



Genetic architecture of grain chalk in rice and interactions with a low phytic acid locus



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ABSTRACT

Grain quality characteristics have a major impact on the value of the harvested rice crop. In addition to grain dimensions which determine rice grain market classes, translucent milled kernels are also important for assuring the highest grain quality and crop value. Over the last several years, there has been increasing concern by the rice industry regarding prevalence of chalky grains which are resulting in a loss of some markets. This study was conducted to identify genetic markers associated with grain chalk that could be used by breeders to develop new varieties that have translucent grains across different environments. A mapping population developed from KBNT-1-1, a translucent, low phytic acid (LPA) mutant derived from the US long grain variety Kaybonnet, crossed with Zhe733, a chalky, long grain variety developed in China, was evaluated in replicated trials conducted across two years and two planting dates that differed by one month. The progeny were evaluated for days to flowering in the field. Grain was harvested at maturity and brown or milled rice were used to determine grain length, width, and percent chalk using an image analysis system. The 187 F12 progeny were evaluated using 174 genome-wide microsatellite markers and one SNP marker, and QTL analysis was performed. A large effect QTL was co-located with the LPA gene, and the mutated KBNT-1-1 LPA allele was associated with increased chalk suggesting that low phytic acid may be one cause of chalk in this cross. Nine additional QTL were detected with the KBNT-1-1 allele associated with reduced chalk and one with increased chalk. Overlaps were identified between chalk QTL, candidate genes for chalk, and QTL for other traits such as grain width. Measures of night temperature and humidity experienced during grain filling were positively correlated with increased chalk. Year and planting time were also shown to significantly affect chalk. However there was no interaction with the pattern of QTL detected and any of the environmental differences, indicating that these QTL are robust across diverse growing conditions.

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1. Introduction

The degree of chalkiness in rice affects grain quality and milling yield. Chalk negatively impacts cooking quality characteristics, such as texture and palatability which subsequently reduces the market value of rice (Chun et al., 2009; Lisle et al., 2000). The presence of chalk also negatively impacts milling yield by increasing the number of broken kernels, which in turn reduces the proportion of whole kernels (Khush et al., 1979). The frequent breakage during milling of chalky rice is caused by less densely packed starch gran-

ules in the chalky areas and less hardness than the translucent areas of the grain (Del Rosario et al., 1968). Broken grains sell for a lower price than unbroken (head rice); over the last ten years the world market price of broken rice has fluctuated between 35 to almost 50% less than that of head rice (Childs, 2016). Reduced milling yield can be especially problematic with long grain rice varieties as their greater length to width ratio makes them more susceptible to grain structure inconsistencies caused by chalk (Wan et al., 2005). In the USA, over 70% of the rice grown in 2015 consisted of long grain varieties (Childs, 2016) and thus, it becomes critical to understand and manage grain chalk that can significantly reduce milling yield.

Chalk is influenced by the environment and genetics. Higher temperatures, and particularly higher night air temperatures (NTAT) during grain filling, significantly increase chalk (Ambardekar et al., 2011; Counce et al., 2005; Lanning et al., 2011). There is a positive quadratic relationship between the 95th percentiles of the NTAT frequencies (NT₉₅) occurring during the grain

Abbreviations: cM, centimorgans; MAS, marker-assisted selection; Mb, megabase pairs in reference to physical location along a chromosome; QTL, quantitative trait locus; SNP, single nucleotide polymorphism; SSR, simple sequence repeat.

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filling stage and the degree of chalk. The amount of chalk is also strongly affected by variety and there is a differential response to increased NT95 between varieties (Ambardekar et al., 2011). High quality rice varieties have been developed to have low chalk, an important factor in grain grading. However, when genetically diverse lines are used as parents in rice hybrids to increase yield through heterosis, or when exotic varieties are used as donors to introgress alleles for improved stress resistance or agronomic traits, there is a potential to increase chalk and reduce grain quality. Thus, it is critical to understand the genetic factors that affect chalk to be able to make full use of rice genetic diversity for variety development while sustaining grain quality in competitive commercial markets.

Chalk in rice occurs as an opaque white discoloration in the endosperm or as localized patches in the center, back or throughout the grain (Ashida et al., 2009). Chalky endosperm contains amyloplasts with a more rounded appearance and a disordered cellular structure than in translucent endosperm. Inside chalky grains the amyloplasts contain small loosely packed starch granules with greater airspace between them (Chun et al., 2009; Lisle et al., 2000). The airspaces hinder the transmission of light resulting in the characteristic opaque chalky appearance, as well as creating mechanical weaknesses within the cellular structure of the rice grain, which in turn may increase the incidence of breakage during milling (Kepiro et al., 2008).

Multiple environmental and genetic factors influence the biochemical pathways involved in the deposition of storage components during the source/sink process of grainfill, which in turn affects chalk formation in the developing grain. Li et al. (2014) recently cloned *Chalk5*, which encodes a vacuolar H⁺-translocating pyrophosphatase (V-PPase). Over expression of *Chalk5* is believed to contribute to chalk formation by disturbing pH homeostasis of the endomembrane trafficking system and interfering with the biogenesis of protein bodies during endosperm development. This in turn leads to the formation of airspaces around starch granules and protein bodies (Li et al., 2014). Other studies have implicated amylose, starch biosynthesis and starch structure as components of chalk formation. Patindol and Wang (2003) performed an analysis of the starch content of chalky kernels and found a greater abundance of amylopectin with long branch chains, and a decrease in overall amylose content. A microarray study performed by Yamakawa et al. (2007) exposed developing rice grains to high temperatures during the milky stage. They found high temperatures caused down regulation of starch branching enzymes (particularly *branching enzyme IIb*), granule-bound starch synthase I and cytosolic pyruvate orthophosphate dikinase while enzymes involved in starch degradation such as α -amylase and heat shock proteins were up regulated.

A review paper by Sreenivasulu et al. (2015) reports over 140 quantitative trait loci (QTL) related to chalkiness have been identified spanning all 12 chromosomes in rice. A wide range of genes involved with starch formation and storage protein regulation have been implicated in grain chalk. Biparental mapping populations have identified QTL responsible for chalk at or near genes such as *Waxy*, *starch synthase III A*, *pyruvate orthophosphate dikinase*, *UDP glucose pyrophosphatase*, *cell wall invertase*, and *H⁺-translocating pyrophosphatases* (Fujita et al., 2007; Kang et al., 2005; Li et al., 2014; Peng et al., 2014; Wang et al., 2008; Woo et al., 2008). Sreenivasulu et al. (2015) point out that QTL studies combined with transcriptome analysis suggest that many high temperature response pathways involved with starch and storage protein metabolism during grain development are co-located with chalk QTL. Storage proteins levels have also been shown to be influenced by higher temperatures during different stages of seed development, which in turn may contribute to the formation of chalk (Li et al., 2011).

Our study involved examining a biparental mapping population consisting of F12-F13 recombinant inbred lines (RIL's) of the Kaybonnet *low phytic acid* mutant, KBNT-1-1, (henceforth referred to as KBNT *lpa*) X Zhe733. The KBNT *lpa* parent was derived from 3632 gamma irradiated M2 lines and the resulting *lpa1-1* mutant is a single gene recessive non-lethal mutation (Larson et al., 2000; Rutger et al., 2004). KBNT *lpa* is from the *tropical japonica* sub-population of *Oryza sativa*, which contains resistance to rice blast (*Magnaportha grisea*) isolates IB-1, IB-49, IC-17, and IG-1 and has translucent grain. Zhe733 is a chalky, high yielding *indica* variety that is resistant to straight head disorder, rice water weevil and some rice blast races (IE1K and IB-33) (Lee et al., 2009; Liu et al., 2008; Yan et al., 2005). The KBNT *lpa* x Zhe733 is a registered mapping population (Rutger and Tai, 2005) which has previously been used for mapping water weevil resistance, disease resistance, and straighthead (Yan et al., 2005). It was chosen for this study as there is a large difference in chalk concentration between the parents (KBNT *lpa* is mean of 3.15% chalk and Zhe733 with an is mean of 25.37% chalk) and because both parents are long grain varieties and thus, grain shape is not a confounding factor (Wan et al., 2005).

Incorporating low phytic acid mutations into rice and other crops can be beneficial for both health and environmental reasons. Phytic acid binds much of the available phosphorus in seeds into an insoluble form that cannot be digested by humans and other monogastric animals. In food products phytic acid has a two-fold negative effect on the environment. The insoluble phosphorus is passed by humans and agricultural animals leading to high phosphorus contents in sewage/waste and contributes to eutrophication of lakes, rivers and drinking water. The resulting insoluble phosphorus in manure is unavailable to agricultural crops until it is broken down by soil microorganisms requiring the additional use of non-renewable inorganic phosphorus fertilizers, which in turn compounds excess phosphorus run off into waterways (Brinch-Pedersen et al., 2002). While a few health benefits have been attributed to phytic acid, the negative aspects of phytic acid in the diet out-weigh the benefits (Raboy, 2009; Schlemmer et al., 2009). Phytic acid is a strong chelator and can bind iron, zinc, calcium, magnesium and manganese into insoluble salts in human and animal digestive systems also. This in turn increases the risk of vitamin and micronutrient deficiencies, especially in developing countries where dietary choices are limited (Raboy, 2007).

In seeds phytic acid, also known as *myo*-inositol-1,2,3,4,5,6-hexakisphosphate, serves as the main storage form of phosphorus and may contain approximately 75% of the total phosphorus in the seed (Raboy, 2009). Phytic acid forms salt complexes with many nutrients that can later be released in the presence of phytases to provide nutrition to the developing embryo during seed germination. The nearest known homolog to the rice *lpa1-1* is a 2-phosphoglycerate kinase found in hyperthermophilic methanogens (Kim et al., 2008; Lehmacher and Hensel, 1994). The exact mechanism by which the *lpa1-1* gene functions is currently unknown. However, Raboy (2009) suggests that the protein encoded by *lpa1* may function similarly to 2-phosphoglycerate kinase by creating an intermediate compound for phytic acid synthesis as well as producing a second compound that protects phytic acid intermediary compounds from degradation.

In the current study, our aims were to identify the QTL that control chalk within long grain rice, and to determine the effect of the *low phytic acid 1-1* allele on chalk (if any). This population was genotyped and phenotyped for chalk and potential interacting agronomic traits, and QTL analysis was performed. The long term objectives are to understand the genetic and biochemical components that cause chalk, and to obtain molecular markers to be used for selection of low chalk grains in rice breeding.

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