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Early anthesis and delayed but fast leaf senescence contribute to individual grain dry matter and water accumulation in wheat

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ABSTRACT

The physiological process of how anthesis time and leaf senescence patterns affect individual grain weight of wheat has only been partially elucidated. In this study, a recombinant inbred line mapping population of bread wheat (*Triticum aestivum* L. 'Forno') and its relative spelt (*Triticum spelta* L. 'Oberkulmer'), contrasting for phasic development and leaf senescence kinetics, was used to understand the physiological and genetic relationships among anthesis time, leaf senescence, grain filling processes, and individual grain weight. Phenotypic measurements were taken in the field over two growing seasons. The results showed that earlier anthesis and delayed leaf senescence were associated with larger grains. Furthermore, early anthesis and delayed but fast leaf senescence promoted grain filling rate (but shortened its duration), grain water absorption rate and maximum grain water content, while individual grain dry matter and water accumulation displayed strong relationships with individual grain weight. A total of 118 significant quantitative trait loci (QTL) were identified in this mapping population, including six QTL for anthesis dates, 24 for flag leaf senescence, 69 for grain filling traits, and 19 for individual grain weight. Frequent QTL coincidences between these traits were observed on chromosomes 2A, 3B, 4A, 4DL, 5A, 5B, 5DL and 7B. Analysis of allelic effects confirmed the above physiological relationships. Therefore, anthesis time and leaf senescence affect individual grain weight at least partly through their effects on individual grain dry matter and water accumulation, resulting from pleiotropy or tight gene linkages. Slightly early anthesis, and delayed but fast leaf senescence, can be used to maximize individual grain weight and yield potential in wheat.

1. Introduction

Flowering in wheat (*Triticum aestivum* L.) is a key event during plant life cycle, as it defines the beginning of the grain filling process for yield formation. Flowering time in wheat is flexible, which allows it to be cultivated in diverse environments around the world, from South America and southern Oceania to North America and northern Europe and Asia, and from sea level to *c.* 3000 m (Slafer and Whitechurch, 2001). For a given genotype, however, an appropriate anthesis date is needed to match its regional environment for adaption. In addition, fine-tuning of this time is also important to maximize grain yield. It has been found that the growth period immediately before anthesis, which coincides with rapid spike growth, determines floret fertility and in turn grain number at maturity (González et al., 2011; Slafer and Rawson, 1994). This critical period also overlaps with the ovary development within florets, and consequently affects individual grain weight (Calderini et al., 1999). Immediately after fertilization, endosperm cell division and enlargement take place (Shewry et al., 2012), an important process determining final individual grain weight (Brocklehurst, 1977). Therefore, optimizing the timing of anthesis can contribute to grain yield potential. On the other hand, wheat production is highly sensitive to environmental changes at and around anthe-

Abbreviations: chl, chlorophyll; Chl_{accum}, accumulated chlorophyll content; Chl_{loss}, duration of rapid chlorophyll loss; Chl_{per}, duration of chlorophyll persistence; Chl_{tot}, total duration of chlorophyll persistence and loss; °Cd, degree day; GA, green area; GA_{accum}, accumulated green area; GA_{loss}, duration of rapid green area loss; GA_{per}, duration of green area persistence; GA_{tot}, total duration of green area persistence and loss; GF, grain filling; GFR, grain filling rate; H^2, broad sense heritability; LOD, logarithm of the odds; Max chl, maximum chlorophyll content; Max CLR, maximum chlorophyll loss rate; Max GALR, maximum green area loss rate; MWC, maximum water content of grain; QTL, quantitative trait locus; RIL, recombinant inbred line; TGW, thousand grain weight; t_{max}, the time at maximum grain filling rate; t_{mwc}, the time at maximum water content; WAR, grain water absorption rate; WLR, grain water loss rate.

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sis. Drought and high temperature during this time, for example, reduce yield (8–30%) and yield components (grain number and grain size) (Lizana and Calderini, 2013; Semenov et al., 2014). These effects can be more common in global warming scenarios, where an increase in frequency of heat stress around anthesis has been predicted in Europe (Semenov et al., 2014). A potential strategy to adapt wheat for climate change is earlier anthesis, by escaping excessive temperature and drought through rapid development. Earliness may also work for wheat growing areas with terminal drought (Izanloo et al., 2008; Lopes and Reynolds, 2011), and with short growing seasons (Iqbal et al., 2007).

From anthesis onwards, grain growth commences, coinciding with leaf senescence. Leaves are the major sites for current photosynthesis, which, together with the preanthesis reserves, supplies assimilates for grain filling. Leaf senescence kinetics during grain filling can be divided into two phases: full functionality and rapid senescence (Wu et al., 2012). Delayed onset of senescence with longer functional photosynthesis (stay-green) may produce more assimilates for developing grains, and thus has potential to maximize grain yield. In fact, higher crop productivity has been well documented to be associated with delayed senescence, for example, in wheat (Bogard et al., 2011; Christopher et al., 2008; Derkx et al., 2012; Gaju et al., 2011; Verma et al., 2004), and other crops as reviewed by Gregersen et al. (2013). The stay-green phenotype is more advantageous when wheat plants grow under stressed conditions during the postanthesis period such as high temperature, drought, elevated ozone, nutrient deficiency and disease infections, where grain yield is more prone to be source-limited (Christopher et al., 2008; Gaju et al., 2011; Gelang et al., 2000; Joshi et al., 2007). Rapid senescence is the final stage of the leaf life cycle. Senesing leaves at this stage display yellowing and loss of photosynthetic capacity, proceeding from lamina tips to the bases close to the stems. This process has been considered as a form of programmed cell death (Gan and Amasino, 1997), and plays an important role in nutrient recycling. During senescence, chloroplasts are broken down; chlorophyll, proteins (e.g., Rubisco), membrane lipids and other macromolecules are then degraded, so that the resultant nutrients can be transported into growing grains. In particular, the remobilization of nitrogen in the forms of glutamate, aspartate, threonine, serine and glutamine from senesing leaves greatly contributes to grain protein concentration at maturity (Distelfeld et al., 2014; Gaju et al., 2014). It has been demonstrated that the functional *Gpc-1* (*NAM-1*) genes confer wheat cultivars or lines with earlier senescence, efficient nutrient remobilization from leaves, and, in turn, higher grain protein and micronutrient (iron and zinc) contents; however, they reduce grain yield under some environments (Distelfeld et al., 2014; Uauy et al., 2006). Delayed leaf senescence favours grain yield improvement, but not nutrient use efficiency, a dilemma of senescence in wheat breeding (Gregersen et al., 2008). Therefore, optimizing leaf senescence kinetics is needed to make better use of both current photosynthetic capacity and degraded nutrients.

The present study aimed to understand how anthesis time and leaf senescence affect individual grain weight, the major determinant of yield during the postanthesis period. A mapping population of bread wheat and spelt with contrasting phasic development and leaf senescence kinetics was used, and then the variation in anthesis time, the onset and progression of leaf senescence, individual grain dry matter accumulation, grain water uptake and loss, and final individual grain weight, was quantified. Physiological and genetic relationships between these processes were established, resulting in a trait interaction model, which can be used to build a wheat ideotype with appropriate anthesis and leaf senescence patterns for breeding.

2. Materials and Methods

2.1. Plant materials and field experiments

A mapping population, consisting of 226 F_5 recombinant inbred lines (RILs) derived from the cross between a Swiss winter bread wheat cultivar 'Forno' (*Triticum aestivum* L.) and a Swiss winter spelt cultivar 'Oberkulmer' (*Triticum spelta* L.) (Messmer et al., 1999), was used in this study. Field experiments were carried out at the University of Nottingham Farm, Leicestershire, UK (52°50'N, 1°15'W, 50 m) in 2011–2012 and 2012–2013. The RILs and two parents were grown in a randomized complete block (RCB) design with three replicates. The soil was a sandy loam (pH 7.6), containing 78.2 (in 2012) and 70.4 (in 2013) kg N ha^{-1} in the top 90 cm. The seeds were sown at 250 seeds m^{-2} on 19 October 2011 (6 × 1.6 m plots) and on 31 October 2012 (12 × 1.6 m plots). A prophylactic program of crop management (disease, weed, pest, and fertilizer) was conducted according to standard agronomic practice. Two subsets (72 RILs in 2012 and 110 RILs in 2013; based on the significant variation in the traits of interest) were selected to quantify all the traits, with the exception of individual grain weight, which was measured on 226 RILs.

2.2. Anthesis time

A spike was judged as flowering when the first anthers were extruded from the middle spikelets. Anthesis date of a plot was recorded when 50% of the spikes started flowering. Evaluation was carried out every day until all plots finished flowering. Calendar dates of anthesis were then converted into accumulated thermal time (degree days, °Cd). Temperature data was obtained from the nearby meteorological station. Daily thermal time was calculated as the average of maximum and minimum air temperature (or the base temperature 0 °C, whichever was higher).

2.3. Leaf senescence

Leaf senescence was assessed based on flag leaves, using two approaches: green area (GA) loss and chlorophyll (chl) loss, at a 5-day interval from anthesis onwards in both seasons. GA of the flag leaves in a plot was rated visually using a scale from 10 (0% yellowing) to 0 (100% yellowing) (Torres and Pietragalla, 2012). Meanwhile, the chl concentrations of flag leaves were nondestructively measured using a chlorophyll meter (SPAD 502, Minolta, USA). For each plot, measurements were taken on five healthy, clean leaves, three points along each leaf (one third, half and two thirds, avoiding the midrib and major veins). The average of 15 readings was recorded, and expressed as chlorophyll concentration index (CCI; ranging from 0 to 99.9).

Data of GA and chl loss of flag leaves were then fitted over the accumulated thermal time after anthesis using the Gompertz growth curve (Fig. 1) (Gooding et al., 2000).

$$G = A + Ce^{-e^{-B(t-M)}}$$

where G is the visual score or SPAD reading; A and $(A+C)$ are the lower and upper asymptotes, respectively; B is the relative senescence rate at the time M; M is the accumulated thermal time when senescence rate is at maximum and when visual scores or SPAD readings decline to $(A+0.37C)$; and t is the accumulated thermal time after anthesis.

Total duration of flag leaves (t_{total}; GA_{tot} or Chl_{tot}) was defined as the period from anthesis to the time at 90% senescence. t_{total} consisted of two components: persistence phase (GA_{per} or Chl_{per}), from anthesis to t_{onset} (the onset of senescence, 10% senescence), and