Quiescence in rice submergence tolerance: an evolutionary hypothesis

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Rice (Oryza sativa) varieties differ considerably in their tolerance to submergence, a trait that has been associated with the SUB1A gene. Recently, this gene was found in some wild rice species and landraces, which along with O. sativa, belong to the AA genome type group. On the basis of geographical and historical data, we hypothesize that SUB1A-1 from wild species may have been introgressed into domesticated rice. This introgression probably occurred in the Ganges Basin, with the subsequent spread of the SUB1A-1 to other areas of South Asia due to human migration. The lack of the SUB1A gene in diploid CC genome type wild rice showing submergence-tolerant traits suggests the presence of a different survival mechanism in this genetic group.

Evolution of submergence tolerance in rice

Various hydrological regimes characterize natural and anthropic habitats where flood events vary in extent, depth, frequency, and seasonal incidence. Extreme hydrological regimes include river floodplains, coastal marshes, the Amazon floodplain, as well as the areas where rice is cultivated, which are characterized by submergence of the plants that can reach several meters but can also be absent [1]. Flood-prone environments determine the distribution and abundance of plant species and exert an evolutionary pressure which selects traits that are advantageous under these environmental conditions [1]. The adaptability of a plant to waterlogging or submergence is enhanced by the development of either metabolic or anatomical characteristics [1]. These traits act in synergy to promote plant tolerance to water submergence and represent a source of genetic variations for crop breeding [2].

Rice is a unique crop due to its adaptability to different flooding conditions. The number of varieties, landraces, and wild relatives covering the large area of production is synonymous with an exceptional plasticity to diverse hydrological regimes. One of the many ways that have enabled rice to adapt to flooding has recently been identified as a ‘quiescence strategy’ [3]. It is characterized by reduced plant elongation during submergence, associated with regrowth when the water recedes. The ethylene responsive factor (ERF) SUBMERGENCE1A (SUB1A), in its allelic form SUB1A-1, is the key determinant of this survival mechanism [4]. SUB1A-1 is induced by ethylene, a gaseous plant hormone that becomes entrapped by water submergence [5]. SUB1A-1 positively regulates the transcription of genes related to the fermentative metabolism, which is required under low oxygen conditions to sustain energy production [6]. SUB1A-1 also represses genes related to the breakdown of carbohydrates, in order to preserve the sugars needed to fuel regrowth when the water recedes [6]. Remarkably, SUB1A-1 also restricts shoot elongation, thus preventing the excessive use of carbohydrates to sustain growth, which would in any case be insufficient for the plant to reach the water surface [5]. Limited shoot elongation under submergence is achieved through the positive action of SUB1A-1 on the gibberellin (GA) signaling repressors SLENDER RICE-1 (SLR1) and SLR1-LIKE (SLRL1) [7]. During the post-hypoxic phase, SUB1A-1 is involved in acclimation to dehydration, paradoxically occurring as natural progression upon desubmergence, by increasing ABA responsiveness and reactive oxygen species (ROS) detoxification [8]. Some submergence tolerance can also be conferred by the intolerant SUB1A-2 allele, when highly expressed [9]. This allele differs in terms of the absence of the SUB1A-1 MITOGEN-ACTIVATED PROTEIN KINASE (MAPK) site [4], which might affect the activation of the protein and the regulation of downstream genes. The introgression of SUB1A-1 in rice varieties with high yields and grain quality traits, but reduced tolerance to submergence, resulted in the production of new varieties with both a high yield and submergence tolerance [10].

Considerable efforts have been made to characterize the presence/absence of the SUB1A gene in Oryza spp. [4,9,11–13]. We summarize these findings on the basis of geographical origin and description of the original habitat of the genotypes studied, in order to examine the evolution of SUB1A-1 and thus the submergence tolerance trait.

SUB1A gene is present in wild and cultivated rice

The genus Oryza L. consists of approximately 23 species harboring several distinct genome groups [14]. The Oryza spp. that belongs to the AA genome type includes Oryza sativa and Oryza glaberrima cultivated rice and wild species (i.e., Oryza rufipogon, Oryza nivara, Oryza barthii, Oryza longistaminata, Oryza meridionalis, and Oryza glumaepatula) [15], which can exchange genetic information when sympatric and flowering at the same time [16]. After being originally associated with the O. sativa small subgroup of indica varieties [4], including the aus landrace Flooding Resistant 13A (FR13A), SUB1A alleles have also been described in other genotypes including some wild
species (e.g., O. nivara and O. rufipogon) [9,12,13] which, together with O. sativa, all belong to the AA type genome group. Of the wild species belonging to the AA genomic group, O. rufipogon and O. nivara are considered to be the most likely ancestors from which O. sativa was domesticated [17].

Figure 1 shows a map of wild and landrace rice accessions belonging to the AA genome type investigated to date for the presence/absence of SUB1A and with the International Rice Germplasm Collection (IRGC) number of the International Rice Research Institute (IRRI). The map shows the presence of various wild rice species harboring the SUB1A-1 allele around the basins of the Ganges and Brahmaputra rivers, which include areas of North India, Nepal, and Bangladesh. One was originally reported to be a hybrid swarm, thus probably a natural population of wild and cultivated rice interspecific hybrids. Most archeological evidence indicates the Yangtze Valley in China as the original area of rice cultivation by humans [18–21]. In addition, genetic evidence suggests that the Ganges Valley in India was a second site of potential rice domestication [22]. A phylogeographic study also showed that the southern Himalayas was the domestication region of the indica group from the O. rufipogon progenitor [23]. Migrants could have disseminated the seeds of submergence-tolerant plants from this area to other parts of Asia, as shown by the presence of landraces with the SUB1A-1 gene in Sri Lanka, Vietnam, and Thailand (Figure 1).

Interestingly, the presence of the intolerant allele SUB1A-2 has also been identified in O. sativa genotypes from China, Cuba, Nigeria, and Guinea–Bissau. The only accession of the African cultivated rice O. glaberrima investigated shows the absence of SUB1A and was collected in Senegal [13]. To date, only a few AA rice accessions from Africa have been analyzed, making it difficult to formulate a hypothesis as to how SUB1A introgressed in this area.

Previous surveys of AA rice genotypes revealed that the SUB1A gene was sometimes, but not always, present in O. nivara, O. rufipogon, and O. sativa [9,11–13]. This supports the theory that submergence tolerance was introgressed from divergent populations of wild relatives into cultivated O. sativa [13]. Wild rice species belonging to the AA genome group evolved in areas characterized by different water regimes, with O. nivara occurring in seasonally dry habitats, and O. rufipogon in permanently wet ones [14]. However, in some places O. nivara and O. rufipogon, which are cross-compatible, are sympatric in areas of rice cultivation. Despite their ecological distinction, O. nivara and O. rufipogon have similar morphological characteristics and a relatively low genetic differentiation, thus O. nivara is also considered as a subspecies or an ecotype of O. rufipogon [14,24]. One hypothesis is that O. nivara evolved from an O. rufipogon ancestor after a habitat shift [17]. The transfer of the SUB1A gene may thus have been successful in environments where flash flooding occurs at the rice seedling stage [25].

Gene flows from AA genome type wild rice species toward nearby O. sativa could have occurred with the introgression of key domestication alleles [26]. However, gene flows from cultivated rice could also have contributed to the genetic diversity of wild relatives in sympatric regions [21]. Studies on the genetic variation of O. rufipogon have shown a higher genetic diversity of the wild rice populations growing adjacent to cultivated rice fields than those found some distance away, thus indicating that gene flows occur from cultivated to wild rice [27,28]. The absence of wild rice harboring SUB1A in Sri Lanka, where SUB1A-containing O. sativa landraces are present, suggests that either they have only been recently introduced in Sri Lanka or that SUB1A was introgressed from wild rice species to O. sativa during domestication in the Indian Basin, and then transferred to Sri Lanka.

The introgression of SUB1A in cultivated rice could have been a relatively recent event. Together with SUB1A (whose presence in rice cultivars is variable), other genes encoding ERFs are invariably present in the SUB1 region, namely SUB1B and SUB1C [6]. Phylogenetic analysis has provided evidence that SUB1A and SUB1B diverged from SUB1C during the differentiation between the AA and CC genome complexes [13], and that SUB1A resulted from the duplication of SUB1B [11]. The recent evolution of SUB1A is also suggested by the occurrence of small allelic variations in this gene (SUB1A-1 and SUB1A-2 only) compared with the highly polymorphic SUB1B and SUB1C (nine and seven alleles, respectively) [4].

**SUB1A is absent in submergence-tolerant wild rice belonging to the CC genome group**

To date, the SUB1A gene has not been found in diploid wild relatives belonging to the CC type genome group Oryza officinalis, Oryza rizomatis, and Oryza eichingeri which, however, have been shown to survive flooding by reducing growth under submergence [13]. Only SUB1C-like genes have been found in these genotypes, suggesting that this ERF may be more primitive than other SUB1 genes [13].

Wild rice belonging to the diploid CC genome type and not harboring the SUB1A gene have shown a disjointed distribution in Africa and Asia (Figure 2). A recent hypothesis suggested that O. eichingeri from Africa may have been introduced to Sri Lanka a very long time ago, because the accessions from the two locations are highly genetically divergent [24]. This species shows morphological and genetic variations in relation to geographical derivation and habitat, thus exhibiting a high degree of intraspecific variation [14]. In South Asia, wild CC and AA genotypes have been found in the same geographical region [24]. Many of the CC genotypes investigated to date have been collected in Sri Lanka where O. sativa landraces harboring SUB1A are also present (Figures 1 and 2). However, trials of breeding programs with O. eichingeri have reported a very low level of success in crosses with O. sativa [15]. Moreover, in Sri Lanka the habitat of O. rizomatis is confined to seasonally dry zones [24], making the genetic exchange between AA and CC rice relatively difficult.

One genetic analysis determined that the SUB1C allele, which is present in O. officinalis, O. rizomatis, and O. eichingeri, does not contribute to submergence tolerance in rice [29]. Moreover, the heterologous ectopic expression of rice SUB1C in Arabidopsis thaliana showed a limited contribution of this gene to the submergence stress response [30]. Overall, this supports the idea of a molecular
Figure 1. Location of the original collection sites of AA genome type wild genotypes (square symbols) and landraces (circle symbols), with or without SUB1A genes [9,11–13]. Wild genotypes and landraces without either SUB1A-1 or SUB1A-2 are represented by blue symbols. Genotypes with the tolerant allele SUB1A-1 are indicated as ‘1A-1’ in the key and yellow squares or circle symbols in the map, while those harboring the intolerant allele SUB1A-2 are indicated with ‘1A-2’ in the key and orange squares or circles in the map. The accessions shown represent those investigated to date for the presence/absence of SUB1A and with the International Rice Germplasm Collection (IRGC) number of the International Rice Research Institute (IRRI). The source country and collection site of the AA genome type wild rice accessions were studied using the original collection forms of the International Rice Information System (IRIS) from the IRRI (http://www.irri.org), whereas landraces were investigated with information obtained by the System-wide Information Network for Genetic Resources (SINGER), now part of the Plant Genetic Resource Gateway (GENESYS, http://www.genesys-pgr.org). The passport data of each accession was checked to locate the site where the sample was originally collected before being sent to the seed bank. The collection site included a wild zone or a field border for the wild species and the germplasm location before being sent to the gene bank for landraces. Rice species with unspecified or other statuses (e.g., improved cultivar and crosses) were not included in the analysis, and neither were the wild accessions lacking the original IRRI collection form. The dotted arrows represent the directions in which domesticated rice may have spread.
mechanism of submergence tolerance which may be unique to the CC type genome group and which still needs to be found. The rice varieties Madabaru and IR72 have recently been shown to harbor novel submergence tolerance quantitative trait loci (QTLs), which are independent of the ethylene-mediated SUB1A pathway [31].

Concluding remarks

Various studies have highlighted that the presence of SUB1A alleles is highly variable in several wild and landrace accessions of rice belonging to the AA genome group. Analysis of the geographical distribution of wild rice and landrace data, together with the molecular analysis for the presence of SUB1 genes, suggests that the introgression of SUB1A-1 from wild into cultivated rice originated around the Ganges Basin. The presence of SUB1A-1 in O. sativa landraces present in other Asian regions suggests that early settlers may have brought with them the seeds of submergence-tolerant plants.

Submergence-tolerant traits have also been shown to be present in some diploid CC type wild rice accessions which, however, lack SUB1A. Only SUB1C-like genes have been found in these genotypes; therefore, it is possible that they harbor a distinctive molecular mechanism of submergence tolerance, which is still unknown. In South Asia, these genotypes are found in the same geographic region where AA rice species grow; however, success in intergenomic crosses is very low.

Novel QTLs associated with submergence-tolerant traits might be useful in enhancing the level of survival. Indeed, the hybridization of wild and cultivated rice with the introgression of alien genes can give rise to new interesting variations, due to the high level of genetic diversity. Rice breeding programs that could overcome the problem of cross-compatibility barriers would be a breakthrough in rice enhancement.

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References


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