Responses of rice (*Oryza sativa* L.) genotypes to repeated drought stress under contrasting temperatures

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Introductory paper at the Faculty of Landscape Architecture, Horticulture and Crop Production Science 2016:1

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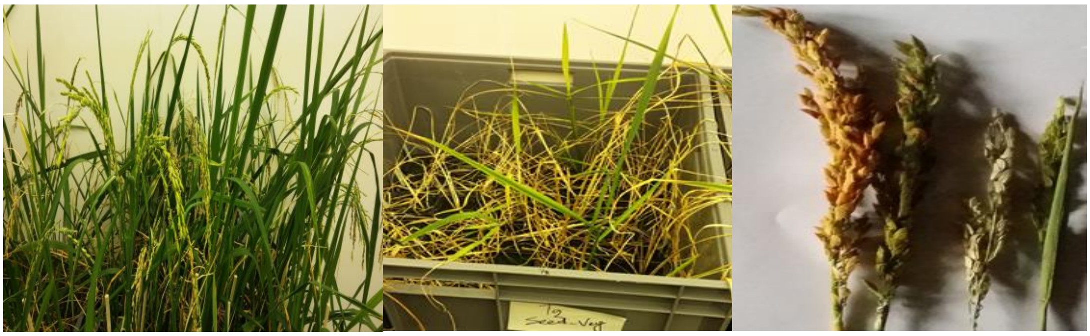

Well watered rice plants throughout the growing season (left) plants that were water stressed at seedling and vegetative stages (middle), stressed panicles (right)

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Abstract

Rice is an important staple food crop for a large part of the world population. Rice is a good source of dietary energy and provides a good proportion of proteins and minerals.

Rice is adapted to diverse environments, although its semi-aquatic characteristic makes paddy rice producing better at high soil moisture content. Rice is largely grown in irrigated systems and drought is one of the most damaging abiotic stress factors, affecting rice growth, productivity and grain quality. Drought hinders rice growth and development and may cause yield losses up to 88% under severe drought.

Various factors including competition from other crops, urbanization and increasing water demand with a growing world population are threatening the rice production. Furthermore, increment of drought frequency and intensity together with rising temperatures due to climate changes constitute a heavy challenge to rice production.

Hence, efforts have been made to find water saving management practices in rice production as well as to breed cultivars for adaptation to drought-prone environment. Intensive studies have been carried out to understand drought adaptation mechanisms, to identify roots and leaf traits as well as quantitative trait loci associated with drought tolerance, and to select or incorporate drought adaptation traits into elite genotypes.

Breeding for highly productive cultivars showing enhanced adaptation to drought-prone environments has been hindered by the complexity of the trait and a strong genotype x environment interaction. Likewise, variability of drought occurrence in time, intensity and pattern are other constraints. The strong genotype x environment interaction makes development of mega-cultivar difficult. Thus, specific screening of cultivars adapted to certain environments, together with development of appropriate water management system is a necessity for successful rice production. Moreover, few researches have focused on combinational effects of drought and temperature on rice quality characteristics.

In Rwanda, rice is mainly produced in irrigated systems where insufficiency of water constitutes one of the limiting factors. Nevertheless, while drought frequency and temperatures are predicted to increase in the future, no research has been carried out to understand how these challenges in Rwandan rice production systems should be dealt with. In this context, the present research study proposes to evaluate the different cultivars suggested to be grown in Rwanda in order to increase the understanding related to how repeated drought and temperature influence yield and quality of rice, and to elucidate what options we have to improve adaptation to drought and high temperatures.

Table of Contents

1. Importance of rice

1.1 Rice in human nutrition

Rice is among the major staple food crops for a large proportion of the world population. Rice nutrient content varies depending on the cultivar and production conditions in addition to the processing method (Rohman et al. 2014).

Rice contains mainly carbohydrates and contributes with 20% of the world's dietary energy. 100gr of raw white rice provide 361 kcal and 6 gr of proteins (Calpe 2006). Good proportions of thiamine, riboflavin, niacin and dietary fibers (FAO 2004) are found in rice. Whole grains, especially from red and black rice are rich in polyphenols and insoluble fibers with nutraceutical and antioxidant benefits (Shao and Bao 2015, Zhang et al. 2015) that play a role in preventing colorectal and intestinal cancer. The low content of fat, cholesterol and sodium in rice contributes to a reduction in obesity and improves cardiovascular health (available at www.organicfacts.net).

Besides its consumption as cooked grain, rice can be processed into different products like rice flour and starch, cakes and puddings, breakfast cereals, rice snacks and noodles, baby food, rice milk and fermented beverages. Milk made from rice can be consumed by people allergic to dairy milk. In addition to its nutritive value, rice is easily conservable even at farm level and thus plays an important role for food security (GRiSP 2013).

1.2 Other uses of rice

In animal feed, rice bran constitutes a cheap product rich in nutrients. Rice hulls and husks may also be incorporated into animal feed production whereas rice straw may be used as litter for animal bedding (GRiSP 2013).

Rice hulls and husks are also used as fuel. They may be incorporated in concrete blocks, tiles, ceramics, cement, filters, charcoal briquettes, and used for cooking gas production. Additionally, the rice straw is used as energy source, roofing material, bedding material and as seedbed cover. All rice by-products serve as good medium for mushroom production. Their incorporation into the soil contributes to nutrient restitution (GRiSP 2013).

In producing countries, rice is often used in religious ceremonies and weddings as a sign of prosperity. In West Africa, some old cultivars are used in traditional medicine. Phenolic compounds in brown rice possess anti-inflammatory properties and thus help in soothing irritated skin as well as delaying signs of premature aging of the skin (available at www.organicfacts.net)

2. Taxonomy, origin and geographical distribution

Rice is classified as belonging to the Gramineae family and the genus *Oryza*. The genus *Oryza* consists of 20 species while only two of the species (*O. sativa* and *O. glaberrima*) are cultivated. *O. sativa* is referred to as the Asian rice while *O. glaberrima* is the African rice.
O. sativa is subdivided into the indica and japonica types which are sometimes considered as subspecies (Garris et al. 2005). Historically, one type of tropical japonica was incorrectly considered as a third separate type of *O. sativa*, termed javanica (Oka 1988). Indica types are tall plants with high tillering ability and slender leaves. The grains of the indica type are long and narrow. Japonica types are short plants with moderate tillering, producing short and round grains.

Besides the conventional cultivars, New Rice for Africa (NERICA) cultivars were bred by AfricaRice (formerly known as WARDA: West African Rice Development Association) using interspecific hybrid germplasm derived from *O. sativa* and *O. glaberrima*. NERICA cultivars have a shorter lifecycle, a higher yield potential as compared to *O. glaberrima*, are resistant to various biotic and abiotic stress factors and are suitable for poor farming systems of sub-Saharan Africa (Jones et al. 1997).

The determination of both the genetic origin and the origin of domestication of rice is complex and controversial. Vaughan et al. (2008) suggested that African and Asian rice might share a common ancestor diverging from *O. longistaminata*, a perennial African species. However, other findings indicate *O. glaberrima* to originate from *O. barthii* and that this event took place in the inland delta of the Niger river approximately 3000 years ago (Wopereis 2009a; Wang et al. 2014). The separate origin of *O. sativa* and *O. glaberrima* was further evidenced when the *O. glaberrima* genome was sequenced (Wang et al. 2014) and compared with the *O. sativa* counterpart. Hence, it has been recently proposed that the domestication of *O. sativa* and *O. glaberrima* took place separately although the two species have a parallel evolution and thus share some evolutionary genes.

The exact origin of the Asian rice constitutes a debate among scientists. *Oryza rufipogon* and *Oryza nivara* are disputed to be the wild progenitors of *O. sativa* (Fuller 2011). The annual life cycle, self-fertilization and high production potential of *O. nivara* (Chang 2003) and the high level of genetic diversity from crosspollination of *O. rufipogon* (Oka 1988) make both these species candidate progenitors of *O. sativa*. Likewise, archeological and molecular-based studies have suggested both a single and a double origin of domestication and evolution for the *indica* and *japonica* types of *O. sativa* (Sang and Ge 2007). Common genomic regions in both types might be a result of introgressions from one species to another (He et al. 2011). However, identical sequences for some traits such as the domestication gene *sh4* responsible of non-shattering and the erect habit locus *prog1* indicate a single origin (Molina et al. 2011). A single origin indicates that *O. rufipogon* is the common ancestor of the *O. sativa* species and the domestication might have taken place in the Yangtze valley in China (Molina et al. 2011; Lu et al. 2002).

Rice cultivation is best suited to a wet tropical climate. However, rice adapts to diverse environments ranging from sea level to an altitude as high as 3000 m above sea level and latitude wise from 35^{o} South (S) to 53^{o} North (N) due to its high genetic diversity and elevated plasticity (Santos et al. 2003). *O. sativa* is spread to all rice growing environments over the world while the spreading of *O. glaberrima* has remained limited to West Africa, its area of origin. Xiong et al. (2011) showed that *indica* cultivars were distributed from 2° S to 40° N whereas *japonica* mostly occupied the latitudes higher than 15° N. The *indica* cultivars followed a normal distribution around a latitudinal temperature peak of 26^{o}C (30^{o}N). The distribution of *Japonica* cultivars was negatively correlated with the average temperatures in the latitude thus confirming the high sensitivity of *japonica* types to increasing temperatures (Xiong et al. 2011).

3. Biology of rice

3.1 Botany

3.1.1 Root system

The radicle is the first to emerge from the coleorhizae of the embryo at germination time (Hochholdinger et al. 2004). A few days after radicle emergence, five embryonic crown roots emerge from the coleoptilar node at the same time as the emergence of the first and second leaf. Later, nodal roots emerge from the stem and tillers' nodes. Embryonic and nodal roots constitute primary roots from which lateral roots are rising. Rice develop many, thin, small lateral roots and a few large lateral roots. Small lateral roots display a determinate lateral growth whereas large lateral roots indeterminably grow downward and develop other small lateral roots (Sasaki et al. 1984). Roots develop root hairs that adsorb water and nutrients. In flooded soils, oxygen is captured from the atmosphere through stomata and transported to the root tips through aerenchyma (Kirk 2003).

About 675 quantitative trait loci (QTLs) have been identified associated with rice root parameters such as root density, maximum root elongation and thickness, root/shoot ratio and root penetration index and most of them have been mapped to chromosomes 1, 2, 3, 7, 9 and 11 (Coudert et al. 2010).

Besides the genetic background, the surrounding environment significantly influences the growth and root architecture of rice. Roots became larger, had less porous and fewer adventitious roots when rice grew in aerobic soil than in anaerobic conditions (Colmer 2003). In addition, plants grown in stagnant solution with high phosphorus (P) level developed shorter but denser adventitious roots with more pores and larger earenchyma than plants grown in aerated conditions with high P supply (Insalud et al. 2006). Moreover, an increasing nitrogen rate resulted in an increase of root weight, root length and surface area (Fan et al. 2010). Furthermore, Fang et al. (2013) noted that root architecture could be modified following a genotype-specific signal from neighbouring roots, or the growth of the root system could be reduced with an increasing number of root tips reaching a physical obstacle.

3.1.2 Shoot system

The aboveground organs of rice comprise the culm, the leaves and the panicle.

Leaves are alternately arranged around the culm and each leaf comprises a blade and a sheath. Blades are flat, sessile and are attached to the culm node by a leaf sheath. The leaf sheath envelops the culm in different form, length and tightness. Leaf morphological traits such as erectness, length, width, thickness, toughness, and senescence contribute to yielding capacity of a cultivar. Erect, thick, and short leaves have been found to permit greater photosynthetic activity by allowing penetration and an even distribution of light as well as less mutual shading (Craufurd et al. 1999; Fageria et al. 2006). Delayed leaf senescence has been considered as a desirable character (Jennings et al. 1979) for active photosynthesis during grain filling which allows more carbohydrates accumulation in the grain.

The stem, also called culm, develops from the plumule of the embryo. The culm is formed by solid centers at the node position and hollow internodes (RKMP 2011). At each node, a leaf and a bud are developed while the last top internode bears the panicle. Internode distance and final plant height vary according to varieties, management practices and environments.

Tillers develop at the end of the seedling stage from the bottom buds of the culm. Tillers produced from the main culm's nodes are primary tillers. The tiller develops its own roots when its fourth leaf emerges. Tillers have the same anatomy and physiology as the main culm. Tillering covers the whole vegetative phase and stops with panicle initiation (Espino 2012). Maximum tiller number has been obtained 35 to 71 days after sowing. After panicle initiation unproductive tillers degenerate (Fageria and Baligar 2001).

3.1.3 Floral organs

The inflorescence of rice is called panicle which is a group of florets (spikelets) borne from the terminal node of the culm. The panicle is sometimes branched into secondary and tertiary branches that bear spikelets.

The floret consists of six stamens and one pistil. The lodicules represent the reduced perianth. The lodicules become turgid, pushing the lemma and palea apart and allowing the stamens to emerge above the open floret. The lemma and palea are modified stems that harden and close after pollination to protect the florets and the developing embryo (RKMP 2011).

3.1.4 Grain

The rice grain is a caryopsis firmly enclosed by the lemma and palea. The lemma and palea and their associated structure form the hull or husk. The embryo is located next to the lemma while the endosperm constitutes the remaining part of the grain (GRiSP 2013).

3.2 Rice development and physiology

Rice development passes through three main phases, namely the vegetative phase from germination to panicle initiation, the reproductive phase from panicle initiation to flowering, and the maturation phase from flowering to maturity (Moldenhauer et al. 2013). From germination to maturity, a rice plant undergoes different physiological and morphological changes according to the growth stage (Figure 1).

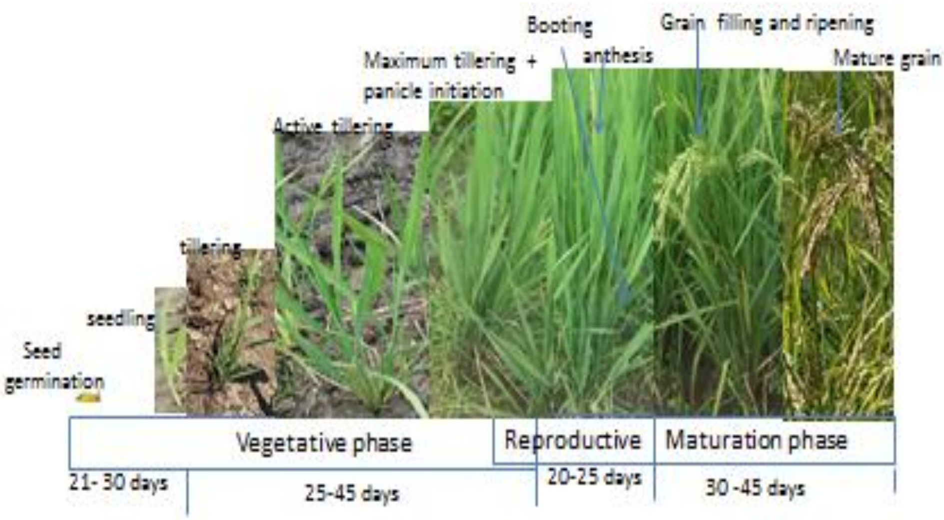

Figure 1: Rice growth and developmental stages

The developmental phases are subdivided into 10 growing stages:

1. Germination and emergence (stage 0): has been described as the projection of the radicle and plumule through the hull followed by the breaking of the first leaf through the coleoptile. Germination takes place when the seed has absorbed sufficient water and the temperature is between 10 and 40^{o}C (Yoshida 1981). The oxygen content of the soil was reported to play an important role for the germination process; the radicle appears first in aerated soils whereas it is the coleoptile that emerges first in anaerobic soils (Yoshida 1981).

2. Seedling (stage 1): starts directly after emergence and lasts up to the first tillering. Early, the seedling is characterized by the development of seminal roots and leaves. At later stages, secondary adventitious roots that form the permanent fibrous root system develop while the radicle and seminal roots die. The development of roots in length is active during seedling stage and early vegetative stage and reaches a plateau at flowering time (Klepper 1992). It has been reported that the root system architecture is genetically determined but it is also greatly influenced by the environment. A high correlation was found between root formation and nitrogen concentration at the stem base (Yoshida 1981). Moreover, thicker and denser roots have been observed in dry and aerobic conditions compared to flooded conditions. Yoshida (1981) reported that 5 to 6 ppm oxygen is required for seedling growth during early seedling stages. In addition, seedlings raised in limited water supply may rapidly recover from transplantation stress thanks to smaller leaves and accumulation of more nitrogen and starch in the plant compared to seedlings that have been water lodged.

The seedling is heterotrophic and lives on seed reserves in the endosperm during the first days of its life and progressively becomes autotrophic at the 3 to 4 leaves stage (Salam et al.

1997) when photosynthesis commences. Optimum seedling growth is attained within the temperature range of 25° to 30°C. In general, emergence of a new leaf requires 100 degree-days before the initiation of panicle primordia and about 170 degree-days thereafter (Salam et al. 1997). Thus, leaves are developing at the rate of one leaf every 3 to 5 days and every 5 to 7 days before and after panicle primordia initiation, respectively (Salam et al. 1997).

3. Tillering (stage 2): begins when tillers emerge from the auxiliary buds of the nodes.

The primary tillers give rise to secondary tillers and tertiary tillers. The plant grows long and wide and develops tillers to the point that they are undistinguishable from the main stem.

Tillering capacity is genetically controlled. Li et al. (2003) isolated and characterized the gene MONOCULM 1 (*MOC1*) that is regulating the tillering in rice and the locus is mapped on the long arm of chromosome 6. Moreover, two independent genes, *OsSPL14* (a member of the squamosa promoter binding protein-like) and strigolactones (*SLs*), have been reported to regulate outgrowth of tiller buds (Luo et al. 2012).

A close relationship has been reported between active tillering / leaf area expansion and active nutrients absorption (especially nitrogen, phosphorus and sulfur) and increased photosynthesis (Murayama 1995). Nitrogen and phosphorus content at, or above, 3.5% and 0.25% respectively, are required to stimulate tillering (Counce 2006). Number of tillers and shoot dry weight decreased in submerged and low phosphorus supply conditions (Insalud et al. 2006).

4. Stem elongation (stage 3): spans from later tillering to panicle initiation although stem elongation might be induced at earlier stages by deep seeding or deep water. At stem elongation, only few of the nodes, normally the five top nodes, elongate whereas the rest of the nodes remain short. The number of elongated nodes varies according to cultivar and environments. For example, internodes increased in number and in total length with a prolonged photoperiod in photo-sensitive cultivars (Yoshida 1981).

5. Panicle initiation to booting (stage 4): the reproductive stage in rice starts with the initiation of the panicle primordium around 30 days before heading. Beginning from the main culm, initiation of panicle primordium continues in the tillers. The panicle develops although additionally 3 leaves emerge before the panicle emerges. The panicle development, that takes place before heading, ends up in booting when the upward extension of the panicle causes the flag leaf sheath to protrude. At the time when the flag leaf sheath protrudes, leaves and nonproductive tillers start to senesce from the base of the plant. Panicle development takes 27 to 46 days depending on variety and weather conditions (Yoshida 1981). Booting is viewed as a crucial stage for the rice plant as meiosis occurs at this time.

6. Heading (stage 5): corresponds to the emergence of the panicle tip from the flag leaf.

Heading takes two to three weeks and ends with complete emergence. Low light intensity and high humidity have been associated with a delayed heading process. Application of exogenous salicylic acid delayed panicle emergence whereas high night temperature (32^{o}C) speeded up panicle emergence (Mohammed and Terplay 2009).

7. Flowering or anthesis (stage 6): occurs one to three days after heading. The florets open, the stamens elongate, the anthers protrude from the glumes, and the pollen is released through both apical and basal pores (Yoshida 1981). Floret opening and filament elongation have been found to be related to potassium-driven uptake of water into lodicules and filament (Liu et al. 2006). Water stress resulted in starch degradation in the pollen of drought sensitive cultivars and pollen grains stuck to one another thereby failing to exit the anther (Liu et al. 2006)

High temperature led to decreased spikelet fertility as a result of a decrease in pollen production and in number of pollen on the stigma (Prasad et al. 2006). Low (<20^{o}C) or elevated (>35^{o}C) temperature at heading and anthesis resulted in increased spikelet sterility (Yoshida 1981). High night temperature led to a 72% decrease in spikelet fertility in comparison to plants grown under ambient night temperature (Mohammed and Tarpley 2009). Moreover, a temperature beyond 40^{o}C can even constrain the stimulating effect of elevated CO_2 concentration on spikelet fertility (Madan et al. 2012). However, exogenous application of vitamin E, glycine betaine and salicylic acid contributed positively to spikelet fertility, especially at high night temperatures, as spikelet fertility increased with 47%, 120% and 195%, respectively, compared to an increase of 9%, 15% and 18%, respectively, at ambient night temperature (Mohammed and Tarpley 2009).

8. Milk grain (stage 7): is noted when a milky liquid fills the grains. The dry weight of the grain increases rapidly as a result of grain filling. The filling starts 15 to 20 days after flowering in the tropics and 25 to 30 days in temperate zones. The upper spikelets on the panicle are the first to be filled and produce heavier grains whereas lower, late-flowering spikelets are sterile or poorly filled and of poor grain quality (Mohapatra et al. 1993). These differences in upper and lower spikelets have been associated with hormonal dynamics during grain filling (Wang et al. 2015). An increase in indole-3-acetic acid (IAA), abscisic acid (ABA) and zeatin riboside (ZR) occurs from 3 to 15 days after pollination (Xu et al. 2007; Abu-Zaitoon et al. 2012) with a maximum content at 6 to 9 and 9 to 15 days after pollination, in superior and inferior spikelets, respectively (Xu et al. 2007). ABA peak values have been positively correlated with maximum filling rate and negatively correlated with active grain filling period. Maximum rate and active period of grain filling correlated also with the peak values of IAA and ZR suggesting that these hormones regulate early grain filling stages through affecting the endosperm cell division (Xu et al. 2007). An early grain filling period was shown positively correlated with high grain fresh weight and with the beginning of the stage of starch synthesis (Abu-Zaitoon et al. 2012).

Environmental factors such as drought, nitrogen deficiency and low solar radiation are largely affecting the grain filling stage. In general, positive correlations have been found among grain filling duration, cumulative mean temperatures, solar radiation and final grain weight. However, the grain filling rate was negatively associated with the above parameters (Yang et al. 2008). Water deficit during the grain filling period induced rapid plant senescence and shortened the grain-filling duration (Xie et al. 2001). The milking stage was significantly affected by salinity as a result of chlorosis of the leaves, reduction in gas exchange and a significant decrease of the photosynthesis rate (Sultana et al. 1999). A high temperature of 35/27.8^{o}C resulted in a drop in percentage of filled grains from 98% to 16% for the rice cultivar IR2006 and from 83% to 3.2% for IR52

9. Dough grain (stage 8): is when the milky liquid progressively becomes hard dough, and the grains turn from green to yellow.

10. Mature grain (stage 9): is achieved when the grain completely develops and is hard. The upper leaves dry rapidly but may remain green in some cultivars.

During the ripening stage, photosynthates accumulate in the grains in the form of starch. In addition, mobile carbohydrates, proteins, and mineral nutrients in leaves, stems, and roots migrate to the panicles while the plant gradually senesce (Murayama 1995).

3.3. Quality of rice grain

Quality of rice grains are defined by the physical appearance, cooking and eating qualities, and nutritional values. Environmental conditions such as drought during plant development may affect the quality of rice. For example, drought during 1-20 and 11-40 days before and after heading, respectively, was found detrimental to brown and milled rice rates, the mid booting stage being the stage when the drought was influencing the quality to the highest extent (Wang et al. 2007).

3.3.1 Physical properties

Grain dimension is used to classify rice into four groups according to its length. namely extra-long, long, medium and short respectively measuring 7.5 mm or above, 6.5 to 7.5 mm, 5.5 to 6.5 mm and below 5.5.

Length to width ratio determines the different grain sizes into slender (>3.0), bold (2.0 to 3.0) and round (<2.0) (Belsnio 1992). Under normal conditions yield was positively correlated with grain width and grain breadth and negatively correlated with grain length (Haider et al. 2015). However, under drought, though a positive correlation existed between grain length and grain width, yield per plant was correlated with grain width whereas no correlation was found with grain length and grain breadth (Haider et al. 2015).

Colour: the grain colour is a varietal property but is also determined by milling level.

Rice grains are normally white or reddish. Whitening and polishing removes the silver skin to make the grain whiter. Wet environmental conditions before the grain is dried causes it to ferment and the starch is partly gelatinized giving the grain a yellowish coloration.

Chalkiness/ translucency: is caused by interruption during the final stages of grain filling which makes the starch granules loosely packed and more prone to breakage during milling (Sampang 1992). Rising temperature immediately after flowering and poor soil fertility and water management affect chalkiness level (Mackill et al. 1996). An interaction effect was observed between moisture stress and nitrogen level on rice quality. Chalkiness was found to increase and palatability to decrease under normal nitrogen level and water stress (Cai et al. 2006). In contrast, under high N rate, the chalkiness percentage was lowered and the palatability improved at water stress (Cai et al. 2006).

3.3.2 Chemical characteristics

Chemical characteristics of rice comprise content of starch, proteins, lipids, minerals and bioactive compounds. Significant differences have been reported between different cultivars for their proteins, crude fibers, fats, ashes and minerals contents (Oko et al. 2012; Anjum et al. 2007; Zeng et al. 2004). However, differences between the two types of rice, i.e. indica and japonica were inconsistent (Zeng et al. 2004).

Cooking and eating characteristics of rice are mainly linked to its starch properties. Starch make up 90% of the dry matter content of milled rice. Important starch characteristics are gelatinization temperature, gel consistency and amylose content (Pandey et al. 2014). Gelatinization temperature (GT) has been correlated with gelatinization time (González et al. 2004) and thereby determines the cooking time. Gel consistency has been described as the tendency of rice to harden upon cooling. Firmness of rice has been positively correlated with cooking resistance and negatively correlated with surface water absorption and cooking time (González et al. 2004). Rice starch characteristics are varying depending on rice cultivar and on the analysed fraction of the starch (Shabbir et al. 2008).

Amylose content classifies the milled rice into waxy (1-2% amylose), very low amylose content (2-9% amylose), low amylose content (10-20% amylose), intermediate amylose content (20-25% amylose) and high amylose content (25-33% amylose). High amylose grains retain less water upon cooking and are associated with a harder gel consistency and a low gelatinization temperature. Rice starch texture has also been determined based on the chain length of amylose and amylopectin (González et al. 2004).

Pasting characteristics have also been shown to be affected by environmental conditions during the growing season, agronomic practices, grain development and isolation procedures (Wani et al. 2012, González et al. 2004). High ambient temperature during ripening related to starch with a higher GT whereas water stress resulted in starch with lower GT and lower peak viscosity compared to starch from rice grown under standard conditions (Veronic et al. 2007). Likewise, high temperature affects amylopectin chains with an increase of long chains at the expense of short ones (Inouchi et al. 2000). Genotype x salinity interaction has been reported to affect starch content. High salinity and alkalinity caused reduction in starch content in tolerant and semi-tolerant genotypes whereas sensitive genotypes did not show such a reduction in starch content (Surekha et al. 2013). Moreover, reduction in amylose content in sensitive genotypes has been recorded only at high salinity while tolerant and semi-tolerant genotypes were significantly affected even at low salinity and alkalinity level (Surekha et al. 2013). Positive correlations have been shown between amylose content in rice grains and the mineral elements K, Na, Mg, Cu, and Mn (Jiang et al. 2007).

Regarding protein content, large variations between cultivars have been reported: 1.58 to 7.94% in cultivars grown in Nigeria (Oko et al. 2012), 7.8 to 8.8% in Pakistani cultivars (Anjum et al. 2007) and 5.9 to 11.0% in Indian cultivars (Devi et al. 2015). Genetic research revealed that rice grain protein content is a multi-genic trait, controlled by a cluster of QTLs (Wang et al. 2008). A major QTL (qPC1) which encodes a putative amino acid transporter (OsAAP6) that controls the synthesis of rice proteins, i.e. the glutelins, prolamins, globulins, albumins, has been mapped to the RM472–RM104 region of the long arm of chromosome 1 (Peng et al. 2014).

Besides genetic control, the content of rice grain protein is influenced by growing conditions. For example, the protein content of NERICA 1 reached 7.5 to 8.0% in well-watered conditions whereas the protein content was 10.1 to 10.5% in water stressed rice (Fofana et al. 2010). Protein content of 7.9% and 8.2%, respectively, was recorded at nitrogen fertilizer applications of 80kg.hm^{-2} and 120kg.hm^{-2} (Chandel et al. 2010). High temperature during the grain development resulted in an increased production of glyceraldehyde-3-phosphate dehydrogenase and prolamine while the amount of proteins such as allergen related proteins and elongation factor 1β decreased (Lin et al. 2005).

Treatment and/or storage conditions of rice are also resulting in alterations of the protein composition. The protein content gradually decreased in parboiled rice bran with increasing heating time in the microwave (Rizk et al. 1994). Moreover, the solubility of the proteins was reduced whereas disulphide bonds as well as the molecular weight of oryzenin (rice storage proteins or glutelins) increased under high storage temperature (Chrastil 1990). Furthermore, high storage temperatures resulted in decreased binding of oryzenin to amylose/amylopectin which led to sticky cooked rice (Chrastil 1990). Structural changes have been observed in globulin and glutelin as a result of rice aging (Guo et al. 2013). In glutelin, an increase of sulfhydryl groups on the expenses of α-helical and unordered coil structures were found while in globulin, an oxidation of sulfhydryl groups was found. In addition, starch and globulin became strongly associated whereas the bonds between glutelin and starch were loosened (Guo et al. 2013).

Mineral elements are chemical compounds in crops that have an important role in human nutrition. Variation in mineral content in rice is dependent on cultivars, growing conditions and milling fraction of rice. In a study of 274 rice genotypes grown in China, the mean contents of K, Ca, Na, Mg, Fe, Zn, Cu, and Mn in milled rice were 804.8, 119.5, 20.8, 194.8, 5.4, 26.0, 10.0, and 10.7µg/g respectively (Jiang et al. 2007). Na and Fe showed the largest variation among genotypes with maximum/minimum content ratios of 19.5 and 27.4, respectively, while Zn varied the least with a ratio of 3.3.

In Indian cultivars, mineral content of 155.5 to 173.5 mg, 1.20 to 1.31 mg, and 1.59 to 1.71 mg per 100 g were found for K, Fe and Zn, respectively. The highest values for Na and K were noted in Basmati 2000 while the values of Fe and Zn were highest in the Super Basmati rice cultivar and the cultivar KS.282 showed the lowest mineral content (Shabbir et al. 2008). In cultivars grown in Nigeria, contents of 0.15 to 0.23%, 0.09 to 0.17%, 0.07 to 0.25%, and 0.07 to 0.25% were recorded for K, Na, Ca and Mg respectively (Oko et al. 2012).

Correlation analyses between different minerals contents have shown significant positive associations between the contents of K and Mg, Ca and Na and Mg, Fe, Zn, Mn and Cu, whereas Cu and K contents were negatively correlated (Jiang et al. 2007). However, negative correlations (though not significant) were noted between Na and K, and between Mg and P, K and Na, while significant positive relation has been observed between Na and P (Oko et al. 2012). In addition, Mg, Ca, and Zn contents have been significantly positively correlated with most of the amino acid contents. Mg, Zn, Cu, and Mn contents were significantly positively correlated with protein content (Jiang et al. 2007).

A genotype × environment interaction has been reported for mineral content in two cultivars and two regions of China where Fe and Zn content were higher and Ca lower in the cultivar TN1 than in the cultivar CJ06 in the Lingshui region whereas the inverse was observed in the Hangzhou region (Du et al. 2013). Genetically, 23 QTLs and 9 QTLs linked to mineral accumulation were identified in the Lingshui and the Hangzhou regions, respectively. However, only two of the detected QTLs were consistent over the two locations, namely RM527-RM3 on chromosome 6 and RM4085-RM1111 on chromosome 8, both linked to the region regulating Mg accumulation (Du et al. 2013).

The mineral contents were found to vary according to the position of the grain on the panicle. Higher contents of minerals were recorded from the top than from the bottom, and from the primary than from the secondary rachis of the panicle, inversely to the concentrations of phytic acid (Su et al. 2014).

Higher content of minerals as well as of proteins, fat, and crude fibers were found in rice bran than in the polished rice (Anjum et al. 2007). Zn and Fe concentrations were highest in the bran and thereafter, in decreasing order, in the hull, whole grain, brown rice and polished rice. The concentrations of Mn and Cu were highest in the hull and thereafter, in decreasing order, in the bran, whole grain, brown rice and polished rice. Polishing of rice resulted in large losses of nutrients, leaving only 2%, 6% and 1% respectively of the total Mn, Zn and Fe, and Cu (Ziarati and Azizi 2013). Brown rice showed higher values than white rice for Na (4.9 vs. 3.9 mg/100 g rice), K (229 vs. 102 mg/100 g rice), Fe (1.7 vs. 0.77 mg/100 g rice) and Zn (2 vs. 1.3 mg/100 g rice) (Ziarati and Azizi 2013).

As many other plants, rice contains bioactive compounds that are beneficial for human health, especially having a protective role against cardiovascular diseases and cancers (Kris-Etherton et al. 2002).

Different fractions of rice contain different quantities of bioactive compounds, such as phenolic acids (ferulic, p-coumaric and vanillic acids), γ-oryzanol and tocopherols. There are also reports of variations in ferric reducing ability power and free-radical scavenging activity in various fractions of rice. The bran fraction has been found to have the highest values for all the mentioned parameters, followed by husk and brown rice, while the lowest values have been found in milled rice (Butsat and Siriamornpun, 2010).

Differences in content of bioactive compounds and antioxidant capacity have also been reported to depend on variation in growing location (Butsat and Siriamornpun, 2010). Moreover, a 110% increase of phenolic acid compounds was reported after 120h of fermentation by *Rizhopus oryzae* (Schmidt et al. 2014). Similarly, Razak et al. (2015) observed increases in phenolic acids content when rice bran was fermented by *Aspergillus oryzae* (*A. oryzae*) and *Rhizopus* oryzae (*R. oryzae*). The highest antioxidant potential in the rice bran was found in samples fermented with a mixture of both the mentioned fungi. However, p-coumaric acid did not show any significant increase after fermentation with *R. oryzae* (Schmidt et al. 2014) or *A. oryzae* (Razak et al. 2015) and the content was even reduced when the rice bran was fermented with *Saccharomyces boulardii* (Ryan et al. 2011). Furthermore, Razak et al. (2015) reported an absence of p-coumaric acid and ferulic acid when rice bran was fermented by *R. oryzae*.

Total phenolic content was reported to be highest in the soluble solution of black rice, and also in the insoluble solution of light-purple rice. White rice instead showed the highest values for ferulic, p-coumaric and isoferulic acids (Zhang et al. 2015). However, total anthocyanin content (TAC) was low (0.02–0.09 mg/g) in white rice while TAC in black rice varied between 1.47 and 2.07 mg/g and was eight fold higher than TAC in light-purple rice (Zhang et al. 2015).

4. Rice cultivation

4.1 Rice cultivation in the world

Although rice evolved in a semiaquatic habitat (Wassmann et al. 2009, Bouman et al. 2007), it adapts to different water regimes. Rice thrives in waterlogged soil and can tolerate submergence more than any other crop but it is highly sensitive to drought. Thus the majority (50%) of rice is grown under irrigated conditions while approximately 34% of the rice is grown in rainfed lowlands. Rainfed upland systems make up 9% and flooded rice cultivation covers 7% of the world rice area (IRRI 2007).

Rice has evolved differently in the lowland and upland environments. Thanks to a developed root system and early maturity, upland cultivars are adapted to limited water availability but their productivity is rather low. Lowland cultivars are adapted to anaerobic conditions, they are more responsive to high inputs compared to the upland cultivars, and they are also in general drought sensitive (Kumar et al. 2014a).

Up to 2010, being produced on more than 114 million farms and 162 million ha, rice occupies the largest area worldwide among crops. The largest rice producers are China and India plus Indonesia, Bangladesh, Vietnam, Thailand, and Myanmar. The Asian top seven producers make up 80% of the world's production (GRiSP 2013). Rice is also produced in Africa mainly in Egypt, Madagascar and Nigeria. In Latin America, rice is principally produced in Brazil, Peru, Colombia and Ecuador. In the United States rice production is dominant in California and the southern states near the Mississippi river. The leading European producers are Italy, Spain and Russia. Rice is also grown in Australia although its production is currently being threatened by recurring drought (GRiSP 2013).

Rice production has increased, mainly due to expansion of the cultivation area. Moreover, thanks to research, high yielding and short duration cultivars have been developed, allowing more than one cultivation season per year (Guimarães 2009). The main achievements of the rice breeding are the development of new rice plant types, hybrid rice and NERICA varieties. Super rice cultivars have been developed that are highly nitrogen responsive and lodging resistant. Nitrogen fertilization has improved rice growth, dry matter accumulation, yield components and grain yield due to increased availability of nutrients and photosynthetic activities (Chaturvedi 2005, Ahmed et al. 1998). However, excessive nitrogen application has been associated with lodging (Bhiah et al. 2010, Zhang et al. 2014), disease promotion (Long et al. 2000), delayed maturity and reduced grain quality (Gu et al. 2015). The development of high yielding and nitrogen-efficient cultivars, improvement of grain filling in inferior spikelets, and increasing harvest index are suggested to give high yields with efficient input use (Yang 2015). Besides breeding programs, improved agricultural practices such as alternate wetting-drying (Zhang et al. 2012), mulching (Zhang et al. 2008), mid-season potassium and nitrogen application (Zhang et al. 2013) have contributed to increased yield with efficient resources use.

Despite the mentioned achievements, a continuous annual yield growth of 1 to 1.2% will be needed beyond 2020 to feed the continuous growing world population (GRiSP 2013, Guimarães 2009). The major challenge for such an increase in yield is the current climate change events. In fact, a yield reduction of 10% is predicted for each 1°C increase in minimum night temperature (GRiSP 2013).

The optimum temperature for growth and productivity of rice ranges between 25^o and 30^{o}C, whereas temperatures below 20^{o}C and above 35^{o}C cause drastic reduction in grain yield. Wopereis (2009b) reported that growth was suppressed at extreme temperatures below 10^{o}C and above 40^{o}C. Cold climate during the vegetative stage has been associated with reduced plant vigor, production of few tillers, increased plant death and delayed flowering (Baruah et al. 2009, Woperies 2009b). Reductions of up to 50%, 83% and 29% for panicle number, spikelet fertility and yield have been reported for plants exposed to a temperature of 13^{o}C during reproductive stage (Ghadirnezhad and Fallah 2014). Night temperatures have been found to be more harmful to rice growth and yield than day temperatures (Cheng et al. 2009). In fact, during grain filling, more carbohydrates are burned as a result of elevated respiration under high night temperatures. This has an impact on the photosynthesis efficiency the next day, resulting in a reduced filling of grains (Moldenhauer et al. 2013). Translocation of carbon and nitrogen to the panicle were stimulated by elevated CO_2 whereas a high night temperature limited the translocation (Cheng et al. 2009).

Baker et al. (1992) and Yang et al. (2006) independently reported a significant positive correlation between total biomass, yield and elevated CO_2 concentration. Conversely, Kim and You (2010) observed a reduction of total biomass, shorter panicles, reduction in number of grains per panicle and ripened grain ratio under elevated CO_2 concentration and elevated temperature. Those results confirm the negative impact of global warming on rice productivity despite the stimulating effects of increased CO_2 concentration.

4.2 Rice cultivation in Rwanda

Rice was introduced in Rwanda in 1950. The current estimated area of rice cultivation is around 12,000 Ha of marshland or flood valleys. Rice cultivation is spread into 29 irrigated schemes country-wide whose 2, 12, 13, and 2 are respectively located in Western, Southern, Eastern, and Kigali City. The altitude ranges from 1,000 m to more than 1,700 m above sea level characterized by high relative humidity, cold nights (10 to 15^{o}C) and hot days (20 to 30^{o}C) (MINAGRI 2011). In Rwanda, rice is considered as a priority crop because of a production potential of 7 T/ha per season and such a high production cannot be reached by any other crop in the marshland ecosystem. Rice production also allows exploitation of additional marshland while leaving arable land on hillsides for other crops. In addition, consumption of rice has increased during later years, making rice relevant both as cash and subsistence crop for farmers and other people involved in rice production and commercialization (MINAGRI 2002). However, the potential yield is not achieved because of low temperatures and insufficient water availability in addition to diseases and pests, and insufficient quality seed (RAB, 2013).

Although rice production has increased in recent years due to the expansion of rice cultivated land (MINAGRI 2011) local production still need to be supplemented by importations to satisfy consumer demand in both quantity and quality (Promar 2012).

The country targets a yield average of 5.8-7tons.Ha and a cultivation area of 28,500 Ha by 2018 (MINAGRI 2011).

4.3 Climate change and rice production in Rwanda

Like elsewhere in the world, the future of rice production in Rwanda may be constrained by climate change effects. Additionally, competition from other crops and urbanisation activities for both land and water are factors impacting rice production in Rwanda (REMA 2011). A SWOT analysis of rice sector has classified climate change and access to water among threats to rice productivity in Rwanda besides demographic pressure, inefficient soil fertility management, pests and diseases attacks, (MINAGRI 2011).

Recent meteorological events, mainly the floods of 1997 and the prolonged drought of 2000, associated with El Nino and La Nina (DFID, 2009) demonstrated that the climate change in Rwanda may have catastrophic consequences. For the period 1970–2004, Africa has registered an average surface temperature increase of 0.2 to 2 °C. A further increase of 1 to 2° C in Rwanda is predicted during the current century: i.e 2010-2100 (MINELA, 2010). The mean annual temperature has risen from 19.8°C in 1971 to 21°C in 2009. This 1.2°C increase in four decades is significantly beyond the 0.8°C that caused the global warming over a period of 150 years (REMA 2011).

Climate change scenarios in Rwanda foresee a substantial increase in both mean temperatures and extremes, especially during the June-September period with an increase in number of hot days and nights. A moderate increase in total rainfall is projected to take place but its distribution is likely to be quite uneven as dry spells during rainy seasons are predicted to increase (CSC 2013). Consequently, there is an imminent risk that rice production will be constrained by increasing temperatures and frequent droughts during the growing season.

5. Drought and rice production

5.1 Effects of drought on rice productivity

Drought is the insufficiency of soil moisture content to meet plant water requirements resulting in reduced growth and development of the plant and hence low yield (Blum 2011). Due to its semiaquatic phylogenetic origin, rice is more vulnerable to drought than any other crop (O' Toole 2004). Drought affects all physiological processes involved in plant growth and development (Lanceras et al. 2004).

At cell level, drought leads to a decrease in cell division and/or cell elongation (Sokoto and Muhammad 2014; Kumar et al. 2014b) as a consequence of the reduction in turgor pressure. Moreover, under water stress, cell expansion is much more impaired than cell division (Jaleel et al. 2009) causing tiny and stunted plants. Thus, water stress results in poor root development both in length and in diameter. Drought also hinders root branching (Clark et al. 2008). Under limited water supply, reduction in leaf size and leaf pubescence as well as a change in shape and leaf yellowing is observed. Furthermore, the development of new leaves and new tillers and stem expansion is slow during drought. Severe drought ends in leaf drying and finally plant death. Moreover, drought is accompanied by reduction in biomass production (Ji et al. 2012). All these modifications in normal status of the different tissues and organs impair with photosynthetic rate and other biochemical processes (Kadan et al. 2015; Usman et al 2013; Blum 2011). The reduction in photosynthetic rate is due to stomatal closure that limits the diffusion of CO_2, which leads to reduction of photosynthetic enzyme activity, and loss or diminution of photosynthetic pigments such as chlorophyll a and b and carotenoids (Yang et al. 2014) resulting from the impairment in their synthesis or their post synthesis degradation. Reduction of photosynthetic rate might also be caused by the loss of the chloroplast membrane.

Drought stress close to the booting stage resulted in disturbance of floret initiation (Pantuwan et al. 2002) whereas the number of unproductive tillers was increased. Furthermore, panicle trap within the flag leaf sheath and an increased amount of spikelet sterility due to anther dehiscence failure, or suppression of starch accumulation in pollen grains was observed at drought stress close to booting (Zhu et al. 2004). Mild drought during grain filling resulted in yield decreases of 11.6% to 14.7% (Cai et al. 2006), while severe drought at panicle initiation, flowering and grain filling resulted in losses of up to 70%, 88% and 52%, respectively (Yambao and Ingram 1988). Reductions of 22% for the number of spikelets per panicle and 15% for 1000-grain weight were observed when drought was applied at 7 days before heading and 10 days after heading (Liu et al. 2006**).**

5.2 Rice adaptation to drought stress

Drought adaptation mechanisms are complex phenomena governed by different physio-biochemical processes (Tripathy et al. 2000).

Three categories of rice adaptation to drought are distinguished:

1. Drought escape was described as an adaptation strategy for short cycle cultivars able to produce grains before drought occurrence (Price et al. 2002; Yue et al. 2006). Such short duration cultivars or cultivars able to shorten grain filling period may escape terminal drought occurring during the reproductive stage.
2. Drought avoidance is achieved by cultivars able to take up water from deeper soils through the development of a deep root system (Price et al. 2002, Yue et al. 2006, Gouda et al. 2012). Root elongations, branching and directions of growth are stress induced and triggered also by other environmental factors such as nutrient availability and hormone status, particularly auxins and ABA. The severity of drought at the seedling and vegetative stages decides the magnitude of the stress avoidance by the plant and whether it will develop a deeper and/or more intensive root system with an increased capacity to accumulate dry matter (Bhatnagar-Mathur et al. 2007) and to recover upon re-watering (Okami et al. 2015 , Xangsayasane et al. 2014).
3. Drought tolerance is considered as an ability of the plant tissues to maintain a good water status under limited water conditions (Guimarães et al. 2015).

Leaf rolling is one of the genetically determined responses of rice to water deficiency. Leaf rolling is leading to a reduced leaf area exposed to light, to a prevention of water loss through transpiration and to limited radiation damage (Ha 2014).

Physiological mechanisms of drought tolerance include among others osmotic adjustment and stomatal conductance. Osmotic adjustment is achieved by the accumulation of proline, soluble sugars, glycinebetaine and other solutes in the cytoplasm (Kato et al. 2011**;** Gowda et al. 2011, Wei et al. 2014) thereby improving water uptake. A sustained stomatal and mesophyll conductance (Comstock 2002; Price et al. 2002, Lauteri et al. 2014), and biomass production and partitioning (Guan et al. 2010, Xangsayasane et al. 2014) allow rice plants to survive water deficit stress.

An active accumulation of abscisic acid (ABA) under drought stress has been shown to significantly trigger antioxidant enzymes (Li et al. 2014) and regulate stomatal movement

(Ahmad et al. 2014) and carbon metabolism (Zhou et al. 2014) in addition to inducing the expression of many genes involved in regulating responses to drought.

Biochemical responses also include an increase in the antioxidant activity, thereby improving drought tolerance by scavenging reactive oxygen species. Moreover, under drought stress, tolerant plants showed higher content of cysteine, palmitoleic acid, oleic acid, arachidic acid, behemic acid, copper, potassium and magnesium, while higher levels of glycine, tyrosine, linoleic acid, linolenic acid, lignoceric acid and calcium were observed in sensitive plants in comparison to their counterpart plants grown under well-watered conditions (Nam et al. 2014). The accumulation of proline is the most important change as proline acts as an osmolyte. Proline chelates metals and is thereby playing a role as an antioxidant and signalling molecule (Fahramand et al 2014).

6. Rice breeding for adaptation to drought-prone sites

Drought tolerance encompasses action and changes in multiple morphological, physio-biochemical and molecular traits. To improve the drought adaptation in rice, we have to focus on how to maintain the water content in the plant tissues, how to keep normal plant function under water stress and how to improve the ability of the plant to recover from drought effects and to thereafter give a high yield.

6.1 Phenotypic selection

Recent research suggests grain yield to be used as a direct selection criterion under drought stress (Kumar et al. 2008; Verulkar et al. 2010) instead of indirect selection based on secondary traits (Jongdee et al. 2002, Pantuwan et al. 2002; Price and Courtois 1999, Fukai et al. 1995). However, as yield is a complex trait, there is a necessity for a genetic and physiological analysis of yield contributing traits and how they are affected by drought (Sellamuthu et al. 2015).

It has been discussed that grain yield is influenced by the moisture retention capacity of the plant which ensures effective evapotranspiration and photosynthesis and the translocation of produced dry matter to the grain (Jain et al. 2013).

Secondary traits like deep, thick, coarse and highly branched roots as well as higher root to shoot ratio are reported as constituents of rice drought adaptation (Blum 2011; Gowda et al. 2011). In addition, lateral root production in response to varying soil water content has been demonstrated as an important trait in maintaining dry matter production and grain yield (Niones et al. 2015).

Traits such as number of leaves, leaf area, leaf angle, leaf rolling plasticity, leaf water potential, canopy temperature, and especially flag leaf traits such as higher flag leaf area and relative dry weight of the flag leaf, leaf glaucousness, higher chlorophyll and lower malondialdehyde content and late senescence are positively associated to yield under drought (Biswal and Kohli 2013, Wei et al. 2014). In addition, drought resistant lines have shown higher leaf water content and less H_2O_2 which allowed stomatal regulation and photosynthetic performance (Siddiqui et al. 2014).

6.2 Molecular tools

Rice is a model crop among cereals with a genome size estimated between 389Mb (IRGSP, 2005) and 430Mb (Eckardt 2000). It was the first sequenced food crop (Swamy and Kumar 2013). The sequence information and availability of molecular markers have made it possible to speed up breeding processes in rice (Collard and Mackill. 2008). Genomic studies have identified more than 20000 SSR markers and over a million of SNPs and InDels (McCouch et al. 2012).

Drought adaptation has been characterized as a complex strategy governed by many small-effect loci under strong genetic control but also strongly influenced by environmental factors (Fukao and Xiong 2013). Numerous loci affecting drought adaptation have been analyzed but few were found useful for marker-assisted selection (Yue et al. 2006). In fact, most of the QTLs were inconsistent across different environments and/or were not associated with grain yield even though they may be associated with secondary traits (Dixit et al. 2014). Possible linkage with negative effect loci has been proposed as the cause of this inconsistency (Dixit et al. 2012).

However, drought adaptation QTLs, such as qTLRN-12 and qLLRN-12 both mapped on chromosome 12, have been found to be associated to lateral root plasticity and dry matter production at seedling and vegetative phases, repectively (Niones et al. 2015). Sellamuthu et al. (2015) identified the QTLs qYLD4.1, qYLD4.2, qYLD6.3, and qYLD12 which are linked to grain yield under drought stress during reproduction stage. The QTL qPHT5, associated with plant height, was also found to collocate with peduncle length, panicle length and panicle exsertion, traits involved in drought adaptation (Sellamuthu et al. 2015). Another QTL associated with increased harvest index, biomass yield, plant height and early flowering has also been mapped on chromosome 12 (Bernier et al. 2007).

Genome-scale analyses showed that dehydration and ABA accumulation resulted in overexpression or down regulation of specific genes connected to the control of photosynthesis and carbohydrate metabolism as well as to signal transduction and survival during stress conditions (Degenkolbe et al. 2009; Lenka et al. 2011). Thus, drought responsive genes may directly react with enhanced osmotolerance and protection of plants by preventing cell dehydration. These direct genes encode late embryogenesis proteins, osmoprotectants and detoxification enzymes. Drought inducible genes may also indirectly intervene in signal transduction and gene expression regulation (Lata et al. 2015), including transcription factors and protein kinase.

Some mitogen-activated protein kinase family genes like the DSM1 gene (Ning et al. 2010, Xiong and Yang 2003) and transcription factors like OsSKIPa (Hou et al. 2009) promote drought tolerance through increasing ROS scavenging capability. A drought and salt tolerance gene (DST) encoding a C2H2 zinc finger protein inhibits stomatal closure through activation of H_2O_2 homeostasis gene expression (Gao et al. 2011). However, other genes like OsMADS26 enhance drought tolerance and tolerance to other stresses by negatively regulating stress-resistance genes (Khong et al. 2015).

7. Current study

7.1 Problem description and rationale

Drought frequency and intensity are predicted to increase in the near future due to climate change (Wassmann et al. 2009, Turral et al. 2011). Furthermore, competition for water between rice and other crops and urbanization activities are predicted to worsen water scarcity in agricultural production (Sinclair 2010). Additionally, the world's population growth will result in increased water demand and food production. In front of these challenges improved yield stability under drought and enhanced water use efficiency should be targeted in all efforts aimed at improving agricultural production.

Rice is among the most widely consumed crops in the world, yet the most vulnerable to drought. Decreasing water availability for agriculture threatens the productivity of irrigated rice ecosystem. Besides rice yield, quality of rice is affected by limited water availability. Thus, studies on how to improve drought adaptation of rice are becoming increasingly important (Serraj et al. 2011, Boote et al. 2011). Nevertheless, the unpredictability of drought occurrence and the complexity of involved mechanisms, a strong genotype × environment interaction and the difficulty of not having an effective drought screening method hinder the development of drought resistant cultivars (Verulkar et al. 2010, Serraj et al. 2009).

The strong genotype × environment interaction calls for specific genotypes and appropriate water management practices in a specific environment. We also have to consider the interaction between the different environment factors that may greatly influence rice productivity. Water and temperature are reported as important factors that affect rice production and quality. With the increasing trend of water shortage and rising temperature, it is imperative to consider combinational effects of these factors. So far, only few researches reported on the combined impact of drought and temperature on rice yield and/or quality.

Rationale

In Rwanda, rice is mostly produced in lowland irrigated schemes. However, insufficient water supply is one of the production constraints (RAB 2013). For example, in Bugarama which has the biggest rice production scheme, fights for water used to be a big issue until water user organizations were formed to take the responsibility of distributing water among the different zones. Thus, time to time, there are cuts of irrigation water in the different zones. Irrigation water needs to be supplemented by rainfall for a higher production (Water users' organization, personal communication). Nevertheless, no research on drought tolerance of rice in the Rwanda environment has been conducted. Yet, the present climate scenario predicts more frequent dry spells even during rainy seasons and a drastic increase in temperature.

With the irregular availability of irrigation water, cultivars that adapt to water regime fluctuations in the Rwandan climate need to be identified and/or improved for drought adaptation, high yield and good quality.

This study was designed to evaluate the responses of rice cultivars to different drought patterns and contrasting temperatures. Field trials will be conducted in two locations with different temperatures. To minimize the effect of other environmental factors, similar experiments will also be performed in two different growth chambers with different temperature sets. In both cases, water stress will be applied at different growth stages of rice.

7.2 Goal and objectives

General objective

This study aims at improved understanding of mechanisms related to drought resistance in rice cultivars grown in Rwanda and options to breed for drought tolerant cultivars for Rwanda under contrasting temperature.

Specific objectives

1. Evaluate the effect of drought pattern and drought intensity on growth, phenology and grain yield of rice cultivars grown in Rwanda
2. Determine the grain quality responses of rice to drought
3. Estimate the interaction effect of drought and temperature on rice yield and quality

7.3 Hypotheses

1. Repeated droughts have different effects than single drought events
2. There is a genetic variation for drought tolerance in rice cultivars grown in Rwanda
3. There is a significant drought x temperature effect on yield and quality of rice

7.4 Interest of the study

We expect that the results from this study will contribute to the understanding of drought tolerance mechanisms. Combinational effects of drought and temperature on rice quality will be elucidated. In addition, adaptation traits which can be used for cultivar improvement to cope with future climate change in Rwanda will be identified among available resources.

Moreover, upon the results of this study an irrigation pattern that efficiently uses available water while preserving rice yield and quality will be proposed.

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