SECOND EDITION

PLANT ABIOTIC STRESS

edited by
MATTHEW A. JENKS
PAUL M. HASEGAWA

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Second Edition

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Preface

Since the last edition of *Plant Abiotic Stress*, insight has come from various research programs that now shines new light on the determinants of plant adaptation to environmental stress. While there are many sources of plant stress, this book will focus as in the first edition on the inanimate components of the environment associated with climatic, edaphic, and physiographic factors that substantially limit plant growth and survival. Categorically, this book places a focus on plant abiotic stresses caused by flooding, drought, salinity, non-optimal temperatures, and poor soil nutrition. Discussions of plant abiotic stress that originate from climate change, and its potential impacts on crop production, are also included in these chapters.

The greatest cause of reduced yield in annual crops worldwide is the combined impact of abiotic stress. For example, the threat of water scarcity to crop production worldwide is increasing as continued overutilization of aquifer-based irrigation by farmers continues unabated, a condition that is now posing a serious threat to the long-term sustainability of many regional agricultural systems. With increasing irrigation in arid and subarid zones comes increased salinization of field soils, a condition already having dramatic negative impacts on crop yield in many parts of the world. Another major threat is temperatures that are too high, too low, or too erratic for efficient crop production, much of this due to changes in climate. Degradation of field soils by increasingly intensive cultivation to satisfy growing world demand for agricultural products is compounding soil degradation and directly limiting crop yield. Although better field management practices can improve production efficiency, there can be no

doubt that new crops with increased resistance to drought, salinity, sub- and supra-optimal temperatures, poor soil nutrient status, and other stresses, like flooding and global climate change, are necessary to meet future food, fiber, and biomass needs globally.

The advent of new technologies for the efficient identification of genetic determinants involved in plant stress adaptation, fostered especially by the use of molecular genetics and high throughput transcriptome, proteome, metabolome, and ionome profiling, as well as the use of genome-wide association and other molecular mapping tools, has improved our understanding of the mechanisms plants use to tolerate abiotic stress and revealed new opportunities for creating improved stress-tolerant crops. This book seeks to summarize the large body of current knowledge about the diverse mechanisms that confer or influence plant stress tolerance, placing special emphasis on the cellular aspects of plant response whose expression is common across diverse environments. Leading scientists involved in plant abiotic stress research worldwide provide a comprehensive treatise to these major stress factors having an impact on world crop production. The material presented in this book emphasizes fundamental genetic, epigenetic, physiological, biochemical, and ecological knowledge of plant abiotic stress, which may lead to novel applications for improving crop performance in stressful environments.

Matthew A. Jenks and Paul M. Hasegawa

1 Flood tolerance mediated by the rice SUB1A transcription factor

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1.1 Introduction

Over one billion people, 15% of the world's population, live in extreme poverty. Most of these people live on farms and barely produce enough food for themselves and their families. The most economic and effective method for improving farm productivity is the planting of high-yielding and more resilient varieties that thrive on these farms. Varieties that are resistant to diseases and/or tolerant of environmental stresses can have dramatic and positive impacts on the lives of the very poor worldwide.

  Rice is the staple food for more than half of the world's population. Flooding is a major constraint to rice production in South and Southeast Asia, where the majority of the

world's rice farmers live. Each year, 25% of the global rice croplands are inundated by flash floods, which are unpredictable and can occur several times a year. Although rice is grown in flooded soil, most rice cultivars die within a week of complete submergence, causing yield losses ranging from 10% to total destruction (Mackill et al., 2012). These losses disproportionately affect the rice farmers in the world, where 70 million people live on less than $1 a day.

Compounding the challenges facing rice production are the predicted effects of climate change. As the sea level rises and glaciers melt, low-lying croplands will be submerged and river systems will experience shorter and more intense seasonal flows, as well as more flooding. Most of the coastal rice production areas in the tropics and subtropics are vulnerable to such conditions, especially low-lying deltas along the coastlines of South, East, and Southeast Asia. Rice production in these deltas is the major agricultural activity. These areas include the Mekong and Red River deltas of Vietnam, the Ayeyerwaddy Delta of Myanmar, and the Ganges-Brahmaputra Delta of Bangladesh. These deltas provide between 34% and 70% of the total rice production in these countries, and any reduction in rice production due to increases in the frequency of flooding will have serious consequences on food security (Wassmann et al., 2009). This is a challenge especially in places like Bangladesh, Eastern India, Vietnam, and Myanmar, where people get about two-thirds of their total calories from rice. Large areas of Bangladesh and India already flood on an annual basis and are likely to flood even more frequently in the future, leading to a substantial loss of agricultural land. In Bangladesh and India alone, 4 million tons of rice, enough to feed 30 million people, is lost to floods each year.

Thus, an important goal for improving the rural economy and livelihood in these vulnerable countries is to develop

rice varieties that can survive flooding. Because most of the world's poorest people get their food and income by farming small plots of land, the availability of rice varieties with enhanced tolerance to flooding is expected to make a major difference in food security for these farmers.

Although rice can withstand shallow flooding, most rice varieties will die if completely submerged for more than a few days. There are a few rice landraces that can survive prolonged submergences, and these are of great interest to rice breeders. For example, the ancient Indian rice landrace, FR13A, has poor grain and yield qualities but is unusual in its ability to endure complete submergence for over 14 days.

FR13A has been known to farmers in Orissa, India, since the 1950s. For over 40 years, breeders at the International Rice Research Institute (IRRI) tried to use FR13A as a donor parent to introduce the submergence tolerance trait into varieties that would be useful to rice farmers. Although submergence tolerant varieties were developed, they were not widely adopted. The main reason is that because breeding was carried out with relatively crude genetic tools based mainly on visual selection, the resulting varieties lacked many of the traits desired by farmers in the major rice-growing areas of Asia. With lack of knowledge on the exact genes needed to confer submergence tolerance, the breeders unknowingly dragged in undesirable traits along with the submergence tolerance trait, which reduced yield and grain quality.

Over the last 15 years, we collaborated with Dave Mackill at the International Rice Research Institute and other researchers and breeders to carry out detailed genetic analyses of submergence tolerance in rice. Our long-term goal was to understand the underlying molecular mechanisms controlling submergence tolerance and generate tools that breeders could use to develop rice

varieties with high yields and good grain quality that are tolerant to submergence. The results of this team effort led to the identification of the *SUB1* locus and associated genes, development of rice "mega varieties" with submergence tolerance for farmers, and elucidation of the gene networks and physiological processes mediated by *SUB1*.

1.2 Isolation of the rice *SUB1* locus

In early genetic studies, rice submergence tolerance derived from FR13A had been shown to have a relatively high heritability, with tolerance being partially to completely dominant (Haque et al., 1989; Mohanty and Khush, 1985; Mohanty et al., 1982; Sinha and Saran, 1988; Suprihatno and Coffman, 1981). The trait was also thought to be controlled by one or a few loci with major effects and loci with smaller, modifying effects. On the basis of these studies, we began to investigate submergence tolerance using an approach combining the power of molecular markers and quantitative trait locus (QTL) analysis. This initial study employed a population (DX18) of 169 F_2 plants and their resulting F_3 families that were derived from a cross between two breeding lines, PI613988 (japonica) and IR40931-26 (indica), the latter of which inherits strong submergence tolerance from FR13A. Kenong Xu and David Mackill demonstrated that a major QTL, *SUB1*, mapped between two restriction fragment length polymorphism (RFLP) markers (C1232 and RZ698) on rice chromosome 9 (Xu and Mackill, 1996). The *SUB1* QTL was supported with a logarithm of odds (LOD) score of 36 and accounted for 69% of phenotypic variation in the F_2 population, concluding that *SUB1* is critical for conferring submergence tolerance in rice.

Simultaneously, other teams (Kamolsukyunyong et al., 2001; Nandi et al., 1997; Toojinda et al., 2003) also reported the strong phenotypic effect of the *SUB1* locus, confirming its effect as the major determinant of tolerance, besides few other minor QTLs.

Previously, the Ronald laboratory had successfully used an approach of "positional cloning" to isolate a rice gene, called *Xa21*, that conferred broad-spectrum resistance to a serious bacterial disease in Asia and Africa (Song et al., 1995). This experience encouraged us to take the same approach to isolate the *SUB1* QTL although it was challenging because a QTL for an important agronomic trait had never before been isolated from a staple crop species, and the rice genome had not yet been sequenced.

We first carried out fine mapping of the *SUB1* QTL to characterize the *SUB1* region with more markers in a large F_2 population (DX202) of 2,950 plants, which was derived from a cross between M202 (a widely grown japonica rice cultivar in California) and DX18-121 (a tolerant line from population DX18, see above). The resulting *SUB1* fine map comprised ten amplified fragment length polymorphism (AFLP) markers. Two of these markers co-segregated with *SUB1* and eight linked to *SUB1* within 0.2 cM (Xu et al., 2000). The significance of this fine map is that it laid a foundation for physically mapping the *SUB1* locus on rice chromosome 9.

We then carried out physical mapping of the *SUB1* locus by identifying a set of five bacterial artificial chromosome (BAC) and 13 binary clones that overlapped each other and that entirely covered the *SUB1* region (Xu et al., 2006). The five BAC clones were obtained from the two BAC libraries constructed from rice cultivars IRBB21 and Teqing, respectively. Both BAC libraries were publically available, but IRBB21 and Teqing do not carry the submergence tolerance trait. The 13 binary clones were achieved from a

genomic library constructed from the submergence tolerance parental line IR40931-26 using a binary vector that could be used to directly engineer rice plants. By developing more markers from these BAC and binary clones and analyzing the expanded F_2 population DX202 of 4,022 plants, we were able to delimit the *SUB1* locus with a region of 182 kb between markers CR25K and SSR1A (Xu et al., 2006).

Complete sequencing of the 182 kb *SUB1* region revealed that the region encodes 13 genes, including 3 that contain ethylene response-factor (ERF) domains, which were designated SUB1A, *SUB1B*, and *SUB1C*. We found that the corresponding *SUB1* region in the sequenced genome of japonica rice Nipponbare (International Rice Genome Sequencing Project, 2005) spans only 142 kb and lacks *SUB1A*.

We next carried out an allelic variation survey of the *SUB1* genes in 21 varieties (17 indica and 4 japonica). We identified two *SUB1A*, nine *SUB1B*, and seven *SUB1C* alleles. The *SUB1A-1* and *SUB1C-1* alleles are specific to all six submergence tolerant accessions studied, including FR13A, Goda Heenati, and Kurkurapan, which are of independent geographic origins. However, there was no such correlation between a specific *SUB1B* allele and submergence tolerance.

Using gene expression analysis, we found that *SUB1A* was rapidly induced upon submergence in the submergence tolerant variety. In contrast, *SUB1C* was upregulated only in the intolerant variety, M202. The expression of *SUB1B* was low and constant in both submergence tolerant and intolerant varieties. These data suggested that *SUB1A* controlled the *SUB1*-mediated submergence tolerance response.

To functionally prove *SUB1A* as the very gene underlying the *SUB1* QTL, we created a construct containing the

SUB1A-1 full-length cDNA under the control of the maize Ubiquitin1 promoter (Christensen and Quail, 1996) to overexpress *SUB1A-1* in Liaogeng, a submergence intolerant japonica rice that also lacks *SUB1A*. Submergence screening of the resulting T_1 transgenic plants identified four independent T_1 families segregating for submergence. A detailed analysis of two of the four T_1 families showed a nearly complete correlation between high expression of the *SUB1A-1* transgene and submergence tolerance. We therefore concluded that *SUB1A-1* is sufficient to confer submergence tolerance to intolerant varieties, signifying the isolation of the *SUB1* QTL (Xu et al., 2006).

This work was significant because it represented the first isolation of a QTL with an important agronomic effect and revealed an important genetic mechanism with which rice plants can control tolerance to submergence. Isolation of *SUB1A* and the 180 kb of genetic sequence surrounding the gene set the stage for advanced marker assisted breeding at the IRRI (Neeraja et al., 2007; Septiningsih et al., 2009; Mackill et al., 2012).

1.3 Sub1 rice in farmers' fields

Initially, the IRRI group monitored the *SUB1* locus using markers closely linked with the gene. However, the availability of the sequences from BAC clone AP005907, which carried the sequences of the *SUB1* genes, soon facilitated the development of six more markers tightly linked to the *SUB1* QTL. This approach allowed for the transfer of the "donor" (Sub1) genetic region to be precisely monitored. The Sub1 donor FR13A variety carries many undesirable agronomic characters; therefore without

knowledge on the precise location of *SUB1A* and the ability to select against other regions of the FR13A genome, these undesirable characteristics are dragged into the new variety along with *SUB1* (Neerja et al., 2007). Thus, with the availability of the *SUB1A* sequence and other sequences in the region, the *SUB1* locus could be precisely introduced into a wide range of recipient rice varieties favored by farmers, while at the same time minimizing the effects of "linkage drag" from the Sub1 donor. This work resulted in the introduction of *SUB1* into eight rice varieties popular in South and Southeast Asia. The first of these was the mega variety Swarna, which is grown on ca. 5 million hectares in India and on additional areas in Bangladesh and Nepal (Xu et al., 2006).

The new rice variety—called *Swarna-Sub1*—was tested in farmers' fields in Bangladesh and India. In the absence of flooding both Swarna and Swarna-Sub1 yield 5–6 tons per hectare. However, in the presence of flooding, fewer plants of the Swarna rice crop survived (0–20% in most cases depending on floodwater conditions and duration; Das et al., 2009), whereas the Swarna-Sub1 rice flourished—80–95% of it survived. This enhanced survival means that farmers growing the Swarna-Sub1 variety gain a 1 to over 3 tons per hectare yield advantage following floods (Singh et al., 2009). Using this marker assisted breeding approach, the IRRI team has now generated and released several Sub1 varieties in six countries (Indonesia [4], Nepal [2], Mynamar [1], India [2], Bangladesh [2], and the Philippines [2]). In 2011, Swarna-Sub1 alone was estimated to have reached over one million farmers in South Asia (Mackill et al., 2012).

Over the last 5 years, our colleagues at IRRI have been working with India's National Food Security Mission, the Ministry of Agriculture, the government of India, and with state governments, non-governmental organizations (NGOs), and public and private seed producers and breeders

in India, Bangladesh, and Nepal to multiply and disseminate Swarna-Sub1 seeds and seeds of other released Sub1 varieties and to strengthen the existing seed systems. The supply will aid various states in South Asia that do not have enough seeds to distribute to farmers.

The Bill and Melinda Gates Foundation is now supporting a large program, called *Stress-Tolerant Rice for Africa and South Asia* (STRASA; www.strasa.org), that is assisting with the development and dissemination of Sub1 rice varieties in three countries (http://irri.org/news-events/irri-news/bill-and-melinda-gates-visit-strasa-and-csisa-projects-at-icar-research-farms-in-patna-india). STRASA was conceived as a 10-year project with the vision of reaching about 20 million farmers in South Asia and Sub-Saharan Africa by 2017. By 2014, Sub1 varieties are predicted to be grown in over 5 million hectares (Mackill et al., 2012).

We initially introduced *SUB1* into a set of popular varieties including Swarna (also widely grown in Bangladesh and Nepal), Samba Mahsuri, and CR1009 (Savitri) from India; BR11 from Bangladesh; Thadkkham 1 (TDK 1) from Laos; and IR64 from IRRI-Philippines. More recently, *SUB1* has been introduced into Ciherang from Indonesia and PSBRc 18 from the Philippines. These varieties were chosen because they are popular among farmers and consumers in rainfed lowland areas, each covering between 1 and over 6 million hectares. The flood-tolerant versions of these high-yielding "mega varieties" are effectively identical to their intolerant counterparts but survive better after severe floods to yield well. The grain quality of all Sub1 lines developed so far is essentially identical to the conventional varieties, with the extra advantages of fast recovery and earlier maturity (by 10–15 days) than their non-Sub1 counterparts following submergence for various durations (Singh et al., 2009). Breeders predict that the most popular Sub1 varieties like Swarna-Sub1 and BR11-Sub1 will soon entirely replace the

existing non-Sub1 versions and spread to other flood-prone areas all over these countries.

Introgression of *SUB1* into these varieties also facilitated the introduction of these varieties to regions where they were not known before; for example, Swarna-Sub1, which previously had only been planted in South Asia, has now been released in Indonesia, and Ciherang from Indonesia is in the final stages of release for flood-prone areas in Bangladesh and India.

We chose to introduce these popular varieties because they were well known to farmers, millers, and consumers, and therefore less time would be needed to evaluate and commercialize the new varieties. One difficulty with such success is that although there are now ample incentives for farmers to grow these mega Sub1 varieties like Swarna-Sub1 and BR11-Sub1, there is still little incentive to introduce additional rice varieties to enhance the overall genetic diversity of the rice planted in large areas as in India and Bangladesh. Breeders, geneticists, and agronomists know from past experience that monocultures can be vulnerable to other problems, such as yield stability. The issue is to balance the demand of farmers for high-yielding, high-quality, flood-tolerant rice varieties with the need to plant genetically diverse rice varieties to minimize possible future losses to pest and disease. For these reasons, IRRI decided to introduce *SUB1* into all varieties being bred for rainfed lowlands, and a considerable number of breeding lines are now being evaluated at target sites in Asia and Africa. In addition, breeding lines combining *SUB1* and drought tolerance as well as *SUB1* and salt tolerance have been developed and are being field tested. These new breeding lines are useful for areas experiencing both flash floods and drought as in most rainfed lowlands, as well as submergence and salt stress as in tropical coastal areas of South and Southeast Asia (Ismail et al., 2008). Substantial

efforts are also being undertaken by national programs to-incorporate *SUB1* into additional local popular varieties as well as into new elite lines as in Vietnam, India, Bangladesh, and Thailand.
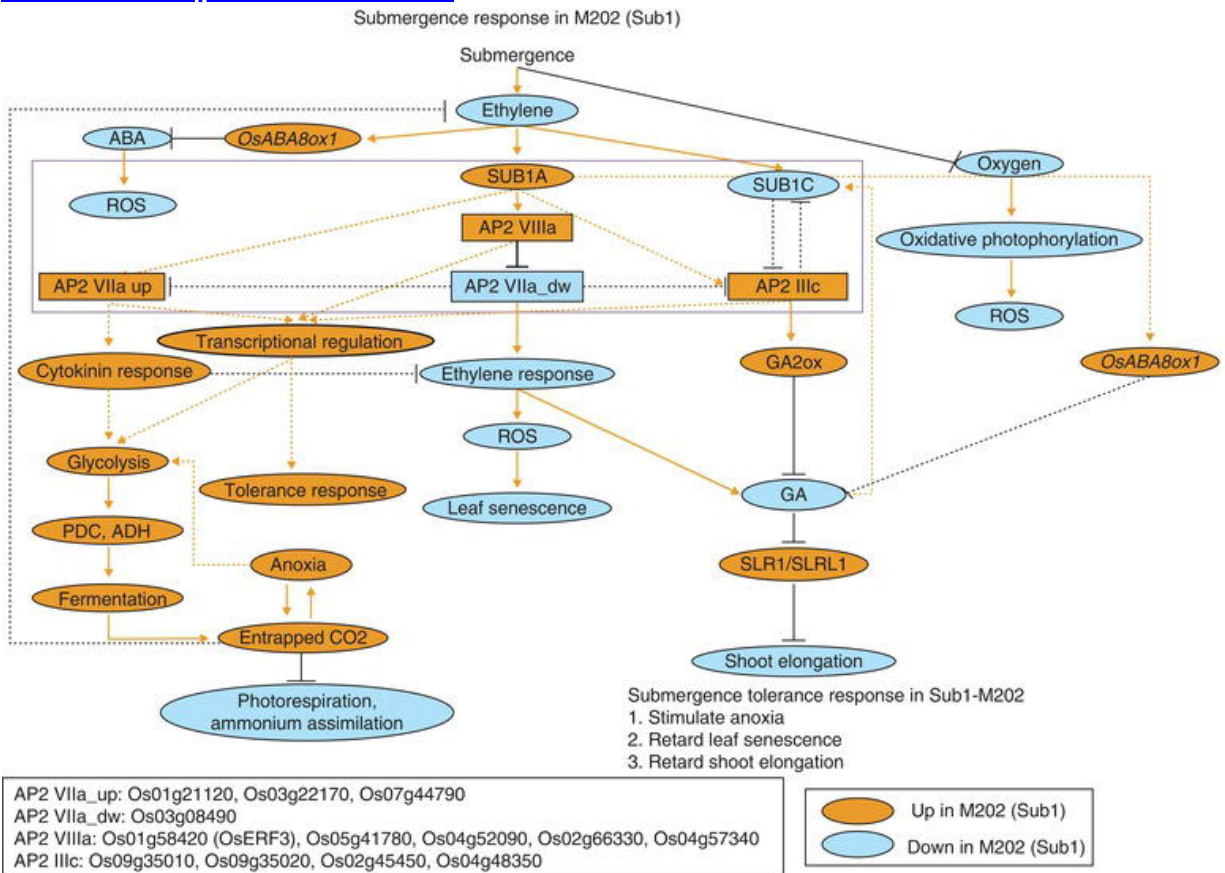
1.4 The SUB1 effect

SUB1 exerts its effect by limiting gibberellic acid (GA)-activated elongation growth and ethylene-induced leaf senescence. Complete submergence restricts light intensity, slows O_2 and CO_2 exchange between shoot tissue and floodwater, and enhances the accumulation of ethylene due to increased synthesis and entrapment. Ethylene accumulation triggers chlorophyll degradation and leaf senescence (Ella et al., 2003) and causes excessive elongation of leaves and internodes of the submerged plants in an attempt to maintain contact with air. This is mediated through ethylene-induced suppression of abscisic acid (ABA) synthesis but enhanced synthesis and sensitivity to GA (Das et al., 2005). Reduced photosynthetic capacity during and following submergence, together with excessive growth during submergence, results in severe carbohydrate starvation and consequent death of the submerged plants. In collaboration with Bailey-Serres at the University of California-Riverside, we have demonstrated that SUB1A exerts its effect by limiting GA-activated elongation growth and conserving carbohydrates (Figure 1.1). The *SUB1* locus enables plants to endure complete submergence for prolonged periods due to activation of a "quiescence strategy" that conserves the shoot meristem and energy reserves until the flood subsides.

1.5 The SUB1-mediated gene network

In addition to flooding, other environmental stresses such as drought, salinity, and heat stress are predicted to be increasingly problematic for farmers as the climate warms. For example, in Africa, three-quarters of the world's severe droughts have occurred over the past 10 years (African Agricultural Technology Foundation, 2010). Losses to pests and diseases are also expected to increase over the next 50 years. Much of the losses caused by these pests, diseases, and environmental stresses, which already result in 30–60% yield reductions globally each year, occur after the plants are fully grown: a point at which most or all of the land and water required to grow a crop has been invested. Thus, there is a need to identify genes that confer robust tolerance to environmental stresses and diseases and to use this information to develop new varieties.

  As part of this goal, we and others are using genomic, molecular-genetic, allelic diversity, and computational approaches to identify other genes and gene networks involved in tolerance to stress and devastating diseases. For example, we recently demonstrated the usefulness of transcriptomics and interactomics approaches to identify genes and proteins that are part of the predicted rice SUB1A-mediated response network, and we have shown, through genetic analysis, that this approach efficiently identifies key genes regulating these biological pathways (Jung et al., 2010; Seo et al., 2011).

Figure 1.1 SUB1A-mediated submergence tolerance responses revealed by integrating omics tools (Jung et al., 2010). Orange boxes indicate events upregulated in M202(Sub1) after submergence, and blue boxes indicate events downregulated in M202(Sub1) after submergence. Several of the AP2/ERF TFs are associated with submergence tolerance response. For color details, please see color plate section.

Submergence response in M202 (Sub1)

Submergence

Ethylene

ABA — OsABA8ox1

Oxygen

SUB1A — SUB1C

ROS

AP2 VIIa

Oxidative photophorylation

AP2 VIIa up — AP2 VIIa_dw — AP2 IIIc

ROS

Transcriptional regulation

Cytokinin response — Ethylene response

GA2ox

OsABA8ox1

Glycolysis

ROS

Tolerance response

Leaf senescence

GA

PDC, ADH

Anoxia

SLR1/SLRL1

Fermentation

Entrapped CO2

Shoot elongation

Photorespiration, ammonium assimilation

Submergence tolerance response in Sub1-M202
1. Stimulate anoxia
2. Retard leaf senescence
3. Retard shoot elongation

AP2 VIIa_up: Os01g21120, Os03g22170, Os07g44790
AP2 VIIa_dw: Os03g08490
AP2 VIIIa: Os01g58420 (OsERF3), Os05g41780, Os04g52090, Os02g66330, Os04g57340
AP2 IIIc: Os09g35010, Os09g35020, Os02g45450, Os04g48350

Up in M202 (Sub1)
Down in M202 (Sub1)

Figure 1.2 The rice SUB1A/SUB1C interactome. The interactome map represents 28 proteins identified from high-throughput Y2H screening using SUB1A and SUB1C as baits. Proteins in blue represent interactors with both SUB1A and SUB1C (Seo et al., 2011). For color details, please see color plate section.