

Genomic dissection of whole-plant responses to water deficit in durum wheat × wild emmer wheat RIL population

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ABSTRACT

Drought is the major environmental stress limiting wheat productivity worldwide. Wild emmer wheat [*Triticum turgidum* ssp. *dicoccoides* (körn.) Thell] gene-pool harbors a rich allelic repertoire for various morpho-physiological traits conferring drought-resistance. The genetic and physiological basis of drought responses was studied in tetraploid wheat population of 152 recombinant inbred lines, derived from a cross between durum wheat (*cv.* Langdon) and wild emmer wheat (acc. G18-16), under contrasting water availabilities. A total of 102 QTLs were mapped for 10 traits. Several QTLs showed environmental specificity, accounting for productivity and related traits under water-limited or well-watered conditions and in terms of drought-susceptibility index. Major genomic regions controlling productivity and related traits were identified on chromosomes 2B, 4A, 5A and 7B. QTLs for productivity were associated with QTLs for drought-adaptive traits suggesting the involvement of several strategies in adaptation to drought-stress. Fifteen pairs of QTLs for the same trait were mapped to seemingly homoeologous positions, reflecting synteny between the A and B genomes. The identified QTLs may facilitate the use of wild alleles for improvement of drought-resistance in elite wheat cultivars.

INTRODUCTION

Drought is the main environmental factor limiting wheat productivity in many parts of the world. Developing crop cultivars with greater drought-resistance is considered a sustainable and economically viable solution to this problem. The multifaceted nature of drought coupled with limited knowledge on the genetic and physiological bases of productivity under water deficit have hindered breeding to improve crop adaptation to such conditions. Better understanding of these strategies and the dissection of genetic factors involved in plant responses to drought stress is expected to provide a solid foundation for genetic improvement of crop productivity under arid conditions. The advent of molecular markers enables to dissect such complex traits like drought resistance via analysis of quantitative trait loci (QTL). Most previous mapping studies focused on QTLs responsible for improved productivity under arid conditions (Tuberosa & Salvi 2006). Several other

studies reported on QTLs associated with morpho-physiological traits underlying drought responses. However, only a few studies reported on QTL mapping of productivity and physiological differences in the same populations, enabling to identify possible associations between these traits. The identification of drought-related QTLs plays a central role in crop improvement through marker assisted selection and eventually can lead to QTL cloning.

Wild emmer wheat [*Triticum turgidum* ssp. *dicoccoides* (körn.) Thell], the tetraploid (2n=4x=28; genome BBAA) progenitor of domesticated wheats, was found to harbor a rich phenotypic diversity in morpho-physiological traits conferring drought resistance (Peleg *et al.* 2005) as well as allelic diversity at the DNA level (Peleg *et al.* 2008a). The aims of the current study were to (i) determine the chromosomal location and phenotypic effects of QTLs associated with wheat response to water-deficit, (ii) dissect the genetic-physiological basis of wheat adaptive mechanisms to such conditions, and (iii) identify potential alleles from the wild for further wheat improvement.

MATERIALS AND METHODS

A population of 152 F₆ recombinant-inbred lines (RILs) was developed by single-seed descent, from a cross between durum wheat cultivar Langdon (LDN hereafter) and wild emmer wheat accession #G18-16. Plants were characterized in the field under contrasting water availabilities. Two irrigation regimes were applied during the winter months (to mimic the natural pattern of rainfall in the Mediterranean region) via drip system: well-watered control (750mm) and water-limited (350mm).

RILs characterization included *plant productivity* (grain yield, spike dry matter, total dry matter and harvest index), *phenological variables* (days from planting to heading, days from heading to maturity and leaf rolling) and *drought related physiological traits* (carbon isotope ratio ($\delta^{13}\text{C}$, an indicator of water-use efficiency), osmotic potential and chlorophyll content). For each measured variable a "drought-susceptibility index" (S) was calculated (Fischer & Maurer 1978). A genetic linkage map of 2,317 cM was developed based on 197 SSR and 493 DaRT markers (Peleg *et al.* 2008b). QTL

analysis was performed with the MultiQTL package (<http://www.multiqtl.com>) using the general interval mapping for a RIL population.

RESULTS AND DISCUSSION

A total of 102 QTLs, in 29 non-overlapping genomic regions, were mapped for 10 traits, with LOD scores ranging between 3.0-35.4. Among the detected QTLs, only 47 (46.1%) showed no significant response to changes in water availability (constitutive effect); 19 QTLs (18.6%) were most influential or exclusively expressed under the water-limited conditions, 15 (14.7%) under the well-watered conditions and 21 QTLs (20.5%) were associated with drought-susceptibility indices (Table 1). QTLs that are specific to arid conditions could be beneficial for improving plant performance rather than solely constitutive QTLs, when breeding for drought-prone environments. Moreover, since different sub-sets of QTLs accounted for productivity under contrasting conditions, a wide environmental-adaptation can be obtained by combining constitutive QTLs with various sets of environment-specific QTLs.

Grain yield, spike DM, total DM and harvest index were used as indicators of plant productivity, revealing jointly 28 QTLs. Drought susceptibility indices, reflecting the stability of these variables across environments, revealed additional 6 QTLs. A total of 15 non-overlapping genomic regions were associated with plant productivity, either in absolute or S terms, with the major QTLs being in chromosomes 2BL, 4AL, 5AS and 7BS. The relationships between plant-productivity and drought-related traits may shed light on drought adaptive mechanisms. Each of the genomic regions associated with plant productivity was co-localized with one or more drought adaptive traits, reflecting escape or drought-resistance strategies. Plant phenology was associated with productivity in 6 genomic regions, confirming the role of earliness (drought escape) under Mediterranean environment. Nevertheless, in four of these cases other physiological traits were also involved. Furthermore, plant productivity was associated with chlorophyll content in 7 genomic regions, osmotic potential in 6 regions, leaf rolling in 5 regions and $\delta^{13}\text{C}$ in two regions. The combination of various strategies and multiple alleles from diverse resources is expected to enhance the productivity of wheat, as well as other cereals, in drought-prone environments.

As many as 30 QTLs (15 pairs) for the same trait were mapped to seemingly homoeologous positions on all seven chromosome groups of the tetraploid wheat. Among the homoeologous-QTLs affecting drought-adaptive traits, in three pairs the wild emmer allele was favourable, in two the LDN allele, and in six pairs reciprocal alleles were favourable, a pattern that seems to be rather random. Interestingly, in all four homoeologous QTL pairs associated with plant-

productivity, each pair was conferred by the same parental allele (two each). It may be speculated that the drought-adaptive QTLs showed genomic plasticity, thus tolerating mutation in one of the loci of their homoeologous group throughout their evolutionary history. At the same time, productivity QTLs showed lower level of genomic plasticity, reflecting the effects of two different selection pressures (natural and anthropogenic) imposed on the respective parental lines.

Table 1. Summary of QTLs associated with plant productivity, drought-related morpho-physiological traits and phenology variables detected in tetraploid wheat (Langdon \times G18-16).

Trait	# of QTLs	Chromosomal locations	Range of LOD
Grain yield	8	1B, 2A, 2B, 2B, 4A, 4B, 5A, 7B	3.3-11.9
Spike dry matter	9	2A, 2A, 2B, 4A, 4A, 4A, 5A, 7A, 7B	3.0-14.4
Total dry matter	6	1B, 2B, 4A, 4B, 5A, 7A	3.3-6.9
Harvest index	11	1B, 2A, 2B, 2B, 3B, 4A, 5A, 5B, 6A, 6B, 7B	4.3-19.4
Carbon isotope ratio	12	1A, 1A, 2A, 2A, 4A, 5A, 5B, 5B, 6A, 6A, 6B, 7B	3.1-12.4
Osmotic potential	11	1B, 2A, 2A, 2B, 3A, 3B, 4B, 5A, 5B, 6A, 6B	3.4-5.2
Chlorophyll content	11	1A, 1A, 1B, 1B, 2B, 4A, 5A, 5B, 6A, 7A, 7A	3.1-6.9
Flag leaf rolling index	14	1A, 2A, 2B, 2B, 2B, 3B, 4B, 5A, 5B, 6A, 6B, 7A, 7B, 7B	3.0-9.6
Days from planting to heading	9	1B, 2B, 2B, 3A, 4B, 5A, 5A, 7B, 7B	4.2-35.4
Days from heading to maturity	11	1B, 1B, 2B, 2B, 4A, 4B, 5A, 5B, 7A, 7B, 7B	3.9-16.8
Total	102		

Conclusions and implication for further wheat improvements

Using a rain-protected facility with precise control of water application enabled to distinguish the effect of water availability from other environmental effects (e.g., temperature, day length, soil type, etc.). Plant adaptations to environmental stresses are regulated through multiple morpho-physiological mechanisms at the whole-plant levels. These physiological mechanisms

are under multigenic control and interact with environmental factors. Wild emmer offers abundant genetic diversity in multiple biotic and abiotic stress adaptive traits, including drought-resistance. The concurrent mapping of QTL for productivity and drought-adaptive traits as well as the dissection of their inter- and intra-relationships provide an insight into the functional basis of the physiology, genomic architecture and evolution of drought response in wheat and other cereal crops. The identification of several complementary favourable alleles on homoeologous chromosomes suggests that re-introducing wild alleles into domesticated wheat cultivars could result in improved drought resistance. Our results exemplify unique opportunities to exploit favourable alleles that were excluded from the domesticated gene pool as a result of the genetic bottleneck involved in the domestication processes.

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