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ARTICLE ADDENDUM

Variation in Arabidopsis flooding responses identifies numerous putative "tolerance genes"

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ABSTRACT
Plant survival in flooded environments requires a combinatory response to multiple stress conditions such as limited light availability, reduced gas exchange and nutrient uptake. The ability to fine-tune the molecular response at the transcriptional and/or post-transcriptional level that can eventually lead to metabolic and anatomical adjustments are the underlying requirements to confer tolerance. Previously, we compared the transcriptomic adjustment of submergence tolerant, intolerant accessions and identified a core conserved and genotype-specific response to flooding stress, identifying numerous 'putative' tolerance genes. Here, we performed genome wide association analyses on 81 natural Arabidopsis accessions that identified 30 additional SNP markers associated with flooding tolerance. We argue that, given the many genes associated with flooding tolerance in Arabidopsis, improving resistance to submergence requires numerous genetic changes.

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KEYWORDS
Dark; genome wide association; submergence; hypoxia

Flooding is a natural phenomenon that shapes plant ecosystems and also negatively affects crop yields in agricultural areas.[1-3] The frequency and intensity of floods are expected to increase with the current climate change and floods are cataloged as one of the most expensive natural disasters to cause widespread crop-damage.[3] The dramatic negative impact of submergence on plants, mainly caused by reduced gas exchange underwater, provides us with a major challenge to understand and improve crop tolerance to flooding. Interestingly, many species occur naturally on floodplains and have evolved a suite of traits to thrive and survive during periods of flooding.[4] These survival strategies can be roughly divided into 2 classes, firstly cessation of growth to retain valuable resources needed for regrowth when the flood recedes, and secondly the creation of improved aeration through the development of adventitious roots and active shoot growth toward the water surface to snorkel for air and light.[5] The molecular mechanisms of these traits in wild species are gradually being elucidated.[6-8] However, these thrive-and-survive traits are naturally not, or only to a limited extent, present in crops, and incorporation of these traits will be challenging. An exception is SUB1A rice, where a naturally occurring allele confers a growth cessation strategy and subsequent tolerance when completely submerged.[9] Despite a lack of specialist traits in other species and crops, large intra-species variation in flooding-tolerance does exist, which could potentially point to key players that modulate tolerance and serve as a basis for crop improvement.

Such within species variation was explored by Vashisht et al. (2011) to uncover a relatively large variation in flooding tolerance among 86 Arabidopsis accessions.[11] A completely submerged plant is challenged with a compound environmental stress consisting of reduced light availability and limited gas exchange. Therefore, the authors estimated tolerance to both the compound stress (submergence and darkness) and to darkness without submergence. Hence not only the ability to withstand compound flooding stress was assessed, but it could also be compared to the ability to tolerate darkness to estimate relative submergence tolerance (hazard ratio). This effectively allowed separation of different stress factors associated with the underwater environment, such as internal ethylene accumulation and a reduction in oxygen availability, from starvation effects caused by a prolonged period in darkness. Interestingly, neither tolerance to complete submergence nor the relative submergence tolerance could be associated with traits considered crucial for survival, such as tissue diameter, length, respiration rate, internal oxygen levels, tissue porosity and initial carbohydrate availability.

In order to understand the processes that govern the observed phenotypic variation in submergence tolerance, the transcriptional shift upon darkness and submergence of tolerant and sensitive accessions were investigated for both the root and shoot.[10] The study identified a strong overlap in the responses between accessions, and a prominent effect of darkness with relatively minor additional response by submergence. Important transcriptomic changes, including alternative splicing, pointed to a major role of autophagy for all accessions, with stronger activation in tolerant genotypes. Additionally, regardless of genotype, several fundamental differences were observed between shoots and roots,

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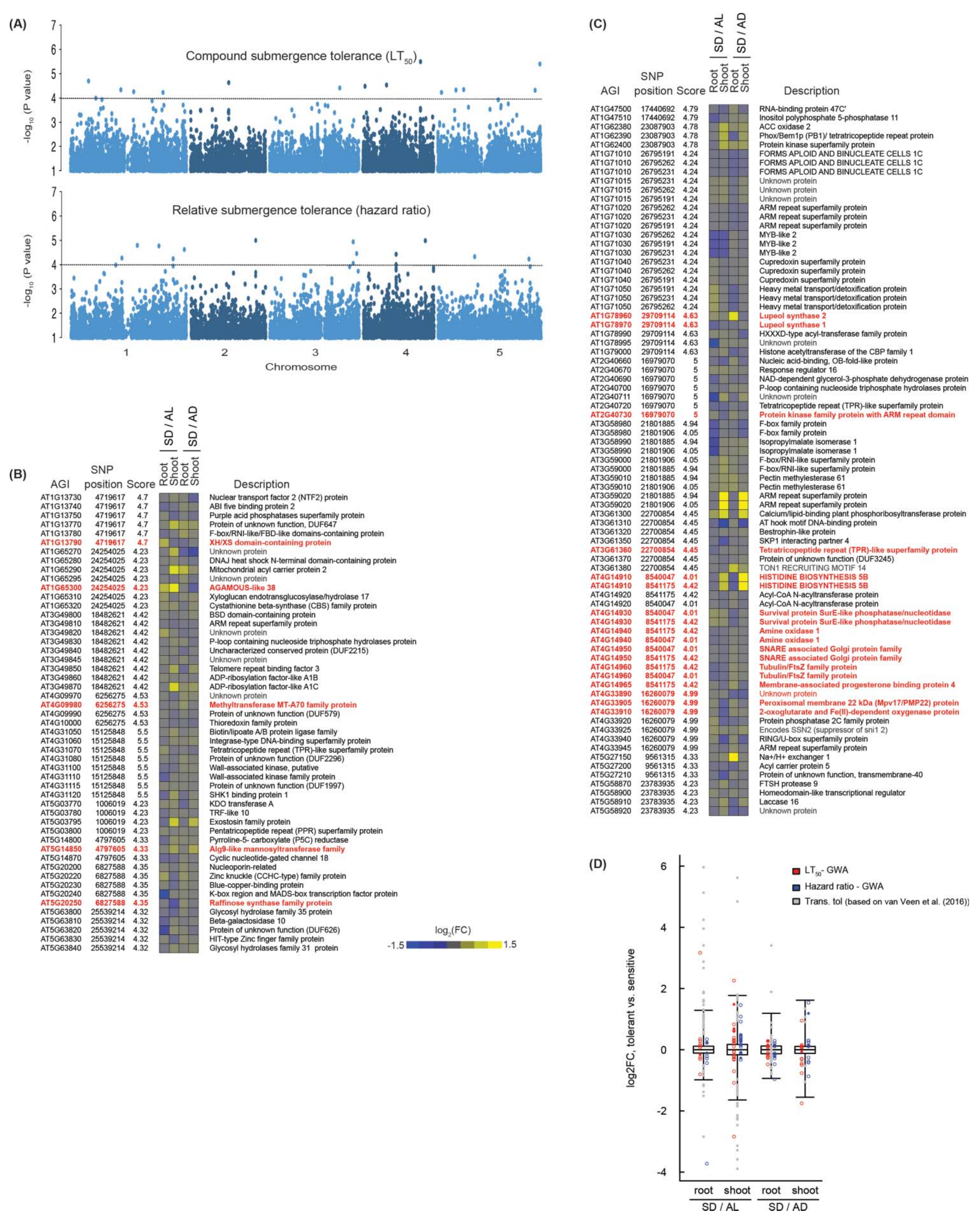

(B)

AGI	SNP position	Score	Description
AT1G13730	4719617	4.7	Nuclear transport factor 2 (NTF2) protein
AT1G13740	4719617	4.7	ABI five binding protein 2
AT1G13750	4719617	4.7	Purple acid phosphatases superfamily protein
AT1G13770	4719617	4.7	Protein of unknown function, DUF647
AT1G13780	4719617	4.7	F-box/RNI-like/FBD-like domains-containing protein
AT1G13790	**4719617**	**4.7**	**XH/XS domain-containing protein**
AT1G65270	24254025	4.23	Unknown protein
AT1G65280	24254025	4.23	DNAJ heat shock N-terminal domain-containing protein
AT1G65290	24254025	4.23	Mitochondrial acyl carrier protein 2
AT1G65295	24254025	4.23	Unknown protein
AT1G65300	**24254025**	**4.23**	**AGAMOUS-like 38**
AT1G65310	24254025	4.23	Xyloglucan endotransglucosylase/hydrolase 17
AT1G65320	24254025	4.23	Cystathionine beta-synthase (CBS) family protein
AT3G49800	18482621	4.42	BSD domain-containing protein
AT3G49810	18482621	4.42	ARM repeat superfamily protein
AT3G49820	18482621	4.42	Unknown protein
AT3G49830	18482621	4.42	P-loop containing nucleoside triphosphate hydrolases protein
AT3G49840	18482621	4.42	Uncharacterized conserved protein (DUF2215)
AT3G49845	18482621	4.42	Unknown protein
AT3G49850	18482621	4.42	Telomere repeat binding factor 3
AT3G49860	18482621	4.42	ADP-ribosylation factor-like A1B
AT3G49870	18482621	4.42	ADP-ribosylation factor-like A1C
AT4G09970	6256275	4.53	Unknown protein
AT4G09980	**6256275**	**4.53**	**Methyltransferase MT-A70 family protein**
AT4G09990	6256275	4.53	Protein of unknown function (DUF579)
AT4G10000	6256275	4.53	Thioredoxin family protein
AT4G31050	15125848	5.5	Biotin/lipoate A/B protein ligase family
AT4G31060	15125848	5.5	Integrase-type DNA-binding superfamily protein
AT4G31070	15125848	5.5	Tetratricopeptide repeat (TPR)-like superfamily protein
AT4G31080	15125848	5.5	Protein of unknown function (DUF2296)
AT4G31100	15125848	5.5	Wall-associated kinase, putative
AT4G31110	15125848	5.5	Wall-associated kinase family protein
AT4G31115	15125848	5.5	Protein of unknown function (DUF1997)
AT4G31120	15125848	5.5	SHK1 binding protein 1
AT5G03770	1006019	4.23	KDO transferase A
AT5G03780	1006019	4.23	TRF-like 10
AT5G03795	1006019	4.23	Exostosin family protein
AT5G03800	1006019	4.23	Pentatricopeptide repeat (PPR) superfamily protein
AT5G14800	4797605	4.33	Pyrroline-5- carboxylate (P5C) reductase
AT5G14850	**4797605**	**4.33**	**Alg9-like mannosyltransferase family**
AT5G14870	4797605	4.33	Cyclic nucleotide-gated channel 18
AT5G20200	6827588	4.35	Nucleoporin-related
AT5G20220	6827588	4.35	Zinc knuckle (CCHC-type) family protein
AT5G20230	6827588	4.35	Blue-copper-binding protein
AT5G20240	6827588	4.35	K-box region and MADS-box transcription factor protein
AT5G20250	**6827588**	**4.35**	**Raffinose synthase family protein**
AT5G63800	25539214	4.32	Glycosyl hydrolase family 35 protein
AT5G63810	25539214	4.32	Beta-galactosidase 10
AT5G63820	25539214	4.32	Protein of unknown function (DUF626)
AT5G63830	25539214	4.32	HIT-type Zinc finger family protein
AT5G63840	25539214	4.32	Glycosyl hydrolases family 31 protein

(C)

AGI	SNP position	Score	Description
AT1G47500	17440692	4.79	RNA-binding protein 47C'
AT1G47510	17440692	4.79	Inositol polyphosphate 5-phosphatase 11
AT1G62380	23087903	4.78	ACC oxidase 2
AT1G62390	23087903	4.78	Phox/Bem1p (PB1)/ tetratricopeptide repeat protein
AT1G62400	23087903	4.78	Protein kinase superfamily protein
AT1G71010	26795191	4.24	FORMS APLOID AND BINUCLEATE CELLS 1C
AT1G71010	26795262	4.24	FORMS APLOID AND BINUCLEATE CELLS 1C
AT1G71010	26795231	4.24	FORMS APLOID AND BINUCLEATE CELLS 1C
AT1G71015	26795231	4.24	Unknown protein
AT1G71015	26795262	4.24	Unknown protein
AT1G71015	26795191	4.24	Unknown protein
AT1G71020	26795262	4.24	ARM repeat superfamily protein
AT1G71020	26795231	4.24	ARM repeat superfamily protein
AT1G71020	26795191	4.24	ARM repeat superfamily protein
AT1G71030	26795262	4.24	MYB-like 2
AT1G71030	26795191	4.24	MYB-like 2
AT1G71030	26795231	4.24	MYB-like 2
AT1G71040	26795231	4.24	Cupredoxin superfamily protein
AT1G71040	26795262	4.24	Cupredoxin superfamily protein
AT1G71040	26795191	4.24	Cupredoxin superfamily protein
AT1G71050	26795191	4.24	Heavy metal transport/detoxification protein
AT1G71050	26795231	4.24	Heavy metal transport/detoxification protein
AT1G71050	26795262	4.24	Heavy metal transport/detoxification protein
AT1G78960	**29709114**	**4.63**	**Lupeol synthase 2**
AT1G78970	**29709114**	**4.63**	**Lupeol synthase 1**
AT1G78990	29709114	4.63	HXXXD-type acyl-transferase family protein
AT1G78995	29709114	4.63	Unknown protein
AT1G79000	29709114	4.63	Histone acetyltransferase of the CBP family 1
AT2G40660	16979070	5	Nucleic acid-binding, OB-fold-like protein
AT2G40670	16979070	5	Response regulator 16
AT2G40690	16979070	5	NAD-dependent glycerol-3-phosphate dehydrogenase protein
AT2G40700	16979070	5	P-loop containing nucleoside triphosphate hydrolases protein
AT2G40711	16979070	5	Unknown protein
AT2G40720	16979070	5	Tetratricopeptide repeat (TPR)-like superfamily protein
AT2G40730	**16979070**	**5**	**Protein kinase family protein with ARM repeat domain**
AT3G58980	21801885	4.94	F-box family protein
AT3G58980	21801906	4.05	F-box family protein
AT3G58990	21801885	4.94	Isopropylmalate isomerase 1
AT3G58990	21801906	4.05	Isopropylmalate isomerase 1
AT3G59000	21801906	4.05	F-box/RNI-like superfamily protein
AT3G59000	21801885	4.94	F-box/RNI-like superfamily protein
AT3G59010	21801885	4.94	Pectin methylesterase 61
AT3G59010	21801906	4.05	Pectin methylesterase 61
AT3G59020	21801885	4.94	ARM repeat superfamily protein
AT3G59020	21801906	4.05	ARM repeat superfamily protein
AT3G61300	22700854	4.45	Calcium/lipid-binding plant phosphoribosyltransferase protein
AT3G61310	22700854	4.45	AT hook motif DNA-binding protein
AT3G61320	22700854	4.45	Bestrophin-like protein
AT3G61350	22700854	4.45	SKP1 interacting partner 4
AT3G61360	**22700854**	**4.45**	**Tetratricopeptide repeat (TPR)-like superfamily protein**
AT3G61370	22700854	4.45	Protein of unknown function (DUF3245)
AT3G61380	22700854	4.45	TON1 RECRUITING MOTIF 14
AT4G14910	**8540047**	**4.01**	**HISTIDINE BIOSYNTHESIS 5B**
AT4G14910	**8541175**	**4.42**	**HISTIDINE BIOSYNTHESIS 5B**
AT4G14920	8541175	4.42	Acyl-CoA N-acyltransferase protein
AT4G14920	8540047	4.01	Acyl-CoA N-acyltransferase protein
AT4G14930	**8540047**	**4.01**	**Survival protein SurE-like phosphatase/nucleotidase**
AT4G14930	**8541175**	**4.42**	**Survival protein SurE-like phosphatase/nucleotidase**
AT4G14940	**8541175**	**4.42**	**Amine oxidase 1**
AT4G14940	**8540047**	**4.01**	**Amine oxidase 1**
AT4G14950	**8540047**	**4.01**	**SNARE associated Golgi protein family**
AT4G14950	**8541175**	**4.42**	**SNARE associated Golgi protein family**
AT4G14960	**8541175**	**4.42**	**Tubulin/FtsZ family protein**
AT4G14960	**8540047**	**4.01**	**Tubulin/FtsZ family protein**
AT4G14965	**8541175**	**4.42**	**Membrane-associated progesterone binding protein 4**
AT4G33890	**16260079**	**4.99**	Unknown protein
AT4G33905	**16260079**	**4.99**	**Peroxisomal membrane 22 kDa (Mpv17/PMP22) protein**
AT4G33910	**16260079**	**4.99**	**2-oxoglutarate and Fe(II)-dependent oxygenase protein**
AT4G33920	16260079	4.99	Protein phosphatase 2C family protein
AT4G33925	16260079	4.99	Encodes SSN2 (suppressor of sni1 2)
AT4G33940	16260079	4.99	RING/U-box superfamily protein
AT4G33945	16260079	4.99	ARM repeat superfamily protein
AT5G27150	9561315	4.33	Na+/H+ exchanger 1
AT5G27200	9561315	4.33	Acyl carrier protein 5
AT5G27210	9561315	4.33	Protein of unknown function, transmembrane-40
AT5G58870	23783935	4.23	FTSH protease 9
AT5G58900	23783935	4.23	Homeodomain-like transcriptional regulator
AT5G58910	23783935	4.23	Laccase 16
AT5G58920	23783935	4.23	Unknown protein

Figure 1. Genetic and transcriptomic associations with flooding tolerance. (A) Manhattan plots of GWA results showing association between SNP markers and tolerance to compound submergence stress (LT_{50}) and relative submergence tolerance (hazard ratio). Alternating shades of blue represents the 5 individual chromosomes of Arabidopsis. SNP markers above the dashed line ($-\log_{10}(P_{val}) > 4$) were explored to identify tolerance associated genes. (B and C) List of genes within +/− 10 kb region of associated SNP markers for compound submergence tolerance (B) and relative tolerance (C). Genes with tolerance specific SNPs among the top 5 tolerant and 5 sensitive accessions[11] are marked red. For these genes a specific variant in the promoter/exon (e.g. SNP) was at least present in 4 tolerant accessions and at most in 1 sensitive accession, and vice versa. The differences in the transcriptomic response ($\log_2$(FC)) to submergence between 3 tolerant and 3 sensitive accessions[10] are shown in the heatmap. (D) Expression values ($\log_2$FC) of GWA and transcriptome[10] derived putative tolerance (trans.tol) genes. Red and blue circles represent GWA genes for compound submergence (LT_{50}) tolerance and relative submergence tolerance (Hazard ratio). Closed circles are GWA derived genes with tolerance specific SNP variation (see B and C). Gray circles depict the transcriptome derived putative tolerance genes (trans.tol) for their corresponding comparison. The boxes show the second and third quartile and the whiskers identify the 2 to 98 % range of all genes transcriptomically investigated by van Veen et al.[10] SD/AL: compound, submergence in dark (SD) compared to air light (AL) conditions; SD/AD: compound submergence compared to air dark (AD) conditions; R, root; S, shoot.

with reprogramming of growth regulatory components in the shoot while chloroplast localized and photosynthesis related genes were common among root-specific genes. With regard to explaining the phenotypic variation, van Veen et al. (2016)[10] identified 126 putative 'tolerance' genes that were induced differently in tolerant and sensitive accessions. Interestingly, there was hardly any overlap between the organs. These 'tolerance' genes were characterized not so much by contrasting regulation, but rather by quantitative differences. This led to the hypothesis that tolerance is due to a relatively large number of small changes. Transcriptomic differences during the initial stress acclimation response are of course of great importance, but can never provide a full picture of the genetic basis of tolerance variation. To provide more information on potential tolerance genes, we revisited the carefully collected dataset by Vashisht et al. (2011) of submergence tolerance variation within Arabidopsis. In order to correlate genetic variants to flooding tolerance, we performed genome wide association (GWA) on the survival score (LT_{50}: the number of days after which 50% of the population is dead) of 81 genotyped accessions under compound submergences and relative submergence tolerance, the latter accounted for sensitivity to darkness w.r.t submergence and darkness together (Hazard ratio).[11]

The genome wide associations between the LT_{50} and hazard ratio with 250K SNP markers of 81 accessions were computed using a linear mixed model (EMMA) on the publically available GWA portal (https://gwas.gmi.oeaw.ac.at). In order to identify phenotype associated genes, we examined SNPs with a minor allele frequency count of more than 10 and peaks with a Bonferroni corrected $-\log_{10}$(Pvalue) of more than four. Our analysis identified 14 and 16 SNP markers that are associated with LT_{50} and hazard ratio respectively (Fig. 1A). Genes within linkage disequilibrium (+/− 10 kb) of the associated SNP markers were identified, enlisting a total of 77 and 68 genes associated with submergence and relative submergence tolerance respectively (Fig. 1B and 1C). No overlap was identified between the GWA and transcriptome derived tolerance genes [10], nevertheless, for some genes there were relatively large estimated differences in the transcriptomic submergence response between tolerant and sensitive accessions (Fig. 1B–D). To highlight the most likely 'tolerance' genes, we compared the SNP variation in the promoter and exonic regions of the top 5 genotyped tolerant (C24, Lp2-6, Kin-0, Ws-2 and NFA-8) and 5 sensitive (Mt-0, Pu2-7, Ler-1, Bay-0 and Cvi-0) accessions.[11] This identified 5 and 18 genes, for compound submergence and relative tolerance respectively, that have SNP variants specific to at least 4 tolerant accessions and allowing one SNP in the sensitive accessions, or *vice versa*.

In summary, both GWA and transcriptome studies points to a relatively large number of genes correlating with flooding tolerance. These findings support the hypothesis that tolerance to flooding, at least in Arabidopsis, requires several genetic changes. We suggest that partly for this reason *in planta* manipulation of single genes has yielded little or unpredictable results. Manipulation of the oxygen sensing mechanism has been reported to strongly increase, but in many cases also to decrease flooding tolerance, without clear explanations for these contrasting results.[5] Furthermore, manipulation of several major transcription factors that are normally activated upon submergence, has done relatively little to improve or decrease tolerance.[12] Among the large number of identified tolerance genes many physiological processes are represented (Fig. 1B).[10] This is not surprising as flooding tolerance requires the ability to deal with severe carbon starvation, generate energy through fermentation driven glycolysis, tolerate build-up of toxic elements in the rhizosphere and deal with the susceptibility to pathogen attacks. Once the flood recedes the plant is prone to desiccation, a surge of oxygen and high light, which leads to a high reactive oxygen species load. Which aspects are most important in Arabidopsis is yet unknown. Nevertheless, to survive and thrive in flood prone areas, mastery of all these aspects is required. The success of SUB1A rice raised the possibility of finding single gene solutions to flood sensitivity also in other species. To the contrary, improving our understanding of what constitutes flooding tolerance will likely require the further dissection of all these crucial individual aspects, with the final aim of stacking all these traits into a single plant to improve flood tolerance.

Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed.

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