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Review

The effects of drought on rice cultivation in sub-Saharan Africa and its mitigation: A review

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Drought is the primary cause of yield loss in agriculture throughout the world, and is currently the most common reason for global food shortages. Three-quarter of the most severe droughts in the last ten years have been in Africa, the continent which already has the lowest level of crop production and drought adaptive capacity. The increased incidences of drought and erratic rainfall have thrown small holder farmers in Africa into deep poverty, hunger and malnutrition. In this paper, the drought situation in sub-Saharan Africa and its impact on rice production was reviewed. Rice is particularly vulnerable to droughts as it has higher water requirement as compared to other crops. The review has also highlighted physiological and molecular plant responses to drought, with special focus on effects of drought stress on rice grain yield and other related-traits. With climate change predicted to exacerbate the problem of water security in Africa, it is imperative that we develop robust, well-planned and informed strategies to mitigate against drought. Various drought mitigation strategies including breeding for drought tolerance and water harvesting and conservation techniques are also outlined. In order to adapt to drought, there is need for a broad based approach that includes development of appropriate policies, putting in place necessary water related investments and institutions as well as capacity building at various levels.

Key words: Drought, tolerance, rice, sub-Saharan Africa, quantitative trait loci (QTL), mitigation, adaptation.

INTRODUCTION

Drought is inadequacy of water availability including periods without significant rainfall, causing a reduction in available water, thereby affecting crop growth. It can also occur when atmospheric conditions cause continuous loss of water by transpiration or evaporation (Singh et al., 2012), also indicated as a period of dry weather that is injurious to crops. In this context, drought is related to

changes in soil and meteorological conditions and not with plant and tissue hydration (Lipiec et al., 2013). Drought is defined as a situation that lowers plant water potential and turgor to the extent that plants face difficulties in executing normal physiological functions (Lisar et al., 2012). Whatever the definition given to drought, it remains perhaps the most serious natural

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hazard, affecting a larger proportion of the human population than any other hazard. It is the most significant environmental constraint for rice production in sub-Saharan Africa (SSA) (Reynolds et al., 2015). Its severity mainly depends on the level of moisture deficiency and the duration.

The challenge of drought is even greater for crops such as rice when compared with other crops such as maize and wheat, as it has relatively higher water needs (Todaka et al., 2015). Rice is sensitive to deficit in soil water content because rice cultivars have been historically grown under flood irrigation conditions where the soil matric potential is zero. About 3,000 to 5,000 L of water is required to produce 1 kg of rice seed, with less than half of that amount needed to produce 1 kg of seed in other crops such as maize or wheat (Bouman et al. 2002). Moreover, as compared to several other field crops, rice has relatively weak resistance to drought and its production systems is more vulnerable to drought than other cropping systems (O'Toole, 2004). In Africa, drought has adversely affected agriculture in different parts of the continent, with production of rice declining in many parts of West Africa due to increasing water stress (Bates and Kundzewicz, 2008). Drought has had significant negative effect on the livelihood of rainfed lowland rice farmers. The increased occurrence of prolonged droughts in SSA is a worrying trend as the region is highly dependent on rainfed agriculture. In order to enhance sustainable crop production in the face of drought and the constantly changing climatic conditions around the world, there is need for constant efforts to adapt our crops and production systems to the existing and emerging environmental challenges. In this review, the challenge of drought and specifically how it impacts rice production in SSA was discussed. Measures that can be undertaken to mitigate the effects of drought are also highlighted.

DROUGHT SITUATION IN AFRICA

The greatest challenges to agricultural production and food security in Africa is drought and climate change. Agriculture in Africa is mainly dependent on rainfall, with only about 5% of Africa's total cultivated land being under irrigation (You, 2008), meaning the region is highly vulnerable to drought. In some sort of fate, drought which continues to degrade some of the most agriculturally productive environments, is predicted to most severely affect the most vulnerable populations particularly those in SSA (FAO/PAR 2011). The recurring droughts in Africa are negatively impacting the livelihoods of a huge proportion of the population, with about 25% of the population facing serious water scarcity (Jarvis et al., 2009). Drought and climate variability are leading to the emergence of novel ecosystems where various plant populations are unable to persist. The proportion of arid and semi-arid areas continues to increase and it is

projected that by 2080, ASAL areas in Africa will increase by 6 to 8% (Jarvis et al., 2009). The continued increase in ASAL areas and the emergence of novel ecosystems could render large sections of land unproductive thereby seriously impacting agricultural production in Africa.

Perhaps, the greatest factor contributing to droughts is the rapidly growing human population, with the latest World Bank projections indicating that by 2060, about 2.8 billion people will be found on the continent (Canning et al., 2015). This increase in population puts enormous pressure on the available resources. It will for example lead to opening up of agricultural lands and other productive ecosystems for human settlement, thus leading to loss of valuable biodiversity. Loss of these genetic resources will reduce the diversity of plant responses to biotic and abiotic stresses thereby reducing the resilience and sustainability of agricultural production systems.

Three-quarters of the most severe droughts in the last ten years have been in Africa, the continent which already has the lowest level of crop production. Moreover, this region has the lowest drought adaptive capacity and among the highest levels of poverty, with about 48% of the total population living on less than \$1.25 a day (Ravallion et al., 2012). This means that this segment of the human population lacks not only the technical capacity to deal with drought but their financial means to address these challenges is also severely limited. Based on this sad reality and predictions of climate change models, the drought situation in Africa does not look promising. The challenge ahead is hugely enormous but with the concerted efforts of all stakeholders, it will be manageable. Successful fighting of droughts is doable.

RICE PRODUCTION AND CONSUMPTION IN AFRICA

Rice is cultivated under a broad range of environmental conditions in terms of topography, soil type, water regime (various degrees and duration of drought) and climatic factors (Khush, 1996). The persistent droughts in SSA have negatively impacted agricultural production systems, with rice production being among the worst hit systems since the crop is more sensitive to droughts than other crops. The situation is particularly worse in SSA where rice is largely grown under rainfed conditions that rely solely on precipitation, making it vulnerable to droughts. Due to this sensitivity, rice yields reduce significantly even under mild drought (Guan et al., 2010). Moreover, rice varieties planted in Africa have only relatively few adaptations to water-limited conditions and are extremely sensitive to drought, thereby worsening the situation. In Africa, the ecosystems under rice cultivation range from rainfed upland (40% of total area), rainfed (38%),irrigated lowland (12%), water/floating (6%) to mangrove swamps (4%). Upland

and lowland rice production which constitute about 80% of the total rice production area in Africa are projected to have the greatest vulnerability to drought (Bimpong et al., 2011a).

Worldwide, more than 3.5 billion people depend on rice for more than 20% of their daily calorie intake (Ricepedia, 2011; Maclean et al., 2013). Rice production is becoming increasingly popular in SSA, especially with the recent release and promotion of new, popular varieties of NERICA (New Rice for Africa) by the Africa Rice Center (formerly known as WARDA). An annual increase in rice consumption of about 6% has been reported (Bernier et al., 2008). With the high urbanization and increase in purchasing power, West Africa is experiencing a significant increase in rice consumption in urban and rural areas.

This increased consumption has also been followed by a concomitant increase in rice production in most African countries. The last 3 decades have recorded a dramatic increase in rice production in Africa, with the production more than doubling in the period between 1982 and 2012 (FAO, 2013). However, despite the increased paddy rice production and the huge potential for rice production in terms of available land area that exists in the sub-region, massive rice imports into SSA are still recorded (Nasrin et al., 2015; AfricaRice, 2009, 2011; Futakuchi et al., 2011). Rice production in West Africa covers only about 60% of the population's needs. This has resulted in increasing rice imports from Asia. With the current trends, according to FAO estimates (Staatz and Dembele 2007). rice imports in West Africa will increase from 6.4 Mt in 2008 to 10.1 Mt in 2020. It is imperative that measures are put in place to boost rice productivity in SSA. These include use of adapted high yielding rice varieties, improved husbandry practices and adoption of various drought and climate change mitigation strategies. Local rice production, processing and marketing will permit African citizens to have access to affordable food. This will contribute to extreme poverty reduction and elimination of food insecurity within the continent, since relying on imports is no longer a sustainable strategy.

EFFECT OF DROUGHT ON YIELD AND PHYSIOLOGY OF RICE

The yield potential of a cultivar under favourable conditions is important in determining the yielding ability under water stress. Drought index which provides a measure of drought related yield loss is an important criterion that has been used for screening of drought tolerance genotypes. Evaluation of eighteen rice genotypes showed reduction in panicle number (72%) and grain yield (12%) (Swain et al., 2010). Singh et al. (2010) evaluated six generations (P1, P2, B1, B2, F1 and F) of six crosses of rice under drought and irrigated conditions and observed a reduction in several characters

including grain yield under drought conditions. The intensity of drought effect on various traits varied with the genetic materials. The study indicated strong relationship between grain yield under drought, leaf rolling and leaf tip burning for moderately tolerant introgression lines and also between grain yield and leaf rolling for tolerant *Oryza glaberrima*. Similar findings were reported by Ndjiondjop et al. (2012). This explains the role of leaf rolling and leaf tip burning potential of a genotype on its development.

Yield decreases are a result of drought effect on several morphological and agronomic traits, including plant height, tillering ability and leaf area (Bocco et al., 2012). Others include various root traits (length, thickness and depth), spikelet fertility, panicle exertion, leaf greenness (SPAD), leaf temperature, time to flowering, time to maturity, leaf tip drying and leaf rolling (Ndjiondjop et al., 2010a). Ndjiondjop et al. (2010a) observed 16.9, 13.7, 6.7, 14.1 and 26.7% reduction in the number of tillers, plant height, number of leaves, leaf width and grain yield, respectively. Drought-related reduction in yield and yield components can be attributed to stomatal closure in response to low soil water content with a resultant decrease in carbon dioxide intake and subsequently a reduction in photosynthesis (Chaves, 1991; Cornic, 2000; Flexas et al., 2004). In summary, drought reduces prevailing plant growth development, leading to hampered flower production and grain filling and thus smaller and fewer grains. A reduction in grain filling occurs due to a reduction in the assimilate partitioning and activities of sucrose and starch synthesis enzymes.

Garrity and O'Toole (1995) observed an increase in leaf temperature by 9°C due to drought and significant correlation between midday leaf temperature on the day of flowering and both grain yield and spikelet fertility. This increase in leaf temperature under drought is a result of lower transpiration rate caused by a reduction (closure) in stomatal aperture. Leaf temperature is, therefore, a very sensitive indicator of plant water status and is associated with leaf stomatal conductance (Jones, 1992). Significant variations among rice cultivars in leaf temperature increase under drought are reported. Cultivars with high drought-avoidance potential consistently remained coolest under drought (Garrity and O'Toole, 1995).

Under drought, flowering time (start, 50 and 100% flowering) and time to maturity are delayed as a result of water shortage. The length of the delays is related to the type of drought, the temperature regimes, the period of occurrence of drought and the rice genotype (Bocco et al., 2012; Wopereis et al., 1996). Spikelet fertility is also influenced by drought. The production of viable pollen, panicle exertion, pollen shed and germination and embryo development, which are involved in fertilization and initiation of grain filling, are all negatively affected by drought. This causes reduced spikelet fertility and dry weight of fertile spikelets thereby leading to grain yield loss (Liu et al., 2006; Rang et al., 2011).

DROUGHT RESISTANCE MECHANISMS

General plant responses to drought

Drought resistance mechanisms include drought escape via a short life cycle or developmental plasticity, drought avoidance via enhanced water uptake and reduced water loss, drought tolerance via osmotic adjustment and antioxidant capacity.

Escape

The first way for the plant to avoid drought is dodging. It is an adaptation to the environment allowing the plants to avoid the critical periods for their good development. Farmers use this plant strategy to place the crop cycle conditions favourable. when are For example, development of varieties with a shorter development cycle in order to avoid the most stressful periods of the year for plants or to shift the date of sowing and/or select varieties to prevent water deficits. This is an important mechanism for avoiding terminal drought. The shortening of growth cycle has improved the yield of many varieties in many annual crop species (Fukai et al., 1999; Turner et al., 2001). Drought evasion can be achieved through two mechanisms (i) completing the crop cycle before the occurrence of a terminal drought; (ii) Avoiding coincidence between periods of low water availability and critical or sensitive phases of crop growth where water is critically required such as flowering and grain filling.

Avoidance

The second way to avoid drought is the ability of the plant to maintain a satisfactory water state. The reduction in soil moisture may have led to lower water content in the leaves causing guard cells to lose turgor pressure and hence the size of stomatal pores are reduced (Tezara et al., 2002), causing stomatal closure (Singh et al., 2012). Avoidance allows plants to limit the effects of stress through adaptations such as wilting or leaf rolling. Drought avoidance consists of mechanisms that reduce water loss from plants due to stomatal control of transpiration, and also maintain water uptake through an extensive and prolific root system.

Drought tolerance

From a physiological point of view, drought tolerance is the ability of the plant to survive and grow under drought. From an agronomic point of view, a plant is tolerant when it is able to obtain a higher yield than sensitive plants. Tolerance allows maintenance of the essential cellular functions for survival, due to specific and targeted responses despite the deficiency of water (Passioura, 1996; Tardieu, 2003, 2005). Keeping of turgor in water deficiency can delay stomatal closure, maintain chloroplastic volume and reduce leaf wilting which confers to the plant a better tolerance to internal water deficit. This tolerance to internal water deficit in turn allows a prolonged operation of photosynthesis. The carbon products can then be used for both osmotic adjustment and root growth. Due to the unpredictability of water stress, tolerance is the most effective strategy in severe and prolonged stress situations.

Rice responses to drought stress

Rice responds and adapts to drought stress by induction of various morphological, physiological and molecular modifications, with these modifications being made according to the developmental stage (Figure 1).

Morphological and phenological modifications

In majority of the plant species, water stress is linked to changes in leaf anatomy and ultrastructure. The first and foremost effect of drought is impaired germination and poor stand establishment (Harris et al., 2002). Cell growth is considered one of the most drought sensitive physiological processes due to reduction in turgor pressure. Growth is the result of daughter-cell production by meristematic cell divisions and subsequent massive expansion of the young cells (Anjum et al., 2011). Under drought stress, plants reduce the number of leaves per plant and individual leaf size as well as leaf longevity by decreasing the soil's water potential. Leaf area expansion depends on leaf turgor, temperature and assimilates supply for growth.

Rice leaf color plays an important role in leaf photosynthesis. The reduction in photosynthetic rate in rice as a result of drought is well documented (Lauteri et al., 2014). Ndjiondjop et al. (2010a) observed an increase in leaf greenness value under drought when compared full irrigation conditions. However. with observations contradict those of Zinolabedin et al. (2008) who reported reduced uptake of water and nutrients by plant root systems causing reduced chlorophyll concentration in plant leaves and therefore the yellowing of the leaves. Under full irrigation conditions, rice leaves normally do not roll and they do not show tip drying symptoms either. But under drought, the first response of the plant is to roll its leaves (Sié et al., 2008) to maintain a favourable internal water status. Therefore, rice genotypes with high leaf water maintenance (high leaf rolling ability) are able to out yield those with lower ability(Fukai and Cooper, 2002). This explains the relationship between leaf rolling and grain yield under drought. Leaf tip drying is also a good indicator of drought

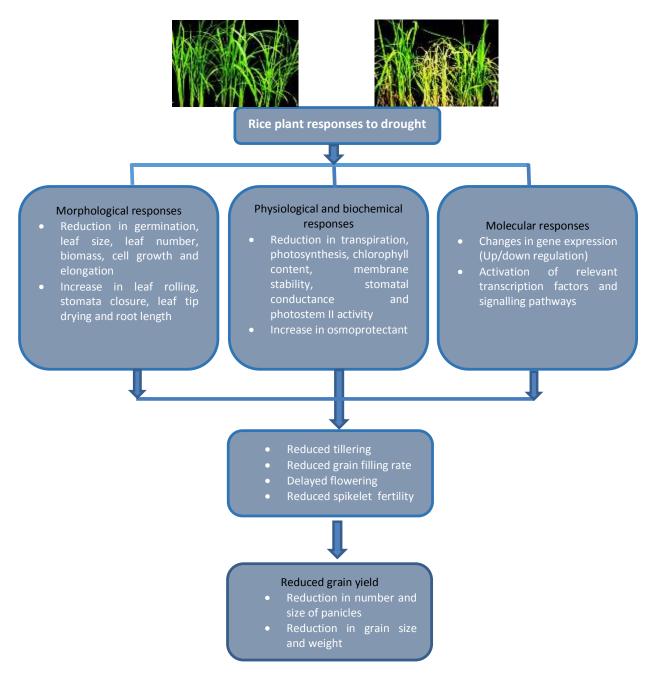


Figure 1. Schematic description of rice plant responses under drought stress.

level (Henderson et al., 1995) and just like leaf rolling, is regarded as a drought avoidance mechanism. The severity of leaf rolling and leaf tip burning is a function of the severity of drought especially on very susceptible rice genotypes. Leaf rolling is reversible but leaf tip drying is irreversible under drought.

Physiological responses

In response to water deficit, plants are able to establish a

series of physiological responses that allow them to act on their own water state in order to adapt to environmental conditions. Some of the physiological responses to drought include:

Decrease in leaf size: Generally, growth decrease is one of the first drought manifestations in rice plant. Drought is manifested in the plant by a slowing down of the initiation of the new aerial organs (leaves and stems) and a reduction in the pre-existing organs (Davies and Zhang, 1991; Boyer and Kramer, 1995; Chaves et al., 2002).

These modifications, will in the long term limit the surfaces through which loss of water by transpiration can take place. Thus growth reduction is not a passive consequence of the lack of water in the cells, but rather a controlled and programmed response of the plant, the result of which is to anticipate the events of drought stress. Studies have shown that these modifications result from a decrease in the rate of division of plant cells (Granier et al., 2000) and a modification of the physicochemical properties of the cell walls which become more rigid thereby inhibiting their growth (Cosgrove, 2005).

Root elongation: Contrary to aerial organs which are reduced under the effect of water stress, these conditions promote the development of the root system. Enhancing the development of the root system traits such as root length allows the plants to access deep ground water resources. Plant production is the function of water use (WU), water use efficiency (WUE) and harvest index (HI). It is therefore vital to understand its effect during defined developmental stage in order to design effective selection methods to improve plant production under dry environment. WUE provides the means of efficient use of water and serves as a breeding target in water saving agriculture. Traditionally, it is defined as the ratio of dry matter produced per unit of water transpired, and constitutes one of the key determinants in controlling plant production. It is also referred to as "transpiration efficiency" and it is estimated from the measures of leaf gas exchange or by using carbon isotope discrimination. Higher WUE in turn lowers photosynthetic rate due to reduced rate of transpiration and consequently slows the rate of plant growth (Condon et al., 2004). Currently, agricultural sectors are slowly moving towards use of genotypes with increased WUE and improved agronomic practices (Pereira et al., 2006).

Leaf water potential (LWP) is a measure of whole plant water status and has long been recognized as an indicator of dehydration avoidance (Pantuwan et al., 2002a). When water deficit in leaf goes beyond a certain threshold level, the stomata closes as a mechanism of lowering the rate of transpiration. Stomatas help to regulate water loss when the tissue water status becomes too low, thereby minimizing the severity of water deficiency in plants. Thus, higher LWP is maintained by stomatal closure and varietal differences in stomatal response to water status have been reported (Jongdee et al., 1998). Genotypes possessing stay-green trait maintain high photosynthetic activity and often protects the plants from premature senescence during the onset of stress. It is reported that stay-green plants assimilate more nitrogen and retain high level of nitrogen content in the leaf, thereby retaining photosynthetic capacity under water limited conditions (Borrell et al., 2001).

Molecular responses to drought stress: As soon as the

stress is detected by plant receptors, a coordinated series of cellular responses is established. In fact, the physiological and morphological reactions are based on these coordinated cellular responses which induce the expression of a large number of genes. In rice, more than 5,000 genes are up-regulated and more than 6,000 are down-regulated by drought stress (Maruyama et al., 2014). Wang et al. (2011) conducted genome-wide gene expression profiling and detected 5,284 genes which were differentially expressed under drought stress, among which were under temporal and spatial regulation. Recently, it has been shown that a CO-like gene, Ghd2 (grain number, plant height, and heading date2), which can increase the yield potential under normal growth condition just like its homologue Ghd7, is involved in the regulation of leaf senescence and drought resistance. This gene is down regulated under drought conditions. Overexpression of Ghd2 resulted in significantly reduced drought resistance, while its knockout mutant showed the opposite phenotype (Liu et al., 2016).

Regulatory transcription factors involved in the response of drought stress have been extensively investigated. This allowed the discovery of two important signaling pathways of transcriptional networks under abiotic stress conditions. One involves a hormone called abscissic acid (ABA) produced when a plant undergoes water stress. Abscissic acid will initiate, at the cellular level, a cascade of signaling involving transcription factors named ABA Responsive Element Binding (AREB) (Abe et al., 1997; Uno et al., 2000). The second pathway is independent of this hormone, and involves other transcription factors, drought responsive element binding (DREB) (Yamaguchi-Shinozaki and Shinozaki, 2005). Many signaling details of ABA have been well elucidated and reviewed (Jiang and Zhang, 2002; Salazar et al., 2015; Sah et al., 2016). ABA is an important messenger that acts as the signaling mediator for regulating the adaptive response of plants to different environmental stress conditions (Sah et al., 2016).

DETECTION OF QUANTITATIVE TRAIT LOCI (QTLS) FOR USEFUL DROUGHT TOLERANCE TRAITS

The recent development of high-density linkage maps has provided the tools for dissecting the genetic basis underlying complex traits such as drought resistance into individual components (Yue et al., 2006). Although, complex traits such as yield are routinely dissected into their component traits namely grain size, test weight and number of productive tillers per plant in rice, sometimes resulting in the development of functional markers, the same is not true in drought stress research (Prakash et al., 2016). Earlier molecular genetic analyses identified several QTLs of secondary traits important to drought tolerance such as root architecture, leaf water status, panicle water potential, osmotic adjustment and relative

water content.

Genes/QTL underlying drought secondary traits

In rice, a number of physio-morphological putative traits have been suggested to confer drought tolerance (Deivanai et al., 2010). Root system architecture plays a primary constitutive role in acquisition of water and nutrient from the soil and maintains appropriate plant water status (Nguyen et al., 1997; Lafitte et al., 2001; Kato et al., 2006). Various root architecture traits among them, rooting depth, root density, root thickness and root distribution pattern (Pantuwan et al., 1996; Wade et al., 1996; Lilley and Fukai, 1994; Fukai and Cooper, 1995) plant water uptake, thereby dehydration. QTLs for morphology and the index of root penetration have been identified in several rice populations (Champoux et al., 1995; Ray et al., 1996; Zhang et al., 2001; Kijoji et al., 2014; Henry et al., 2014). Liu et al. (2009) identified and cloned a gene named OsDHODH1 which encodes a putative cytosolic dehydrogenase (DHODH) dihydroorotate in Overexpression of the OsDHODH1 gene in rice increased the DHODH activity and enhanced plant tolerance to salt and drought stresses.

Deep rooting is a very important trait for plants drought avoidance mechanism and it is usually represented by the ratio of deep rooting (RDR). The root growth angle (RGA) is another important trait in drought tolerance. which determines the direction of root elongation in the soil and affects the area in which roots capture water and nutrients. Courtois et al. (2009) conducted a metaanalysis of QTLs in 12 populations and detected 675 root trait QTLs. Although, many QTLs for root trait have been mapped, only 5 major QTLs for deep rooting have been reported (Kitomi et al., 2015; Uga et al., 2015, 2011) and only the DRO1 gene has been cloned (Uga et al. 2013a). DRO1 has been detected on chromosome 9 in recombinant inbred lines (IK-RILs) derived from a cross between the shallow-rooting cultivar IR64 and the deeprooting cultivar Kinandang Patong (Uga et al., 2011). This QTL has subsequently been cloned. It has been shown that the functional allele of DRO1 introduced from Kinandang Patong (Dro1-NIL) had a significantly larger RGA and higher grain yield than the parental variety IR64, which had a non-functional allele of DRO1. The DRO1 is the first gene associated with root system architecture (RSA) that has been shown to improve the ability to avoid drought. Another major QTL for RGA named DRO2 has been identified on chromosome 4 in three F2 populations derived from crosses between each of three shallow-rooting cultivars (ARC5955, Pinulupot1 and Tupa729) and Kinandang Patong (Uga et al., 2013b).

A new QTL for RGA was recently identified on the long arm of chromosome 7. This QTL named DRO3 is involved in the DRO1 genetic pathway as its effect on

RGA in plants have been detected only with a functional DRO1 allele (Uga et al., 2015). The Phosphorus Uptake 1 (PUP1) is a QTL that contributes to phosphorus (P) uptake in low P content soils. The gene underlying the QTL, later termed Phosphorus-Starvation Tolerance 1 (PSTOL1), was cloned and appeared to encode a receptor-like cytoplasmic kinase (Gamuyao et al., 2012). Recently, a novel gene, OsAHL1, was identified through genome-wide profiling and analysis of mRNAs. Analysis showed that OsAHL1 has both drought avoidance and drought tolerance mechanisms and when overexpressed. it enhances multiple stress tolerances in rice plants during both seedling and panicle development stages. Functional studies revealed that OsAHL1 regulates root development under drought condition to enhance drought avoidance, participates in oxidative stress response and also regulates the chlorophyll content in rice leaves (Zhou et al., 2016). Two QTLs for the root gravitropic response, and 4 QTLs for seminal root morphology (SRM) have been reported (Norton and Price, 2009). These 2 traits are well known to be important components of RGA. The QTL designed, quantitative trait locus for Soil Surface (qSOR1) has been fine-mapped on Rooting 1 chromosome 7, using 124 recombinant inbred lines (RILs) derived from a cross between Gemdjah Beton, an Indonesian lowland rice cultivar with soil-surface roots, and Sasanishiki, a Japanese lowland rice cultivar without soil-surface roots (Uga et al., 2012).

Liu et al. (2005) identified 2 and 6 main effect QTLs for canopy temperature and leaf water potential respectively in RILs (F9) from a cross between Zhenshan97B and IRAT109. Recently, 6 QTLs for RDR were identified using 1 019 883 single-nucleotide polymorphisms (SNPs) (Lou et al., 2015). Prince et al. (2015) identified two QTLs for canopy temperature, 1 QTL for leaf drying and 1 for SPAD under managed stress and in a rainfed target drought stress environment, respectively. introduction of traits that contribute to drought avoidance or tolerance should improve resistance of rice to drought and this strategy therefore has considerable potential to increase rice production in areas prone to drought (Fukai and Cooper, 1995; Nguyen et al., 1997). For rice, considerable research effort has been devoted to mapping QTL for osmotic adjustment (Lilley et al., 1996), but only a few loci with major effects have been identified.

QTL for yield and yield related-traits under drought

Several studies using different mapping populations have identified QTLs for traits related to drought tolerance (Khowaja and Price, 2008). Bernier et al. (2007) identified large-effect QTLs for grain yield under drought stress. If confirmed, these identified QTLs have to be fine mapped for use in breeding programs. A drought experiment conducted by Lanceras et al. (2004) using 154 doubled haploid lines derived from a cross between two rice

cultivars, CT9993-510 and IR62266-42, allowed identification of 77 QTLs for grain yield and its components under various drought intensities. Among them were 7 for grain yield, 8 for biological yield, 6 for harvest index, 5 for days to flowering, 10 for total spikelet number, 7 for percent spikelet sterility, 23 for panicle number and 11 for plant height. A recombinant inbred population obtained from a cross between high-yielding lowland rice IR64 and Cabacu was used to identify 10 QTLs for grain yield and component traits under reproductive-stage drought stress (Trijatmiko et al., 2014). The qDTY12.1 is the first reported large-effect QTL for grain yield under severe upland reproductivestage drought conditions and was identified in a population of 436 F3-derived lines from a cross between Vandana and Way Rarem (Bernier et al., 2007). Two other large-effect QTLs, qDTY2.1 and qDTY3.1, well known to affect grain yield under lowland reproductivestage drought, were identified in a back cross inbred line (BIL) population derived from a cross between Swarna and Apo. Both QTLs showed a very high effect (R2 = 16.3 and 30.7%) under severe lowland reproductivestage drought. These QTLs also showed pleiotropic effects on other traits such as DTF and PHT (Venuprasad et al., 2009). Another QTL, qDTY6.1 had strong effect on yield in aerobic drought stress conditions (Venuprasad et al., 2012b).

A large-effect QTL qDTY1.1 has been identified as having an effect on grain yield under severe lowland reproductive-stage drought across F3-derived populations developed from a cross between N22 and Swarma, N22 and IR64 and N22 and MTU1010 (Vikram et al., 2011). This QTL has also been reported in CT9993-5-10-1-M/IR62266- 42-6-2 and Apo/IR64 populations (Kumar et al., 2007; Venuprasad et al., 2012a).

In the same way, qDTY2.2, qDTY4.1, qDTY9.1 and qDTY10.1 were identified to have a large effect on grain yield in BIL population from a cross between Aday Sel and IR64 (Swamy et al., 2013). Table 1 presents a summary of large effect QTLs for grain yield reported in rice.

MITIGATION AGAINST DROUGHT

Mitigating drought and climate change requires robust, well-planned and informed strategies in order to enhance agricultural sustainability and ensure that human livelihood is not negatively affected. Improved rice technologies that help reduce losses from drought can play an important role in long-term drought mitigation.

Important scientific progress is being made in understanding the physiological mechanisms that impart tolerance to drought (Blum, 2005; Lafitte et al., 2006). Similarly, progress is being made in developing drought-tolerant rice germplasm through conventional breeding and the use of molecular tools (Korres et al., 2017). Improving the resilience of rice production systems to

climate change requires the development and dissemination of appropriate combinations of improved stress-tolerant rice germplasm, natural resource management strategies and creation of appropriate policy environments to help increase and stabilize yields in variable cultivation conditions.

Breeding for drought tolerance and adaptation

One of the main strategies in confronting drought is breeding for drought tolerance which helps to deliver adapted genotypes. These breeding efforts will require characterization and evaluation of diverse germplasm with the aim of identifying genotypes possessing traits that are important in enhancing drought tolerance. The replacement of diverse and adapted traditional rice varieties with genetically narrow based genotypes has significantly increased the vulnerability of the agricultural production systems. The use of a wide range of genetic resources is critical in the development of varieties that adapted to drought. Crop wild relatives are particularly useful sources of genes for adapting crops to drought. There exists a variety of physiological traits that are associated with drought tolerance. Some of these traits include root traits, early flowering, water use efficiency, amount of water transpired, transpiration efficiency, osmotic adjustment and stay green. Breeding for increased yields under drought tolerance will require proper understanding of the various traits that are associated with yield (Pandey et al., 2015). The exact trait to target in a breeding programme in order to obtain the best response in terms of drought tolerance may not always be clear to a breeder.

Africa Rice has been spearheading efforts aimed at delivering rice varieties that are tolerant to drought. This has involved screening of a wide range of genetic resources including indigenous Africa species such as O. glaberrima and Oryza barthii. A key goal of the breeding programme has been to develop a rice variety that can escape terminal drought that frequently occurs at the end of the wet season through its short growth duration. Short duration varieties are also preferred to avoid late season fungus diseases (Jones et al., 1997). Several upland interspecific O. sativa × O. glaberrima (NERICA) varieties were evaluated at AfricaRice and it was observed that they have potential for escaping drought due to their short growth duration. The capacity of NERICA varieties to maintain growth under mild drought, their survival under severe drought, recovery from drought and their water use efficiency need to be incorporated into breeding programs (Futakuchi et al., 2011).

Exploitation of drought tolerance traits in African rice in rice breeding

African rice is one of the two independently domesticated

Table 1. Large effect QTLs reported for grain yield under drought stress conditions.

QTL name	Chrom	Interval	Population	Ecosystem	R2	References	
qDTY1.1	1	RM11943-RM12091	N22/Swarna	Lowland	13	Vikram et al. (2011)	
qDTY1.1	1	RM11943-RM12091	N22/IR64	Lowland	17	Vikram et al. (2011)	
qDTY1.1	1	RM11943-RM12091	N22/MTU1010	Lowland	13	Vikram et al. (2011)	
qDTY1.1	1	RM486-RM472	Apo/IR64	Upland	58	Venuprasad et al. (2012a)	
qDTY1.2	1	RM259-RM315	Kali Aus/MTU1010	Upland	7	Sandhu et al. (2014)	
qDTY 1.3	1	RM488-RM315	Kali Aus /IR64	Upland	5	Verma et al. (2014)	
qDTY2.1	2	RM327-RM262	Apo/Swarna	Lowland	16	Venuprasad et al. (2009)	
qDTY2.2	2	RM236-RM279	Aday Sel./ IR64	Lowland	11	Swamy et al. (2013)	
qDTY2.2	2	RM236-RM555	Aday Sel./ IR64	Lowland	3	Swamy et al. (2013)	
qDTY2.2	2	RM236-RM555	Aday Sel./ IR64	Lowland	9	Swamy et al. (2013)	
qDTY2.2	2	RM211-RM263	Kali Aus/ MTU1010	Upland	6	Sandhu et al. (2014)	
qDTY2.2	2	RM211-233A	Kali Aus/ MTU1010	Lowland	16	Palanog et al. (2014)	
qDTY3.1	3	RM520-RM16030	Apo/Swarna	Lowland	31	Venuprasad et al. (2009)	
qDTY3.1	3	RM168-RM468	IR55419-04/TDK1	Lowland	8	Dixit et al. (2014)	
qDTY3.1	3	RM168-RM468	IR55419-04/TDK1	Upland	15	Dixit et al. (2014)	
qDTY 3.2	3	RM569-RM517	Aday Sel./ Sabitri	Lowland	23	Yadaw et al. (2013)	
qDTY 3.2	3	RM60-RM22	N22/Swarna	Lowland	19	Vikram et al. (2011)	
qDTY 3.2	3	id3000019-id3000946	Moroberekan/Swarna	Lowland	8	Dixit et al. (2014b)	
qDTY 3.2	3	id3000019-id3000946	Moroberekan /Swarna	Upland	19	Dixit et al. (2014b)	
qDTY 4.1	4	RM551-RM16368	Aday Sel./IR64	Lowland	11	Swamy et al. (2013)	
qDTY6.1	6	RM589-RM204	Vandana/IR72	Upland	40	Venuprasad et al. (2012b)	
qDTY6.1	6	RM589-RM204	Apo/IR72	Upland	63	Venuprasad et al. (2012b)	
qDTY6.1	6	RM586-RM217	IR55419-04/TDK1	Lowland	9	Dixit et al. (2014)	
qDTY6.1	6	RM586-RM217	IR55419-04/TDK1	Upland	36	Dixit et al. (2014)	
qDTY6.2	6	RM121-RM541	IR55419-04/TDK1	Lowland	9	Dixit et al. (2014)	
qDTY6.2	6	RM121-RM541	IR55419-04/TDK1	Upland	20	Dixit et al. (2014)	
qGY8.1	8	RM38-RM331	MASARB25 / Pusa Basmati; HKR47/ MAS26	Upland	34	Sandhu et al. (2014)	
qDTY10.1	10	MTU1010/N22	RM216-RM304	Lowland	5	Vikram et al. (2011)	
qDTY10.2	10	Aday Sed./IR64	RM269-G2155	Lowland	17	Swamy et al. (2013)	
qDTY11.1	11	id11002304-id11006765	Moroberekan- Swarna	Upland	25	Dixit et al. (2014b)	
qDTY12.1	12	RM28166-RM28199	IR74371-46-1-1 / Sabitri	Lowland	24	Mishra et al. (2013)	
qDTY12.1	12	RM28048 -RM511	Way Rarem/ Vandana	Upland	33	Bernier et al. (2007)	

rice species, with its distribution being limited to West Africa. Its genetic potential in terms of resistance to both biotic and abiotic stresses has been well documented and deployed in rice improvement (Wambugu et al., 2013). Its tolerance to drought is a particularly valuable trait during these periods that are characterized by increased occurrences of drought and erratic rainfall. Some alien introgression lines derived from an interspecific cross between *O. sativa* and *O. glaberrima* under drought conditions had higher yield than the parents (Bimpong et al., 2011b). This demonstrates the potential of transferring drought related traits from African rice to Asian rice. In this study, novel QTLs for drought related traits such as yield and yield components were identified with about 50% of the beneficial alleles being

contributed by African rice.

A total of 2000 African rice accessions conserved at AfricaRice genebank were evaluated by Shaibu et al. (2018) for drought tolerance in three locations in West Africa over a period of 3 years. Results of this screening showed that four *O. glaberrima* genotypes had significantly higher yields under both drought and rainfed conditions than the *O. glaberrima* check, CG14, which is considered a drought tolerant variety. Though, these genotypes were not significantly different from the *O. sativa* checks (Table 2), they will serve to widen the African rice genepool that can be used for breeding for drought tolerance. African rice has several drought avoidance mechanisms such as early flowering. It has also been reported to have thin leaves which easily roll

Table 2. Grain yield (g/m²) of selected *Oryza glaberrima* accessions and standard checks under drought, rainfed and control conditions during 2013-14 at three locations in West Africa.

	Drought			Rainfed			Control	
Entries	Ibadan	Ibadan	Ibadan	Badeggi	Cotonou	Ibadan	Ibadan	Cotonou
	DS 2013	DS 2013	DS 2014	DS 2014	WS 2014	WS 2014	WS 2014	WS 2014
No. of <i>O. glaberrima</i> genotypes evaluated	200	285	74	74	30	30	30	30
Selected <i>O. glaberrima</i> genotypes								
TOG 7400	-	236	236	25	83	270	399	368
TOG 6520	401	-	301	7	-	349	403	455
TOG 6519-A	393		226	5	72	303	286	308
TOG 7442-B	327	-	152	7	69	251	292	443
Checks								
O. glaberrima check								
CG 14	217	238	51	6	60	104	415	339
O. sativa check								
Apo	432	397	472	9	48	242	255	401
FARO 52	472	447	216	9	-	55	-	619
IR 77298-14-1-2-B-10	363	451	298	12	56	263	418	285
Trial mean	246	161	122	6	51	171	241	310
LSD _{0.05}	142	142	103	5	43	130	119	149
Heritability	0.87	0.75	0.71	0.69	0.70	0.85	0.90	0.84

Adapted from Shaibu et al. (2018).

during drought to retain water, in addition to having small diameter roots which easily extract water from the soil (Dingkuhn et al., 1999). The phenological responses of African rice during times of drought have been found to be superior to those of traditional and improved *O. sativa* cultivars (Dingkuhn et al., 1999). African rice has also been found to possess the capacity to close stomata earlier in response to drought as compared to *O. sativa* (Bimpong et al., 2011c).

Challenges in breeding for drought tolerance

In most rice breeding programs, grain yield as an important trait of interest is widely used as an index for adaptation to drought stress. But several researchers have reported inconsistency in yield production by rice genotypes across environments and years (Fukai and Cooper, 1995; Pantuwan et al., 2002a, b, c). A genotype performing well in one type of drought environment may not perform well in other environments (Pantuwan et al., 2002a, c). It is unclear whether promising materials selected under drought condition will yield well in full irrigation/wet-season condition. This explains the large genotype-by-environment (GxE) interactions and the low heritability of grain yield of rainfed lowland rice under drought and the uncertainty in the selection of drought resistant genotypes (Fukai and Cooper, 1995). To

accommodate the effects of GxE interactions and improve selection efficiency, a large number of multi-location trials over years in various drought intensity conditions could be a solution (Nyquist and Baker, 1991; Fukai and Cooper, 1995). Unfortunately, such evaluation processes are costly and time-demanding for making selections in the breeding program. Therefore, it has become necessary to identify more efficient breeding options based on the use of indirect selection methodology (Falconer, 1989).

Even though there is extensive evidence that selection under target stresses may accelerate breeding gains for stress environments (Atlin and Frey, 1990; Ceccarelli et al., 1992; Ud-Din et al., 1992; Bänziger et al., 1997), the difficulty of choosing appropriate selection environments, given a highly variable target environment, may limit the identification of superior genotypes. While breeding programs in high-income countries may resort to realtime GIS information for adequately weighting information from METs (Podlich et al., 1999), these opportunities rarely exist in low-income countries as there is a lack of both real-time GIS information and resources for conducting a large number of METs. Progress in improving drought resistance has been slow. This is partly due to the complexity of the drought environment, the number of different mechanisms of drought resistance exploited by rice and the interaction between the two as well as the genetic complexity of most traits.

Other drought mitigation strategies

In addition to crop improvement and selection of drought tolerant genotypes, other strategies for mitigating against long term impacts of drought include development of irrigation facilities and water harvesting structures such as dams. Development of water resources is an important area of protection against drought that is emphasized in SSA. The large-scale development of irrigation schemes that was a hallmark of the green revolution is limited now by high costs and increasing environmental concerns (Rosegrant et al., 2002). Moreover, the rationale of establishing new large scale irrigation schemes may be questioned as many such schemes have and continue to stall. The collapse of these schemes, many of which have been established in partnership with various development partners, brings to the fore critical issues such as feasibility sustainability of such projects. In some cases, the long term availability of water for these projects is usually not guaranteed. The technical and financial capacity to maintain these projects need to be explored before their establishment. However, there are still substantial opportunities to provide some protection from drought through small and minor irrigation schemes and through land-use approaches that generally enhance soil moisture and water retention (Shah, 2001; Moench, 2002). Public-sector support for further development, maintenance and rehabilitation of small and minor irrigation schemes could make them more effective in mitigating drought. Public-sector involvement, however, should be limited to the provision of technical assistance. while the actual management of these small-scale schemes is better left to local communities (Kerr et al., 2002). Hand dug shallow wells are another option for sourcing water resources particularly for small holder farmers.

Watershed-based approaches implemented in drought prone areas of India are providing opportunities to achieve long-term drought-proofing by improving overall moisture retention within watersheds (Rao, 2000). As already stated, one of the causes of drought in Africa is habitat destruction especially due to population pressure. Most habitats in many African countries are currently severely degraded and non-productive. Consequently, one of the ways to mitigate drought is through the rehabilitation of these degraded habitats through ecological restoration. Drought forecasting and timely provision of such advice to farmers is an important drought mitigation strategy that can help reduce the overall economic cost of drought. It also helps improve preparedness, thereby helping in managing the risk more effectively. Various indicators such as the Southern Oscillation Index (SOI) are routinely used to forecast drought in several countries (Wilhite, 2000; Meinke and Stone, 2005). Forecasting is especially important in assisting farmers make more informed decisions regarding the choice of crops and cropping practices.

CONCLUSION

Drought is one of the major climatic hazards even in the sub humid rice-growing areas of Asia and Africa. It is an event that reoccurs, affecting agriculture and the livelihoods of millions of farmers and agriculture laborers. The socio-economic impact of drought is enormous. It has huge economic costs, in terms of both actual economic losses during drought years and losses arising from foregone opportunities for economic gains. Drought contributes directly to an increase in the incidence and severity of poverty.

It is therefore critical that we establish effective strategies to mitigate the effects of drought in order to ensure agricultural productivity and environmental sustainability. Use of adapted genotypes and improvement in rice production technology are some of the components of an overall strategy for effective drought mitigation. Increased moisture availability to crops through water conservation and harvesting, and watershed development is an important component. Improvements in drought forecasting and efficient provision of such information to farmers can improve their decisions regarding crop choice and input use.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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