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Genetic analysis of tolerance to photo-oxidative stress induced by high light in winter wheat (*Triticum aestivum* L.)

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Abstract

High light induced photooxidation (HLIP) usually leads to leaf premature senescence and causes great yield loss in winter wheat. In order to explore the genetic control of wheat tolerance to HLIP stress, a quantitative trait loci (QTL) analysis was conducted on a set of doubled haploid population, derived from two winter wheat cultivars. Actual values of chlorophyll content (Chl), minimum fluorescence level (*Fo*), maximum fluorescence level (*Fm*), and the maximum quantum efficiency of photosystem II (*Fv/Fm*) under both HLIP and non-stress conditions as well as the ratios of HLIP to non-stress were evaluated. HLIP considerably reduced Chl, *Fm*, and *Fv/Fm*, but increased *Fo*, compared with that under non-stress condition. A total of 27, 16, and 28 QTLs were associated with the investigated traits under HLIP and non-stress and the ratios of HLIP to non-stress, respectively. Most of the QTLs for the ratios of HLIP to non-stress collocated or nearly linked with those detected under HLIP condition. HLIP-induced QTLs were mapped on 15 chromosomes, involving in 1A, 1B, 1D, 2A, 2B, 2D, 3A, 3B, 4A, 4D, 5B, 6A, 6B, 7A, and 7D while those expressed under non-stress condition involved in nine chromosomes, including 1B, 1D, 2A, 2B, 3B, 4A, 5A, 5B, and 7A. The expression patterns of QTLs under HLIP condition were different from that under non-stress condition except for six loci on five chromosomes. The phenotypic variance explained by individual QTL ranged from 5.0% to 19.7% under HLIP, 8.3% to 20.8% under non-stress, and 4.9% to 20.2% for the ratios of HLIP to non-stress, respectively. Some markers, for example, *Xgwm192* and *WMC331* on 4D regulating Chl, *Fo*, *Fm*, and *Fv/Fm* under HLIP condition, might be used in marker assistant selection.

Keywords: *Triticum aestivum*; photooxidation; high light; chlorophyll content; chlorophyll fluorescence; grain filling; QTL

Introduction

It was predicated that wheat, the largest food source in the world, should have massive increment from current 590 million metric tons per year to 840 million metric tons per year by 2025 to meet the demand (Murchie et al., 2009). However, in comparison with 1.6% increase of demand for wheat per year (Rosengrant et al., 1995), its genetic yield potential increased at 0.9% annual rate (Calderini et al., 1999), revealing a serious situation for wheat genetic yield improvement. As the final source for grain yield, photosynthesis is considered as an important avenue

Abbreviations: HLIP, high light induced photooxidaition; QTL, quantitative trait locus; Chl, chlorophyll content; *Fo*, minimum fluorescence level; *Fm*, maximum fluorescence level; *Fv/Fm*, maximum quantum efficiency of photosystem II; PSII, photosystem II.

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to enhance wheat genetic yield potential (Reynolds et al., 2000b). In fact, many researchers have uncovered an association between light saturated assimilation rates (A_{max}) in flag leaf and yield (Reynolds et al., 1994, 2000a; Fischer et al., 1998; Jiang et al., 2003; Hubbart et al., 2007), even though such association was not always straightforward (Evans, 1993). Moreover, evidences from elevated CO_2 concentration confirmed that the enhancement of photosynthetic rate leads to yield increase (Kimball 1983; Bender et al., 1999; Mitchell et al., 1999).

However, A_{max} in flag leaves is often inhibited by high light at noon in sunny days, often termed as "mid-day-depression of photosynthesis" (Xu and Shen, 2005), which is usually a result from high light induced photoinhibition. It affects field production to a large extent (Long et al., 1994). For example, it could cause approximately 10% loss of potential carbon assimilation under natural condition (Ögren et al., 1992). Nevertheless, a dynamic photoinhibition has also been suggested as regulation of photosynthetic apparatus against high light avoid of over-excitation of PSII, which is peculiarly important for senescent leaves during the grain filling stage (Lu et al., 2001). PSII reaction center was considered the most susceptible site to photoinhibition (Kok, 1956; Demmig-Adams et al., 1992). The reduction of *Fv/Fm*, which is correlated linearly with the quantum efficiency of electron transport (Russell et al. 1995), has been often taken as an indicator of photoinhibition (Maxwell and Johnson, 2000). In addition to *Fv/Fm*, *Fo* and *Fm* had also been used to evaluate chilling dependent photoinhibition in maize (Fracheboud et al., 2004; Pimentel et al., 2005; Jompuk et al., 2005) as well as drought tolerance in barley (Guo et al., 2008) and wheat (Yang et al., 2007a). During the grain filling period, other adverse environments such as high temperature and/or drought will eventually change the reversible photoinhibition into irreversible photooxiation of photosynthetic apparatus. Persistent photo-oxidative stress induced by high light will decrease photosynthetic function (Long et al., 1994).

Several studies demonstrated that responses to high light stress in winter wheat were dependent upon genotypes (Wang, 2000; Monneveux et al., 2003; Yang et al., 2006; Yang et al., 2007b) as well as upon light intensity, suggesting that high light induced photosynthetic loss may represent an important approach for improving wheat photosynthesis and yield (Murchie et al. 1999). However, it is difficult for breeders to screen for tolerant lines from a number of offspring efficiently for the uncontrolled photo-oxidative weather as well as for a lot of laborious and time-consuming assessing works in the field. Therefore, understanding the genetics of tolerance to HLIP stress in wheat will be favor for breeding HLIP tolerant varieties.

Although many documents have focused on the mechanisms of plants for adaptation to high light stress, such as leaf and chloroplast movement, D1 protein, energy dissipation by xanthophylls cycle, and ROS scavenging enzymes and antioxidants (Powles, 1984; Long et al., 1994; Takahashi et al., 2008), we still know less about the genetic basis of wheat tolerance to HLIP stress at the whole-genome level. High-density genetic linkage map enables to dissect genome regions which regulate complex traits. Many QTLs have been identified for chilling-dependent photoinhibition in maize (Fracheboud et al., 2004; Jompuk et al., 2005; Pimentel et al., 2005) and tomato (Oyanedel et al., 2000 and 2001). In contrast, to our knowledge, no QTL linked with HLIP tolerance has been reported in plants. The current work was to determine genomic regions and the effects of QTLs controlling HLIP tolerance in winter wheat.

Materials and methods

Plant materials

A doubled haploid population consisting of 148 doubled haploid lines (DHLs) and their parents Hanxuan10 (HX, female parent) and Lumai14 (LM, male parent) were used in this study. HX, released in 1966 with light-green leaves, is mainly grown in Northwestern China while LM, a high yield variety released in 1986 with dark-green leaves, is mainly cultivated in Northern China (Jing et al., 1999; Hao et al., 2003). They were planted in the experimental station of Institute of Genetics and Developmental Biology (116°41′27″E, 40°10′1″N), Chinese Academy of Sciences in Beijing in the growing seasons of 2004–2005 and 2005–2006. At the end of September, seeds were sown in four 1.5-m-long rows spaced 23-cm apart with 50 seeds in each row. In next May representative healthy flag leaves, five for each line, were collected at 0, 7, and 14 days post anthesis (DPA) in 2005 and at 7 DPA in 2006, and then were used in HLIP treatment.