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Title

Genomic-Physiological Dissection of Grain Protein and Mineral Nutrient Concentrations in Wild Emmer Wheat Under Contrasting Water Availabilities

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INTRODUCTION

Mineral nutrients play fundamental roles in the biochemical and physiological functions of biological systems. While higher plants obtain their mineral nutrients primarily from the soil, animal and humans depend mostly on higher plants to supply them with mineral nutrients. Mineral nutrient malnutrition, and particularly deficiency in Zn and Fe, afflicts over three billion people worldwide, resulting in overall poor health, anaemia, increased morbidity and mortality rates (Cakmak 2008). Enhancement in grain concentrations of mineral nutrients (biofortification), either agronomically or genetically, is considered the most promising and cost-effective approach to alleviate malnutrition and related health problems (Welch and Graham 2004; Cakmak 2008; Peleg et al. 2008a). This solution, however, requires a comprehensive exploration of potential genetic resources and an in-depth understanding of the physiological and genetic basis of mineral nutrients accumulation.

Wheat (*Triticum* spp.) is the major staple food crop in many parts of the world. Therefore, the composition and nutritional quality of the wheat grain has a significant impact on human health and well-being, especially in the developing world. The joint effects of domestication and its associated evolutionary phenomena (*i.e.*, founder effect) following modern breeding processes has eroded the genetic basis of crop species (Ladizinsky, 1998; Tanksley & McCouch, 1997). Domesticated wheat contains very low levels of minerals and shows a narrow genetic variation as compared with its wild relatives. Wild emmer wheat [*T. turgidum* ssp. *dicoccoides* (körn.) Thell] is the tetraploid ($2n=4x=28$; genome BBAA) progenitor of both domesticated tetraploid durum wheat [*T. turgidum* ssp. *durum* (Desf.) MacKey] and hexaploid ($2n=6x=42$; BBAADD) bread wheat (*T. aestivum* L.). Wild emmer germplasm harbors a valuable source of allelic repertoire for improving of various economically important traits (e.g. Nevo et al., 2002) including drought resistance (Peleg et al., 2007) and grain mineral concentrations (Cakmak et al., 2004; Peleg et al., 2008a, 2009).

The aims of this study were (i) to characterize the genetic variation in grain protein and mineral nutrient concentrations of wild emmer wheat under two levels of water availability; (ii) determine the chromosomal location and phenotypic effects of QTLs associated with grain mineral nutrient concentration in a recombinant-inbred line (RIL) population, derived from a cross between durum wheat and wild emmer; and (iii) identify potential alleles from the wild for future wheat improvement.

MATERIALS AND METHODS

Plant material included: (1) Twenty two wild emmer accessions, representing a range of drought resistance capacity (Peleg et al. 2005), as well as two durum wheat cultivars (Inbar and Svevo); and (2) a mapping population of 152 F₆ RILs developed by single-seed decent procedure from a cross between durum wheat (*cv.* Langdon; LDN hereafter) and wild emmer wheat (accession G18-16) (Peleg et al. 2008b). Plants were grown in a rain-out shelter under two irrigation regimes, well-watered control (750 mm) and water-limited (350 mm) (termed hereafter as "wet" and "dry", respectively). Plants were characterized for grain yield (GY) and grain mineral concentrations. Nitrogen in the grain was determined by using a C/N analyzer (TruSpec CN, Leco Co., USA). Grain nitrogen concentration was multiplied by 5.83 to obtain grain protein concentration (GPC). Grain macronutrients (calcium, Ca; magnesium, Mg; potassium, K; phosphorus, P; and sulphur, S) and micronutrients (zinc, Zn; iron, Fe; copper, Cu; and manganese, Mn) concentrations were determined by inductively coupled plasma-optical emission spectroscopy (ICP-OES; Vista-Pro Axial; Varian Pty Ltd, Australia), after digesting

samples in a closed microwave system.

RESULTS AND DISCUSSION

World cereal demand is growing at the present in accordance with the global expansion of human populations. During the past several decades, the primary objective of plant breeding programs has been to increase yield, a quest that will remain a principal concern in providing the calorie intake required for the growing world population. However, equally important, but largely overlooked in breeding programs, is the nutrient composition and concentration, particularly the micronutrients, in the grains of staple food crops (Cakmak 2008). Among grain mineral nutrients, Zn and Fe deficiencies are the most important global challenges.

The results obtained in the current study show that wild emmer wheat accessions exhibited higher grain Zn concentration under both treatments (68.8-139.5 mg kg⁻¹ and 71.1-133.5 mg kg⁻¹ for the dry and wet treatment, respectively) as compared to the durum cultivars (49.4-54.7 mg kg⁻¹ and 52.6-56.2 mg kg⁻¹, respectively; Fig. 1). Grain Zn concentration was positively correlated with grain Fe concentration ($r=0.83^{***}$ and $r=0.86^{***}$ for the dry and wet treatments, respectively) and GPC ($r=0.65^{***}$ and $r=0.51^{**}$, respectively). Analysis of variance showed highly significant irrigation \times accession interactions for grain Zn, Fe and GPC concentrations. While certain accessions exhibited a stable ranking of Zn concentrations across the two treatments (*i.e.* MM5/2), the ranking of other accession was greatly affected by the water availability (*i.e.* 18-39).

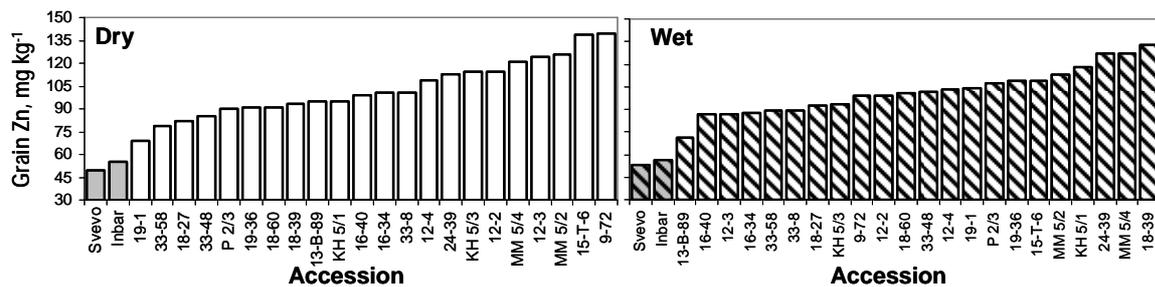


Figure 1. Grain zinc concentrations of 22 wild emmer wheat accessions and two durum wheat cultivars (in gray) grown under well watered and water limited irrigation regimes.

Eighty two significant QTLs, scattered across all 14 chromosomes of the tetraploid wheat, were detected for 10 grain mineral nutrient concentrations characterized under three environments (Table 1). In 50 QTLs (61%) the wild allele (G18-16) contributed to improved grain mineral concentrations and in the remaining 32 QTLs (39%) the domesticated allele (LDN) was favorable. Forty four QTLs (54%) showed no interaction with environmental conditions, whereas 38 QTLs exhibited G \times E interaction, of which 25 QTLs were detected under all environments with different effects and 13 QTLs were detected under one environment.

Abundant experimental evidence shows that GPC increases with N application up to a certain point, after which it remains stable, while the straw N concentration keeps increasing (Barneix 2007). Genetic improvement is the most promising strategy to increase GPC under either optimal or sub-optimal N availability. In the present study, 10 QTLs associated with GPC were identified (Table 1). The wild emmer alleles (G18-16) were favorable in most (80%) GPC QTLs, thus confirming the potential of wild emmer germplasm for wheat improvement. **Micronutrients** (Zn, Fe, Cu and Mn) are required by plants at very low concentrations, while at high concentrations they may become toxic. Thus, plants have evolved a complex regulation

networks to control minerals homeostasis. In the current study, Zn was conferred by 6 QTLs (2A, 2A, 5A, 6B, 7A, 7B), with the wild allele being favorable in five cases. Fe was conferred by 11 QTLs, with the wild allele being favorable in five cases. Cu was conferred by 10 QTLs, with the wild allele being favorable in six cases. Mn was conferred by 2 QTLs, both with the domesticated allele being favorable. QTLs for Mn were found only in the WW07 environment, indicating a pronounced G×E interaction (Table 1). **Macronutrients** (Ca, Mg, K, P and S) are essential elements used by plants in relatively large amounts. Unlike micronutrients, which have only functional roles, macronutrients have both structural and functional roles. Ca was conferred in the current study by 9 QTLs, with the wild allele being favorable in four cases. Mg was conferred in the current study by 8 QTLs, with the wild allele being favorable in six cases. K was conferred in the current study by 8 QTLs, with the wild allele being favorable in only two cases. P was conferred in the current study by 8 QTLs, with the wild allele being favorable in five cases. S was conferred in the current study by 10 QTLs, with the wild allele being favorable in nine cases (Table 1).

Table 1. Summary of QTLs detected in tetraploid wheat (LDN × G18-16) RIL population associated with grain protein and nine mineral nutrient concentrations.

Trait, grain concentration	# QTLs	LOD	Favorable allele		Environment			
			G18-16	LDN	All env ¹	WL05	WW05	WW07
Protein	10	3.2-10.4	8	2	7	-	2	1
Zinc	6	3.7-16.4	5	1	5	1	-	-
Iron	11	4.6-16.7	5	6	9	-	-	2
Copper	10	4.9-10.4	6	4	10	-	-	-
Manganese	2	3.9-4.1	-	2	-	-	-	2
Calcium	9	6.0-16.0	4	5	9	-	-	-
Magnesium	8	5.0-9.8	6	2	7	1	-	-
Potassium	8	3.9-12.2	2	6	5	2	1	-
Phosphorus	8	5.3-15.3	5	3	8	-	-	-
Sulfur	10	3.4-9.3	9	1	8	-	-	2
Total	82	3.2-16.7	50	32	69	4	3	6

¹. In one case QTL conferring Ca (on chromosome 4B) was detected in two environments (WW05 and WW07)

The 82 QTLs discovered in the current study were located in 32 non-overlapping genomic regions. Relationships between QTLs conferring grain protein and mineral concentrations may shed light on possible common mechanisms influencing mineral concentrations in the grain of wheat and other cereal species. There was a significant positive correlation between GPC, Zn and Fe, which was supported by a significant overlap between QTLs, suggesting a common physiological-genetic control of these minerals. These identified genetic resources and QTLs may facilitate the use of wild alleles for improvement of grain protein and mineral concentrations in elite wheat cultivars. When breeding for improved grain quality, special attention should be given to avoid negative effects on grain yield. In wild emmer, neither negative nor positive associations between grain mineral concentrations and productivity were noted (Peleg et al. 2008a). Three out of 10 QTLs conferring GPC were significantly associated with QTLs conferring GY (2B, 4A, 7B). Higher GPC and lower yield were conferred by wild alleles in two genomic regions (2B, 4A) and by the domesticated allele in one region (7B). This was further supported by a negative correlation between GPC and GY ($r = -0.29$, $P = 0.0003$).

Conclusions and prospects for wheat improvement. During a long evolutionary history, wild emmer wheat has accumulated high genetic diversity for various biotic and a-biotic stress adaptations. The notion of using wild emmer gene resources in wheat improvement has been

repeatedly advocated since the discovery of the wild progenitor of the cultivated wheats about a century ago. A high genetic diversity was found among wild emmer wheat accessions in terms of drought resistance and grain mineral nutrient concentrations, with a considerable potential to improve both traits in cultivated wheat grown in zinc poor soils, suggesting that wild emmer is a potential source for improvement of cultivated wheats. Likewise, in most QTLs detected in the current study in a segregating population derived from a cross of domesticated × wild wheat, the wild parent allele was favourable.

QTLs conferring high grain mineral concentrations may reflect genes acting in one or more different steps, such as root uptake, root-to-shoot translocation, storage (in leaves or grain) and remobilization, as well as genes that encode regulatory proteins. The identified associations between QTLs affecting different mineral nutrients suggest physiological coupling of certain processes that govern mineral accumulation in wheat grain. Few genomic regions (Chr. 2A, 5A, 6B, 7A) were found to harbor clusters of QTLs for GPC and other minerals. These regions offer unique opportunities for synchronous improvement of GPC, Zn, Fe and other mineral nutrients in wheat grain. Our results exemplify unique opportunities to exploit favorable alleles that were excluded from the domesticated gene pool as a result of the genetic bottleneck involved in the domestication processes. The concurrent mapping of QTL for several minerals as well as the dissection of their inter- and intra-relationships provides an insight into the functional basis of the physiology, genomic architecture and evolution of minerals accumulation in wheat and other cereal crops.

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