ISABELA PEREIRA DE LIMA

PHENOTYPING AND MORPHO-PHYSIOLOGICAL BEHAVIOR OF RICE GENOTYPES UNDER WATER DEFICIT

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FENOTIPAGEM E COMPORTAMENTO MORFOFISIOLÓFICO DE GENÓTIPOS DE ARROZ SOB DÉFICIT HÍDRICO

Tese apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Agronomia/Fitotecnia, área de concentração em Produção Vegetal, para a obtenção do título de Doutora.

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À minha mãe, meu exemplo de vida.

Ao meu pai, meu exemplo de força.

Dedico

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ABSTRACT

Given the current climate change, understanding and selectimg of the drought tolerant genotypes become extremely important. The upland rice is sensitive to climatic conditions and it is damaged by the occurrence of water deficit. Once the variability has been found for drought tolerance, upland rice crop can be studied and worked by breeders in order to solve the problem. Thus, the objective of this work was to fine phenotype upland rice genotypes, contrasted by behavior under water deficit, using analysis of morpho-physiological characteristics, and phenotypic correlations estimation between index of response variation from evaluated characters. For this, two trials were conducted using six previously selected genotypes, and stress start was at panicle initiation. A trial was conducted in a randomized block design, with three repetitions and two water treatments, irrigated (IRR) and stressed (STR), at Embrapa Rice and Beans, Santo Antônio de Goiás, Brazil. And a second one, at CIRAD, Montpellier France, was conducted in a completely randomized design, with three repetitions and two water treatments, IRR and STR. Several characters were evaluated and used for fine phenotyping plant development, until panicle emergence, determining in this phase water stress end. To better understand data obtained, were done analyzes of variance, means grouping by Scott-Knott test, orthogonal contrasts and phenotypic correlations between response index to evaluated characters were performed. Through the analyzes was possible to conclude that CIRAD 409 presents potential drought tolerance, without behavior change and a significant increase in water use efficiency for dry weight production under water stress. The spikelet number reduction is strongly related to panicle branch number reduction, but not related with panicle length reduction. The flag leaf width and length reduction is directly related with panicle spikelet number of the main stem.

Keywords: *Oryza sativa*; Genotypes; Phenotyping; Drought tolerance.

RESUMO

Diante da atual conjuntura de mudanças climáticas, torna-se extremamente importante, o entendimento do comportamento e a seleção de genótipos, que apresentem tolerância ao déficit hídrico. O arroz de terras altas, apresenta sensibilidade às condições climáticas, sendo altamente prejudicado pela ocorrência de déficit hídrico. Uma vez encontrada variabilidade para tolerância ao estresse hídrico, a cultura do arroz de terras altas, vem sendo muito estudada e trabalhada por melhoristas, a fim de solucionar o problema. Com isso, com o presente trabalho objetivou-se, realizar uma fenotipagem morfofisiológica de genótipos de arroz de terras altas, contrastantes em relação ao comportamento frente ao déficit hídrico, por meio da análise de características morfofisiológicas, e a estimação de correlações entre os índices de variação de respostas dos caracteres avaliados. Para tal, foram conduzidos dois experimentos utilizando seis genótipos previamente selecionados, tendo o início do estresse marcado pela fase de iniciação da panícula. Um experimento, na Embrapa Arroz e Feijão, Santo Antônio de Goiás, Brasil, conduzido em blocos casualizados, com três repetições e dois tratamentos hídricos, irrigado (IRR) e estressado (STR). E o segundo, no CIRAD, Montpellier França, conduzido em delineamento inteiramente casualizado, com três repetições e dois tratamentos hídricos, IRR e STR. Foram avaliados diversos caracteres, os quais fenotiparam de forma detalhada o desenvolvimento da planta até a emissão da panícula, determinando nessa fase o fim da aplicação do estresse hídrico. A fim de compreender os dados obtidos, foram realizadas análises de variância, agrupamento de médias pelo teste de Scott-Knott, contrastes ortogonais e correlação fenotípica entre os índices de respostas dos caracteres avaliados. Por meio das análises foi possível concluir que, o genótipo CIRAD 409 apresenta potencial tolerância ao déficit hídrico, sem alteração de comportamento e aumento significativo na eficiência no uso da água para produção de matéria seca, sob estresse hídrico. A redução do número de espiguetas está fortemente relacionada à redução do número de ramos da panícula, mas não à redução do comprimento total da panícula. A redução da largura e comprimento da folha bandeira afetam diretamente o número de espiguetas da panícula do perfilho principal.

Palavras chaves: *Oryza sativa*; Genótipos; Fenotipagem; Tolerância ao déficit hídrico.

CONTENTS

1 INTRODUCTION

Given the current climate changes, weather forecasting indicates an intensification to water limitation situations over the next decades (CECCARELLI, 2014). On the other hand, the population growth and the increasing demand for food will reflect directly in the agricultural production, which is expected to double over the next 12 years (FRANKARD et al., 2011). Thus, maintaining crop productions under such climate changes is expected to be one of the greatest challenges of modern agriculture. The lack of water might be the main factor that will limit the increase in production around the world (CECCARELLI, 2014). Furthermore, there is strong pressure regarding the impact of water use in agricultural activities and competition with urban population (FRANKARD et al., 2011).

With respect to rice cultivation, there are currently two predominant production systems in Brazil, called irrigated or upland rice. Upland rice is extremely productive when associated with the use of high technology and proper climatic conditions. However, when these requirements are not complied with, it causes great losses, which makes the crop uncompetitive in the agricultural market.

Water deficit causes a number of problems that affect plant growth significantly. Generally, these problems may cause cycle increase, plant height reduction, yield reduction and low grain quality (TAIZ and ZEIGER, 2013; TERRA et al., 2013).

Plant breeding is an area that can bring contributions to plant adaptation to water deficit. The development of drought tolerant cultivars is an alternative that has been used by researchers (GRENIER et al., 2015, RAMALHO et al., 2012). In this sense, the identification of drought tolerant upland rice genotypes will make a contribution to maintaining and increasing the yield of this crop, once this is considered the basis of the daily diet of more than half population in the world (SNEYD, 2016). The development of drought tolerant upland rice cultivars has a strong social appeal, because it will be difficult to sustain the growing demand for food only with the irrigated production system.

One of the main goals of the upland rice breeding program is to increase yield stability under water stress. Significant differences among rice cultivars have been observed in field experiments under different water stress conditions (CASTRO et al., 2013; NDJIONDJOP et al., 2012). In rice crops, there is genetic variability for different mechanisms of tolerance to water deficit. However, the genetic control of drought tolerance is complex and difficult to evaluate at the field level (CECARELLI, 2014; TERRA et al., 2013).

The key to the progress of plant breeding and the development of tolerant cultivars is better understanding cellular, physiological, biochemical and molecular changes that occur in

response to water stress (OYANG et al., 2010; STITT; SULPICE; KEURENTJES, 2010). In this sense, it is difficult to characterize precisely which genotypes are tolerant to the different levels of water deficit, which also makes it hard to determine which characters should be evaluated (ARIAS et al., 2011). Thus, it is important to use the upland rice genetic diversity to explore physiological and genetic bases of drought tolerance.

Working with drought tolerance in upland rice, researchers from Embrapa Rice and Beans, in partnership with researchers from CIRAD (International Center for Agronomic Research for Development), developed the DRYCE project, called “Identification, validation and introgression within elite lines and recurrent selection population of key alleles contributing to tolerance to water deficit in rainfed rice”. DRYCE is a large project with several stages, one of which is represented by this thesis.

Given the above, this dissertation aimed at making a morphophysiological phenotyping of upland rice genotypes with contrasting behaviors under water deficit. It also aimed at exploring correlations among genotype behaviors, under water deficit in the reproductive phase using organogenesis and morphogenesis processes, and the relation among components of the reproductive and vegetative phases.

2 LITERATURE REVIEW

2.1 Morphological development of plant rice

Rice (*Oryza sativa* L.) is a monocotyledon, belonging to Poaceae family. As such, it is characterized by hollow stems, reduced flowers organized as inflorescences, and cariopse-type fruit (CHANG; BARDENAS, 1965).

Rice has a fasciculate root system, which is not provided with a main root, and is characterized by three root types: seminal, mesocotyl and nodal. The seminal root appears after germination, at radicle emergence, and remains active until the emergence of the seventh leaf. Afterwards, the seminal root is replaced by the mesocotyl and nodal roots. The mesocotyl roots grow from the axis between the coleoptile node and radicle base, and the nodal root appears in the tiller basal region (MATSUO; HOSHIKAWA, 1993).

The plant stem consists of a main tiller, added with a variable number of primary and secondary tillers. In the vegetative phase, the tillers are formed by a set of nodes that is located at the tiller base, which is only visible through dissection. In the reproductive phase, the internode elongation occurs and the nodes get distant from each other, allowing their complete visualization, surrounded by the leaf sheath (MATSUO; HOSHIKAWA, 1993).

Growing from buds located at the nodes, the leaves are elongated and distributed alternately in the plant tiller. The complete leaf is formed by the sheath, ligule and blade. The sheath is the elongated, cartridge-shaped organ that begins at the node and surrounds the tiller. The ligule is part of the leaf collar, and is the limit between the sheath and the leaf blade, the blade is the hanging part of the leaf (CHANG; BARDENAS, 1965). The period between the ligulation of a leaf and the ligulation of the next leaf is named phyllochron. In other words, phyllochron is the intervening period between the sequential appearance of two complete leaves (RICKMAN; KLEPPER, 1995). 8 to 14 leaves grow from the main stem, according to genotype cycles. The last leaf to appear in each tiller is called flag leaf. The genotype leaves differ from each other as to length, width, insertion angle, pubescence and color (CHANG; BARDENAS, 1965).

Rice flowers are called spikelets and are grouped in a panicle-type inflorescence, located on the peduncle. The peduncle extension varies considerably from genotype to genotype. In general, the panicle consists of a main rachis composed by primary and secundaries branches, from which the spikelets grow (CHANG; BARDENAS, 1965).

Spikelets are formed by two pairs of bracts and glumes. The inferior pair is rudimentary and the glumes are sterile. The superior glumes are called palea and lemma and contain floral organs composed by a pistil with an ovule, and six stamens. The sterile glumes, along with the

lemma and the palea, form the grain shell. Sometimes and depending on the genotype, the lemma has a filiform extension called arista (MATSUO; HOSHIKAWA, 1993).

The rice fruit is formed by the fertilized ovary and contains only one seed in the pericarp, surrounded by the lemma and the palea. The grain without the shell is called cariopse (CHANG; BARDENAS, 1965).

Any plant development begins with fertilization of the ovule cell, to form the zygote. From the first zygotic division, plant development begins with a sequence of phases that differ from each other based on certain key events (MATSUSHIMA, 1966).

In plant growth and development, there are two basic processes: morphogenesis and organogenesis. Briefly, organogenesis is the process of formation of new organs through cell differentiation, and morphogenesis is the process of elongation of these organs through cell division (TAIZ and ZEIGER, 2013). The presence of water is extremely important in cellular elongation, since the cell wall relaxation by the hormonal action allows the water to enter the cell, thus elongating it (TAIZ; ZEIGER, 2013).

The rice plant development can be roughly divided into three phases: embryogenesis, vegetative phase and reproductive phase. A particularity of rice is the simultaneous occurrence of the end of the vegetative phase and the beginning of the reproductive phase (COUNCE; KEISLING; MITCHELL, 2000), which occur at the phenological phases corresponding to V_{F-4} and R_0. Seed dormancy and germination, and the beginning of inflorescence formation typically delimit the three stages of plant development, which can be divided into subphases, with more specific events (MATSUSHIMA, 1966).

Embryogenesis begins with the zygote formation and continues until seed germination. In this phase, plant architecture is determined, that is, zygotic cell divisions occur without morphogenetic events to form the embryo. Then, the apical meristem and radicle differentiate, fixing specific positions in the stem (ITOH et al., 2005). To better categorize embryogenesis, this phase can be divided into ten stages, as described in Figure 1.

Figure 1 – Stages of rice embryogenesis phase.

Symbol	Stage	Events
Em_1	Zygote	Fertilization.
Em_2 to Em_4	Globular stage	First fertilized ovule division, globule formation and intense cell division and elongation.
Em_5	Apical meristem and radicle formation	Beginning of the coleoptile, apical meristem and radicle differentiation.
Em_6	First leaf formation	First leaf primordium protrusion
Em_7	Second and third leaves formation	Second and third leaves protrusion in alternate phyillotaxis
Em_8	Organ elongation	Organ elongation and complete morphology.
Em_9	Maturation	Maturation expression.
Em_{10}	Dormancy	Dormancy.

Source: Adapted from Itoh et al., 2005.

As observed in Figure 1, the formation of leaf primordia at embryogenesis is not a characteristic exclusive to rice plant, but to grasses in general, and it means that the early stages of the vegetative phase occur before dormancy (ASAI et al., 2002). Seed germination is the process of embryo transformation into a seedling (Berlyn, 1972).

From germination, the plant begins its vegetative development, which is usually the longest period, where leaf and tiller formation occurs. Vegetative growth occurs differently in two processes of organogenesis and morphogenesis (ITOH et al., 2005).

The successive emergence of complete leaves is what determines the different development stages of the vegetative phase (COUNCE; KEISLING; MITCHELL, 2000), as described in Figure 2. The vegetative development consists of stages called V_1, V_2, V_3 ... V_F. Number 1 corresponds to the first complete leaf emergence and F the final number of ligulated leaves in the main stem, called the flag leaf.

Figure 2 – Stages of rice vegetative phase.

Symbol	Stage	Events
V_1	Formation of the first complete leaf collar on the main stem.	
V_2	Formation of the second complete leaf collar on the main stem.	Nodal root formation.
V_3	Formation of the third complete leaf collar on the main stem.	Possible tillering.
V_4	Formation of the fourth complete leaf collar on the main stem.	Tiller formation.
V_5 to V_x	Formation of the fifith/others complete leaf collars on the main stem.	Tiller formation.
$V_{F-4} = R_0$	Formation of the V_{F-4} leaf collar on the main stem.	Panicle initiation. Internode elongation in the main stem.
V_{F-3}	Formation of the V_{F-3} leaf collar on the main stem.	Internode elongation in the main stem.
V_{F-2}	Formation of the V_{F-2} leaf collar on the main stem.	Panicle branch differentiation. Internode elongation in the main stem.
V_{F-1}	Formation of the V_{F-1} leaf collar on the main stem.	Palea, lemma e glume differentiation. Last internode elongation in the main stem.
V_F	Formation of the V_F leaf in the main stem.	Microsporogenesis. Last complete leaf appearance. Peduncle elongation.

Source: Adapted from Counce; Keisling; Mitchell, 2000.

When the environmental conditions and internal factors of the plant become favorable for floral induction, the apical meristem, which coordinates the successive emergence of leaves and tillers, is then converted into floral meristem. This will initiate the panicle and also mark the beginning of the reproductive phase.

The floral meristem will be responsible for the formation of branches and spikelets, which will create the panicle (ITOH et al., 2005). The nine different stages and events that characterize the rice reproductive phase are described in Figure 3.

Figure 3 – Stages of rice reproductive phase.

Symbol	Stage	Events
R_0	Panicle initiation.	
R_1	Panicle differentiation and branch formation.	Glume, palea and lemma differentiation.
R_2	Complete flag leaf formation.	Microsporogenesis.
R_3	Panicle emergence.	Peduncle elongation.
R_4	Anthesis	Pollination.
R_5	Beginning of grain filling.	Cariopse expansion.
R_6	End of grain filling.	Full grains. Milk stage.
R_7	At least one grain presents typical shell color.	Soft and tough mass stage.
R_8	Some grains mature and reach typical shell color.	Physiological maturity
R_9	All grains filled in R_6 have typical color shell.	Dry grains.

Source: Adapted from Counce; Keisling; Mitchell, 2000.

2.2 Plants mechanisms related to water deficit tolerance

Plant productivity is limited to and dependent on water, therefore water availability is as important as the efficient use of this resource by plants (TAIZ AND ZEIGER, 2013). Improper climatic conditions, long dry seasons and periods with less rainfall cause water deficit in plants, in general and limit crop yield (TAIZ AND ZEIGER, 2013)

According to Taiz and Zeiger (2013), water deficit can be defined as the situation in which the water content in the cell or tissue is lower than the state of greater hydration and can be varied according to intensity and duration of such stress. This deficit causes water stress to the plant. The term “stress” is widely used, and can be defined as a deviation in the optimal conditions for plant growth and development (LARCHER, 2004).

The stress caused by the water deficit affects several biochemical, physiological and morphological processes in the plants, and the responses usually depend on the genotype, the development stage, stress duration and severity (VIDAL; CARVALHO; MENESES, 2005). Stress severity depends on several factors, including rainfall distribution, plant evaporative demand, and soil capacity for water storage (WERY et al., 1994).

The effects of water stress on plants are not always evident during the phenological stages of growth and development, depending on the stage affected by the stress, the stress intensity and the genotype tolerance or susceptibility to drought. Plant growth and development

are directly related to cell division, elongation and differentiation, and involve genetic, physiological, ecological and morphological factors (FAROOQ et al., 2009).

Under water deficit conditions, mitosis is impaired, limiting cell division. This limitation indirectly affects cell elongation, causing a reduction in plant growth and development, as well as plant height and leaf area. As a consequence, leaf area reduction, lower leaf expansion, and senescence cause the decrease in the active photosynthetic area (NONAMI, 1998; TERRA et al., 2013). Wopereis et al. (1996) reported that delays in flowering and maturation can increase growth and biomass accumulation in water-deficient environments. Water stress during the reproductive phase is also a great cause of yield reduction.

In order to deal with water deficit, plants develop mechanisms of tolerance to stress, being the water deficit tolerance defined as the ability to grow, flower and produce grains under conditions of water deficit (CHAVES; OLIVEIRA, 2004). These mechanisms can be classified as morphological, physiological and molecular processes that promote changes to the entire plant, being able to act solely or jointly, and determine the plant ability to sustain growth and development, even under conditions of water deficit (FAROOQ et al., 2009).

Among the morphological mechanisms involved in the process of water deficit tolerance, escape mechanisms, avoidance and phenotypic plasticity are mentioned. For crops in general, escaping from water deficit is a mechanism related to plant cycle reduction, which is not observed in rice crops (TERRA et al., 2013), or seasonal growth, which allows the plant to reproduce before the environment becomes dry enough to prevent it (ARAUS et al., 2002). The duration of the crop cycle is determined by genotype and environment, and may determine the plant's ability to escape climatic stresses, such as water deficit (ARAUS et al., 2008). Escaping from water deficit occurs when the complete phenological development coincides with good moisture availability in the soil, water deficit affects only the final plant development, and this, as a way of escaping, shortens the reproductive phase (ARAUS et al., 2002).

Flowering time is a characteristic of crop adaptation to the environment, especially when plant growth and development are restricted by water deficit and high temperatures at the end of plant development (TAIZ; ZEIGER, 2013). In order to minimize yield decreases caused by dry periods, early crop maturity prevents the period of water deficit (KUMAR; ABBO, 2001). However, yield is generally correlated with the the duration of a crop cycle at favorable growth and development conditions, and some yield reductions can be observed with shortening of the cycle (TURNER et al., 2001). In the upland rice crop, some authors have related the crop cycle increase to stress caused by water deficit (FISHER et al., 2003; TERRA et al., 2013).

Another mechanism plants use is the avoidance of water deficit, which consists of reducing water loss by the plant, with the control of stomatal closure and the reduction of transpiration, and maintaining water absorption by better developing root system (TURNER; WRIGHT; SIDDIQUE, 2001). The root system biomass, length and density are the main avoidance characteristics, which contribute to the final production in an environment under water deficit (SUBBARAO et al., 1995; TURNER; WRIGHT; SIDDIQUE, 2001).

Stomatal closure control and transpiration reduction help maintain the green leaves with high foliar osmotic potential, thus avoiding leaf senescence and reduction of active photosynthetic area; however, photosynthesis is also reduced, damaging plant growth and development (NONAMI, 1998, TAIZ and ZEIGER, 2013).

Phenotypic plasticity is related to the plant's ability to change its physiology and morphology according to environmental conditions, maintaining plant growth and development even under water deficit conditions. At morphological level, stem and roots are the most affected parts, and those are the keys to plant adaptation to water deficit (SCHUPPLER et al., 1998).

Rice reacts to water deficit by reducing plant height, foliar area, leaf number and biomass production, in addition to aborting tillers, increasing cycle, reducing the number and length of panicles, increasing spiklet sterility and reducing yield (AHMADIKHAH; MARUFINIA, 2016; TERRA et al., 2013).

To select water deficit tolerant genotypes, it is important for them to have mechanisms that reduce water loss and maintain plant development and biomass production. For this, increasing water use efficiency is highly important, which is possible by increasing the water absorption, biomass production per transpirated water unit, and dividing the biomass produced towards the grains (CODON et al., 2004).

As morphological and avoidance mechanisms that contribute to drought tolerance, we can mention the increase in root length and density. This inductive mechanism helps plants to continuously absorb available water even under water stress (KAVAR et al., 2007; TURNER, 1986).

As a physiological mechanism, we can mention osmotic adjustment and antioxidant defense system, which have been important bases related to the response to water stress tolerance. (FAROOQ et al., 2009). There is evidence of variability among genotypes for osmotic adjustment, which is measured by leaf water potential, for rice crops (JONGDEE; FUKAI; COOPER, 2002).

The antioxidant defense system in plant cells consists of enzymatic and non-enzymatic components that protect cells from oxidative damage and act on the regulation of ROS (Reactive Oxygen Species), by both limiting their formation and instituting their removal (VRANOVÁ; INZÉ; VAN BREUSEGEM, 2002). These enzymatic components include superoxide dismutase, catalase, peroxidase and glutathione reductase, while the non-enzymatic components contain reduction of glutathione and ascorbic acid (GONG et al., 2005). Tolerance to abiotic stress, such as the water deficit, has such important constituents as high antioxidant enzymatic activity and high contents of non-enzymatic constituents (FAROOQ et al., 2009).

Molecular mechanisms are related to changes in gene expression under water stress conditions. Several genes are expressed as a response to drought, and the product of several of those genes has water deficit tolerance function (KAVAR et al., 2008). One of the most studied advancements regarding water deficit tolerance is the DREB's (dehydratation-responsive element binding). DREB's are transcription factors that bind to specific genes promoters, inducing expression in response to stresses (KASUGA et al., 1999).

In rice, some genes have already been mentioned, such as *OsNAC10*, which refers to the gene expression of root thickening and increased production under water deficit (JEONG et al., 2010); *RWC3,* which refers to relative water content in roots and leaves, and transpiration control (LIAN et al., 2004); *HVA1*, which relates to membrane stabilization (BABU et al., 2004); *HARDY,* which increases water use efficiency (KARABA et al., 2007); *SNAC1*, which relates to stomatal control (HU et al., 2006); *DSM2* that increases synthesis of xanthophyll and abscisic acid, acting on photochemical efficiency (DU et al., 2010); *OsSIK1* that reduces water loss by stomatal regulation and increases antioxidant activity (OUYANG et al., 2010), among others.

Furthermore, the metabolites produced by plants may reveal variations in growth process, adaptation strategies or physiological processes (STITT; SULPICE; KEURENTJES, 2010). Among these metabolites are non-structural carbohydrates, such as glucose, fructose, hexose, sucrose and starch, which were used to discriminate response mechanisms of genotype subjected to water deficit (SHAO et al., 2009). Luquet et al. (2008) reported that water deficit in rice seedlings reduces the source of starch concentration in the leaf. Other studies also show sugars acting as a water deficit sign, participating in the plant growth and development regulation, maintaining the accumulation of biomass (LIU; LAFITTE; GUAN, 2004; ROLLAND; BAENA-GONZALEZ; SHEEN, 2006; STITT; SULPICE; KEURENTJES, 2010). However, Rebolledo et al. (2012) did not confirm the efficiency of using non-structural sugars in responses of upland rice genotypes under water deficit.

2.3 Plant breeding estrategies for water deficit tolerant genotype selection

Understanding plant diversity is fundamental to comprehend plant behavior in different environments, favorable to water deficit (ALONSO-BLANCO et al., 2009). Rice comes from regions propitious to flood – flooded system – and is frequently exposed to drought – upland systems. This crop was domesticated in areas with different rainfall availabilities, and this process resulted in a wide genetic and phenotypic diversity, which has high value for plant breeding for water deficit tolerance (NI; Colowit; Mackill, 2002)

Some difficulties in selecting and working with water deficit tolerant genotypes have been reported, for example, determining the critical level of water limitation, identifying the environment and ideal stage to start stress, and choosing the characters to be evaluated (CECCARELLI; GRANDO, 1996).

Great efforts have been made to obtain rice genotypes tolerant to water deficit, by using knowledge on plant responses to water stress and mechanisms involved in the processes of plant growth and development. The most used strategy is the development and selection of tolerant genotypes, by means of conventional selection techniques or molecular and biotechnological breeding techniques, including the production of genetically modified plants (FAROOQ et al., 2009).

Conventional plant breeding strategies have been based on empirical selection for yield. Conventional breeding is considered a good strategy for the development of water deficit tolerant genotypes. When experiments are run in several places, the progenies are tested in different environments, representing a random variation in the water deficit conditions (BABU et al., 2003). This fact allows the exploration of yield stability of the progenies in different environments, under varied water deficit situations occurred during the conduction of the trials.

The empirical selection for production may not be the best option, since production is characterized as quantitative character, with low heritability and high interaction genotypes x environments (RAMALHO et al., 2012). The modification of selection strategies for the use of probable secondary characteristics of adaptation to water deficit, solely or as part of selection indexes, has been studied, but those may have undesirable secondary responses (LUDLOW; MUCHOW, 1990). Like the selection of genotypes that reduce transpiration in places with water deficit, for example, they may result in low yield, when in an environment that propitious to the plant development (FAROOQ et al., 2009). However, other secondary characters that are positively correlated with production, and have functions such as maintenance of plant development and growth, may be cited, for example, the increase of water use efficiency, biomass production, the maintainance of flag leaf length and width (Table 1), the percentage of

non-structural carbohydrates, among others (FAROOQ et al., 2009; LUQUET et al., 2008; REBOLLEDO et al., 2012; TERRA et al., 2013).

Understanding these morphological, physiological and molecular processes can be the key to discover the characteristics that limit grain yield when submitted to water stress. This approach can complement conventional breeding programs to reduce deleterious impacts of stress and accelerate yield increase, while also exploiting the maximum potential of the genotype (CATTIVELLI et al., 2008).

Phenotyping, using secondary characters, has been used as a tool to identify characters genetically associated with the yield of grains that have high heritability, stability and are easy to evaluate. For this tool to be successful, those characters should not be associated with yield decrease when the crop is cultivated in an environment without water deficit (VENUPRASAD; LAFITTE; ATLIN, 2007).

The use of phenotyping for drought tolerance in natural environments is difficult, since there might be irregular and unpredictable genotype responses when submitted to the water deficit (FAROOQ et al., 2009). However, phenotyping in an environment with controlled water stress, without the occurrence of undesired rainfall, is more easily managed and more reliable regarding the data obtained. Venuprasad; Lafitte e Atlin. (2007) reported that, in rice crops, the response of selected genotypes under a controlled water deficit environment can be considered correlated with the responses, of those same genotypes, under natural field conditions.

In Brazil, to use phenotyping strategies in environment with controlled water deficit, Embrapa Rice and Beans uses a phenotyping platform named SITIS (Integrated System for Induced Treatment of Drought). This platform has been improved and used for various crops such as rice, bean, cotton, etc.

Some studies were done with non-selected upland rice populations, characterizing grain yield upon the water deficit applied in the reproductive phase; the results were compared with the grain yield in environment with and without water deficit. The results showed that it is possible to obtain water deficit tolerant genotypes, with a high yield potential under optimum climatic conditions of cultivation, in upland rice crops (VENUPRASAD; LAFITTE; ATLIN, 2007).

Still regarding plant breeding strategies, Beebe et al. (2008), Edmeas et al. (1993), Grenier et al. (2015) and Ramya et al. (2016) suggest recurrent selection as an effective plant breeding strategy for the selection of water deficit tolerant genotypes. Using recurrent selection, an increase in the mean of the character is expected, maintaining the genetic variability for future progress with selection (HALLAUER, 1986), being considered the most indicated plant

breeding strategy when there are quantitative characters involved (RAMALHO et al., 2012). An advantage of recurrent selection includes the accumulation of favorable alleles of many parents in a single superior genotype (RAMALHO et al., 2012).

In a study on wheat, using recurrent selection as a plant breeding strategy for drought tolerance, the authors observed a biomass yield reduction, but an average 17% increase in grain yield (RAMYA et al. 2016). According to the authors, this growth was due to the increase in the harvest index (ratio between grain yield and biomass accumulation) and better grain filling under stress conditions.

Recurrent selection as a plant breeding strategy for drought tolerance is widely popularized in maize (BOLAÑOS; EDMEADES, 1993). The use of this strategy increased grain yield by 30-50% in genotypes under water deficit, along with the indirect selection of secondary characters (EDMEADES et al., 1999).

For upland rice crop, the use of recurrent selection has been facilitated by the use of genes that promote male sterility in rice genotypes, which facilitates recombination (FUJIMAKI 1979; FROUIN et al., 2004; GRENIER et al., 2015; PANG et al., 2017). Since 1992, CIAT (International Center for Tropical Agriculture) and CIRAD (International Center for Agronomic Research for Development) have been using recurrent selection in upland rice breeding programs (CHÂTEL et al., 1995).

Grenier et al. (2015) also affirm that besides the use of recurrent selection, genomic selection is another strategy that can be used with recurrent selection. According to the authors, genomic selection can accelerate genetic gains by increasing selection intensity, thus shortening the selection cycle, by approximate genomic predictions of the performance of future lineages in early generations.

3 MATERIAL AND METHODS

To accomplish this project, two different experiments were run. The first one called Sitis 2015, carried out in year 2015 at Embrapa Rice and Beans (Brazilian Agricultural Research Corporation), Santo Antônio de Goiás, Brazil.

The second one, named Phytotron 2017, was run in year 2017 at CIRAD, (International Center for Agronomic Research for Development), Montpellier, France.

3.1 Obtaining the genotypes

The panel called 2K is composed of about two thousand accessions from groups of the species *Oryza sativa*, in addition to representing other species of the genus *Oryza*. From panel 2K, we obtained PRAY (Phenomics of rice adaptation and yield), which consists of two sub-panels (indica and tropical japonica), each with three hundred accessions that capitalize genetic diversity within the important subgroups (CGIAR, 2018).

An experiment was conducted in 2014, using eight controls (Guarani, Aimoré, BRSGO Serra Dourada, BRS Esmeralda, BRS Soberana, Douradão, AN Cambará and BRSMG 355) and 217 accessions of the tropical japonica subpanel, which were sent to Brazil by the International Rice Research Institute (IRRI) at the end of 2011. In Brazil, they were put in quarantine at the National Center for Research on Genetic Resources and Biotechnology (CENARGEN). The seeds were multiplied by transplanting of seedlings, in a protected area of the Palmital farm (Embrapa Rice and Beans, in the city of Goianira - GO).

Through the experiment conducted in 2014, 20 contrasting accessions were selected, and another trial was run to select the six early and contrasting genotypes with respect to water deficit tolerance, used in both trials conducted in this study (Table 1).

Table 1 – Upland rice genotypes used in the trials SITIS 2015 and Phytotron 2017. Embrapa Rice and Beans, Santo Antônio de Goiás, Brazil, 2015 and CIRAD, Montpellier, France, 2017.

	Genotypes	Parents	Country of origin
1	CIRAD 392	Latsidahy x FOFIFA 62	Madagascar
2	CIRAD 409	CT11537 x CT10035	Colombia
3	EARLY MUTANT IAC 165	Dourado precoce x IAC 1246	Brazil
4	GUARANI	IAC 25 x 63-83	Brazil
5	HD 1-4	IRAT 146 x Beira Campo	France
6	IAC 25	Dourado precoce x IAC 1246	Brazil

Source: From author (2018).

3.2 Sitis 2015

3.2.1 Place of trial

The trial was conducted in 2015, at Embrapa Rice and Beans, in Santo Antônio de Goiás, Goiás, Brazil, at an altitude of 823 meters, latitude 16º28'00"S and longitude 49º17'00"W. We used SITIS phenotyping platform (Integrated System for Induced Treatment of Drought), which characterizes a greenhouse with transparent glass walls and ceilings, consisting of PVC tube columns placed under scales for weight control and irrigation.

3.2.2 Installation and conduction of the trial

The trial, containing the six selected genotypes, was conducted in a randomized block design with three repetitions and two water treatments, irrigated (IRR) and stressed (STR), totalizing 36 plots. Each plot consisted of a PVC column, with 100 cm length by 25 cm internal diameter, containing three plants in each column.

Sowing occurred on September 24, 2015, each column was filled with medium texture red latosol, which was homogenized with a 1.25 cm mesh sieve to remove larger aggregates. Fertilization was performed with 4g of fertilizer 04-14-08 (NPK), in each column, according to recommendations for rice cultivation according to soil nutrient analysis.

To ensure three plants in each column, a germination test was done (BRASIL, 2009). The sowing of the trial was done in order to ensure the presence of three plants, by sowing seeds according to the germination test. After plant emergence, thinnings were performed until three plants per column were left in all plots.

For weekly evaluations, one of the three plants in the column was tagged with a colored woolen thread, being named 'plant 1', used reference for all the evaluations until panicle emergence. ‘Plant 1' was marked during vegetative stage V_4.

The climatic characteristics under which the trial was conducted are presented in Table 2. These data were obtained by means of the installation of a digital thermometer (brand AKSO®) in the center of the greenhouse, SITIS platform, from which values for maximum, minimum temperature and radiation rate were obtained.

Table 2 – Climatic conditions in the Sitis 2015 trial. Embrapa Rice and Beans, Santo Antônio de Goiás, Brazil, 2015.

	Sitis		
	Min	**Mean**	**Max**
TºC min	17.4	20.3	24.8
TºC max	24.6	31.8	37.6
Radiation ($MJ.m^{-2}.day^{-1}$)	1.9	16.7	26.0
VPD (Vapour pressure déficit - kPa)	0.67	3.35	5.87

Source: From author (2018).

After filling the columns with soil, they were soaked until water remained in the column plate. This water was removed and the column weight related to the field capacity was obtained. Before the stress application, the columns in both water treatments were irrigated until the weight corresponding to the field capacity was reached.

To ensure the application of water stress in the reproductive phase of the genotypes, we used the number of days for flowering (Table 3). This value represents the average of three previous trials. The beginning of stress application was determined as 20 days before the estimated flowering. The end of the stress was determined as the panicle emergence in the genotypes of the irrigated treatment.

Table 3 – Upland rice genotypes and mean of days after sowing (DAS). Embrapa Rice and Beans, Santo Antônio de Goiás, Brazil, 2015.

	Genotypes	**Flowering (DAS)**
1	CIRAD 392	58
2	CIRAD 409	56
3	EARLY MUTANT IAC 165	61
4	GUARANI	58
5	HD 1-4	59
6	IAC 25	59

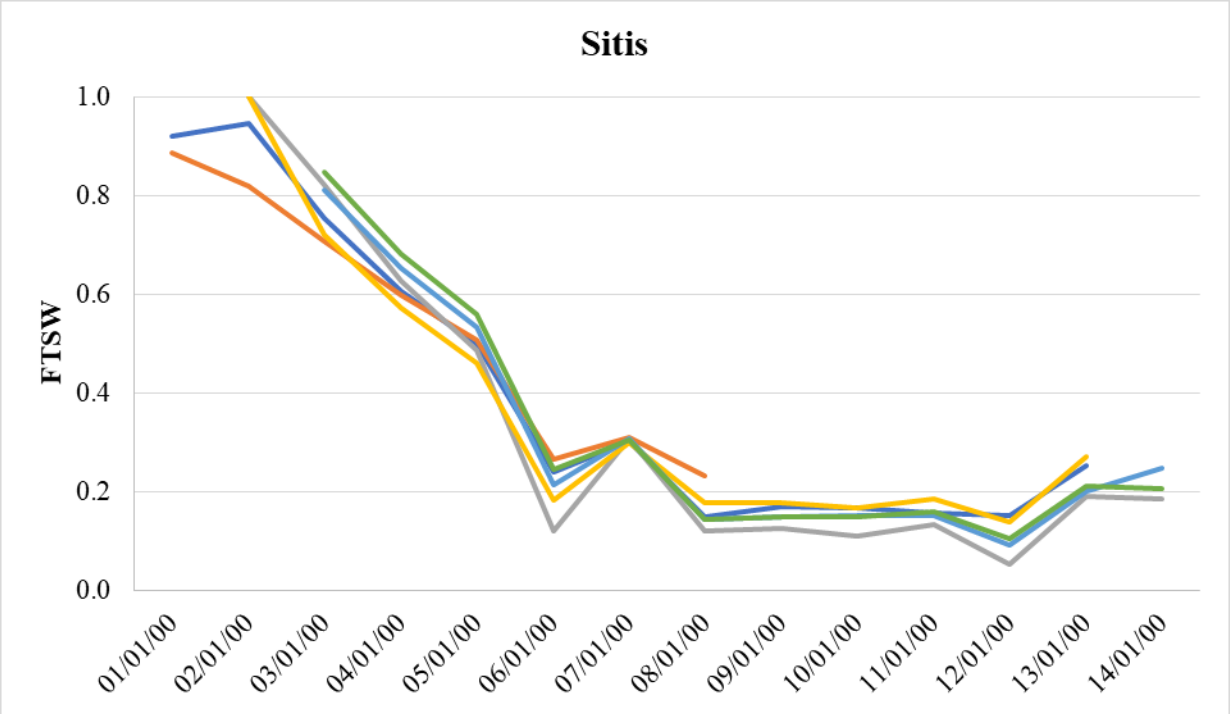
Source: From author (2018).

The applied water stress corresponded to FTSW = 0.4 (Fraction of the Transpirable Soil Water), that is, an irrigation up to 40% of field capacity. This index was reduced to FTSW = 0.2 (Figure 4) in the period between irrigations. The irrigations were performed daily, at the end of the afternoon, and water was replaced to the column plate, using the lysimeter by weight method, where the volume of evapotranspirated water was replaced until the weight balance returned to the reference weight, to obtain FTSW = 0.4. The water was replaced in the lower part of the column (in the column plate), because at the beginning of the water stress

application, all the genotypes already had roots appearing on the plate, and then all colonization of the column could be considered.

On the other hand, in the irrigated environment, the water was replaced until it reached FTSW = 0.8, also using the lysimeter by weight method, at the top of the column.

Figure 4 – FTSW average during the water stress applied in the reproductive phase, period between irrigations. Embrapa Rice and Beans, Santo Antônio de Goiás, Brazil, 2015.



Source: From author (2018).

After panicle emergence and the end of stress, the columns of the stressed treatment were irrigated again, until FTSW = 0.8. Two plants per column were maintained, grown until the grain maturation in the cycle end, to evaluate the yield components.

3.3 Phytotron 2017

3.3.1 Place of trial

The trial was conducted in 2017 at the CIRAD (International Center for Agronomic Research for Development) in Montpellier, France, at an altitude of 27 meters, latitude 43º41'03"N and longitude 3º52'37"E. A Phytotron-type growth chamber was used. Six genotypes were evaluated (Table 1), the same as the ones selected for the Sitis 2015 trial.

3.3.2 Installation and conduction of the trial

The trial was conducted in a fully randomized design with three repetitions and two water treatments, irrigated (IRR) and stressed (STR), totalizing 36 plots. Each repetition consisted of a polyethylene pot with volume of 3.5 liters, containing one plant per pot. Pre-germination of the seeds in an incubator at 30ºC was conducted for 3 days. After that, three seedlings were transplanted to each pot, with subsequent thinning, leaving one plant in each of the 36 pots.

The pots were filled with approximately 1473 grams of commercial substrate with known reference and physicochemical characteristics; no additional fertilization was performed. We used a photoperiod of 12/12 hours, daytime humidity of 65 % and nighttime of 90% and approximate daytime temperature 28ºC and nighttime 20ºC.

The climatic conditions under which the trial was conducted are described in Table 4. This information was obtained from a digital thermometer located strategically inside the phytotron growth chamber, from which we obtained values for maximum and minimum temperature, and radiation rate.

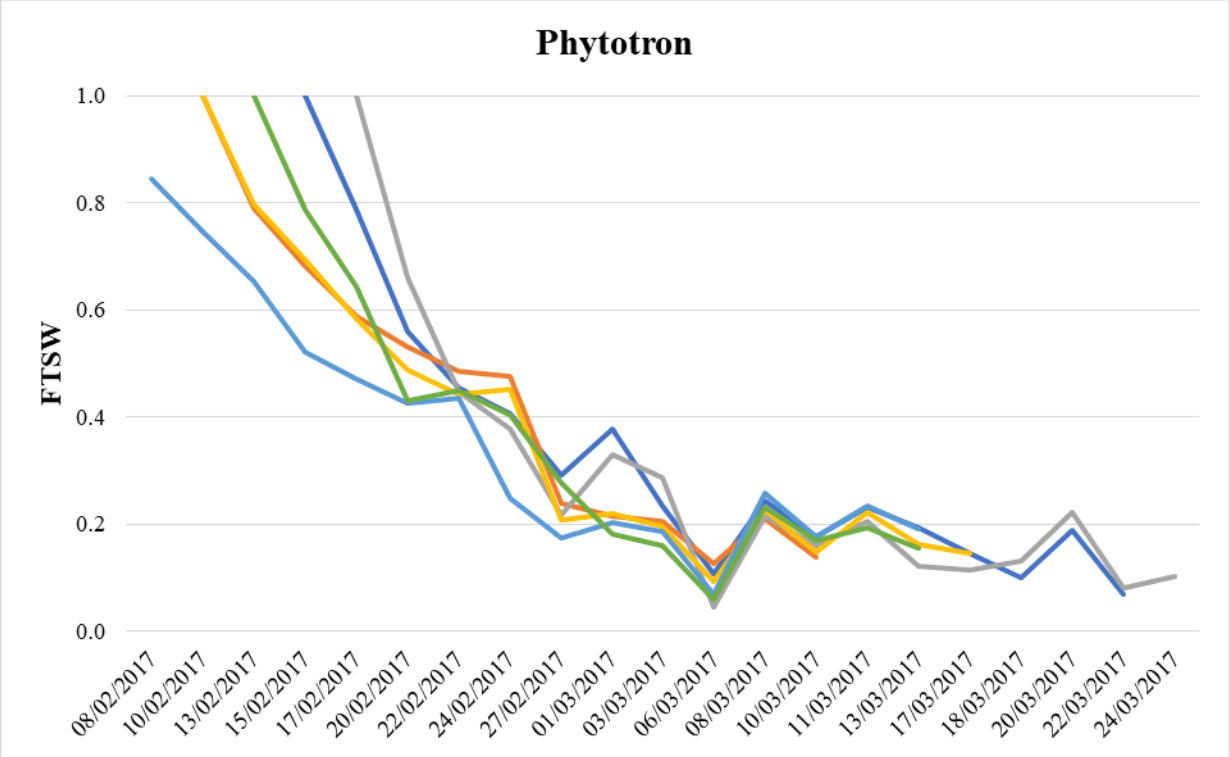
Table 4 – Climatic conditions in the Phytotron 2017 trial. CIRAD, Montpellier, France, 2017.

	Phytotron		
	Min	**Mean**	**Max**
TºC min	19.9	20.1	21.6
TºC max	26.7	27.8	28.4
Radiation ($MJ.m^{-2}.day^{-1}$)	1.3	5.8	9.0
VPD (Vapour pressure déficit - Kpa)	1.2	1.4	1.54

Source: From author (2018).

Initially, the water stress applied corresponded to FTSW = 0.6 (Fraction of the Transpirable Soil Water), corresponding to an irrigation up to 60 % of field capacity for 10 days; after that, the FTSW was reduced to 0.4. This index was reduced to FTSW = 0.2 (Figure 5) in the period between irrigations. Irrigations were done every two days at the end of the afternoon, and the water was replaced on the top of the pot, using the lysimeter by weight method, where the volume of evapotranspirated water was replaced until the weight balance returned to the reference weight, so as to obtain an FTSW = 0.4. In the irrigated treatment, the water was replaced until FTSW = 0.8, also using the lysimeter by weight method.

Figure 5 – Average FTSW during the water stress applied in the reproductive phase, period between irrigations. CIRAD, Montpellier, France, 2017.



Source: From author (2018).

In the beginning of the water stress application, the pots were covered with polystyrene micro balls to avoid losing water by soil transpiration, and to measure the amount of water absorbed by the plant.

To ensure the application of water stress in the reproductive phase, a pre-trial was conducted in the same growth chamber, using the six genotypes. Thus, an estimate of the panicle initiation date (Table 5) was determined by Haun's index (counting of the complete leaves number plus the percentage of the last leaf in emergence on the main stem). The application of water stress was performed 10 days after the estimated date. And the end of stress was determined as the panicle emergence in the genotypes of the irrigated treatment.

Table 5 – Upland rice genotypes and the estimation of number of days after sowing until panicle initiation, obtained in the pre-trial. CIRAD, Montpellier, France, 2017.

	Genotypes	Panicle initiation estimation (DAS)
1	CIRAD 392	35
2	CIRAD 409	29
3	EARLY MUTANT IAC 165	36
4	GUARANI	30
5	HD 1-4	26
6	IAC 25	32

Source: From author (2018).

3.4 Characteristics evaluated in the trials

- *Panicle initiation estimation:* Twice a week, the Haun Index (IH) was visually estimated, by counting the number of complete leaves plus the percentage of the last leaf in emergence on the main stem. Through HI it is possible, at the end of the trial, to return to the leaf number and determine in which phase the water stress application was initiated, considering the emergence of panicle in V_{F-4}.

- *Phyllochron*: twice a week, from the beginning of the trial to the end, Haun index evaluations were done. The phyllochron was determined by the number of day for the emergence of a complete leaf in the main stem during the period of water stress application.

$$Phyllochron = \frac{Stress\ duration\ (days)}{Complete\ leaf\ number}$$

- *Transpiration at the beginning and end of stress (mmol $H_2O.m^{-2}.s^{-1}$)*: these results were obtained using the LC-Pro-IRGA® equipment in Sitis 2015 and Walz GFS 3000® in the Phytotron 2017. On the beginning of water stress application and on the day of panicle emergence, the transpiration rate was measured. The balance time established for reading was one minute for Sitis 2015 and six minutes for Phytotron 2017.

- *Growth rate ($g.day^{-1}$)*: was determined by the daily accumulation of biomass during the stress period. For Sitis 2015, the biomass of the plant at the beginning of stress was estimated using the biomass of the seedlings removed during the thinning 12 days after

sowing. In Phytotron trial, the biomass of the plant at the beginning of the stress was done using the biomass of the plants collected at the beginning of water stress application, present in supplementary pots.

$$Growth\ rate\ (g.day^{-1}) = \frac{Final\ biomass\ (g) - Start\ biomassa(g)}{Stress\ duration\ (days)}$$

- *Elongation rate (mm.day^{-1})*: twice a week, from the beginning to the end of the trial, the height of the main stem was measured from the soil to the last ligule. The elongation rate was determined by daily elongation of the main stem during the stress period.

$$Elongation\ rate\ (mm.day^{-1}) = \frac{Final\ height\ (mm) - Start\ height\ (mm)}{Stress\ duration\ (days)}$$

- *Total biomass (g):* corresponds to the plant's total biomass at the end of the water stress application. In the panicle emergence, the plant was removed from the pot, dissected and placed in a stove at 65 ºC for 72 hours.

- *Flag leaf length and width (mm):* at the end of water stress application, the largest flag leaf length and width were measured, using an experimental ruler.

- *Total number of panicle branches:* at the end of water stress application, the panicle was removed from the main stem sheath, and the number of primary and secondary branches of the panicle was counted.

$$Panicle\ branch\ number = Primary\ branches + Secondary\ branches$$

- *Panicle length (mm):* was measured just for Phytotron 2017, at the end of water stress application, the panicle was removed from main stem sheath, and measured from the top of the peduncle to the apex of the panicle main rachis using an experimental ruler.

- *Length of panicle branches (mm):* was measured just for Phytotron trial, at the end of water stress application. The panicle was removed from main stem sheath. A picture of

the panicle was taken, and using the software P-TRAP®, total lengh of the primary and secondary branches was obtained.

Length of panicle branches (mm) = primary branch length + secondary branch length

- *Spikelet number:* at the end of water stress application, the panicle was removed from the main stem sheath, and the number of panicle spikelets was counted.

- *Length and width of internodes 1 and 2 (mm):* at the end of water stress application, the main stem was dissected, exposing nodes and internodes. The length and width of Internodes 1 and length and width were measured using an experimental ruler. Internode 1 was considered the first one below the penduncle.

- *Plant height (mm):* at the end of water stress, the main stem height was measured from the soil until the flag leaf ligule, using an experimental ruler.

- *Soluble sugars and starch concentration in the flag leaf (mg.g^{-1}):* at the end of water stress application, after measurements, the flag leaf was stored in liquid nitrogen, and then lyophilized, triturated and in freezer at -20 ºC. Soluble sugars and starch concentrations were determined as detailed by Luquet et al. (2006).

- *Total water consumption during the water stress period (g):* was measured only for Phytotron 2017, during water stress application, before and after irrigation, the pot weigth was measured using digital scale.

$$Total\ water\ consuption = \sum \frac{(Last\ weight(g) - Weight\ before(g))}{Days\ between\ irrigations}$$

- *Water use eficiency (g.g^{-1}):* was measured only for Phytotron 2017, by total biomass accumulated over total water consumption during water stress application.

$$Water\ use\ eficency\ (g.g^{-1}) = \frac{Biomass\ accumulated\ (g)}{Water\ consumption\ (g)}$$

- *Number of tillers:* at the end of water stress application, the number of tillers per plant was counted, except for the main stem.

- *Grain yield (g/plant):* was measured only for Sitis 2015. Two plants were conducted until the end of the cycle, to grain maturation. The panicles were harvested, threshed and the grains filled at 13% of moisture were then weighed.

- *Spikelet sterility (%):* was assessed only for Sitis 2015. The total number of grains, both empty and full, was counted in the panicle of the main stem.

$$Sterility\ (\%) = \frac{(Spiklet\ number\ empty\ x\ 100)}{Total\ spikelet\ number}$$

- *Thousand-grain weight (g):* was measured only for Sitis 2015. Eight samples of one hundred filled grains were removed, each sample was weighed separately, the mean was multiplied by ten to obtain the estimated weight of a thousand grains, according to the rules of seeds analysis - RAS (BRASIL, 2009).

3.5 Statistical data analyses

3.5.1 Analyses of variance

The individual analyses of variance for each trial, Sitis 2015 and Phytotron 2017, were performed according to the statistical models:

For Sitis 2015:

$$Y_{ikd} = \mu + p_i + b_k + a_d + ap_{di} + e_{ikd}$$

Where:

Y_{ikd}: value observed in the plot that received genotype *i*, in block *k*, within water treatment *d*.

μ: constant associated with observations;

b_k: random block effect *k* (*k* = 1,2,3), where $b_k \sim N(0, \sigma_b^2)$;

p_i: fixed genotype effect *i* (*i* = 1, 2, ... , 6);

a_d : fixed water treatment effect *d* (*d* = 1,2);

ap_{di}: interaction effect between water treatments *d* (*d* = 1,2) and the genotypes *i* (*i* = 1, 2, ... , 6);

e_{ikd}: experimental error effect associated with observation, where e_{ikd} ~N$(0, \sigma_e^2)$

And for Phytotron 2017:

$$Y_{ikd} = \mu + p_i + a_d + ap_{di} + e_{ikd}$$

Where:

Y_{ikd}: value observed in the plot that received genotype *i*, in repetition *k*, within water treatment *d*.

μ: constant associated with observations;

p_i: fixed genotype effect *i* (*i* = 1, 2, ... , 6);

a_d : fixed water treatment effect *d* (*d* = 1,2);

ap_{di}: interaction effect between water treatments *d* (*d* = 1,2) and the genotypes *i* (*i* = 1, 2, ... , 6);

e_{ikd}: experimental error effect associated with observation, where e_{ikd} ~N$(0, \sigma_e^2)$;

The experimental precison of each character under evaluation was measured by accuracy estimating (RAMALHO et al., 2012) and the coefficient of variation, using the estimators below.

Accuracy (Rgg'):

$$Rgg'(\%) = \sqrt{1 - \frac{1}{F_c}}\ x\ 100$$

Where:

Rgg' is the accuracy expressed as a percentage;

F_c is the calculated F value for variation source in the variance analyses;

Coefficient of variation (CV%):

$$CV\ \% = \frac{\sqrt{QME}}{\bar{x}}\ x\ 100$$

Where:

QME is the mean squared error;

$\bar{x}$ is the phenotypic mean;

The adjusted means were obtained and grouped by Scott-Knott (1974) test at 5% of probability. To support the analyses of variance, statistical software R (2012) was used.

3.5.2 Orthogonal contrasts

To better understand the behavior of the genotypes under different water treatments, variation response indexes were estimated using means adjusted for each water treatment in each trial separately. According the estimator below:

$$Response\ index = \frac{STR - IRR}{IRR}$$

Where:

STR is the phenotypic adjusted mean for treatment stressed;

IRR is the phenotypic adjusted mean for treatment irrigated;

The response index was validated by a test of orthogonal contrasts, where the adjusted means of the irrigated treatment were compared to the adjusted mean of the stressed treatment using F Test and the software R (2012).

3.5.3 Correlation analyses

The phenotypic correlations were estimated (RAMALHO et al., 2012) between response indexes for the characters evaluated to six genotypes, using t-Student test and software R (2012). The correlations were estimated using response index for both trials, Sitis 2015 and Phytotron 2017, thus, each genotype was represented twice, totalizing twelve points per analyzed character. Moreover, the correlation analyses using just Phytotron 2017 trial datas were run.

4 RESULTS AND DISCUSSION

For phenotyping of the selected genotypes and the analyses of correlations among genotype behaviors under water deficit applied in the reproductive phase, 21 traits were evaluated in 2015 in Embrapa Rice and Beans (Sitis 2015) and 22 traits in 2017 in CIRAD (Phytotron 2017). The phenotypic characteristics employed to perform the evaluations were selected according to Counce; Keisling; Mitchell, (2000), because these characters are more affected by the water stress in the reproductive phase.

The summaries of the individual analyses of variance for each trial are described in Tables 6 and 7. Through coefficients of variation (CV %) and accuracy estimations, it was possible to observe high experimental precision in the conduction of trials, since most characters studied presented values of CV% below 20% and accuracy above 66% (PIMENTEL-GOMES, 2009; RESENDE; DUARTE, 2007). However, for some traits, considering Sitis 2015, phyllochron and internode 1 length, and to Phytotron 2017, internode 1 length and starch concentration in the flag leaf, presented a high CV%, associated to moderate accuracy estimation, except for internode 1 length, in Phytotron 2017 (RESENDE; DUARTE, 2007). The high CV% values, observed for internode 1 length, in Sitis 2015 and Phytotron 2017 (Tables 6 and 7), and low accuracy for Phytotron 2017 (Table 7 are likely to be due to the fact that internode 1 is a character that develops at the end of the reproductive phase, when the evaluation and the end of water stress application occurred (COUNCE; KEISLING; MITCHELL, 2000). That is, at the moment of panicle emergence, which characterizes the end of water stress application, the internode 1 was in full development.

In both trials (Sitis 2015 and Phytotron 2017) most evaluated characters differed significantly as to the source of variation genotypes (Tables 6 and 7), confirming existence of variability among the evaluated genotypes. The presence of significance for source of variation genotypes x water treatments was also observed for most characters. Since that interaction is significant, the genotypes present different behavior responses under water stress in the reproductive phase. This makes it possible to infer that, even using a reduced number of six genotypes, there is variability to study behavior response and water stress tolerance in the reproductive phase.

Between both trials conducted, different estimates were obtained, considering soluble sugars (SS FL ($mg.g^{-1}$)) and starch (STH FL ($mg.g^{-1}$)) present in the flag leaf. Those characters presented significant difference to source of variation genotypes, only in Sitis 2015. The non-existence of variability for those traits in Phytotron 2017 is easily explained by the difference in

climatic conditions, between environments where the trials were conducted, with radiation average about 16,76 $MJ.m^{-2}.dia^{-1}$ in Sitis 2015 which was reduced to 5,89 $MJ.m^{-2}.day^{-1}$ in Phytotron 2017.

According to Farooq et al. (2009), transpiration rate is directly related to photosynthetic rate. Taiz and Zeiger (2013) reported that during photosynthesis the plant transforms energy of solar radiation into chemical energy that is used in the photosynthetic process to produce metabolites. When radiation rate is low, the formation of metabolites is also reduced, which did not allow the maximum exploration of the genotype potential, a fact that may explain the non-occurrence of significant difference for genotypes, in Phytotron 2017, for the characters SS FL ($mg.g^{-1}$) and STH FL ($mg.g^{-1}$) (Table 7).

A significant difference was observed among genotypes for the source of variation of a thousand-grain weight (Table 6). It is a tropical japonica subpanel, with a high presence of variability between the accessions, there is probably variability as to the grain type and size of the genotypes evaluated in the trials.

Table 6 – Variance analyses summaries to Sitis 2015 trial with representative traits of phenotyping of upland rice genotypes for drought tolerance in the reproductive phase. Embrapa Rice and Beans, Santo Antônio de Goiás, Brazil, 2015. Continues.

SV	Block	Genotypes	Water treatments	Genotypes * Water treatments	Error	CV (%)	Accuracy (%)
DF	2	5	1	5	22		
			Pr(>F)				
Tiller number	0.10	**0.02**	**0.03**	0.67		14.62	83.86
Phyllochron	0.22	0.14	0.11	0.57		33.85	68.86
Transpiration - stress start (mmol $H_2O.m^{-2}.s^{-1}$)	0.77	**0.00**	0.47	0.44		7.96	99.48
Transpiration – stress end (mmol $H_2O.m^{-2}.s^{-1}$)	0.43	**0.00**	**0.00**	0.63		12.41	96.95
Growth rate ($g.day^{-1}$)	0.53	**0.00**	**0.00**	**0.05**		14.23	96.31
Elongation rate ($mm.day^{-1}$)	0.94	**0.05**	**0.00**	0.30		15.87	78.82
Total biomass (g)	0.47	**0.00**	**0.00**	**0.08**		15.10	92.51
Flag leaf length (mm)	0.12	0.19	0.63	0.27		11.79	99.99
Flag leaf width (mm)	0.10	**0.00**	0.86	0.28		5.32	99.18
Total panicle branch number	0.12	**0.00**	**0.00**	**0.06**		13.39	96.62
Spikelet number	0.53	**0.00**	**0.00**	**0.03**		11.74	89.87
Internode 1 length (mm)	0.44	0.16	**0.00**	0.11		24.80	66.59
Internode 1 width (mm)	0.59	**0.00**	**0.05**	0.38		11.73	90.67

Bold numbers are significant by F Test;
Source: From author (2018).

Table 6 – Variance analyses summaries to Sitis 2015 trial with representative traits of phenotyping of upland rice genotypes for drought tolerance in the reproductive phase. Embrapa Rice and Beans, Santo Antônio de Goiás, Brazil, 2015. Conclusion.

SV	Block	Genotypes	Water treatments	Genotypes * Water treatments	Error	CV (%)	Accuracy (%)
Internode 2 length (mm)	0.88	**0.00**	**0.00**	0.54		19.89	94.53
Internode 2 width (mm)	0.10	**0.00**	**0.08**	0.37		7.61	97.82
Plant height (mm)	0.32	**0.00**	**0.00**	**0.05**		7.98	93.85
SS FL ($mg.g^{-1}$)	0.31	**0.03**	**0.00**	**0.03**		8.15	82.66
STH FL ($mg.g^{-1}$)	0.59	**0.00**	**0.00**	**0.08**		9.04	91.84
Yield (g/plant)	0.23	**0.09**	**0.03**	0.67		26.79	73.72
Spikelet sterility (%)	0.94	**0.01**	**0.00**	**0.01**		41.55	86.34
Thousand grains weight (g)	0.90	**0.00**	**0.06**	0.61		6.30	95.70

Bold numbers are significant by F Test;
Source: From author (2018).

In both trials, the transpiration rate, measured at the beginning of the water stress applicayion, did not present a significant difference for the water treatment, which is essential to perform the work. The same condition was not observed for the transpiration rates at the end of the water stress application, at panicle emergence. At the end of the water stress application, the transpiration rate presented a significant difference for water treatments, proving that stress was applied effectively and affected plant metabolism (Tables 5 and 6). With water stress, plants tend to reduce water loss with stomatal closure and consequently reduce transpiration rates (TAIZ; ZEIGER, 2013).

In Sitis 2015, phyllochron, which corresponds to the average number of days for appearance of a complete leaf, during the stress application, and leaf length were not significant for neither source of variation (Table 6). Phyllochron evaluation is essential to verify response to the vegetative development under water stress. These inferences can be explained by the fact that water stress, applied in Sitis 2015, was late, since it was applied when the plants already had 52% to 72% of the corresponding phase between panicle initiation and complete flag leaf emergence. In Phytotron 2017, water stress was applied earlier, varying from 13 % to 31 % of the phase between panicle initiation and complete flag leaf emergence, already concluded at the beginning of water stress. Returning in the Haun Index datas, allows estimate the percentage between panicle initiation and complete falg leag emergence. In this case, the phyllochron presented a significant difference for variation sources genotypes and water treatments, and the flag leaf length was significantly different as to variation source of water treatment (Table 6). Under water stress, a phyllochron is expected to increase, that is, more days are required for

complete leaf emergence. The lack of water directly affects mitosis, impairing cell division, and consequently, cell elongation and expansion, thus reducing plant development (NONAMI, 1998; FAROOQ et al., 2009).

Table 7 – Variance analyses summaries to Phytotron 2017 with representative traits of upland rice genotypes phenotyping for drought tolerance in the reproductive phase. CIRAD, Montpellier, France, 2017.

SV	Genotypes	Water treatments	Genotypes * Water treatments	Error	CV (%)	Accuracy (%)
DF	5	1	5	24		
			Pr(>F)			
Tiller number	**0.00**	1.00	0.19		20.40	95.80
Phyllochron	**0.00**	**0.08**	0.34		13.76	94.77
Transpiration - stress start (mmol $H_2O.m^{-2}.s^{-1}$)	**0.00**	0.75	0.29		21.08	91.87
Transpiration – stress end (mmol $H_2O.m^{-2}.s^{-1}$)	**0.00**	**0.01**	**0.02**		14.41	94.93
Growth rate ($g.day^{-1}$)	**0.00**	**0.01**	**0.00**		18.83	93.34
Elongation rate ($mm.day^{-1}$)	**0.00**	**0.00**	**0.09**		12.18	97.31
Total biomass (g)	**0.00**	**0.01**	**0.00**		17.17	96.58
Flag leaf length (mm)	0.30	**0.00**	0.96		12.14	47.40
Flag leaf width (mm)	**0.00**	**0.01**	0.15		8.75	95.05
Total panicle branch number	**0.00**	**0.00**	**0.06**		17.23	89.07
Panicle length (mm)	**0.00**	**0.00**	0.51		7.73	93.23
Total panicle branch length (mm)	**0.00**	**0.00**	**0.03**		16.36	90.84
Spikelet number	**0.00**	**0.00**	**0.02**		15.39	90.81
Internode 1 length (mm)	0.26	**0.00**	0.94		30.27	53.90
Internode 1 width (mm)	**0.00**	**0.00**	0.21		8.06	88.22
Internode 2 length (mm)	**0.00**	**0.00**	**0.05**		15.15	97.15
Internode 2 width (mm)	**0.00**	**0.00**	0.11		7.69	95.83
Plant height (mm)	**0.00**	**0.00**	**0.01**		6.31	97.91
SS FL ($mg.g^{-1}$)	0.14	**0.00**	0.83		15.00	67.54
STH FL ($mg.g^{-1}$)	0.14	0.76	0.74		132.01	67.42
Total water consumption (g)	**0.00**	**0.00**	**0.00**		9.41	98.29
Water use efficiency ($g.g^{-1}$)	**0.00**	**0.00**	**0.02**		13.53	93.05

Bold numbers are significant by F Test; Source:
From author (2018).

In Tables 8 and 9, it is possible to observe the water deficit response index applied in the reproductive phase, for six genotypes used, in Sitis 2015 and Phytotron 2017, respectively, the response index was calculated for all evaluated characters.

Tabela 8 – Response index to representative traits of upland rice genotypes for drought tolerance in the reproductive phase. Embrapa Rice and Beans, Santo Antônio de Goiás, Brazil, 2015.

Genotypes	CIRAD 392	CIRAD 409	EARLY MUTANT IAC 165	GUARANI	HD 1-4	IAC 25
Tiller number	-0.12^{ns}	0.04^{ns}	-0.10^{ns}	-0.13^{ns}	-0.07^{ns}	-0.27*
Phyllochron	0.25^{ns}	-0.03^{ns}	0.53*	0.18^{ns}	-0.14^{ns}	0.45*
Transpiration – stress end (mmol $H_2O.m^{-2}.s^{-1}$)	-0.17^{ns}	-0.05^{ns}	-0.06^{ns}	-0.15^{ns}	-0.17*	-0.20*
Growth rate (g.day^{-1})	-0.15^{ns}	-0.01^{ns}	-0.16^{ns}	-0.19^{ns}	-0.21*	-0.38**
Elongation rate (mm.day^{-1})	-0.44**	-0.20^{ns}	-0.55**	-0.38**	-0.31*	-0.41**
Total biomass (g)	-0.14^{ns}	-0.01^{ns}	-0.16^{ns}	-0.19^{ns}	-0.21*	-0.38**
Flag leaf length (mm)	0.16^{ns}	0.03^{ns}	-0.16^{ns}	0.00^{ns}	-0.02^{ns}	-0.09^{ns}
Flag leaf width (mm)	0.08^{ns}	0.04^{ns}	0.03^{ns}	-0.02^{ns}	-0.07^{ns}	-0.03^{ns}
Total panicle branch number	0.09^{ns}	-0.07^{ns}	-0.12^{ns}	-0.13^{ns}	-0.23*	-0.31**
Spikelet number	0.06^{ns}	-0.01^{ns}	-0.17*	-0.19*	-0.17*	-0.33**
Internode 1 length (mm)	-0.49**	-0.04^{ns}	-0.61**	-0.55**	-0.36**	-0.60**
Internode 1 width (mm)	-0.07^{ns}	0.00^{ns}	0.00^{ns}	-0.07^{ns}	-0.25**	-0.06^{ns}
Internode 2 length (mm)	-0.39*	-0.04^{ns}	-0.32*	-0.26*	-0.27*	-0.22*
Internode 2 width (mm)	-0.03^{ns}	0.00^{ns}	0.03^{ns}	-0.03^{ns}	-0.14*	-0.09^{ns}
Plant height (mm)	-0.26**	-0.03^{ns}	-0.28**	-0.21**	-0.15*	-0.20**
SS FL (mg.g^{-1})	0.90**	-0.02^{ns}	0.82**	0.66**	0.97**	0.68**
STH FL (mg.g^{-1})	-0.18**	-0.28**	-0.13^{ns}	-0.34**	-0.27**	-0.39**
Yield (g/plant)	-0.14^{ns}	0.02^{ns}	-0.15^{ns}	-0.19^{ns}	-0.12^{ns}	-0.50*
Spikelet sterility (%)	9.33**	0.69*	1.15*	5.11*	0.52^{ns}	2.29**
Thousand grains weight (g)	-0.06^{ns}	-0.01^{ns}	0.00^{ns}	0.00^{ns}	-0.09*	-0.07^{ns}

** significant by F test at 1% probability;
* significant by F test at 5% probability;
^{ns} not significant;
Source: From author (2018).

The response index represents difference between stressed and irrigated treatments. Through response index, it is possible to confirm the presence of variability for tolerance to water deficit applied in the reproductive phase, among the genotypes studied, once they responded differently to water stress application in the reproductive phase. Those response indexes demonstrate whether there were behavioral differences among the genotypes under water stress application in the reproductive phase, for the traits evaluated. This variation allows selection of genotypes with similar behavior in such conditions, with or without water stress application, which can be widely explored and desired in plant breeding programs.

Through response index, it is possible to select genotypes that are more tolerant to water stress. Low and non-significant response index are representative of more tolerant genotypes and the opposite is observed for genotypes more susceptible. For CIRAD 409, a low response

to the water stress was observed, with no significant difference among indexes for the majority of evaluated characters, except for the starch concentration in the flag leaf and spikelet sterility in Sitis 2015 (Table 8); and internode 1 length, total water consumption during water stress apllication and water use efficiency in Phytotron 2017 (Table 9). In other words, under water stress in the reproductive phase, a similar behavior was observed for CIRAD 409, in different water treatments, with or without stress application. The genotype stands out because it presents low indexes with non-significant responses in both trials, in addition to not reducing yield in Sitis 2015. Even with a large difference in weather conditions, the genotype showed potential tolerance to drought in both trials. These facts suggest that, in principle, CIRAD 409 has a potential behavior stability. This genotype has already been selected by CORPOICA, CIAT and CIRAD, as a cultivar recommended in Colombia, being named Llanura11, indicated for rotating cultivation with corn and soybean crops, and characterized by presenting precocity, tolerance to high aluminum saturations and adaptation to savanna region (TAPIERO et al., 2012).

However, genotype CIRAD 409 showed a significant difference for the spikelet sterility response index, with a 69% increase (0.69) in relation to stressed treatment (Table 8). The genotype presented the second lowest increase (0.69), when compared to the other genotypes, where the increase was higher than 900% (9.33), for CIRAD 392 (Table 8). In general, increased spikelet sterility reached large magnitudes, which can be explained by the fact that sterility is related to high temperatures (WU; CHANG; LUR; 2016), which occurred in the Sitis phenotyping platform. Spikelet sterility was strongly affected in the execution of the trial, once water stress and high temperature affected the viability of the reproductive organs, as spikelet.

Table 9 - Response index to representative traits of upland rice genotypes for drought tolerance in the reproductive phase. CIRAD, Montpellier, France, 2017. Continues.

Genotypes	CIRAD 392	CIRAD 409	EARLY MUTANT IAC 165	GUARANI	HD 1-4	IAC 25
Tiller number	0.13^{ns}	-0.26^{ns}	0.26^{ns}	0.06^{ns}	-0.11^{ns}	-0.06^{ns}
Phyllochron	0.06^{ns}	-0.06^{ns}	0.32**	0.03^{ns}	0.10^{ns}	0.06^{ns}
Transpiration – stress end (mmol $H_2O.m^{-2}.s^{-1}$)	-0.36**	-0.05^{ns}	-0.31*	-0.05^{ns}	0.15^{ns}	-0.25*
Growth rate ($g.day^{-1}$)	-0.39**	0.03^{ns}	0.41*	-0.17^{ns}	-0.38*	-0.21^{ns}
Elongation rate ($mm.day^{-1}$)	-0.34**	-0.01^{ns}	-0.33**	-0.17*	-0.26**	-0.28**

** significant by F Test at 1 % probability;
* significant by F Test at 5 % probability;
^{ns}not significant;
Source: From author (2018).

Table 9 - Response index to representative traits of upland rice genotypes for drought tolerance in the reproductive phase. CIRAD, Montpellier, France, 2017. Conclusion.

Genotypes	CIRAD 392	CIRAD 409	EARLY MUTANT IAC 165	GUARANI	HD 1-4	IAC 25
Biomassa total (g)	-0.40**	0.04 ns	0.31*	-0.15 ns	-0.36*	-0.21 ns
Flag leaf length (mm)	-0.17 ns	-0.15 ns	-0.25 ns	-0.18 ns	-0.13 ns	-0.16 ns
Flag leaf width (mm)	0.00 ns	0.07 ns	-0.17**	-0.12 ns	-0.11 ns	-0.05 ns
Total panicle branch number	-0.31*	-0.08 ns	-0.46**	-0.19 ns	-0.17 ns	-0.25 ns
Total panicle branch length (mm)	-0.31*	-0.01 ns	-0.44**	-0.09 ns	-0.29**	-0.24*
Panicle length (mm)	-0.16*	-0.09 ns	-0.21**	-0.06 ns	-0.10 ns	-0.06 ns
Spikelet number	-0.28*	-0.03 ns	-0.45**	-0.24 ns	-0.10 ns	-0.26*
Internode 1 length (mm)	-0.53*	-0.44*	-0.36*	-0.37*	-0.32*	-0.47**
Internode 1 width (mm)	-0.24**	-0.08 ns	-0.24**	-0.16*	-0.12*	-0.14*
Internode 2 length (mm)	-0.34*	0.21 ns	-0.12 ns	-0.06 ns	-0.13 ns	-0.28**
Internode 2 width (mm)	-0.18**	0.01 ns	-0.17**	-0.09 ns	-0.16*	-0.16**
Plant height (mm)	-0.23**	0.02 ns	-0.18**	-0.12*	-0.19**	-0.19**
Total water consumption (g)	-0.44**	-0.45**	-0.18**	-0.46**	-0.50**	-0.42**
Water use efficiency ($g.g^{-1}$)	0.10 ns	0.87**	0.75**	0.53**	0.24 ns	0.38**
SS FL ($mg.g^{-1}$)	0.26 ns	0.18 ns	0.27*	0.29*	0.06 ns	0.15 ns
STH FL ($mg.g^{-1}$)	-0.43 ns	1.16 ns	-0.38 ns	0.14 ns	-0.18 ns	-0.37 ns

** significant by F Test at 1 % probability;
* significant by F Test at 5 % probability;
nsnot significant;
Source: From author (2018).

On the other hand, IAC 25 and HD 1-4 can be considered the ones with the largest difference in phenotypic behavior between both conditions of water stress in the reproductive phase, since they present high and significant values for the most part of the characters evaluated (Tables 7 and 8). However, IAC 25 can be classified as the most susceptible genotype, because it presents higher values for the presented indexes, indicating greater difference in behavior between the water treatments.

Genotype HD 1-4, in Phytotron 2017, despite being significant for the majority of indexes, does not present a significant response index for the number of spikelets. In other words, plants reduced several morphological aspects, but kept the number of spikelets, keeping high yield potential.

Another genotype with a peculiar behavior in Phytotron 2017, Guarani presented significant response indexes only for plant height and main stem elongation rate. The plant was

reduced in height without changing the number of spikelets under water stress in the reproductive phase.

In Phytotron 2017, the amount of water consumption by the plant during water stress application was measured. With exception Early Mutant IAC 165, which presented a difference of only 18% (-0.18) less in the water consumption, between stressed and irrigated treatment, the other genotypes showed a reduction of 42 % (-0.42) to 50 % (-0.50) (Table 9). This reduction in water consumption confirms that there was a decrease in the amount of water absorbed by plants during water stress application.

The water use efficiency (WUE) for dry matter production was measured in grams of total accumulated biomass per grams of water consumption during water stress application. For this character, it was possible to observe a large variability for response indexes, varying from an increase of 10% to 87% (0.10 to 0.87) in stressed ones compared to the irrigated ones (Table 9). The highest response index found (0.87) belongs to CIRAD 409, that even at water limitation, produced almost as much dry matter as the irrigated treatment. The large increase in WUE in the stressed treatment, for CIRAD 409, may have great influence in the maintenance of other response indexes. Matsubara et al. (2016) reported that the accumulation of biomass is directly correlated with the number of spikelets and consequent grain yield, panicle length, flag leaf length and plant height.

Among the genotypes evaluated, CIRAD 392, Early Mutant IAC 165 and Guarani presented large variation in response to water stress applied in the reproductive phase, between both trials conducted. It is possible to observe that the significance of estimated response indexes was not similar between both trials. This information evidences that those three genotypes, in the evaluated trials, presented large discrepancies in the phenotypic behavior when submitted to different weather conditions.

The variation in response observed for CIRAD 392, Early Mutant IAC 165 and Guarani genotypes can be explained by the climatic difference between both trials. Genotypes more or less sensitive to photoperiod and thermal amplitude tend to have great behavior changes when there is a weather change, and, changes in the cycle, development and yield of grains may occur, depending on which development phase was more or less affected (DINGKUHN et al. al., 2015).

It was possible to observe, an increase in water use efficiency of 75 % (0.75) (Table 9) for Early Mutant IAC 165. However, the genotype is not considered to have a potential tolerance to drought, as it also presented a 45% reduction (-0.45) in the number of spikelets, the

panicle component that expresses yield potential (Table 9). Under water stress, the plants extended the reproductive phase, with large leaf and tiller production.

In order to understand the relationship between response indexes and water stress among traits analyzed, Pearson's phenotypic correlations were estimated. Initially, the phenotypic correlations were obtained from the response indexes for six genotypes, 17 traits, using both trials (Table 10). Each genotype was represented twice in the correlation analysis. This was possible due to same phenotypic behavior of most genotypes, among the trials (Tables 7 and 8). The similar values among the estimated indexes allow, at first, to infer the presence of stability of the genotype responses under different environmental conditions, which allowed the use of both trials in the correlations analysis.

Table 10 – Phenotypic correlation between response indexes of representative traits of the phenotyping of upland rice genotypes regarding drought tolerance in the reproductive phase. Embrapa Rice and Beans, Santo Antônio de Goiás, Brazil, 2015 and CIRAD, Montpellier, France, 2017.

	GR	ER	TBIO	FL L	FL W	PBN	SN	In1 L	In1 W	In2 L	In2 W	T End	ALT	SS FL	STH FL
ER	0.23														
TBIO	**0.99*** **	0.28													
FL L	-0.20	-0.21	-0.16												
FL W	-0.18	-0.06	-0.13	**0.57** **											
PBN	-0.17	0.04	-0.09	**0.74*** **	**0.74*** **										
SN	-0.15	0.21	-0.07	**0.71*** **	**0.71*** **	**0.94*** **									
In1 L	0.35	**0.54***	0.38	0.15	-0.16	0.10	0.30								
In1 W	-0.10	-0.15	-0.04	0.40	**0.63** **	**0.65** **	**0.55***	-0.01							
In2 L	0.43	**0.87*** **	0.47	-0.31	-0.04	0.02	0.15	0.47	0.12						
In2 W	0.14	-0.02	0.22	0.42	**0.72*** **	**0.72*** **	**0.61** **	-0.03	**0.84*** **	0.25					
T End	-0.18	0.29	-0.11	0.13	0.05	**0.51***	**0.57** **	0.35	0.50	0.43	0.40				
ALT	0.35	**0.91*** **	0.41	-0.07	0.11	0.12	0.29	**0.63** **	0.08	**0.90*** **	0.25	0.31			
SS FL	-0.18	**-0.67** **	-0.19	0.45	0.21	0.21	0.05	**-0.56***	0.04	**-0.59** **	0.23	-0.20	**-0.54***		
STH FL	0.23	**0.68*** **	0.30	-0.14	0.34	0.37	0.42	0.03	0.19	**0.77*** **	0.47	0.41	**0.66** **	-0.20	
Phyllo	0.03	**-0.76*** **	-0.01	-0.11	0.01	-0.13	-0.33	**-0.58** **	0.37	-0.40	0.20	0.13	**-0.66** **	-0.32	0.33

Growth rate (GR); Elongation rate of main stem (ER); Total biomass accumulated (TBIO); Flag leaf length (FL C); Flag leaf width (FL W); Total panicle branch number (PBN); Spikelet number (SN); Internode 1 length (In1 L); Internode 1 width (In1 W); Internode 2 length (In2 L); Internode 2 width (In2 W); Transpiration rate at stress end (T end); plant height (ALT); Soluble sugars in the flag leaf (SS FL); Starch in the flag leaf (STH FL); Phyllochron (Phyllo).

*** significant at 1 % probability;

** significant at 5 % probability;

* Significant at 10 % probability;

Source: From author

When the correlation estimates were studied, a significant correlation between the elongation of existing organs – morphogenesis – and new organ formation – organogenesis – was not found (Table 10). Counce; Keisling; Mitchell, (2000) reported that panicle initiation occurs in the phenological stage of V_{F-4}, approximately in the beginning of water stress application; after panicle initiation occurs branches and spikelets differentiation. Thus, the panicle components are considered characters that suffered organogenesis during the water stress application, while the other characters were in morphogenesis process.

Significant correlations were not found between the genotype response index for the panicle components (total number of panicle branches and spikelet number) and the genotype response index for the characters related to plant height (internode 1 length, internode 2 length, plant height and elongation rate of the main stem). Likewise, significant correlations were not observed between the genotype response index for the panicle components and growth rate, total biomass accumulated and soluble sugars and starch concentration present in the flag leaf. These results do not corroborate the ones found by Matsubara et al. (2016). The authors reported a significant correlation between panicle length, spikelet number, plant height and plant biomass; however, under optimum conditions without water stress.

It was possible to observe a positive and highly significant correlation between response index of the main stem elongation during water stress application ($mm.day^{-1}$) and plant height index (0.91) (Table 10). Those correlations express a large reduction of the plant height when there was a large elongation rate reduction of main stem in the period of stress application. Furthermore, a positive and significant correlation was observed between response index of the main stem's elongation rate during the stress period and indexes of the internode 1 length (0.54) and internode 2 length (0.87) (Table 10). The elongation period of the rice plant begins along with panicle initiation (COUNCE; KEISLING; MITCHELL, 2000), therefore the elongation rate is expected to decrease in this phase, consequently, reducing plant height.

A positive and significant correlation was observed between the plant height response index and index estimated to internode 1 length (0.63) and internode 2 length (0.90) (Table 10). The difference between the values obtained for the correlations allows to infer that plant height decrease is strongly related to internode 2 length; when this is more affected, there is a large reduction in the plant height. According to Dunand and Saichuk (2009), the number of internodes in the rice plant varies with the genotype; however, literature lacks data on which internode is the most correlated to the plant height.

Another highly significant positive correlation was observed between the response index of growth rate during stress application ($g.day^{-1}$) and response index for the final biomass accumulated (0.99) (Table 10). A large reduction of the daily biomass accumulation in the stress application period provided a large total biomass reduction. The largest development of plant rice occurs in the reproductive phase (COUNCE; KEISLING; MITCHELL, 2000). Thus, as plant height, the reduction in the total biomass accumulated during this phase reduces the total biomass accumulated as a consequence.

The number of spikelets is one of the most important yield components of rice crop and is directly related to grain yield, since it expresses the panicle yield potential (FREITAS et al., 2007; MARCHEZAN et al., 2005). As it was possible to obtain grain yield data only for Sitis 2015, the number of spikelets in the main stem panicle was considered the most imposing character in the analyses, allowing to infer the yield potential.

Regarding water stress response index of spikelet number, there were highly significant correlations between indexes of the characters flag leaf length, flag leaf width and total number of panicle branches. The positive and significant correlation between response indexes of spikelet number and response index to flag leaf length and width allows to infer that the reduction in the flag leaf width and length induces a reduction of spikelet number. Farooq et al. (2010) confirm this behavior in trials working with rice crop and water deficit. The authors state that plants with larger leaves have better yield performance than plants with smaller leaves, under water deficit.

The significant correlations found between the response index to panicle components and indexes to flag leaf length and width allow the early genotype selection in plant breeding programs for drought tolerance. In other words, as soon as the emergence of the flag leaf occurs, it would be possible to select genotypes that would not possibly reduce the number of spikelets under water deficit in the reproductive phase.

A positive and significant correlation was also found between the genotype response index to panicle components and the response index internode 1 and internode 2 width. Yamagishi et al. (1992) found a positive correlation between the number of spikelets in the main stem panicle and width of the first internode from the top of the plant, referring to internode 1, and correlate these characters with the diameter of the apical meristem.

The positive and significant correlation between spikelet number response index and response index to transpiration rate at the end of the stress indicate that when rice plant reduces the transpiration rate, the number of spikelets also decreases. The transpiration rate is

related to photosynthetic rate, however, plants that reduce transpiration rate under water stress, probably has a tendency to reduce the grain yield (FAROOQ et al., 2009).

In addition, Pearson's phenotype correlation analysis between the genotype responses indexes for panicle components was also run only for Phytotron 2017, which did not have these characters (total panicle branch length and panicle length) in Sitis 2015 (Table 11). The maintenance of a highly significant correlation between the response indexes to spikelet number and total number of panicle branches number. Likewise, there is a significant correlation between the response index of total panicle branch length and the response index to spikelet number. However, when the correlation between the indexes to spikelet number and panicle length was not observed, a significant correlation was not found either (Table 11). Under water stress in the reproductive phase, the reduction of spikelet number is strongly related to the reduction in the number of panicle branches, but not with the reduction of panicle length. Ranawake and Amarasinghe (2014), did not observe a direct correlation between the spikelet number and panicle length either, under optimal conditions of culture. Other studies in literature, also without water stress, affirm the opposite and present significant positive correlations between panicle length and spikelet number (AKINWALE et al., 2011; MATSUBARA et al., 2016).

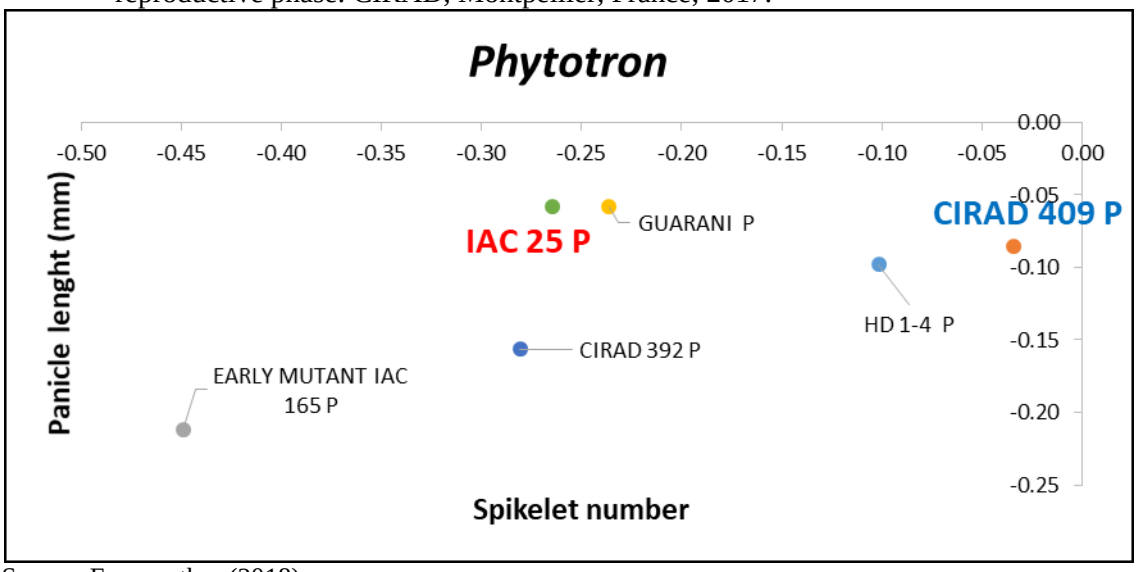
Table 11 - Phenotypic correlation between response indexes to panicle representative traits of the phine phenotyping of upland rice genotypes to drought tolerance in the reproductive phase. CIRAD, Montpellier, France, 2017.

	PBN	**NTR C**	**PL**
PBL	**0.88****		
PL	**0.80***	**0.75***	
SN	**0.96*****	**0.74***	0.63

Panicle branch number (PBN); Panicle branch length (PBL); Panicle length (PL); Spikelet number (SN).
*** significant at 1 % probability;
** significant at 5 % probability;
* significant at 10 % probability;
Source: From author (2018).

The lack of correlation between the response index to spikelet number and panicle length is given in Figure 6. For IAC 25, considered the most susceptible genotype, a significant reduction in the spikelet number in the order of 26% (-0.26) was observed; however, a significant reduction in panicle length was not observed, which reduced only 6% (-0.06) (Table 9).

Figure 6 - Phenotypic correlation between response indexes between response indexes to panicle length and spikelet number of upland rice genotypes for drought tolerance in the reproductive phase. CIRAD, Montpellier, France, 2017.



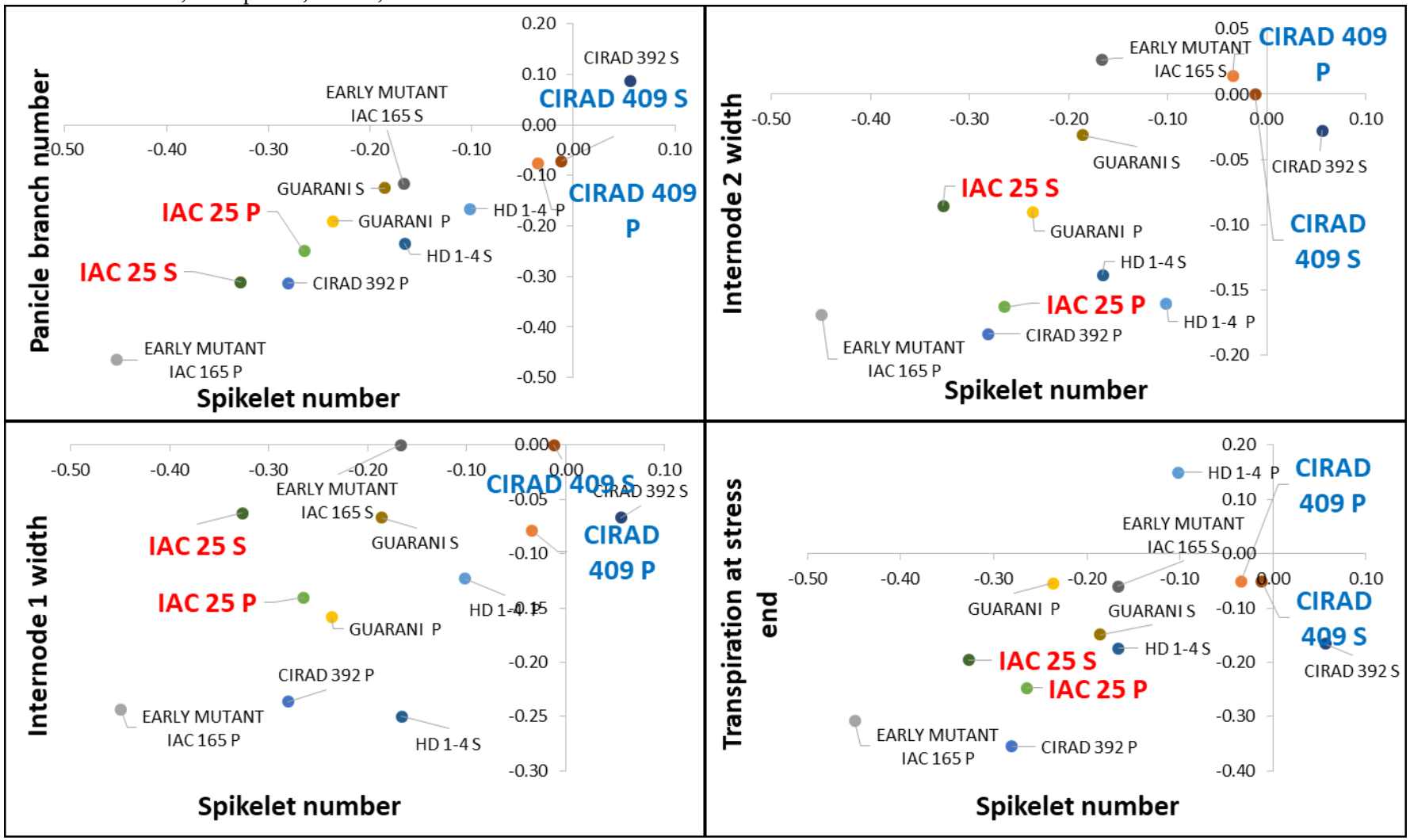
Source: From author (2018).

Phenotypic correlation is a statistical parameter that measures degree of association between two variables, it helps in the indirect selection for important characters, such as the spikelet number, from secondary traits of easier and faster evaluations (RAMALHO et al., 2012). According to Coimbra et al. (2004), the phenotypic correlation may help in the discovery of yield components that influence the obtainment of larger estimates of grain yield.

In Figure 7, the letter 'S' in front of the genotype identification represents trial Sitis 2015 and letter 'P' Phytotron 2017. The same behavior was observed for both genotypes, CIRAD 409 and IAC 25, selected as contrasting for drought tolerance, and in Figure 7 it is possible to observe the proximity of the representative points of two trials in the graph (Figure 7).

The positive and highly significant correlation between response index to spikelet number and total number of panicle branches, internodes 1 and 2 width and transpiration rate at the end of stress can explain the maintenance of spikelet number for CIRAD 409 and the large difference between irrigated and stressed treatments for IAC 25 (Figure 7).

Figure 7 – Phenotype correlation between response index to spiklet number and panicle brench number internode 1 and 2 with and tranpiration at stress end to upland rice genotypes for drought tolerance in the reproductive phase. Embrapa Rice and Beans, Santo Antônio de Goiás, Brazil, 2015 and CIRAD, Montpellier, France, 2017.



Source: From author (2018).

In Sitis 2015, such environmental conditions as better radiation rate and normal production of metabolites allow the analysis of the characters soluble sugars ($mg.g^{-1}$) and starch concentration ($mg.g^{-1}$). Those characteristics present a good experimental precision with a variation coefficient of less than 20% and an accuracy of more than 85%, except for the concentration of soluble sugars in the irrigated treatment (PIMENTEL-GOMES, 2009; RESENDE; DUARTE, 2007) (Table 12). For soluble sugar ($mg.g^{-1}$) and starch concentration ($mg.g^{-1}$), a significant difference was found for genotypes in the individual analysis only for the stressed treatment (Table 12).

Table 12 – Variance analyzes summaries to Sitis 2015 trial with concentrations of soluble sugars ($mg.g^{-1}$) and starch ($mg.g^{-1}$) in the flag leaf of upland rice genotypes phenotyping for drought tolerance in the irrigated and stressed treatment. Embrapa Rice and Beans, Santo Antônio de Goiás, Brazil, 2015.

SV		**Block**	**Genotype**	**Error**		
DF		2	5	10		
Traits	**Teatment**		**Pr (>F)**		**CV (%)**	**Accuracy (%)**
SS FL ($mg.g^{-1}$)	**Sitis**	Irrigated	0.24	0.41	19.78	31.43
STH FL ($mg.g^{-1}$)		Irrigated	0.69	2.47	8.65	99.35
SS FL ($mg.g^{-1}$)		Stressed	0.73	**0.04**	17.56	85.58
STH FL ($mg.g^{-1}$)		Stressed	0.14	**0.00**	8.74	93.88

Concentration of soluble sugars in the flag leaf (SS FL); Concentratio of starch in the flag leaf (STH FL).
Source: From author (2018).

Studies report that sugars act as a metabolic resource when the plant is under water deficit, participating in the growth and development organs regulation (LIU; LAFITTE; GUAN, 2004; ROLLAND; BAENA-GONZALEZ; SHEEN, 2006). Meyer et al. (2007) and Muller et al. (2011) state that plant growth under water deficit is considered a limited sink, because the development is more sensitive than carbon assimilation. The plant continues to produce assimilated for development, but as it is not used by the sink, it is stored in the different organs of the plant.

CIRAD 409 shows a lower concentration of soluble sugars in the flag leaf under water stress (Table 13), initially supported by the hypothesis that the sink is not limited in this genotype under water deficit. Instead of storing sugars, the plant continued to export the assimilates and maintained the plant development in the same way as performed by the plants of the irrigated treatment, which made the response indexes low and non-significant. On the other hand, ththere was an accumulation of starch in the flag leaf, which does not corroborate

the results found by Luquet el al. (2008), who reported that under water deficit, the rice plant tends to reduce the starch concentration in the leaf.

Table 13 – Phenotypic means to concentrations of soluble sugars ($mg.g^{-1}$) and starch ($mg.g^{-1}$) in the flag leaf of upland rice genotypes under water stress. Embrapa Rice and Beans, Santo Antônio de Goiás, Brazil, 2015.

Genotypes	SS FL ($mg.g^{-1}$)		STH FL ($mg.g^{-1}$)	
CIRAD 392	133.79	a	55.38	a
CIRAD 409	70.67	b	52.94	a
Guarani	109.05	a	52.53	a
IAC 25	120.43	a	41.37	b
Early Mutant IAC 165	103.78	a	43.87	b
HD 1-4	114.23	a	38.89	b

Concentration of soluble sugars in the flag leaf (SS FL); Concentration of starch in the flag leaf (STH FL). Means followed by the same letter in the column belong the same group by Scott-Knott test at 5% probability. Source: From author (2018).

Rebolledo et al. (2012) have not confirmed the efficiency of use of sugar concentration estimates as metabolic markers for adaptation to water stress, and state the need for further studies in this area of knowledge.

This study, on the other hand, finds a possible hypothesis of adaptation to sustained water stress tolerance with soluble sugars concentration. This result may be the way for future studies in an attempt to elucidate the problem.

5 CONCLUSIONS

CIRAD 409 shows potential tolerance to drought in the reproductive phase in the evaluated trials, with a significant increase in water use efficiency and maintenance of grain yield under water deficit in the reproductive phase.

The reduction of the yield component and spikelet number is strongly associated with the reduction of total number of panicle branches, but not associated to reduction of panicle length, under water deficit in the reproductive phase. Likewise, there is a link between the reductions in the flag leaf width and length with the spikelet number of the main stem.

The reduction of plant height is strongly associated with the reduction of internode 2 length. When this is more affected, a larger reduction in the plant height occurs.

REFERENCES

AHMADIKHAH, A.; MARUFINIA, A. Effect of reduced plant height on drought tolerance in rice. **3 Biotech**, [s. l.], v. 6, p. 221, 2016.

AKINWALE, M. G. et al. Heritability and correlation coefficient analysis for yield and its components in rice (*Oryza sativa L.*). **African Journal of Plant Science,** [s.l.], v. 5, n. 3, p. 207-212, 2011.

ALONSO-BLANCO, C. et al. What has natural variation taught us about plant development, physiology, and adaptation? **The plant Cell**, Rockville, v. 21, n. 7, p. 1877–1896, 2009.

ARAUS, J. L et al. Plant breeding and Drought in C_3 cereals: what should we breed for? **Annals of Botany**. London, v. 89, n. 7, p. 925–940, 2002.

ARAUS, et al. Breeding for yield potential and stress adaptation in cereals. **Critical Reviews in Plant Sciences**, [s. l.], v. 27, n. 6, p. 377–412, 2008.

ARIAS, C. A. A. et al. Desenvolvimento de cultivares de soja com tolerância à deficiência hídrica. In: SIMPÓSIO SOBRE TOLERÂNCIA À DEFICIÊNCIA HÍDRICA EM PLANTAS: ADAPTANDO AS CULTURAS AO CLIMA DO FUTURO, 2010, Goiânia. **Trabalhos apresentados...** Santo Antônio de Goiás: Embrapa Arroz e Feijão, 2011. p. 130-134

ASAI, K. et al. A rice heterochronic mutant, mori1, is defective in the juvenile-adult phase change. **Development**, [s. l.], v. 129, n. 1, p. 265–273, 2002.

BABU, R. C. et al. Genetic analysis of drought resistance in rice by molecular markers: Association between Secondary Traits and Field Performance, **Crop Science,** Madison, v. 43, n. 4, p. 1457–1469, 2003.

BABU, R. C. et al. HVA1, a LEA gene from barley confers dehydration tolerance in transgenic rice (*Oryza sativa L.*) via cell membrane protection. **Plant Science**, Limerick, v. 166, n. 4, p. 855–862, 2004.

BEEBE, S. et al. Selection for drought resistance in common bean also improves yield in phosphorus limited and favorable environments. **Crop Science**, Madison, v. 48, n. 2, p. 582-592, 2008.

BERLYN, G. P. Seed germination and morphogenesis. In: Kozlowski, T. T. **Seed biology.** New York: Academic Press. 1972. v. 1, p. 223-312.

BOLAÑOS, J.; EDMEADES, G. O. Eight cycles of selection for drought tolerance in lowland tropical maize. I. Responses in grain yield, biomass, and radiation utilization. **Field Crops Research,** Amsterdam, v. 31, n. 3-4, p. 233–252, 1993.

BRASIL. Ministério da Agricultura, Pecuária e Abastecimento. Secretaria de Defesa Agropecuária. Regras para análise de sementes. Brasília, DF: MAPA: SDA, 2009. 395 p.

CONSULATIVE GROUP FOR INTERNATIONAL AGRICULTURAL RESEARCH - CGIAR. **Diversity Panels**. Disponível em: < http://ricephenonetwork.irri.org/diversity-panels/pray-diversity-panel >. Acesso em 06 mar. 2018.

CASTRO, A. P. et al. Avaliação de cultivares de arroz (*Oryza sativa*) de terras altas quanto à deficiência hídrica. In: CONGRESSO BRASILEIRO DE MELHORAMENTO DE PLANTAS, 7., 2013, Uberlândia. **Anais…** Viçosa: SBMP, 2013, p. 1918-1922.

CATTIVELLI, L. et al. Drought tolerance improvement in crop plants: An integrative view from breeding to genomics. **Field Crop Research,** Amsterdam, v. 105, n. 1-2, p. 1–14, 2008.

CECCARELLI, S. Drought. In: JACKSON, M.; FORD-LLOYD, B.; PARRY, M. L. **Plant Genetic Resources and Climate Change,** Boston: Ed. Cabi, 2014, cap. 13, p. 221-235.

CECCARELLI, S.; GRANDO, S. Drought as a challenge for the plant breeder. **Plant growth regulation**, v. 20, n. 2, p. 149-155, 1996.

CHANG, T. ; BARDENAS, E. A. **Morphology and varietal characteristics of the rice plant**. 4th ed. Los Baños: International Rice Research Institute, 1965.

CHAVES, M. M.; OLIVEIRA, M. M. Mechanisms underlying plant resilience to water deficits: prospects for water saving agriculture. **Journal Experimental Botany**, Oxford, v. 55, n. 407, p. 2365-2384, 2004.

CHATEL, M.; GUIMARAES, E. P. Recurrent selection in rice using male sterility gene. **CIAT publication**, Cali, n. 276. p: 77, 1997.

COIMBRA, J. L. M. et al. Análise de trilha dos componentes do rendimento de grãos em genótipos de canola. **Ciência Rural**, Santa Maria, v. 34, n. 5, p.1421-1428, 2004.

CONDON, A. G. et al. Breeding for high water-use efficiency. **Journal Experimental Botany**, Oxford, v. 55, n. 407, p. 2447–2460, 2004.

COUNCE, P. A.; KEISLING, T. C.; MITCHELL, A. J. A uniform, objective, and adaptative system for expressing rice development. **Crop Science**, Madison, v. 40, n. 2, p. 436-443, 2000.

DINGKUHN, M. et al. Improving yield potential of tropical rice: Achieved levels and perspectives through improved ideotypes. **Field Crop Research**, Amsterdam, v. 182, n. 1, p. 43–59, 2015.

DU, H. et al. Characterization of the beta-carotene hydroxylase gene DSM2 conferring drought and oxidative stress resistance by increasing xanthophylls and abscisic acid synthesis in rice. **Plant Physiology**, v. 154, n. 3, p. 1304–18, 2010.

DUNAND, R.; SAICHUK, J. Rice growth development. In: SAICHUK, J. K. **Louisiana Rice Production Handbook**, Louisiana: LSU Ag. Center, 2009, cap. 4, p. 41-53.

EDMEADES, G. O. et al. Selection improves drought tolerance in tropical maize populations: I. Gains in biomass, grain yield, and harvest index. **Crop Science,** Madison, v. 39, n. 5, p. 1306–1315, 1999.

FAROOQ, M. et al. Broader leaves in better performance of indica rice under drought stress. **Journal of Plant Physiology,** Stuttgart, v. 167, n. 3, p. 1066-1075, 2010

FAROOQ, M. et al. Plant drought stress: effects mechanisms and management. **Agronomy for sustainable development,** Paris, v. 29, n. 1, p. 185-212, 2009

FISHER, K. S. et al. (Eds.). **Breeding rice for drought-prone environments**. Los Baños: IRRI, 2003.

FRANKARD, V. et al. Identification of genes for yield enhancement and abiotic stress tolerance by high throughput phenotyping. In: SIMPÓSIO SOBRE TOLERÂNCIA À DEFICIÊNCIA HÍDRICA EM PLANTAS: ADAPTANDO AS CULTURAS AO CLIMA DO FUTURO. 2010. Goiânia. **Trabalhos apresentados...** Santo Antônio de Goiás: Embrapa Arroz e Feijão, 2011. p. 33-34.

FREITAS, J. G. de et al. Produtividade de cultivares de arroz irrigado resultante da aplicação de doses de nitrogênio. **Bragantia**, Campinas, v. 66, n. 2, p. 317-325, 2007.

FROUIN, J. et al. Positional cloning of the rice male sterility gene ms-IR36, widely used in the inter-crossing phase of recurrent selection schemes. **Molecular Breeding**, [s. l.], v. 33, n. 3, p. 555–567, 2014.

FUJIMAKI, H. Recurrent selection by using genetic male sterility for rice improvement. **Japan Agricultural Research Quarterly**, Tokyo, v. 13, n. 3, p. 153–156, 1979.

GONG H., et al. Silicon alleviates oxidative damage of wheat plants in pots under drought. **Plant Science**, Limerick, v. 169, n. 2, 313–321, 2005.

GRENIER, C. et al. Accuracy of genomic selection in a rice synthetic population developed for recurrent selection breeding. **PLoS ONE,** v. 10, n. 8, p. e0136594, 2015.

HALLAUER, A. R.; DARRAH, L. L. Compendium of recurrent selection methods and their applications. **Critical Reviews in plant Science**, [s. l.], v. 3, n. 1, p. 1-33, 1985.

HU, H. et al. Overexpressing a NAM, ATAF, and CUC (NAC) transcription factor enhances drought resistance and salt tolerance in rice. **Proceedings of the National Academy of Sciences of the United States of America,** Washington, v. 103, n. 35, p. 12987–12992, 2006.

ITOH, J. et al. Rice plant development: from zygote to spikelet. **Plant and Cell Physiology,** Kyoto, v. 46, n. 1, p. 23-47, 2005.

JEONG, J. S. et al. Root-specific expression of OsNAC10 improves drought tolerance and grain yield in rice under field drought conditions. **Plant Physiology**, Bethesda, v. 153, n. 1, p. 185-197, 2010.

JONGDEE, B.; FUKAI, S. COOPER, M. Leaf water potential and osmotic adjustment as physiological traits to improve drought tolerance in rice. **Field Crops Research**, Amsterdam, v. 76, n. 2-3, p. 153–163, 2002.

KARABA A. et al. Improvement of water use efficiency in rice by expression of HARDY, an Arabidopsis drought and salt tolerance gene. **Proceedings of the National Academy of Sciences of the United States of America,** Washington, v. 104, n. 39, p. 15270–15275, 2007.

KASUGA, M. et al. Improving plant drought, salt, and freezing tolerance by gene transfer of a single stress-inducible transcription factor. **Nature biotechnology**, New York, v. 17, n. 3, p. 287-291, 1999.

KAVAR, T. et al. Identification of genes involved in the response of leaves of *Phaseolus vulgaris* to drought stress, **Molecular Breeding**, [s. l.], v. 21, n. 2, p. 159–172, 2008.

KUMAR, J.; ABBO, S. Genetics of flowering time in chickpea and its bearing on productivity in semiarid environments. **Advances in Agronomy**, San Diego, v. 72, p. 107–138, 2001.

LARCHER, W. **Ecofisiologia Vegetal**, São Carlos: ed. Rima, 2004.

LIAN, H. et al. The role of aquaporin RWC3 in drought avoidance in rice. **Plant and Cell Physiology**, Kyoto, v. 45, n. 4, p. 481-489, 2004.

LIU, L.; LAFITTE, R.; GUAN, D. Wild *Oryza* species as potential sources of drought-adaptive traits. **Euphytica**, Wageningen, v. 138, n. 2, p. 149-161, 2004.

LUQUET, D. et al. Orchestration of transpiration, growth and carbohydrate dynamics in rice during a dry-down cycle. **Functional Plant Biology**, Victoria, v. 35, n. 8, p. 689-704, 2008.

LUQUET, D. et al. *EcoMeristem*, a model of morphogenesis and competition among sinks in rice. 1. Concept, validation and sensitivity analysis. **Functional Plant Biology,** Victoria, v. 33, n. 4, p. 309-323, 2006.

LUDLOW, M. M.; MUCHOW, R. C. A critical evaluation of traits for improving crop yields in water-limited environments. **Advances in Agronomy**, San Diego, v. 43, p. 107-153, 1990.

MARCHEZAN, E. et al. Análise de coeficiente de trilha para os componentes de produção em arroz. **Ciência Rural**, Santa Maria, v. 35, n. 5, p. 1027-1033, 2005.

MATSUO, T.; HOSHIKAWA, K. **Science of the rice plant**. Tokyo: Food and Agriculture Policy Research Center. 1993.

MATSUBARA, K. et al. Improvement of Rice Biomass Yield through QTL Based Selection. **PLoS ONE**, [s. l.], v. 11, n. 3, p. e0151830, 2016.

MATSUSHIMA, S. **Crop science in rice. Theory of yield determination and its application**. Tokyo: Fuji publishing, 1966

MEYER, R. C. et al. The metabolic signature related to high plant growth rate in *Arabidopsis thaliana*. **Proceedings of the National Academy of Sciences of the United States of America,** Washington, v. 104, n. 11, p. 4759–4764, 2007.

MULLER, B. et al. Water deficits uncouple growth from photosynthesis, increase C content, and modify the relationships between C and growth in sink organs. **Journal of Experimental Botany,** Oxford, v. 62, n. 6, p. 1715-1729, 2011.

NDJIONDJOP, M. N. et al. Field evaluation of rice genotypes from the two cultivated species (*Oryza sativa L.* and *Oryza glaberrima Steud.)* and their interspecifics for tolerance to drought. **Crop Science**, Madison, v. 52, n. 2, p. 524-538, 2012.

NI, J. J.; Colowit, P. M.; Mackill, D. J. Evaluation of genetic diversity in rice subspecies using microsatellite markers. **Crop Science,** Madison, v. 42, n. 2, p. 601–607, 2002.

NONAMI, H. Plant water relations and control of cell elongation at low water potentials, **Journal Plant Research**, Tokyo, v. 111, n. 3, p. 373-382, 1998.

PANG, Y. et al. Recurrent selection breeding by dominant male sterility for multiple abiotic stresses tolerant rice cultivars. **Euphytica**. Wageningen, v. 213, p. 268, 2017.

PIMENTEL-GOMES, F. **Curso de estatística experimental**. 15. ed. Piracicaba: Fealq, 2009.

OUYANG, S. Q. et al. Receptor-like kinase OsSIK1 improves drought and salt stress tolerance in rice (*Oryza sativa*) plants.**The Plant Journal**. [s. l.], v. 62, n. 2, p. 316–329, 2010.

R Development Core Team **R: A linguagem e ambiente para computação estatística.** Viena, R. Foundation for Statistical Computing, R versão 3.0.1, Disponível em: http://www.Rproject.org, 2012

RAMALHO, M. A. P. et al. **Aplicações da genética quantitativa no melhoramento de plantas autógamas**. Lavras: Editora UFLA. 522p, 2012.

RAMYA, P. et al. Effect of recurrent selection on drought tolerance and related morpho physiological traits in bread wheat. **PLoS ONE**, [s. l.], v. 11, n. 6, p. e0156869, 2016.

RANAWAKE, A. L.; AMARASINGHE, U. G. S. Relationship of yield and yield related traits of some traditional rice cultivars in Siri Lanka as described by correlation analysis. **Journal of Scientific Research & Reports**. v. 3, n. 18, p. 2395-2403, 2014.

REBOLLEDO, M. C. et al. Phenomics of rice early vigour and drought response: Are sugar related and morphogenetic traits relevant? **Rice**, [s. l.], v. 5, n. 22, p. 1-25, 2012.

RESENDE, M. D. V.; DUARTE, J. B. Precisão e controle de qualidade em experimentos de avaliação de cultivares. **Pesquisa Agropecuária Tropical**, Goiânia, v. 37, n. 3, p.182-194, 2007.

RICKMAN, R. W.; KLEPPER, B. L. The phyllochron: where do we go in the future? **Crop Science**, Madison, v. 35, n. 1, p.44-49, 1995

ROLLAND, F.; BAENA-GONZALEZ, E.; SHEEN, J. Sugar sensing and signaling in plants: conserved and novel mechanisms. **Annual Review Plant Biology**.[s. l.], v. 57, p. 675–709, 2006.

SCHUPPLER, U.et al. Effects of water stress on cell division and cell-division-cycle-2-like cell-cycle kinase activity in wheat leaves. **Plant Physiology**, Stuttgart, v. 117, n. 2, p. 667–678, 1998.

SCOTT, A.; KNOTT, M. A Cluster-analysis method for grouping means in analysis of variance. **Biometrics**, Washington, v. 30, n. 3, p. 507- 512, 1974.

SHAO, H. B. et al. Higher plant antioxidants and redox signaling under environmental stresses. **Comptes Rendus Biologies**, Paris, v. 331, n. 6, p. 433–441, 2008.

SNEYD, L. Wild food consumption and urban food security. In: CRUSH, J.; BATTERSBY, J. **Rapid urbanisation, Urban Food Deserts and Food Security in Africa**.Suiça: Springer International Publishing, 2016, p. 143-155.

STITT, M.; SULPICE, R.; KEURENTJES, J. Metabolic networks: how to identify key components in the regulation of metabolism and growth? **Plant Physiology,** Stuttgart, p. 152, n. 2, p. 428–444, 2010.

TAIZ, L.; ZEIGER, E. **Fisiologia vegetal**. 5. ed. Porto Alegre: Artmed, 2013.

TAPIERO, A. L. et al. Arroz Corpoica Llanura 11 : Variedad mejorada de alta precocidad para sistemas prouctivos de la altillanura plana. **Corpoica**. Bogota, n. 60, 2012.

TERRA, T. G. R. et al. Tolerância de linhagens de arroz de terras altas à seca. **Pesquisa Agropecuária Tropical**, Goiânia, v. 43, n. 2, p. 201-208, 2013.

TURNER, N. C.; WRIGHT, G. C.; SIDDIQUE, K. H. M. Adaptation of grain legumes (pulses) to water-limited environments, **Advances in Agronomy,** San Diego, v. 71, p. 123-231, 2001.

TURNER, N. C. Crop water deficits: a decade of progress. **Advances in Agronomy**, San Diego, v. 39, p. 1–51, 1986.

VENUPRASAD, R.; LAFITTE, H.R.; ATLIN, G.N. Response to direct selection for grain yield under drought stress in rice. **Crop Science**, Madison, v. 47, n. 1, p. 285–293, 2007.

VIDAL, M. S.; CARVALHO, J. M. F. C.; MENESES, C. H. S. G. Déficit hídrico: aspectos morfofisiológicos. Campina Grande: Embrapa Algodão. 2005. Documentos 142.

VRANOVÁ, E.; INZÉ, D.; VAN BREUSEGEM, F. Signal transduction during oxidative stress. **Journal Experimental Botany**, Oxford, v. 53, n. 372, p. 1227–1236, 2002.

WERY, J. et al. Screening techniques and sources and tolerance to extremes of moisture and air temperature in cool season food legumes, **Euphytica**, Wageningen, v. 73, p. 73-83, 1994.

WOPEREIS, M. C .S. et al. Drought-stress responses of two lowland rice cultivars to soil water status. **Field Crop Research**, Amsterdam, v. 46, n. 1-3, p. 21-39, 1996.

WU, Y. C.; CHANG, S-J.; LUR, H-S. Effects of field high temperature on grain yield and quality of a subtropical type *japonica* rice - Pon-Lai rice. **Plant Production Science.** [s. l.], v. 19, n. 1, p. 145-143, 2016.

YAMAGISHI, Y. et al. Relation of number of spikelet per panicle to the characteristics of shoot and size around growing point at panicle initiation stage in rice varieties. **Japanese Journal of Crop Science**, Tokyo, v. 61, n. 4, p. 568-575, 1992.

APPENDICES A – Mean tables

Table 1 – Phenotypic adjusted means of upland rice genotypes, irrigated, without water stress in the reproductive phase. Embrapa Rice and Beans, Santo Antônio de Goiás, Brazil, 2015.

Genotypes	CIRAD 392	CIRAD 409	EARLY MUTANT IAC 165	GUARANI	HD 1-4	IAC 25
			Sitis			
Tiller number	11.00	9.00	10.33	10.33	9.00	8.67
Phyllochron	8.23	8.74	9.26	7.36	7.50	6.27
Transpiration – stress end (mmol $H_2O.m^{-2}.s^{-1}$)	3.30	3.33	4.81	5.13	5.13	5.66
Growth rate ($g.day^{-1}$)	0.70	1.17	1.29	1.00	1.17	1.52
Elongation rate ($mm.day^{-1}$)	25.82	26.15	25.00	26.12	24.45	30.45
Total biomass (g)	11.80	12.85	18.04	16.99	16.32	21.32
Flag leaf length (mm)	397.00	441.00	511.33	421.33	395.00	453.33
Flag leaf width (mm)	13.33	13.17	19.17	18.33	19.33	20.67
Total panicle branch number	23.00	32.33	42.67	26.67	42.67	44.00
Spikelet number	118.67	141.00	180.00	145.67	159.00	186.67
Internode 1 length (mm)	180.67	151.33	188.00	162.00	142.67	174.67
Internode 1 width (mm)	5.00	4.00	5.67	5.00	5.33	5.33
Internode 2 length (mm)	144.67	73.33	145.33	160.67	139.33	184.67
Internode 2 width (mm)	6.00	4.00	6.33	5.33	6.00	5.83
Plant height (mm)	699.67	564.33	720.67	751.67	645.33	806.00
Soluble Sugar – Flag feaf ($mg.g^{-1}$)	70.34	72.07	60.03	72.66	52.76	67.98
Starch – Flag leaf ($mg.g^{-1}$)	67.61	73.18	60.04	62.26	60.45	63.30
Yield (g/plant)	35.45	24.08	35.12	35.85	38.00	31.95
Spikelet sterility (%)	3.63	16.55	6.39	3.57	8.34	8.03
Thousand grains weight (g)	36.42	30.74	38.49	38.86	40.73	38.48

Source: From author (2018).

Table 2 – Phenotypic adjusted means of upland rice genotypes, stressed, with water stress in the reproductive phase. Embrapa Rice and Beans, Santo Antônio de Goiás, Brazil, 2015.

Genotypes	CIRAD 392	CIRAD 409	EARLY MUTANT IAC 165	GUARANI	HD 1-4	IAC 25
			Sitis			
Tiller number	9.67	9.33	9.33	9.00	8.33	6.33
Phyllochron	10.28	8.52	14.12	8.65	6.46	9.08
Transpiration – stress end (mmol $H_2O.m^{-2}.s^{-1}$)	2.76	3.16	4.52	4.36	4.23	4.56
Growth rate ($g.day^{-1}$)	0.59	1.16	1.08	0.81	0.92	0.94
Elongation rate ($mm.day^{-1}$)	14.41	20.85	11.29	16.23	16.93	18.00
Total biomass (g)	10.12	12.68	15.13	13.75	12.88	13.12
Flag leaf length (mm)	459.33	455.67	429.67	422.67	387.00	414.33
Flag leaf width (mm)	14.33	13.67	19.67	18.00	18.00	20.00
Total panicle branch number	25.00	30.00	37.67	23.33	32.67	30.33
Spikelet number	125.33	139.33	150.00	118.67	132.67	125.67
Internode 1 length (mm)	91.67	146.00	86.67	72.33	58.00	70.67
Internode 1 width (mm)	4.67	4.00	5.67	4.67	4.00	5.00
Internode 2 length (mm)	88.67	70.67	99.33	119.00	102.00	144.67
Internode 2 width (mm)	5.83	4.00	6.50	5.17	5.17	5.33
Plant height (mm)	520.33	546.67	520.00	590.67	549.00	642.00
Soluble sugar – Flag leaf ($mg.g^{-1}$)	133.79	70.67	109.05	120.43	103.78	114.23
Starch – Flag leaf ($mg.g^{-1}$)	55.38	52.94	52.53	41.37	43.87	38.89
Yield (g/plant)	30.33	24.50	29.68	29.05	33.35	16.08
Spikelet sterility (%)	37.54	27.97	13.75	21.84	12.67	26.40
Thousand grains weight (g)	34.26	30.28	38.68	38.69	36.88	35.94

Source: From author (2018).

Table 3 – Phenotypic adjusted means of upland rice genotypes, irrigated, without water stress in the reproductive phase. CIRAD, Montpellier, France, 2017.

Genotypes	CIRAD 392	CIRAD 409	EARLY MUTANT IAC 165	GUARANI	HD 1-4	IAC 25
			Fitotron			
Tiller number	10.00	7.33	6.33	5.67	6.33	5.33
Phyllochron	9.95	6.88	7.95	7.28	6.50	8.45
Transpiration – stress end (mmol $H_2O.m^{-2}.s^{-1}$)	5.07	4.61	3.93	4.19	5.03	3.83
Growth rate ($g.day^{-1}$)	0.59	0.26	0.29	0.42	0.35	0.46
Elongation rate ($mm.day^{-1}$)	11.17	11.30	14.08	16.50	14.86	19.74
Biomassa total (g)	23.58	8.50	15.54	15.64	13.71	17.36
Flag leaf length (mm)	550.00	615.33	607.33	591.00	653.67	641.00
Flag leaf width (mm)	15.00	15.33	21.00	19.67	20.33	20.67
Total panicle branch number	33.00	39.33	51.67	33.33	38.00	32.00
Total panicle branch length (mm)	112.11	136.21	188.46	132.26	178.98	141.08
Panicle length (mm)	270.33	287.67	285.67	314.33	319.67	303.33
Spikelet number	133.00	145.67	217.33	139.67	161.00	143.67
Internode 1 length (mm)	181.67	150.33	182.67	202.67	198.67	227.67
Internode 1 width (mm)	5.63	4.67	5.97	5.04	5.60	5.70
Internode 2 length (mm)	123.00	80.00	162.33	143.33	125.00	208.33
Internode 2 width (mm)	6.41	4.70	6.86	5.17	5.95	6.53
Plant height (mm)	717.00	648.00	887.67	854.33	806.00	967.67
Total water consumption (g)	5354.28	2919.32	4427.03	4245.30	5233.37	3969.67
Water use efficiency ($g.g^{-1}$)	0.0036	0.0025	0.0023	0.0032	0.0024	0.0032
Soluble sugar – Flag leaf ($mg.g^{-1}$)	53.06	59.41	67.60	59.98	63.68	60.61
Starch – Flag leaf ($mg.g^{-1}$)	0.46	1.11	0.53	0.53	1.03	0.47

Source: From author (2018).

Table 4 – Phenotypic adjusted means of upland rice genotypes, stressed, with water stress in the reproductive phase. CIRAD, Montpellier, France, 2017.

Genotypes	CIRAD 392	CIRAD 409	EARLY MUTANT IAC 165	GUARANI	HD 1-4	IAC 25
			Fitotron			
Tiller number	11.33	5.33	8.00	6.00	5.67	5.00
Phyllochron	10.53	6.48	10.54	7.48	7.16	8.96
Transpiration – stress end (mmol $H_2O.m^{-2}.s^{-1}$)	3.27	4.37	2.72	3.97	5.78	2.89
Growth rate ($g.day^{-1}$)	0.36	0.27	0.41	0.35	0.22	0.36
Elongation rate ($mm.day^{-1}$)	7.32	11.17	9.38	13.62	10.97	14.15
Biomassa total (g)	14.10	8.86	20.39	13.23	8.82	13.74
Flag leaf length (mm)	451.67	524.00	520.00	520.00	509.33	538.33
Flag leaf width (mm)	15.00	16.33	17.33	17.33	18.00	19.67
Total panicle branch number	22.67	36.33	27.67	27.00	31.67	24.00
Total panicle branch length (mm)	76.80	135.51	104.80	120.87	127.27	106.64
Panicle length (mm)	228.00	263.00	225.00	296.00	288.33	285.67
Spikelet number	95.67	140.67	119.67	106.67	144.67	105.67
Internode 1 length (mm)	85.00	83.67	117.00	127.67	134.33	121.00
Internode 1 width (mm)	4.30	4.30	4.51	4.24	4.91	4.90
Internode 2 length (mm)	81.00	96.67	142.33	135.33	109.33	151.00
Internode 2 width (mm)	5.23	4.77	5.70	4.70	4.99	5.47
Plant height (mm)	550.67	663.67	731.67	753.67	650.00	785.67
Total water consumption (g)	3010.42	1615.30	3615.56	2310.24	2610.21	2283.52
Water use efficiency ($g.g^{-1}$)	0.0040	0.0047	0.0040	0.0050	0.0029	0.0045
Soluble sugar – Flag leaf ($mg.g^{-1}$)	66.81	70.22	85.54	77.52	67.73	69.76
Starch – Flag leaf ($mg.g^{-1}$)	0.26	2.40	0.33	0.60	0.85	0.30

Source: From author (2018).