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Comparative QTL analysis of maize seed artificial aging between an immortalized F_2 population and its corresponding RILs

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ABSTRACT

Seed aging decreases the quality and vigor of crop seeds, thereby causing substantial agricultural and economic losses in crops. To identify genetic differences in seed aging between homozygotes and heterozygotes in maize, the seeds of a set of recombinant inbred lines (RILs) and an immortalized F_2 (IF_2) population were subjected to artificial aging treatments for 0, 2, 3, and 4 days under 45 ºC and 85% relative humidity and seed vigor was then evaluated in a field experiment. Seed vigor of all entries tested decreased sharply with longer aging treatment and seed vigor decreased more slowly in heterozygotes than in homozygotes. Forty-nine QTL were detected for four measured seed vigor traits in the RIL (28 QTL) and IF_2 (21 QTL) populations. Only one QTL, *qGP5*, was detected in both populations, indicating that the genes involved in anti-aging mechanisms differed between inbred lines and hybrids. Several QTL were identified to be responsible for multiple seed vigor traits simultaneously in the RIL and IF_2 populations under artificial aging conditions. These QTL may include major genes for seed vigor or seed aging. QTL *qVI4b* and *qGE3a* detected in the RIL population coincided with genes *ZmLOX1* and *ZmPLD1* in the same respective chromosomal regions. These QTL would be useful for screening for anti-aging genes in maize breeding.

1. Introduction

Crop seeds, for example, maize (*Zea mays* L.) kernels, are consumed directly as human food and animal feed, providing more than 70% of caloric intake worldwide. Seeds are also a fundamental component of the plant life cycle because they store the genetic information necessary for the next generation [1]. In seed production, seed quality is defined as the

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ability to maintain high vigor and stable content during storage. Seed with high vigor usually shows advantages in growth and production potential, positively affecting germination rate, resistance to environmental stresses, and crop yield [2,3]. Seeds gradually lose their ability to germinate during long periods of storage [4]. During storage, seed vigor depends mainly on the ability to withstand prolonged storage and the deleterious effects of aging [5]. The ability of seeds to withstand storage is influenced by many factors, including seed mass, oil content, carbohydrate composition, taxonomy, seed maturity, and climate factors [6–11]. Investigating the effects of seed aging on seed vigor will facilitate understanding the mechanisms underlying seed tolerance of prolonged storage.

With extended storage, seeds of most crops age and deteriorate. Aging and deterioration may lead to seedling abnormalities, delay field establishment, or even result in emergence failure [12]. Aging rate has been reported to be strongly influenced by seed moisture content, storage temperature, seed quality, and genetic factors [10]. At the molecular level, seed vigor and longevity are controlled mainly by protein damage and repair [13]. During the seed aging process, free radical-mediated lipid peroxidation, enzyme inactivation or protein degradation, disruption of cellular membranes, and damage to genetic material (nucleic acids) are the major factors determining loss of seed vigor [4,8,14–16]. In general, seeds are treated at high temperature and high relative humidity to accelerate seed aging for analysis of the seed aging process [12,17]. In maize, the floury parts of the seed endosperm become more corneous with aging under high temperature and high relative humidity. This physiological change is strongly associated with starch and protein changes [18]. Aged maize seeds also showed lower plasma membrane H^+-ATPase activity, inhibiting germination and post-germination root growth [19].

In seed plants, a few studies have focused on the genetic mechanisms of seed aging or seed vigor [5, 11, 20–29]. In *Arabidopsis*, *AtOGG1*, *PLDα1* (*phospholipase D alpha*), and *DOG1* (*delay of germination 1*) have been identified as being involved in regulation of seed vigor and longevity [5,21,27,29]. Interestingly, the homolog of *PLDα1* in soybean (*Glycine max* L.) also proved to be associated with seed longevity [28]. Quantitative trait loci (QTL) analyses seed aging and vigor have been performed in rice (*Oryza sativa* L.) [20,24] and wheat (*Triticum aestivum* L.) [23]. In maize, Li et al. reported that the mutant *ZmLOX-1,2* (*low lipoxygenase-1,2*) showed decreased germination, suggesting that *LOX-1, 2* was a factor influencing seed vigor [22]. Two proteomic analyses for maize seed germination showed that seed aging responses are regulated mainly by signal transduction, metabolism, energy, and stress-response proteins [25,26]. Some QTL have been identified to be responsible for seed vigor in maize. Presterl et al. [30] identified nine and 10 QTL for fresh seedling weight in a set of doubled haploid (DH) populations and their corresponding testcrosses, respectively, and Liu et al. [11] detected 16 seed vigor-related QTL for the seeds harvested at three developmental stages (32, 40, and 45 days after pollination). Although these genetic studies made considerable advances in dissecting the genetic mechanism of seed vigor, longevity, and aging responses, there is still much to be learned about the genetic mechanisms underlying these important traits in plants. Particularly in maize, the mechanism of seed aging is largely unknown. QTL analyses of maize seed aging will help identify the genes of the associated regulatory mechanisms.

Maize is one of the most important cereal crops in the world [31]. In 2012, the total world production of maize was 854 million tons on a total planting area of 154 million hectares [32]. The annual demand for hybrid seed for the maize production of the world is estimated to be 2.5 million tons [32]. Maize hybrids are widely used in production. Hybrid maize offers genetic mechanisms distinct from those of inbred lines for controlling various traits and metabolisms. For this reason, comparing the genetic basis of seed vigor or aging between homozygous and heterozygous materials will have important economic and agricultural significance. Previous genetic studies on maize seed vigor and aging have been developed using mainly RIL and DH populations, as well as inbred lines and hybrids [11,22,25,26,30]. However, few genetic analyses have been performed in heterozygous maize populations. In this study, we performed a comparative QTL analysis between a RILs and an IF_2 population to identify genetic effects of artificial seed aging on homozygous and heterozygous maize varieties.

2. Materials and methods

2.1. Development of the experimental population

Nongda 108 (Huang C × Xu 178) is an elite hybrid that was widely planted in China around 1999–2002. The parent Huang C has low seed vigor but high lysine content and stress resistance. Xu 178 is a high-nitrogen-efficiency inbred line with high seed vigor and low lysine content. A set of 166 RILs was constructed by single-seed descent from the hybrid. Using this RIL population, an IF_2 population was constructed using random RIL single-crossing. According to the procedure described by Hua et al. [33,34], 166 RILs were randomly divided into two groups, each consisting of 83 RILs. Then, pairwise crosses were made randomly between the lines of two groups without repeats, so that 83 different crosses were generated. The procedure was repeated three times, resulting in 249 (83 × 3) pairwise crosses between the two groups of RILs. Because insufficient seeds were harvested from six of these single crosses, 243 crosses (the IF_2 population) were used in this study.

2.2. Artificial aging treatment of seeds

The seeds of all plant materials, including RILs, the IF_2 population, two parents (Huang C and Xu 178), and the hybrid Nongda 108, were multiplied in winter 2010 in Hainan province. After harvest, the ears of the materials were fully dried under natural conditions, and uniform ears from each material were selected and threshed by hand. For each material, 1200 kernels were collected from the middle part of the ear and divided into four portions for artificial aging treatments with 300 kernels each. For ensuring uniform treatment conditions, the seed of each portion of the RIL