Preanthesis biomass accumulation of plant and plant organs defines yield components in wheat

Quan Xie, Sean Mayes, Debbie L. Sparkes *

Division of Plant and Crop Sciences, The University of Nottingham, Sutton Bonington Campus, Loughborough, Leicestershire LE12 5RD, UK

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ABSTRACT

The preanthesis period in wheat is critical for growth of plant organs including leaves, stems, spikes and roots. However, the roles of the preanthesis biomass accumulation of plant and plant organs in yield determination are only partially elucidated, and the underlying genetic basis remains largely unknown. This study aimed to understand the physiological and genetic relationships between preanthesis biomass accumulation and yield determination. In a mapping population of bread wheat (*Triticum aestivum* 'Forno') and its relative spelt (*Triticum spelta* 'Oberkulmer') contrasting for biomass, the dry weight of above-ground whole shoots and different organs, and leaf area, were analysed at GS39 (full flag leaf emergence) and anthesis. Yield components (thousand grain weight, grains per spike, final shoot biomass and grain weight per spike) and plant height were measured at maturity, followed by identification of quantitative trait loci (QTL) for all above traits. Field experiments were carried out in UK in 2011–2012 and 2012–2013 seasons, each using a randomised complete block design with three replicates. The results showed that there was a significant variation in biomass and its partitioning to organs at different stages. Consistent with the previous findings, stem water soluble carbohydrates and spike dry weight at anthesis contributed to thousand grain weight and grains per spike, respectively. In addition, this study revealed many other traits positively associated with one or more yield components, including biomass and leaf area at GS39, leaf and structural stem growth as well as whole shoot biomass at anthesis, and higher dry matter accumulation and crop (and spike) growth rates between the two stages. Increasing shoot biomass by removing other tillers at GS39 led to higher grain number and grain weight per spike. These results indicate the importance of the preanthesis growth of plant and plant organs for yield determination. Plant height was only weakly correlated with final biomass at maturity so it is possible to produce high-biomass genotypes without increasing plant height. Genetic analysis revealed 193 QTL associated with biomass and biomass-related traits. Frequent QTL coincidences between biomass and yield traits were observed, mainly on chromosomes 2B, 3A, 4A, 4B, 5A, 6A and 7B, indicating pleiotropy or tight gene linkages, consistent with their phenotypic associations. The preanthesis biomass traits associated with yield components and the underlying QTL, would facilitate the trait-based physiological and molecular breeding in wheat.

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1. Introduction

Wheat (*Triticum aestivum* L.) alone provides 19% of the calories and 20% of the protein for human diets (Braun et al., 2010),

* Corresponding author.
E-mail address: debbie.sparkes@nottingham.ac.uk (D.L. Sparkes).

and hence is a key contributor to global food security. A substantial increase in wheat production is required to keep pace with the burgeoning world population, being over 9 billion by 2050, as projected by the United Nations. However, the annual growth rates of wheat production and yield have slowed down, that is, only around 1.0% for both in last decades, less than those of demand (1.7%) (Reynolds et al., 2012; Ray et al., 2013). Future yield gain has also been challenged by global climate change, diminishing natural resources, rising prices for fertilisers and pesticides, and competition for arable land (Reynolds et al., 2012). From a breeding perspective, wheat cultivars need to be improved for further genetic gain. Conventional breeding has been mainly based on grain yield *per se*, together with the resistance to lodging, and biotic and

abiotic stresses. Such a strategy can be substantially enhanced by understanding the physiological and genetic basis of yield. Given its complexity, wheat grain yield can be dissected into relatively simpler traits: grain number and individual grain weight (numerical components), or biomass and harvest index (HI, biomass partitioning to grains) (physiological components). Traits influencing these components during plant growth and development have to be clarified so that the pathways of yield determination can be understood. Favourable traits and their underlying genes will be assembled to form ideotypes for wheat breeding. This strategy, i.e. trait-based physiological and molecular breeding, is more fundamental for yield improvement (Foulkes et al., 2011).

For numerical components, yield progress has been highly associated with an increase in grain number rather than individual grain weight (Slafer and Andrade, 1993; Shearman et al., 2005; Sanchez-Garcia et al., 2013). In some regions, grain weight has also been improved and contributed most to yield gain, especially in recent decades (Sadras and Lawson, 2011; Wu et al., 2014). Grain number is mainly determined by the preanthesis floret survival within spikelets. Each spikelet produces up to ten florets, but fewer than five (mainly those closest to rachis) can set grains, and the remaining ones die just before anthesis (Kirby, 1988; González-Navarro et al., 2015). It seems that the proportion of fertile florets, rather than the total number of floret primordia, is the main factor that determines the final number of fertile florets at anthesis (Brooking and Kirby, 1981; González-Navarro et al., 2015). There is a strong and positive relationship between spike dry weight (DW) at anthesis and floret survival (Fischer, 1985, 2011; González et al., 2011). As spike DW can be expressed as a function of spike growth duration (SGD), crop growth rate (CGR), and biomass partitioning to spikes (spike partitioning index, SPI), an increase in these traits during the critical period before anthesis would favour spike growth and in turn floret survival (Fischer, 2011; Garcia et al., 2014). On the other hand, biomass partitioning to stems should be decreased to minimise the competition between spikes and stems for assimilates (Kirby, 1988).

Individual grain weight is largely determined during grain filling, but a short period before anthesis is also important. It has been proposed that carpel size prior to anthesis may set an upper limit for grain development, as there is a strong and positive relationship between them (Calderini et al., 1999; Hasan et al., 2011; Xie et al., 2015). Carpel growth seems to be responsive to preanthesis biomass accumulation and partitioning; for example, increasing assimilate availability through de-graining at heading leads to greater carpel size (Calderini and Reynolds, 2000). After fertilisation, there is evidence that endosperm cell number, as affected by the assimilate availability during the first two weeks after anthesis, defines a threshold of potential grain weight (Brocklehurst, 1977; González et al., 2014). Rapid dry matter accumulation is then initiated, followed by grain maturation and desiccation. During grain filling, the assimilates are supplied from the current photosynthesis and dry matter translocation of leaves, spikes and stems. The amount of newly synthetic biomass between anthesis and maturity depends on the timing of plant senescence, and delayed senescence is usually believed favourable (Gregersen et al., 2013). Water soluble carbohydrates (WSCs) in vegetative parts (mainly stems) show positive associations with grain weight and yield (Foulkes et al., 2007; Rebetzke et al., 2008), and the estimated contribution of total WSCs to yield can be as high as 50%, depending on growing conditions (e.g. more significant under drought) (van Herwaarden et al., 1998a; Rebetzke et al., 2008). In addition, structural nutrients (particularly nitrogen) can be partly recycled during terminal senescence for growing grains (Distelfeld et al., 2014).

Physiologically, yield is a product of plant biomass and HI. HI has been largely improved with the use of dwarfing genes, and closely associated with yield progress (Shearman et al., 2005; Sadras and Lawson, 2011; Sanchez-Garcia et al., 2013). HI currently reaches approximately 0.45–0.50 in spring wheat and 0.50–0.55 in winter wheat, approaching its theoretical maximum value (approximately 0.64 in winter wheat) (Foulkes et al., 2011; Reynolds et al., 2012). To further increase HI, biomass partitioning to different plant organs needs to be optimised. Genetic variation in biomass partitioning has been observed in elite wheat lines, and this variation can be broadened by introducing desirable traits from wild species existing in Triticeae (Foulkes et al., 2011; Reynolds et al., 2012). However, given no systematic progress in HI since the early 1990s, future yield gain will depend more on an increase in biomass (Fischer, 2011; Reynolds et al., 2012). Recent yield improvement has showed an association with increased biomass (Shearman et al., 2005; Sadras and Lawson, 2011). Biomass is a function of light interception (LI) and radiation use efficiency (RUE, biomass per unit of radiation intercepted) (Reynolds et al., 2012). LI can be improved by optimising canopy size (e.g. large leaves and spikes), architecture (e.g. erect leaves) and longevity (e.g. early vigour and late senescence), while increasing plant photosynthesis is required for higher RUE (Reynolds et al., 2012).

As stated above, there are quite a number of studies focusing on the pre-anthesis phase in wheat, including stem elongation period and spike dry weight at anthesis as related to floret fertility, and carpel size and stem WSCs as related to individual grain weight. However, whether the other traits such as leaf growth, structural stem development, spike growth dynamic, competition between plant parts and overall crop growth before anthesis, would determine the process of yield formation is rarely elucidated in detail. Furthermore, little is known about the underlying genetic elements bridging the preanthesis plant growth with yield production. This work aimed to provide a comprehensive understanding of the physiological and genetic associations of the preanthesis growth of plant and plant organs with yield determination. Plant-level biomass accumulation and partitioning at key growth stages (GS), namely GS39 (full flag leaf emergence), anthesis and maturity, were analysed in a mapping population of bread wheat (*T. aestivum* 'Forno') and spelt (*T. spelta* 'Oberkulmer') contrasting for biomass production. Although observation of biomass in this study was based on single-plant level rather than crop scale, these results help to elucidate formation of yield components in terms of physiology and genetics in a simpler way. The physiological traits of biomass associated with yield components were determined, and subsequently the genetic dissection of biomass, biomass-related traits, and yield components, were carried out via a detailed quantitative trait locus (QTL) analysis.

2. Materials and methods

2.1. Plant materials and field experiments

Spelt is a relative of bread wheat, and has higher biomass but lower harvest index than the latter (Koutroubas et al., 2012). A cross between the Swiss winter bread wheat 'Forno' and Swiss winter spelt 'Oberkulmer' was carried out to introduce genetic variation in biomass, and a total of 226 F_5 recombinant inbred lines (RILs) were derived (Messmer et al., 1999). This population was grown in a sandy loam soil (pH 7.6, *c.* 80 and *c.* 70 kg nitrogen ha^{-1} available in 0–90 cm depth as measured before the growing seasons in 2011 and 2012, respectively) at University of Nottingham Farm, Leicestershire, UK. Field experiments were conducted in 2011–2012 and 2012–2013 (referred hereafter as 2012 and 2013, respectively), and arranged according to a randomised complete block design with three replicates. The seeds were sown at 250 seeds m^{-2} in plots of 6 × 1.6 m in 2011 and 12 × 1.6 m in 2012. An additional *c.* 140 (in 2012) and *c.* 160 (in 2013) kg nitrogen ha^{-1} in the form of