Invited Review

Genetic regulation of root traits for soil flooding tolerance in genus Zea

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Flooding stress caused by excessive precipitation and poor drainage threatens upland crop production and food sustainability, so new upland crop cultivars are needed with greater tolerance to soil flooding (waterlogging). So far, however, there have been no reports of highly flooding-tolerant upland crop cultivars, including maize, because of the lack of flooding-tolerant germplasm and the presence of a large number of traits affecting flooding tolerance. To achieve the goal of breeding flooding-tolerant maize cultivars by overcoming these difficulties, we chose highly flooding-tolerant teosinte germplasm. These flooding-tolerance-related traits were separately assessed by establishing a method for the accurate evaluation of each one, followed by performing quantitative trait locus (QTL) analyses for each trait using maize × teosinte mapping populations, developing introgression lines (ILs) or near-isogenic lines (NILs) containing QTLs and pyramiding useful traits. We have identified QTLs for flooding-tolerance-related root traits, including the capacity to form aerenchyma, formation of radial oxygen loss barriers, tolerance to flooded reducing soil conditions, flooding-induced adventitious root formation and shallow root angle. In addition, we have developed several ILs and NILs with flooding-tolerance-related QTLs and are currently developing pyramided lines. These lines should be valuable for practical maize breeding programs focused on flooding tolerance.

Key Words: adventitious roots at the soil surface, aerenchyma, reducing soil conditions, radial oxygen loss (ROL) barrier, root angle, teosinte, waterlogging.

Introduction

Many regions of the world, including Southeast Asia, peninsular India, eastern Africa and the northern half of the Andes, have experienced a dramatic increase in flooding due to an increase in precipitation events associated with climate change (Hirabayashi et al. 2013, Sasidharan et al. 2017, Voesenek and Bailey-Serres 2015). In South and Southeast Asia, for example, over 18% of the maize (Zea mays subsp. mays) production area is affected by soil flooding (waterlogging) (Caíns et al. 2012, Zaidi et al. 2010). Flooding stress threatens upland crop production and food sustainability (Pedersen et al. 2017), so upland crop cultivars with greater tolerance to soil flooding (waterlogging) are needed for these areas. Apart from flooding related to climate change, Japan is faced with a unique situation: in order to counteract the decreases in land productivity and food self-sufficiency caused by overproduction of rice for human consumption, maize is grown in uncultivated upland fields converted from rice paddies, which are frequently flooded or waterlogged during the rainy season (Fig. 1). To develop flooding-tolerant maize, an understanding of genetic and physiological aspects of tolerance is essential.

Despite the importance of developing flooding-tolerant upland crops, there are no reports of highly flooding-tolerant maize cultivars for two main reasons: (1) the lack of flooding-tolerant germplasm useful for practical breeding approaches and (2) the presence of multiple and complex genetic factors related to flooding tolerance, which reduces the repeatability of experiments and increases environmental interactions (Mano and Oyanagi 2009). To overcome these difficulties, we and our colleagues at the Institute of Livestock and Grassland Science, NARO, and at Nagoya University followed a unique approach using highly flooding-tolerant teosinte germplasm in the following strategy: (1) separate flooding-tolerance-related traits and establish methods for the accurate evaluation of each one, (2) perform quantitative trait locus (QTL) analyses for each trait using maize × teosinte mapping populations, (3) develop introgression lines (ILs) or near-isogenic lines (NILs) of maize containing QTL alleles for flooding...
sameable root traits from teosinte and (4) pyramid useful traits. In this review, we present the current status of investigations regarding flooding tolerance in genus Zea, which are focused on root traits.

**Teosinte germplasm**

Wild relatives of crops offer a diversity of traits useful for increasing tolerances to multiple stresses (Harlan 1976, Warburton et al. 2017). In the genus Zea, for example, teosinte (a set of species related to maize) is tolerant to insects, diseases (de Lange et al. 2014, Mammadov et al. 2018) and flooding (Mammadov et al. 2018, Mano and Omori 2007). Teosinte consists of three polytypic annual subspecies of Zea mays (Z. mays subsp. parviglumis, Z. mays subsp. mexicana and Z. mays subsp. huehuetenangensis) and four additional species: a diploid perennial, Z. diploperennis; a tetraploid perennial, Z. perennis; and two diploid annual species, Z. luxurians and Z. nicaraguensis (Doebly and Itis 1980, Itis and Doebly 1980, Itis and Benz 2000). Of these, Z. nicaraguensis is found in flooded lowlands in the northwest coastal plain of Nicaragua (Bird 2000, Itis and Benz 2000) and Z. luxurians accession JSG-593 is adapted for high-precipitation regions in Oaxaca, Mexico (e.g., receiving 3669 mm during the growing season; Sánchez et al. 2011, 2018). These teosintes adapted to flooded or wet environments are considered to possess unique and favorable genes that would be useful for breeding flooding-tolerant maize. Because it is easier to obtain, we have been using mainly Z. nicaraguensis for flooding studies. An advantage to the use of teosinte in the development of flooding-tolerant maize lines is that all of the teosinte species, with the exception of Z. perennis, can be easily crossed to maize, followed by selfing or backcrossing.

**Root traits related to flooding tolerance**

Flooding tolerance is a complex quantitative trait controlled by multiple genes. Flooding-tolerance-related traits have widely been reported in several wetland and upland plants (e.g., Mustroph 2018, Pedersen et al. 2021a, Vartapetian and Jackson 1997), and many of them are root traits. Root traits related to flooding tolerance include (1) the capacity to form aerenchyma, (2) formation of a barrier to radial oxygen loss (ROL), (3) tolerance to toxic soil constituents under reducing soil conditions, (4) flooding-induced adventitious root formation at the soil surface (ARF-SS) and (5) shallow root angle. In addition, a higher cortex-to-stele ratio (CSR; Yamauchi et al. 2021) was recently found to promote oxygen transport from the shoot base to root tips of plants (Pedersen et al. 2021a), and comparison of upland and wetland crops suggested a positive relationship between CSR and flooding tolerance (Yamauchi et al. 2019).

Flooding-tolerant Z. nicaraguensis has all of the flooding-tolerance-related root traits listed above (Mano and Omori 2007, Mano et al. 2016), with the exception that its CSR has not been well investigated. These different root traits are considered to be controlled by different genetic mechanisms, so we analyzed these components separately. For genetic analyses using segregants of a cross between maize and Z. nicaraguensis, we used maize inbred line Mi29 as a female parent, because this line is widely used in Japanese breeding programs (Ikegaya et al. 1999, Ito et al. 2004). In addition to performing QTL analyses for root traits, we have developed a series of ILs each possessing a chromosome segment of Z. nicaraguensis in the genetic background of Mi29 (Mano and Omori 2013a). The ILs, and subsequently developed NILs possessing QTLs introduced by backcrossing, can be used as breeding materials directly as well as for genetic, physiological and anatomical analyses.

**Constitutive aerenchyma formation**

Root aerenchyma in cortical tissue contains air spaces that provide plant roots with oxygen under flooded or low-oxygen conditions. In upland crops, lower capacity for oxygen transport from shoot to root tip under flooded conditions inhibits plant growth and induces yield loss because of incomplete or partial aeration through root aerenchyma. Therefore, higher capacity for oxygen transport from shoot to root tip via aerenchyma is essential for improving flooding tolerance (summarized in Takahashi et al. 2014 and Yamauchi et al. 2013).

In some wetland crops such as rice (Oryza sativa), lysigenous aerenchyma, which is produced by cortical cell death, is constitutively formed even in drained soil, and its formation is further induced by waterlogged or low-oxygen conditions (Shiono et al. 2011). These mechanisms are
respectively described as constitutive and inducible aerenchyma formation (Yamauchi et al. 2018). On the other hand, flooding-sensitive upland crops such as maize, wheat and barley form inducible aerenchyma under flooded or low-oxygen conditions but lack constitutive aerenchyma (Drew et al. 1979, Yamauchi et al. 2016). Because the induction of aerenchyma after exposure to flooding or low-oxygen conditions takes several hours or days, roots of upland crops without constitutive aerenchyma are damaged by flooding until they form sufficient amounts of inducible aerenchyma (Herzog et al. 2016, Rajhi et al. 2011, Yamauchi et al. 2014). The importance of constitutive aerenchyma, which enables the plant to adapt more rapidly to flooding conditions, is widely known (Pedersen et al. 2021a); however, accurate comparisons between materials with and without aerenchyma were not made in earlier studies because these investigations compared different genera or species.

In an earlier study, Ray et al. (1999) revealed that 2- to 3-month-old plants of Z. luxurians and F₁ hybrids of Z. luxurians × maize formed clear constitutive aerenchyma in well-aerated environments. Mano et al. (2006b) evaluated constitutive aerenchyma formation in the seedlings of Zea species grown under drained soil conditions and found that accessions of Z. nicaraguensis and Z. luxurians formed clear aerenchyma. Because diploid teosinte can be crossed to maize, development of NILs for constitutive aerenchyma formation and precise comparisons between aerenchyma-forming and -non-forming maize became possible. QTLs for constitutive aerenchyma formation have been mapped in several chromosome regions by using F₂ and backcross populations of maize × teosinte crosses and self-pollinated Z. nicaraguensis (Table 1). Among these, QTL for aerenchyma formation on the long arm of chromosome 1 at bin 1.06-1.07 (Qaer1.06-1.07) showed the largest effect (Mano et al. 2007, Mano and Omori 2008).

Recently, we developed a pyramided line, IL-AE91, possessing four QTLs (Qaer1.06-1.07, Qaer1.11, Qaer5.09n and Qaer8.05) in the genetic background of Mi29 (Fig. 2A, Table 2) and found greater flooding tolerance than in Mi29 at the seedling stage under both oxygen-deficient stagnant hydroponic growth and flooded potting-mix soil conditions (Gong et al. 2019). By measurement of ROL and cell viability in IL-AE91 and Mi29, effective O₂ transport and cell survival in root tips under stagnant conditions were verified in IL-AE91. Although Mano and Omori (2013b) revealed that a greater capacity to form constitutive aerenchyma enhanced flooding tolerance by comparing Z. nicaraguensis accessions with high and low levels of its formation, a study by Gong et al. (2019) was the first to reveal the advantage of constitutive aerenchyma formation to flooding tolerance in materials with a similar genetic background. Because IL-AE91 still contains ~14% of the Z. nicaraguensis genome, deletion of undesirable Z. nicaraguensis genome regions is necessary to use IL-AE91 for practical breeding. For this purpose, detailed mapping of Qaer1.06-1.07, which has the highest genetic effect among the four aerenchyma QTLs, is now in progress.

**Formation of barrier to radial oxygen loss (ROL)**

The presence of a ROL barrier in adventitious roots, which facilitates oxygen diffusion to root apices by preventing radial loss of oxygen from the roots, is an important adaptation under low-oxygen conditions in plants (Colmer 2003, Watanabe et al. 2013). Flooding-tolerant rice and some wetland species induce a ROL barrier under stagnant or flooded conditions (referred to as inducible ROL barrier formation; Colmer et al. 1998, Colmer 2003, Shiono et al. 2011), whereas a few wetland species form ROL barriers under aerated or well drained conditions (constitutive ROL barrier formation; McDonald et al. 2002, Visser et al. 2000). In recent investigations, wild species of Echinochloa and Amazonian wild rice (Oryza glumaepatula) were found to constitutively form ROL barriers under aerated conditions (Ejiri and Shiono 2019, Ejiri et al. 2020). In this review, we focus on genetic mechanisms for inducible ROL barrier formation in Z. nicaraguensis.

By screening of a series of ILs derived from a cross between Mi29 × Z. nicaraguensis for ROL barrier formation, we found that only IL#11, which contains segments of chromosomes 1, 3 and 4 from Z. nicaraguensis, formed ROL barriers. In further genetic analyses using backcross progeny of the same cross combination, we found that the capacity to produce an inducible ROL barrier is controlled by a single major locus on the short arm of chromosome 3 (bin 3.04), and the mode of gene action was complete dominance (Watanabe et al. 2017). This locus was tentatively named RBF1 (ROL Barrier Formation 1; Table 1), and we developed a NIL, designated NIL468-3, possessing RBF1 in the genetic background of maize Mi29 (Table 2). By detailed mapping, the chromosome region containing RBF1 was narrowed down to 232 kb, and candidate genes were selected (Ide et al. 2017). In the most recent investigation, RBF1 induced a ROL barrier both in the main axis of adventitious roots and in the lateral roots when grown in stagnant, deoxygenated solution (Pedersen et al. 2021b). Isolation of RBF1 and investigations of the mechanism of ROL formation (e.g., the signal for ROL formation and the composition of the barrier) are now in progress using Agrobacterium-transformed Mi29 containing the RBF1 allele from Z. nicaraguensis.

**Tolerance to toxic soil constituents under flooded reducing soil conditions**

During the rainy season in Japan (late spring to early summer) in upland paddies, toxic soil constituents (e.g., Fe²⁺, Mn²⁺ and H₂S) induced by reducing soil conditions (low redox potential) are a severe problem in addition to the stress caused by excessive water or low oxygen.
Genetic regulation of flooding tolerance in Zea

Table 1. QTL and genes for flooding-tolerance-related traits in Zea species

| Trait                        | Namea                  | Chr. | Bin | PVEb     | Populationc | References                  |
|------------------------------|------------------------|------|-----|----------|-------------|-----------------------------|
| Constitutive aerenchyma      | Qaur1.02-1.03          | 1    | 1.02–1.03 | 0.11    | B64 × Z. nicaraguensis | Mano et al. (2007)          |
| formation                    | Qaur1.05-1.06          | 1    | 1.05 | 0.25    | Mi29 × Z. nicaraguensis | Mano and Omori (2009)       |
| Qaur1.06-1.07                | 1                      | 1.06 | 0.17 | Z. nicaraguensis (S1) | Mano et al. (2012)         |
| Qaur1.11                     | 1                      | 1.11 | 0.12 | Mi29 × Z. nicaraguensis | Mano and Omori (2008)       |
| Qaur2.06                     | 2                      | 2.06 | 0.09 | B73 × Z. luxurians | Mano et al. (2008)         |
| Qaur5.09                     | 5                      | 5.09 | 0.11 | B64 × Z. nicaraguensis | Mano et al. (2007)         |
| Qaur5.09a                    | 5                      | 5.09 | 0.06 | Mi29 × Z. nicaraguensis | Mano and Omori (2008)       |
| Qaur7.01                     | 7                      | 7.01 | 0.12 | Z. nicaraguensis (S1) | Mano et al. (2012)         |
| Qaur8.05                     | 8                      | 8.05 | 0.07 | Mi29 × Z. nicaraguensis | Mano and Omori (2009)       |

| ROL barrier formation       | (RBF1)                | 3    | 3.04 | Major locus | Mi29 × Z. nicaraguensis | Watanabe et al. (2017)      |
| Flooding tolerance under    | (Qft-rd-1.3.04)        | 1    | 1.03–1.04 | 0.14    | F1649 × H84 | Mano et al. (2006a)         |
| reducing soil conditions    | (Qft-rd-0.7-4.11)      | 4    | 0.7–4.11 | 0.13–0.42 | Mi29 × Z. nicaraguensis | Mano and Omori (2013a)      |
| Adventitious root formation | (Qarf1.04)             | 3    | 3.04 | 0.06    | Mi29 × Z. nicaraguensis | Mano et al. (2009)         |
| at the soil surface (ARF-SS) | (Qarf1.07-3.08)        | 3    | 3.07–3.08 | 0.10    | B64 × Na4 | Mano et al. (2005)          |
| | (Qarf1.07)               | 4    | 4.07 | 0.09   | B64 × Z. mays subsp. huehuetenangensis | Mano et al. (2005b)        |
| | (Qarf1.05)               | 5    | 5.03 | 0.14   | B64 × Z. nicaraguensis | Mano et al. (2005b)        |
| | (Qarf1.07)               | 7    | 7.04 | 0.21   | B64 × Na4 | Mano et al. (2005)        |
| | (Qarf1.04)               | 8    | 8.03 | 0.04   | Mi29 × Z. nicaraguensis | Mano et al. (2009)         |
| | (Qarf1.05)               | 8    | 8.05 | 0.25   | B64 × Z. mays subsp. huehuetenangensis | Mano et al. (2005b)        |

| Root angle                   | CRA1                   | 1    | –    | 0.04   | DHIM × T877 | Li et al. (2018)           |
|                             | CRA4                   | 1    | –    | 0.03–0.04 | DHIM × T877 | Li et al. (2018)           |
|                             | Qra3rd2.08–2.04        | 2    | 2.03–2.04 | 0.13    | B73 × Z. luxurians | Omori and Mano (2007)      |
| Qra2nd4.05                  | 4                      | 4.05 | 0.16 | B73 × Z. luxurians | Omori and Mano (2007)      |
| Qra2nd4.07                  | 4                      | 4.07 | 0.13 | B73 × Z. luxurians | Omori and Mano (2007)      |
| CRA3                        | 6                      | –    | 0.03 | DHIM × T877 | Li et al. (2018)           |
| CRA4                        | 9                      | –    | 0.03–0.04 | DHIM × T877 | Li et al. (2018)           |
| Root relative dry weight    | rdw1                   | 1    | 1.04 | 0.04   | HZ32 × K12 | Qiu et al. (2007)          |
|                             | rdw3                   | 3    | 3.04 | 0.05   | HZ32 × K12 | Qiu et al. (2007)          |
|                             | jWT5.04                | 5    | 5.04 | 0.10–0.12 | A3237 × A3239 | Yu et al. (2019)          |
| Root dry weight (treatment) | rdw4-1                 | 4    | 4.05 | 0.07   | HZ32 × K12 | Osman et al. (2013)        |

a QTL or gene names in parentheses are tentative and are based on our previous nomenclature.
b Proportion of phenotypic variance explained.
c Mapping populations; boldface indicates parent contributing higher-value allele.
d Unknown.
e The parent contributing the allele with a positive effect differed depending on the environment.

(Ponnamperuma 1984). Under artificial reducing soil conditions produced by adding 0.1% or 0.2% soluble starch solution to the soil, wide variations were observed among maize inbred lines (Mano et al. 2006a) and between maize Mi29 and Z. nicaraguensis for the amount of leaf injury (Mano and Omori 2013a). Adventitious roots of sensitive maize Mi29 seedlings became black, whereas those of Z. nicaraguensis showed only a slight visible change, if any (Fig. 2C). We evaluated tolerance to toxic soil constituents as leaf injury (possibly correlated to root damage) under artificial reducing soil conditions.

Mano et al. (2006a) found a QTL for flooding tolerance in reducing soil conditions on chromosome 1 by using a maize mapping population from a cross between F1649 (tolerant) × H84 (sensitive) (Table 1). Because the effect of the QTL found in F1649 was not very large, we used Z. nicaraguensis as a donor for further genetic analyses. By screening ILs derived from a cross between Mi29 × Z. nicaraguensis under reducing soil conditions, we identified a tolerant line, IL#18a (Fig. 2C; Mano and Omori 2013a). IL#18a contains most of the long arm of chromosome 4 of Z. nicaraguensis in the genetic background of Mi29, and we named the QTL as Qft-rd-0.7-4.11 (QTL for flooding tolerance under reducing soil conditions at bin 4.07–4.11).
We introgressed Qft-rd4.07-4.11 into maize inbred lines Mi47 and Na50 by backcrossing eight times and developed two ILs, Mi47 Qft-rd4.07-4.11 and Na50 Qft-rd4.07-4.11 (Table 2; Y. Mano and F. Omori, unpublished). The effectiveness of Qft-rd4.07-4.11 for flooding tolerance in these two different genetic backgrounds of maize (Y. Mano and F. Omori, unpublished) and in F1 hybrids (Mano and Omori 2015) was confirmed in our greenhouse experiments. However, no recombination was observed in the Qft-rd4.07-4.11 region. This recombination suppression is caused by a large chromosome inversion, which was verified by linkage analyses (Mano and Omori 2013a) and modifications of the FISH signal patterns (Brazet al. 2020).

We have been targeting QTLs in addition to Qft-rd4.07-4.11 for tolerance to toxic soil constituents under reducing soil conditions because the region of Qft-rd4.07-4.11 on chromosome 4 may contain genes for undesirable traits (linkage drag) such as lower kernel row number, late flowering and low pollen amount, but they cannot be eliminated because of recombination suppression. We identified another IL (IL#39) containing mainly the short arm of chromosome 9 of Z. nicaraguensis (Table 2), which showed equivalent tolerance under reducing soil conditions (Mano and Omori 2013a; Supplemental Fig. 1). Because IL#39 contains teosinte chromosome fragment(s) other than the short arm of chromosome 9 and the precise position of the QTL was not determined, detailed mapping is now in progress. Unlike Qft-rd4.07-4.11, the QTL for tolerance to toxic soil constituents in IL#39, possibly located on the short arm of chromosome 9, may be useful for practical breeding after the elimination of undesirable chromosome segments of Z. nicaraguensis by backcrossing.

Flooding-induced adventitious root formation at the soil surface (ARF-SS)

Adventitious (i.e., stem-base crown) root formation at the soil surface (ARF-SS) is one of the most important adaptations to soil flooding, because adventitious roots that develop close to or above the soil surface can obtain oxygen directly from the air. Similar to many flooding-tolerant wetland species (Justin and Armstrong 1987, Visser et al. 1996), some maize lines induce ARF-SS under flooded conditions (Lizaso et al. 2001, Mano et al. 2005a). Furthermore, Z. nicaraguensis, Z. luxurians and Z. mays subsp. huehuetenangensis formed larger numbers of adventitious soil-surface roots than did maize (Bird 2000, Mano et al. 2005a, 2009). This trait was observed in both greenhouse and field experiments (Mano and Omori 2007).

QTL analyses using parents with contrasting degrees of

![Fig. 2. Flooding-tolerance-related traits in Z. nicaraguensis and various introgression lines.](image-url)
| Trait                                      | Name          | QTL      | Chr. | Bin     | Genetic background | Donor            | Fig. showing line   | References                  |
|--------------------------------------------|---------------|----------|------|---------|--------------------|------------------|---------------------|---------------------------|
| Constitutive aerenchyma formation          | IL-AE91       | Qaer1.06-1.07 | 1    | 1.06–1.07 | Mi29 | Z. nicaraguensis  | Fig. 2A  | Gong et al. (2019)       |
|                                            |               | Qaer1.11  | 1.11 |          |                   |                  |                     |                           |
|                                            |               | Qaer5.09n | 5    | 5.09    |                   |                  |                     |                           |
|                                            |               | Qaer8.05  | 8    | 8.05    |                   |                  |                     |                           |
| ROL barrier formation                      | IL#11         | (RBF1)   | 3    | 3.04    | Mi29 | Z. nicaraguensis  | Fig. 2B  | Watanabe et al. (2017)   |
|                                            |               | (RBF1)   | 3    | 3.04    | Mi29  | Z. nicaraguensis  |                     |                           |
| Flooding tolerance under reducing soil     | IL#18a, IL#18b| Qft-rd4.07-4.11 | 4    | 4.07–4.11 | Mi29 | Z. nicaraguensis  | Fig. 2C | Mano and Omori (2013a)   |
|                                            |               | Qft-rd4.07-4.11 | 4    | 4.07–4.11 | Mi47 | Z. nicaraguensis  |                     |                           |
|                                            |               | Qft-rd4.07-4.11 | 4    | 4.07–4.11 | Na50 | Z. nicaraguensis  |                     |                           |
|                                            | IL#39         |          |      |         | Mi29 | Z. nicaraguensis  | Supplemental Fig. 1| Mano and Omori (2013a) |
| Adventitious root formation at the soil     | IL#468-4      | Qarf3.04  | 3    | 3.04    | Mi29 | Z. nicaraguensis  | Fig. 2D  | Y. Mano and F. Omori (unpublished) |
| surface (ARF-SS)                           | IL#32         | Qarf7.04  | 7    | 7.04    | Mi29 | Z. nicaraguensis  | Supplemental Fig. 2| Y. Mano and F. Omori (unpublished) |
|                                            | Na110         | Qarf5.03  | 5    | 5.03    | Mi29 | Z. mays subsp. huehuetenangensis |         | H. Tamaki et al. (unpublished) |
|                                            |               | Qarf8.05  | 8    | 8.05    | Mi29 | Z. mays subsp. huehuetenangensis |         |                           |
| Shallow root angle                         | IL#32         | Qra7.04  | 7    | 7.04    | Mi29 | Z. nicaraguensis  | Fig. 2E  | Y. Mano and F. Omori (unpublished) |

a QTL or gene names in parentheses are tentative and based on our previous nomenclature.
b Detailed mapping is now in progress.
c Near isogenic line possessing RBF1 (undesirable segments of Z. nicaraguensis from IL#11 have been eliminated).
d BC$_3$F$_4$ generation.
e Developed to BC$_3$ generation in this study; subsequent backcrosses were made by Y. Mano and F. Omori (unpublished).
f Different from Qft-rd4.07-4.11, but precise position was not determined.
ARF-SS revealed QTLs controlling ARF-SS on chromosomes 3, 7 and 8 in a mapping population from maize B64 × maize Na4 (Mano et al. 2005c), on chromosomes 4 and 8 in a population from B64 × Z. mays subsp. haejutanengensis (Mano et al. 2005b), and on chromosomes 3, 7 and 8 in a population from Mi29 × Z. nicaraguensis (Mano et al. 2009) (Table 1). Three of the identified QTL regions could be detected in two different populations: bin 7.04–7.05 (donor parents were Z. nicaraguensis and maize Na4), bin 8.03 (Z. nicaraguensis and Z. mays subsp. haejutanengensis) and bin 8.05 (Z. mays subsp. haejutanengensis and maize Na4) (Table 1).

By selecting the series of ILs described above and backcrossing, we have developed two ILs for ARF-SS: IL#468-4, possessing QTL for adventitious root formation at the soil surface at bin 3.04 (Qarf3.04; Fig. 2D), and IL#32 (Qarf7.04; Supplemental Fig. 2). These lines should be useful for verifying the effect of ARF-SS on flooding tolerance and revealing its genetic and physiological mechanisms. In addition, we have generated pyramided line Na110, which contains both Qarf5.03 and Qarf8.05 (derived from Z. mays subsp. haejutanengensis) in the genetic background of Mi29 (Table 2). Since 2013, yield-related data for F1 hybrids (Na110 × Mi47 and Mi29 × Mi47 [control]) have been obtained under both flooded and unflooded field conditions (Mano et al. 2016).

**Shallow rooting angle**

Root angle is related to tolerance to several abiotic stresses such as flooding, drought and low soil P conditions (Lynch and Wojciechowski 2015, Oyanagi et al. 2004, Wasson et al. 2012). Research on root angle is focused mainly on drought tolerance, and deep rooting is an important means of reaching water stored deep in the soil. Genetic factors controlling deep rooting include DRO1–DRO5 in rice (e.g., Uga et al. 2013, 2015), nine root-growth-angle QTL clusters in wheat (Maccacerri et al. 2016) and Root-ABA1 and CRA1–CRA4 in maize (Table 1). Regarding shallow rooting, Kitomi et al. (2020) recently identified a gene responsible for a QTL associated with root growth angle in rice, qSOR1, and demonstrated that a shallower root growth angle could enhance rice yields in saline paddies.

Shallow-rooting wheat lines had higher tolerance to flooding under paddy field conditions than deep-rooting lines (Oyanagi et al. 2004). In Zea species, Omori and Mano (2007) reported four QTLs controlling the angle of root emergence from the 2nd and 3rd nodes from the bottom at the seedling stage: QTL for root angle emerged from 3rd node from the bottom at bin 2.03–4 (Qra3rd2.03–4), Qra2nd4.05, Qra3rd4.07 and Qra3rd7.04 (Table 1). Some QTLs for root angle overlap with those for ARF-SS. For example, both Qra3rd4.07 and Qarf4.07 were located at bin 4.07 on chromosome 4, and Qra3rd7.04 and Qarf7.04 were located at bin 7.04 on chromosome 7 (Table 1). The overlap in QTL regions for these two root traits suggests that shallow roots can easily emerge from the soil surface under flooding. IL#32, which contains only a chromosome segment corresponding to bin 7.03–7.06 of Z. nicaraguensis in the genetic background of Mi29 (Fig. 2E, Table 2), should be useful for understanding the relationship between root angle and ARF-SS by backcrossing and subsequent dissection of Qra3rd7.04 (root angle QTL) and Qarf7.04 (ARF-SS).

Although QTLs for flooding tolerance in Zea have been widely investigated (Mano et al. 2006a, Zaidi et al. 2015, Zhang et al. 2013), QTLs associated with root traits other than those in our investigations are limited. Some examples of QTLs controlling root relative dry weight (Qiu et al. 2007, Yu et al. 2019) and root dry weight under waterlogged conditions (Osman et al. 2013) are listed at the bottom of Table 1.

**Breeding strategy and perspective**

Table 2 summarizes ILs possessing flooding-tolerance-related traits developed at the Institute of Livestock and Grassland Science, NARO, and at Nagoya University. Because combinations of root traits (e.g., constitutive aerenchyma formation plus a ROL barrier) should increase flooding tolerance by increasing oxygen transport to the root tip via aerenchyma under flooded conditions, pyramiding of these root traits would be valuable for maize breeding. The genetic background of most of these lines is Mi29, so it should be relatively easy to pyramid multiple genes in Mi29 by crossing and selfing together with marker-assisted selection. Indeed, we have developed pyramided lines possessing several flooding-tolerance-related traits (Y. Mano and F. Omori, unpublished).

In addition to generating ILs and pyramided lines, understanding the physiological mechanisms for flooding-tolerance-related traits is essential to applying QTLs for efficient breeding of maize and other flooding-sensitive upland crops. The ILs and NILs listed in Table 2 can be useful for physiological and functional analyses. Indeed, we used IL-AE91 for physiological analysis of constitutive aerenchyma (Gong et al. 2019) and NIL#468-3 or IL#11 for physiological and functional analyses of ROL barrier formation (Ide et al. 2017, Pedersen et al. 2021b, Watanabe et al. 2017). Through these investigations, the relationships between QTLs for flooding-tolerance-related traits and physiological mechanisms such as ethylene-induced aerenchyma formation (reviewed by Drew et al. 2000), suberin-related ROL barrier formation (reviewed by Watanabe et al. 2013) and auxin-induced adventitious root development (reviewed by Steffens and Rasmussen 2016) are being revealed.

As mentioned in this review, we have been applying a unique approach using a highly flooding-tolerant teosinte germplasm to develop flooding-tolerant maize. During the development of NILs or ILs possessing flooding-tolerance-related traits, recombination suppression caused by a large
chromosome inversion (a problem often seen in crosses involving wild relatives) was observed in the Qft-rd4.07-4.11 region on the long arm of chromosome 4 (Mano and Omori 2013a). The recombination suppression prevented us from fine-mapping of Qft-rd4.07-4.11 by linkage analysis, so we could not generate a NIL for the Qft-rd4.07-4.11 locus. To overcome this difficulty, the following approach is now in progress: we have constructed a high-density F2 linkage map of the long arm of chromosome 4 derived from a cross between Z. nicaraguensis × Z. luxurians, both of which possess an inverted chromosome segment in this region (Mano and Omori 2013a). Because these parents showed a clear difference in flooding tolerance under reducing soil conditions (Y. Mano, unpublished), it may be possible to perform fine-mapping of Qft-rd4.07-4.11 by linkage analysis and subsequent isolation of the responsible gene. By using genome editing targeting the orthologous gene in maize, it may be possible to improve flooding tolerance in maize without introducing teosinte’s undesirable traits. These efforts can be used to prevent the flooding damage promoted by global climate change and other causes.

Author Contribution Statement

YM wrote the main text and generated figures and tables; MN wrote the main text and generated a figure.

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Literature Cited

Bird, R.M. (2000) A remarkable new teosinte from Nicaragua: growth and treatment of progeny. Maize Gen. Coop. Newsl. 74: 58–59.
Braz, G.T., L.D.V. Martins, T. Zhang, P.S. Albert, J.A. Birchler and J. Jiang (2020) A universal chromosome identification system for maize and wild Zea species. Chromosome Res. 28: 183–194.
Caíns, J.E., K. Sonder, P.H. Zaidi, N. Verhulst, G. Mahuku, R. Babu, S.K. Nair, B. Das, B. Govaerts, M.T. Vinayan et al. (2012) Maize production in a changing climate: impacts, adaptation, and mitigation strategies. Adv. Agron. 114: 1–58.
Colmer, T.D., M.R. Gibberd, A. Wiengweera and T.K. Tinh (1998) The barrier to radial oxygen loss from roots of rice (Oryza sativa L.) is induced by growth in stagnant solution. J. Exp. Bot. 49: 1431–1436.
Colmer, T.D. (2003) Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. Plant Cell Environ. 26: 17–36.
de Lange, E.S., D. Balmer, B. Mauch-Mani and T.C.J. Turlings (2014) Insect and pathogen attack and resistance in maize and its wild ancestors, the teosintes. New Phytol. 204: 329–341.
Doebly, J.F. and H.H. Ilitis (1980) Taxonomy of Zea (Gramineae). I. A subgeneric classification with key to taxa. Am. J. Bot. 67: 982–993.
Drew, M.C., M.B. Jackson and S. Giffard (1979) Ethylene-promoted adventitious rooting and development of cortical air spaces (aerenchyma) in roots may be adaptive responses to flooding in Zea mays L. Planta 147: 83–88.
Drew, M.C., C.J. He and P.W. Morgan (2000) Programmed cell death and aerenchyma formation in roots. Trends Plant Sci. 5: 123–127.
Ejiri, M. and K. Shiono (2019) Prevention of radial oxygen loss is associated with exodermal suberin along adventitious roots of annual wild species of Echinochloa. Front. Plant Sci. 10: 254.
Ejiri, M., Y. Sawazaki and K. Shiono (2020) Some accessions of Amazonian wild rice (Oryza glumaepatula) constitutively form a barrier to radial oxygen loss along adventitious roots under aerated conditions. Plants 9: 880.
Giuliani, S., M.C. Sanguineti, R. Tuberosa, M. Bellotti, S. Salvi and P. Landi (2005) Root-ABA1, a major constitutive QTL, affects maize root architecture and leaf ABA concentration at different water regimes. J. Exp. Bot. 56: 3061–3070.
Gong, F.P., H. Takahashi, F. Omori, W. Wang, Y. Mano and M. Nakazono (2019) QTLs for constitutive aerenchyma from Zea nicaraguensis improve tolerance of maize to root-zone oxygen deficiency. J. Exp. Bot. 70: 6475–6487.
Harlan, J.R. (1976) Genetic resources in wild relatives of crops. Crop Sci. 16: 329–333.
Herzog, M., G.G. Striker, T.D. Colmer and O. Pedersen (2016) Mechanisms of waterlogging tolerance in wheat—a review of root and shoot physiology. Plant Cell Environ. 39: 1068–1086.
Hirabayashi, Y., R. Mahendran, S. Koizala, L. Konoshima, D. Yamazaki, S. Watanabe, H. Kim and S. Kanae (2013) Global flood risk under climate change. Nat. Clim. Chang. 3: 816–821.
Ide, K., K. Watanabe, H. Takahashi, H. Takahashi, F. Omori, Y. Mano and M. Nakazono (2017) Identification of a major locus involved in the formation of the radial oxygen loss barrier in roots of Zea nicaraguensis. Breed. Res. 19 (Suppl. 2): 209.
Ikegaya, F., K. Koimura, E. Ito, Y. Inoue, K. Nozaki, K. Fujita and N. Mochizuki (1999) Development and characteristics of new inbred line “Mi29” for silage maize. Bull. Kyushu Natl. Agric. Exp. Stn. 35: 71–83.
Ilitis, H.H. and J.F. Doebly (1980) Taxonomy of Zea (Gramineae). II Subspecific categories in the Zea mays complex and a generic synopsis. Am. J. Bot. 67: 994–1004.
Ilitis, H.H. and B.F. Benz (2000) Zea nicaraguensis (Poaceae), a new teosinte from Pacific coastal Nicaragua. Novon 10: 382–390.
Ito, E., F. Ikegaya, K. Koimura and K. Eguchi (2004) Development and characteristics of new silage maize cultivar “Yumechikara”. Bull. Kyushu Natl. Agric. Exp. Stn. 43: 1–24.
Justin, S.H.F.W. and W. Armstrong (1987) The anatomical characteristics of roots and plant response to soil flooding. New Phytol. 106: 465–495.
Kitomi, Y., E. Hanzawa, N. Kuya, H. Inoue, N. Hara, S. Kawai, N. Kanno, M. Endo, K. Sugimoto, T. Yamazaki et al. (2020) Root angle modifications by the DRO1 homolog improve rice yields in saline paddy fields. Proc. Natl. Acad. Sci. USA 117: 21242–21250.
Li, P., Y. Zhang, S. Yin, P. Zhu, T. Pan, Y. Xu, J. Wang, D. Hao, H. Fang, C. Xu et al. (2018) QTL-by-environment interaction in the response of maize root and shoot traits to different water regimes. Front. Plant Sci. 9: 229.

Lizaso, J.I., L.M. Melendez and R. Ramirez (2001) Early flooding of two cultivars of tropical maize. I. shoot and root growth. J. Plant Nutr. 24: 979–995.

Lynch, J.P. and T. Wojciechowski (2015) Opportunities and challenges in the subsoil: pathways to deeper rooted crops. J. Exp. Bot. 66: 2199–2210.

Maccferri, M., W. El-Feki, G. Nazemi, S. Salvi, M.A. Canè, M.C. Colalongo, S. Stefanelli and R. Tuberosa (2016) Prioritizing quantitative trait loci for root system architecture in tetraploid wheat. J. Exp. Bot. 67: 1161–1178.

Mammadov, J., R. Buyyaratu, S.K. GuttiKonda, K. Parliament, I.Y. Abdurakhmonov and S.P. Kumpta (2018) Wild relatives of maize, rice, cotton, and soybean: treasure troves for tolerance to biotic and abiotic stresses. Front. Plant Sci. 9: 886.

Mano, Y., M. Muraki, M. Fujimori and T. Takamizo (2005a) Varietal difference and genetic analysis of adventitious root formation at the soil surface during flooding in maize and teosinte seedlings. Jpn. J. Crop Sci. 74: 41–46 (in Japanese with English summary).

Mano, Y., M. Muraki, M. Fujimori, T. Takamizo and B. Kindiger (2005b) Identification of QTL controlling adventitious root formation during flooding conditions in teosinte (Zea mays ssp. huehuetaenangensis) seedlings. Euphytica 142: 33–42.

Mano, Y., F. Omori, M. Muraki and T. Takamizo (2005c) QTL mapping of adventitious root formation under flooding conditions in tropical maize (Zea mays L.) seedlings. Breed. Sci. 55: 343–347.

Mano, Y., M. Muraki and T. Takamizo (2006a) Identification of QTL controlling flooding tolerance in reducing soil conditions in maize (Zea mays L.) seedlings. Plant Prod. Sci. 9: 176–181.

Mano, Y., F. Omori, T. Takamizo, B. Kindiger, R.McK. Bird and C.H. Loaisiga (2006b) Variation for root aerenchyma formation in flooded and non-flooded maize and teosinte seedlings. Plant Soil 281: 269–279.

Mano, Y. and F. Omori (2007) Breeding for flooding tolerant maize using “teosinte” as a germplasm resource. Plant Root 1: 17–21.

Mano, Y., F. Omori, T. Takamizo, B. Kindiger, R.McK. Bird, C.H. Loaisiga and H. Takahashi (2007) QTL mapping of root aerenchyma formation in seedlings of a maize × teosinte “Zea nicaraguensis” cross. Plant Soil 295: 103–113.

Mano, Y. and F. Omori (2008) Verification of QTL controlling root aerenchyma formation in a maize × teosinte “Zea nicaraguensis” advanced backcross population. Breed. Sci. 58: 217–223.

Mano, Y., F. Omori, B. Kindiger and H. Takahashi (2008) A linkage map of maize × teosinte Zea luxurians and identification of QTLs controlling root aerenchyma formation. Mol. Breed. 21: 327–337.

Mano, Y. and F. Omori (2009) High-density linkage map around the root aerenchyma locus Qaer1.06 in the backcross populations of maize Mi29 × teosinte “Zea nicaraguensis”. Breed. Sci. 59: 427–433.

Mano, Y., F. Omori, C.H. Loaisiga and R.McK. Bird (2009) QTL mapping of above-ground adventitious roots during flooding in maize × teosinte “Zea nicaraguensis” backcross population. Plant Root 3: 3–9.

Mano, Y. and A. Oyanagi (2009) Trends of waterlogging tolerance studies in the Poaceae. Jpn. J. Crop Sci. 78: 441–448 (in Japanese with English summary).

Mano, Y., F. Omori and K. Takeda (2012) Construction of intra-specific linkage maps, detection of a chromosome inversion, and mapping of QTL for constitutive root aerenchyma formation in the teosinte Zea nicaraguensis. Mol. Breed. 29: 137–146.

Mano, Y. and F. Omori (2013a) Flooding tolerance in interspecific introgression lines containing chromosome segments from teosinte (Zea nicaraguensis) in maize (Zea mays subsp. mays). Ann. Bot. 112: 1125–1139.

Mano, Y. and F. Omori (2013b) Relationship between constitutive root aerenchyma formation and flooding tolerance in Zea nicaraguensis. Plant Soil 370: 447–460.

Mano, Y. and F. Omori (2015) Flooding tolerance in maize (Zea mays subsp. mays) F1 hybrids containing a QTL introgressed from teosinte (Zea nicaraguensis). Euphytica 205: 255–267.

Mano, Y., F. Omori, H. Tamaki, S. Mitsuhashi and W. Takahashi (2016) DNA marker-assisted selection approach for developing flooding-tolerant maize. Jpn. Agric. Res. Q. 50: 175–182.

McDonald, M.P., N.W. Galwey and T.D. Colmer (2002) Similarity and diversity in adventitious root anatomy as related to root aeration among a range of wetland and dryland grass species. Plant Cell Environ. 25: 441–451.

Mustroph, A. (2018) Improving flooding tolerance of crop plants. Agronomy 8: 160.

Omori, F. and Y. Mano (2007) QTL mapping of root angle in F2 populations from maize ‘B73’ × teosinte ‘Zea luxurians’. Plant Root 1: 57–65.

Osman, K.A., B. Tang, Y. Wang, J. Chen, F. Yu, L. Li, X. Han, Z. Zhang, J. Yan, Y. Zheng et al. (2013) Dynamic QTL analysis and candidate gene mapping for waterlogging tolerance at maize seedling stage. PLoS ONE 8: e79305.

Oyanagi, A., C. Kiribuchi-Otobe, T. Yanagisawa, S. Miura, H. Kobayashi and S. Muranaka (2004) Growth and grain yield of wheat experimental lines with deep and shallow root system in wet paddy fields. Jpn. J. Crop Sci. 73: 300–308 (in Japanese with English summary).

Pedersen, O., P. Perata and L.A.C.I. Voeseke (2017) Flooding and low oxygen responses in plants. Funct. Plant Biol. 44: iii–vi.

Pedersen, O., M. Sauter, T.D. Colmer and M. Nakazono (2021a) Regulation of root adaptive anatomical and morphological traits during low soil oxygen. New PhytoL 229: 42–49.

Pedersen, O., Y. Nakayama, H. Yasue, Y. Kurokawa, H. Takahashi, A.H. Floytrup, F. Omori, Y. Mano, T.D. Colmer and M. Nakazono (2021b) Lateral roots, in addition to adventitious roots, form a barrier to radial oxygen loss in Zea nicaraguensis and a chromosome segment introgression line in maize. New PhytoL 229: 94–105.

Ponnampuruma, F.N. (1984) Effects of flooding on soils. In: Kozlowski, T.T. (ed.) Flooding and plant growth. Academic Press, Orlando, Florida, USA, pp. 9–45.

Qiu, F., Y. Zheng, Z. Zhang and S. Xu (2007) Mapping of QTL associated with waterlogging tolerance during the seedling stage in maize. Ann. Bot. 99: 1067–1081.

Rajhi, I., T. Yamauchi, H. Takahashi, S. Nishiuchi, K. Shiono, R. Watanabe, A. Mikyi, Y. Nagamura, N. Tsutsui, N.K. Nishizawa et al. (2011) Identification of genes expressed in maize root cortical cells during lysigenous aerenchyma formation using laser microdissection and microarray analyses. New PhytoL 190: 351–368.

Ray, J.D., B. Kindiger and T.R. Sinclair (1999) Introgressing root aerenchyma into maize. Maydica 44: 113–117.

Sánchez, G.J.J., L.L.D.L. Cruz, M.V.A. Vidal, P.J. Ron, S. Tabo, F. Santacruzu-Ruvalcaba, S. Sood, J.B. Holland, C.J.A. Ruiz, S. Carvajal et al. (2011) Three new teosintes (Zea spp., Poaceae) from México. Am. J. Bot. 98: 1537–1548.
Genetic regulation of flooding tolerance in Zea

Sánchez, G.J.J., C.J.A. Ruiz, G.M. García, G.R. Ojeda, L.D.I.C. Larios, J.B. Holland, R.M. Medrano and R.G.E. García (2018) Ecogeography of teosinte. Plant Breeding Science 71(1): 1–14.

Sasidharan, R., J. Bailey-Serres, M. Ashikari, B.J. Atwell, T.D. Colmer, K. Fagerstedt, T. Fukao, P. Geigenberger, K. Hebelstrup, R.D. Hill et al. (2017) Community recommendations on terminology and procedures used in flooding and low oxygen stress research. New Phytol. 214: 1403–1407.

Shiono, K., S. Ogawa, S. Yamazaki, H. Isoda, T. Fujimura, M. Nakazono and T.D. Colmer (2011) Contrasting dynamics of radial $O_2$-loss barrier induction and aerenchyma formation in rice roots of two lengths. Ann. Bot. 107: 89–99.

Steffens, B. and A. Rasmussen (2016) The physiology of adventitious roots. Plant Physiol. 170: 603–617.

Takahashi, H., T. Yamauchi, T.D. Colmer and M. Nakazono (2014) Aerenchyma formation in plants. In: van Dongen, J.T. and F. Licausi (eds.) Plant Cell Monographs: Low-oxygen stress in plants. Springer 21: 247–265.

Uga, Y., K. Sugimoto, S. Ogawa, J. Rane, M. Ishitani, N. Hara, Y. Kitomi, Y. Inukai, K. Ono, N. Kanno et al. (2013) Control of root system architecture by DEEPER ROOTING 1 increases rice yield under drought conditions. Nat. Genet. 45: 1097–1102.

Uga, Y., Y. Kitomi, E. Yamamoto, N. Kanno, S. Kawai, T. Mizubayashi and S. Fukuoka (2015) A QTL for root growth angle on rice chromosome 7 is involved in the genetic pathway of DEEPER ROOTING 1. Rice (N Y) 8: 8.

Vartapetian, B.B. and M.B. Jackson (1997) Plant adaptations to anaerobic stress. Ann. Bot. 79: 3–20.

Visser, E.J.W., C.W.P.M. Blom and L.A.C.J. Voesenek (1996) Flooding-induced adventitious rooting in Rumex: morphology and development in an ecological perspective. Acta Bot. Neerl. 45: 17–28.

Visser, E.J.W., T.D. Colmer, C.W.P.M. Blom and L.A.C.J. Voesenek (2000) Changes in growth, porosity, and radial oxygen loss from adventitious roots of selected mono- and dicotyledonous wetland species with contrasting types of aerenchyma. Plant Cell Environ. 23: 1237–1245.

Voesenek, L.A.C.J. and J. Bailey-Serres (2015) Flood adaptive traits and processes: an overview. New Phytol. 206: 57–73.

Warburton, M.L., S. Rauf, L. Marek, M. Hussain, O. Ogunola and G.J.J. Sanchez (2017) The use of crop wild relatives in maize and sunflower breeding. Crop Sci. 57: 1227–1240.

Wasson, A.P., R.A. Richards, R. Chatterth, S.C. Misra, S.V. Prasad, G.J. Rebetzke, J.A. Kirkgaard, J. Christopher and M. Watt (2012) Traits and selection strategies to improve root systems and water uptake in water-limited wheat crops. J. Exp. Bot. 63: 3485–3498.

Watanabe, K., S. Nishiuchi, K. Kulichkhin and M. Nakazono (2013) Does suberin accumulation in plant roots contribute to waterlogging tolerance? Front. Plant Sci. 4: 178.

Watanabe, K., H. Takahashi, S. Sato, S. Nishiuchi, F. Omori, A.I. Malik, T.D. Colmer, Y. Mano and M. Nakazono (2017) A major locus involved in the formation of the radial oxygen loss barrier in adventitious roots of teosinte Zea nicaraguensis is located on the short-arm of chromosome 3. Plant Cell Environ. 40: 304–316.

Yamauchi, T., S. Shimamura, M. Nakazono and T. Mochizuki (2013) Aerenchyma formation in crop species: A review. Field Crops Res. 152: 8–16.

Yamauchi, T., K. Watanabe, A. Fukazawa, H. Mori, F. Abe, K. Kawaguchi, A. Oyanagi and M. Nakazono (2014) Ethylene and reactive oxygen species are involved in root aerenchyma formation and adaptation of wheat seedlings to oxygen-deficient conditions. J. Exp. Bot. 65: 261–273.

Yamauchi, T., A. Tanaka, H. Mori, I. Takamure, K. Kato and M. Nakazono (2016) Ethylene-dependent aerenchyma formation in adventitious roots is regulated differently in rice and maize. Plant Cell Environ. 39: 2145–2157.

Yamauchi, T., T.D. Colmer, O. Pedersen and M. Nakazono (2018) Regulation of root traits for internal aeration and tolerance to soil waterlogging-flooding stress. Plant Physiol. 176: 1118–1130.

Yamauchi, T., F. Abe, N. Tsutsumi and M. Nakazono (2019) Root cortex provides a venue for gas-space formation and is essential for plant adaptation to waterlogging. Front. Plant Sci. 10: 259.

Yamauchi, T., K. Noshita and N. Tsutsumi (2021) Climate-smart crops: key root anatomical traits that confer flooding tolerance. Breed. Sci. 71: 51–61.

Yu, F., K. Liang, X. Han, D. Du, Z. Pan and F. Qiu (2019) Major natural genetic variation contributes to waterlogging tolerance in maize seedlings. Mol. Breed. 39: 97.

Zaidi, P.H., P. Maniselvan, A. Srivastava, P. Yadav and R.P. Singh (2010) Genetic analysis of water-logging tolerance in tropical maize (Zea mays L.). Maydica 55: 17–26.

Zaidi, P.H., Z. Rashid, M.T. Vinayan, G.D. Almeida, R.K. Phagna and R. Babu (2015) QTL mapping of agronomic waterlogging tolerance using recombinant inbred lines derived from tropical maize (Zea mays L) germplasm. PLoS ONE 10: e0124350.

Zhang, X., B. Tang, F. Yu, L. Li, M. Wang, Y. Xue, Z. Zhang, J. Yan, B. Yue, Y. Zheng et al. (2013) Identification of major QTL for waterlogging tolerance using genome-wide association and linkage mapping of maize seedlings. Plant Mol. Biol. Rep. 31: 594–606.