

Journal of Pharmacognosy and Phytochemistry

Available online at www.phytojournal.com



E-ISSN: 2278-4136 P-ISSN: 2349-8234 JPP 2018; 7(5): 813-816 Received: 25-07-2018 Accepted: 26-08-2018

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Breeding for drought tolerance: A major challenge for rice cultivation under water limiting conditions

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Abstract

Rice is a drought-susceptible crop because of its shallow root system, rapid stomatal closure and little epicuticular wax on the leaves. It is highly sensitive to drought stress at the reproductive stage. The reduction in grain yield under drought stress is mainly caused due to the sterility of spikelet at maturity. Deep and thick root systems have been correlated with better grain yield under drought stress in rice. Many QTLs have been identified under upland and rainfed lowland conditions for various root traits as well as grain yield under drought stress. The successful introgressions of these QTLs through Marker Assisted Breeding (MAB) followed by precise phenotyping have resulted in the development of several drought tolerant varieties. To be more effective, the breeding programme should aim at introgressing QTLs for root traits as well as grain yield under drought stress for development of drought tolerant high yielding rice variety.

Keywords: Rice, QTLs, grain yield, drought tolerance

Introduction

Rice, is the most important crop and staple food for more than half of the world's population (Todaka *et al.*, 2012) ^[33]. It covers 2.54 million (M) ha of the total 3.3 M ha cropped area. More than 90 per cent of the world's rice is grown and consumed in Asia, where 60 per cent of the global population lives. Rapid growth in human population throughout the world is boosting demand for a corresponding increase in grain yield (Liang *et al.*, 2010) ^[8] and there is need to increase production 50 per cent more by 2025 (Khush, 2001) ^[11]. To achieve this ambitious goal various rice varieties with greatly improved agronomic traits such as, high yield potential and stress tolerance should be developed. Worldwide, water for agriculture is becoming increasingly scarce, day by day, due to uncertain and uneven rainfall distribution patterns, shrinking groundwater resources, increasing level of salts in soil solution and diverting the fresh water resources to competing urban and industrial uses. In the coming future, water availability may be more affected due to ongoing changes in global climate.

The predominantly rice-growing areas in Asia are often threatened by severe abiotic stresses, of which the most common is drought. Drought is the major constraint to rice production in rainfed areas. Throughout the world, about 34 per cent (~54 million hectare) of the total land under rice cultivation is under rainfed conditions (Maclean et al., 2002 and Yoichi et al., 2011) ^[20, 44]. Asia occupies 32.1 per cent rainfed low land rice of the total rice area which currently averages production of 2.3 tonnes per hectare (Tuong and Bouman, 2003) ^[35]. Drought is the most devastating among abiotic stresses and it depresses yield by 15-50 per cent depending on the vigour and period of stress. Water-deficit may occur early in the growing season or any time from flowering to grain filling, and the intensity of the stress depends on the duration and frequency of water-deficit. Rice is highly sensitive to water stress at the reproductive stage (O'Toole 1982 and Venuprasad *et al.*, 2007) ^[24, 2]. Drought stress suppresses leaf expansion, tillering, photosynthesis (Kramer and Boyer, 1995) ^[12] and reduces leaf area due to early senescence. Reduction of photosynthetic activity, accumulation of organic acids and osmolytes and changes in carbohydrate metabolism, are typical physiological and biochemical responses to drought stress (Tabaeizadeh, 1998) [32]. Water deficit also increases the formation of reactive oxygen species resulting in lipid peroxidation, protein denaturation and nucleic acid damage with severe consequences on overall metabolism. The requirement of drought tolerant rice varieties have long been felt to ensure crop production in rainfed areas. The global reduction in rice production due to drought stands at an average of 18 million tonnes annually. Therefore, drought mitigation, through development of drought tolerant varieties with higher yields under water-limiting environments will be a key to improve rice availability and ensure food security to 3 billion people in Asia.

Root traits associated with drought tolerance

Roots are essential organs for exploiting soil resources, such as water and mineral nutrients. The deeper, thicker and more branched root system with a high root to shoot ratio can enhance the tolerance of rice to water deficits (Gowda et al., 2011)^[7,8]. The increase in length and thickness of root in rice is correlated with drought tolerance and grain yield (Jeong et al., 2010)^[9]. The prevalence of branched roots, the rate of root growth and the direction of root growth relative to limiting resources are important root traits that can be used for breeding purpose. The tropical japonica types have fewer tillers and deeper root systems than *indica* and *aus* types (Lafitte et al., 2006)^[15]. Variability in the root thickness, root depth, and root mass among the rice cultivars was observed under drought stress (Gowda et al., 2011)^[7, 8]. Indica types, grown mostly in lowland, have thinner and shallow roots, while aus types are often grown in upland conditions and exhibit intermediate diameter with length similar to japonica (which include upland Asian and temperate cultivars). Several rice cultivars were screened for root traits under stress and some promising cultivars such as Salumpikit, Azucena, Dular, Black Gora were identified for use in breeding programme (Henry et al., 2011) [7, 8]. Two deep rooted drought tolerant rice cultivars from Assam viz., ARC10372 and Banglami were also reported by Verma et al. (2017)^[41]. In addition to cultivated forms, root systems of wild rice germplasm have also been characterized and O. longistaminata and O. rufipogon were identified as potential sources of novel genes for drought tolerance (Liu et al., 2004) ^[17]. Among the root morphological traits, maximum root length, root dry weight, root volume, root to shoot weight and length ratios are associated with drought tolerance in upland rice (O'Toole and Soemartono, 1981; Yoshida and Hasegawa, 1982; Babu et al., 2001 and Kanbar et al., 2009) [43, 1, 10].

As compared to above-ground organs, roots have undergone very little direct selection during cereal domestication, so most modern cultivars have insufficient root systems for optimum uptake of water and nutrients for maximum grain yield. Therefore, QTLs for various root traits were identified and used in Marker Assisted Breeding (MAB) in order to improve root system of shallow rooted high yielding mega rice varieties under drought.

Major QTLs associated with root traits under drought stress

A number of studies have reported QTLs associated with various root traits such as root length (Price et al., 2002; MacMillan et al., 2006 and Courtois et al., 2009) [25, 21, 4], root biomass (Courtois et al., 2003)^[5], and root number (Zheng et al., 2000, 2003 and Courtois et al., 2009) [47, 5, 4]. In rice, root length, diameter, dry weight and total absorbing surface area were positively correlated with grain yield (Liu et al., 2014) ^[17]. A major root QTL (DRO1) was identified in the Near Isogenic Lines (NIL) derived from a cross between IR64 and Kinandang Patong (Uga et al., 2013)^[23]. Four QTLs (OTL2, QTL7, QTL9 and QTL11) were identified in the Recombinant Inbred Lines (RILs) derived from the cross between 'Bala' and 'Azucena' for various root traits such as root penetration, deep root weight, root thickness and maximum root length (Steel et al., 2013). The introgression of QTLs for increased root size enables plant to take up more water and nutrients, and thereby increase photosynthesis and carbohydrate accumulation resulting in mobilization of assimilates towards grain yield. Apart from these secondary traits, it was also reported that the marker assisted breeding using QTLs

associated with grain yield under drought has much been effective in rice for improvement to drought stress. Many QTLs for high grain yield under drought have been identified (Kumar *et al.*, 2014 and Verma *et al.*, 2017) ^[41, 13] and breeding lines have been developed for upland and rainfed lowland conditions (Verulkar *et al.*, 2010) ^[40] by using this approach. The breeding programmes have to combine favourable root traits with grain yield under stress as the selection criteria in order to develop drought tolerant rice variety.

Yield traits associated with drought tolerance

Traits such as tiller number and plant height modify the expression of secondary and integrative traits by affecting transpirational demand. Plant type traits are highly heritable and are extensively used in traditional plant breeding. Plant height is an important developmental and yield related trait (Zhao et al., 2011) [45]. It was slightly lowered in aerobic conditions than the flooded conditions. The plant height in rice was associated with thick and deep root system (Tomar and Prasad, 1996) [28]. A significant positive correlation was observed for number of tillers with effective booting tillers, spikelet fertility and grain yield under drought stress. Higher number of tillers and effective booting tillers were observed in drought tolerant cultivars whereas, low tillering was observed in drought susceptible cultivars under drought stress (Verma et al., 2017)^[41]. The most important cause of yield reduction under drought stress is the sterility of spikelets (Liu et al., 2006) ^[18] therefore higher spikelet fertility was observed in drought tolerant cultivars. A significant positive correlation of spikelet fertility was observed with number of tillers, effective booting tillers, plant height, panicle length, number of grains per panicle and grain yield per plant under drought stress (Verma et al., 2017)^[41]. It showed that the various yield component traits associated with enhancement of grain yield in rice under drought stress. The QTLs for various yield component traits under drought stress were identified in rice (Suji et al., 2012; Muthu kumar et al., 2015 and Verma et al., 2017) [41, 22]. These traits can be used for indirect selection of grain yield under drought stress conditions. Moderate heritability of grain yield under drought stress was observed by Kumar et al. (2009) [14] therefore, large number of breeding programme have been started using grain yield as a selection criteria for development of high vielding drought tolerant rice variety and OTL mapping.

Major QTLs identified for grain yield under drought stress

A large number of QTLs for grain yield under reproductivestage drought stress under both upland and lowland conditions have been identified. Among these, qDTY12.1 was the first reported large-effect QTL with R² value of 33% in the F₃derived lines from the upland rice cultivars Vandana and Way Rarem (Bernier et al., 2007)^[2]. The two large-effect QTLs (qDTY2.1 and qDTY3.1), were identified in a backcross inbred lines derived from a cross of high-yielding lowland rice variety 'Swarna' and upland rice variety 'Apo' with an R² of 16.3% and 30.7% respectively (Venuprasad et al., 2009) ^[14]. *QDTY6.1* was identified under aerobic and irrigated lowland conditions in the same population with an R^2 of 66% and 39% respectively (Venuprasad et al., 2012) [37]. A major QTL for grain yield *qDTY1.1*, was reported in F₃-derived populations developed from the cross between Nagina22/ Swarna, Nagina22/ IR64 and Nagina22/MTU1010 with an R² of 13.4%, 16.9%, and 12.6% respectively (Vikram et al.,

2011) ^[42]. Four large-effect QTLs, qDTY2.2, qDTY4.1, qDTY9.1, and qDTY10.1, were identified in the backcross inbred lines derived from the cross between Aday Sel and IR64 (Swamy *et al.*, 2013) ^[30]. Among the various QTLs reported for grain yield qDTY1.1, qDTY2.2, qDTY2.3, qDTY3.1, qDTY3.2, qDTY6.1, and qDTY12.1 have shown an effect across multiple genetic backgrounds (Kumar *et al.*, 2014) ^[13] Therefore, these are the most suitable QTLs to be used for development of drought tolerant rice variety in different genetic backgrounds.

MAB for drought tolerance

In MAB the different QTLs combinations were found effective in specific genetic background due to interaction of QTLs with genetic background as well as among the QTLs. In India several drought tolerant cultivars were released with very high degree of drought tolerance (Verulkar et al. 2010 and Gowda et al. 2011) [40, 8]. The introgression of DRO1 QTL in a shallow-rooting variety (IR64) resulted in development of deep rooted plants with high yield performance under drought conditions (Uga et al., 2013 and Deshmukh et al., 2017)^[36]. The introgression of multiple root QTLs increased root penetration, root thickness and nodal root apex stiffness (Clark et al., 2008). Similarly, a root QTL 9 was reported to increase the root length by 9.6 cm under both drought and well-watered conditions and a deep rooted variety "Birsa Vikas Dhan 111" was developed through MAB (Steele et al., 2006) [28].

Recently, different combinations of grain yield QTLs were utilized in drought breeding programme. The combination of *qDTY12.1* with *qDTY2.3* and *qDTY3.2* results in significant vield advantage in Vandana and Way Rarem F₃ derived population under upland drought stress conditions (Swamy et al., 2013) ^[30]. Similarly, in an IR64 background, plants with qDTY2.2 and qDTY4.1 showed a higher yield advantage under lowland drought stress. The OTL combinations (qDTY3.1,qDTY2.2 and qDTY3.1,qDTY12.1) provided a higher yield advantage under reproductive stage drought stress in the background of elite Malaysian rice cultivar, MR219 (Shamsudin et al., 2016) [26]. The various combinations of QTLs were found effective in enhancement of grain yield in variable genetic backgrounds under drought stress. Therefore, the breeding strategies based on root traits and grain yield were utilized effectively through MAB for the development of drought tolerant rice variety across the rainfed rice growing areas of India and other countries. In future these two strategies for drought tolerance can be combined together. The plants will be selected for deep root along with high grain yield under drought stress in order to develop drought tolerance rice variety.

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