis have demonstrated differences in submergence tolerance [11, 42–44]. However, since Arabidopsis is also rather flooding-sensitive, the analysis of flooding-tolerant Brassicaceae, for example from the *Rorippa* genus [211,212], might be more suitable.

9. Conclusions

Over recent years, many studies have been published on flooding-tolerant cultivars of temperate crop species. In several cases, QTLs could be discovered, and certain tolerance-related traits were described. However, in most studies, the underlying mechanism(s) or the responsible gene(s) have not yet been identified. It is therefore of great importance to continue with well-designed QTL analyses in order to truly improve crop resistance to flooding. All studies so far have demonstrated that a QTL analysis is only promising when it is associated with a specific, well-defined tolerance trait. The most promising traits so far have been related to morphological adaptations that appear to be similar across genera, such as enhanced root porosity, a barrier against ROL, and the formation of adventitious roots. Metabolic adaptations could be related to the antioxidant system, and to primary metabolism, mainly to carbohydrate availability. However, metabolic traits are rather hard to compare in a large collection of cultivars. The knowledge on the overall crop response to the stress at the transcriptomic, proteomic, and metabolomic level will certainly help to understand the molecular mechanisms that provide the basis for underlying tolerance traits.

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