



Influence of high temperature during filling period on grain phytic acid and its relation to spikelet sterility and grain weight in non-lethal low phytic acid mutations in rice



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ABSTRACT

Low phytic acid (*lpa*) crop is considered as an effective strategy to improve crop nutrition. However, the inferior agronomic performance of *lpa* crops and their environmental growth adaptation have not yet been fully understood. Three rice *lpa* lines and their corresponding wild-types were used to compare their differences in grain phytic acid (PA) in response to high temperature (HT) and its relation to spikelet sterility and grain weight at a controlled temperature at the filling stage. Results showed that HT caused an increase in grain PA and inorganic phosphate contents, with more substantial increase of PA content for *lpa* lines compared with corresponding wild-types. This increase in PA content in high temperature-ripened grains was not simply attributed to the reduction in grain weight and relatively enhanced proportion of aleurone-layer fraction to whole grains. Significant increase in PA contents was also detected in milled rice. Moreover, spikelet sterility and grain plumpness of *lpa* lines were more susceptible to HT stress than those of wild-types. Exogenous PA spraying with an appropriate concentration could increase grain PA content, but it had only a slight contribution to the enhancement of heat-tolerance and injury alleviation for rice exposed to stressful HT.

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1. Introduction

Phytic acid (PA) is the main storage form of phosphorus in cereal and legume seeds (Miller et al., 1980). Typically, it accounts for >70% of total seed phosphorus and approximately 1% of seed dry weight (Raboy and Dickinson, 1987). In the seed-filling period, PA is synthesized and gradually accumulated in seeds as a phosphorus reservoir. This reservoir is present in the form of mixed-phytate with several mineral cations, such as potassium, calcium, iron, and zinc (Brinch-Pedersen et al., 2002). However, PA phosphorus and cation minerals complexed with phytate are almost indigestible by monogastric animals and humans. As a result, the bioavailability of these nutrient elements is remarkably reduced (Brinch-Pedersen et al., 2002). In human nutrition, PA in staple foods is undesirable and commonly considered as an anti-

nutritional component (Loewus and Murthy, 2000). Moreover, animals possibly excrete a higher amount of phosphorus when they are fed with diets containing high PA, which can cause a threat of contaminating water sources (Kuwano et al., 2009). Therefore, the concentration of PA in cereals should be reduced to improve crop nutritive quality and address relevant environmental problems.

The development of low phytic acid (*lpa*) genotypes is an effective strategy to reduce PA in crop breeding. Since the mid-1990s, mutation breeding by gamma-irradiation or chemically-induced mutagenesis and has been successfully applied to generate germplasm breeding materials of an *lpa* background for various crops, including maize, barley, rice, wheat, soybean, and common bean. This strategy may result in a significant reduction in seed PA from 50 to 95% (Liu et al., 2007; Raboy et al., 2000; Rutger et al., 2004; Yuan et al., 2007). In addition, animal feeding tests have extensively shown the potential of *lpa* seeds to promote the use of phosphorus, and the bioavailability of minerals, and reducing phosphorus-induced pollution. The *lpa* barley variety Herald has been released for commercial use (Bregitzer and Raboy, 2007). However, *lpa* mutant crops are generally characterized by lower yield and seed viability than wild types. For instance, *lpa* mutant

Abbreviation: HT, high temperature; NT, normal temperature; PA, phytic acid; Pi, inorganic phosphorus.

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rice KBNT exhibits approximately 5–14% of yield loss compared with other standard rice varieties (Rutger et al., 2004). A similar phenomenon has been found in other cereals and legumes (Raboy et al., 2000; Yuan et al., 2007). Zhao et al. (2008) showed that the deterioration of seed viability and yield performance of *lpa* mutant crops was negatively correlated with the extent of PA reduction, with a decrease of 12.5–25.6% in grain yield in four *lpa* rice lines (38–63.6% of grain PA reduction). On the other hand, one *lpa* mutation in barley and one in soybean have not elicited a negative effect on yield performance, seed germination capacity, and other phenotype defects (Dorsch et al., 2003; Yuan et al., 2007). This suggests that the reduction of PA content in low-phytate crops does not always lead to deterioration of plant growth and poor agronomic performance under normal growth conditions.

Evidence has indicated that PA contributes to various physiological functions, such as stress responses (Loewus and Murthy, 2000), energy triggering, phosphate sensing and homeostasis in addition to phosphorus storage (Doria et al., 2009; Hanke et al., 2012). Brinch-Pedersen et al. (2002) reported that PA was involved in plant cell protection and resistance to oxidative stress by inducing the synthesis of enzymatic systems responsible for antioxidant metabolism. Khurana et al. (2012) revealed that PA and other inositol phosphates also functioned in signal transduction in guard cells, by which the drought-stress and abscisic acid induced stomatal closure. Moreover, salinity stress remarkably enhances *MIPS* transcripts, which catalyze the initial step of the PA biosynthetic pathway (Iwai et al., 2012; Loewus and Murthy, 2000), implying that the PA metabolic pathway may be closely associated with the perception and resistance response of plants to abiotic stress. Doria et al. (2009) found that the knockdown of the *GmMIPS1* gene altered the susceptibility of soybean plants to drought stress. Previous study with four *lpa* barley lines revealed that the contents of total phosphorus and inorganic phosphorus (Pi) in grains produced in a rain-fed environment were significantly higher than those in an irrigated environment (Bregitzer and Raboy, 2006). In *lpa* soybean, the field emergence percentages of the *mips* allele were significantly lower than those of *Mips* lines (normal PA phenotype), and the environment of seed production had a marked impact on the seed viability and germination capacity of *lpa* soybean lines. This was termed a so-called “seed source effect” (Anderson and Fehr, 2008; Meis et al., 2003). However, whether or not the agronomic performance and grain yield of *lpa* crops are susceptible to stressful environments, such as high temperature and drought stress, remains unclear.

High temperature (HT) is a major environmental constraint affecting rice productivity (Lin et al., 2010). In recent decades, global warming has been predicted to be more variable with frequent episodes of stressful HT during rice growing seasons. HT at the reproductive stage is particularly injurious to yield and quality (Prasad et al., 2006). Previous studies had widely demonstrated that HT can cause reduced filled grains, decreased grain weight, and low harvest index compared with normal growth temperature (Hiromoto et al., 2007; Lin et al., 2010). Prasad et al. (2006) further revealed that the heat-tolerance of rice genotypes was independent of differing subspecies, ecotypes and cultivar original regions. However, little information is available on the difference in response to high temperature and heat tolerance among rice genotypes differing in PA contents. Nevertheless, there were great concerns on their possible alteration in the sensitivity and adaptation to stressful growth environment for the *lpa* mutant crops (Khurana et al., 2012; Thavarajah et al., 2010).

In this study, three rice *lpa* lines and their corresponding wild types were used: (i) to investigate the effect of increased filling temperature on grain PA concentration and its relation to rice yield performance; (ii) to identify if there are genotypic differences in the

response of spikelet sterility and grain plumpness to HT at the filling stage between *lpa* lines and wild-types; (iii) to examine the alleviating effects of exogenous PA spraying on the reduction of spikelet sterility and grain plumpness when rice plants were exposed to HT, as well as their association with the varying grain PA contents for *lpa* rice lines. Such results could provide helpful information to improve *lpa* crop breeding and production management.

2. Materials and methods

2.1. Rice genotypes and plant husbandry

The experiments were conducted during rice growing seasons from 2010 to 2012, using controlled environment facilities at the experimental station of Zhejiang University, China. Three rice *lpa* lines, including *Os-lpa-XQZ*, *Os-lpa-9B* and *Os-lpa-Xiushui110* were used in this study together with their wild-types. These *lpa* mutant lines were initially generated through gamma irradiation in Zhejiang University, China (Liu et al., 2007), and the wild types were commercial rice cultivars, namely Xieqingzao (*indica*), Zhong9B (*indica*) and Xiushui110 (*japonica*). Moreover, 22 *indica* cultivars, which had been extensively used in rice production, were also employed to conduct an extensional experiment for further investigating the interrelationship of grain PA contents with their heat tolerance performance.

Rice seed was sown in a paddy field and the 25–30 day old seedlings were laterally transplanted into the plastic pots filled with the clayed soil from the paddy field. The soil type in plastic pots was clay-loam, being air-dried, fully mixed and then soaked prior to rice transplanting, with total N at 1.36 g/kg, available P at 24.5 mg/kg and exchangeable K at 79.3 mg/kg, respectively. The pots were placed in a greenhouse under natural light conditions and similar temperature environment (28 °C day/22 °C night) until rice plants were exposed to different temperature treatments at their flowering dates. Rice plants grown in different pots inside the greenhouse were also uniformly managed and usually irrigated every 2–3 days, depending on the requirements.

2.2. Temperature treatments for rice *lpa* lines in growth phytotrons

In 2010 and 2011, three rice *lpa* lines (*Os-lpa-XQZ*, *Os-lpa-9B* and *Os-lpa-Xiushui110*) together with their corresponding wild types were used. Rice plants in pots were transferred from greenhouse to growth phytotrons (Model PGV-36, Canada) at their flowering dates. Two different temperatures were imposed in the two phytotrons, 4 pots per phytotron for each genotype as the repetitions in a complete randomized block design. The daily mean temperatures were 33 °C (high temperature, HT) and 23 °C (Normal temperature, NT). The diurnal change of temperature was designed by a simulation of temperature fluctuation in the wild. The daily maximum and minimum temperatures were set at 2:00 p.m. and 5:00 a.m., with 38 °C and 28 °C for HT, 26 °C and 20 °C for NT, respectively. The two phytotrons were kept under the same climatic conditions except for the temperature setup. The photoperiod was from 5:30 a.m. to 7:00 p.m. with 150–180 J m⁻² s⁻¹ of light intensity, and the relative humidity was maintained around 75–80% with a wind speed of 0.5 m s⁻¹.

At maturity, the seed-setting rate was examined as the ratio of the number of filled grains per panicle to the total number of spikelets per panicle, and the different pots of each genotype were separately sampled for the statistical replications. The number of filled grains included both completely and partially filled grains. Grain weight was measured using an electronic balance after being dried to constant weight.

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