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Yield of chromosomally engineered durum wheat-*Thinopyrum ponticum* recombinant lines in a range of contrasting rain-fed environments

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ABSTRACT

Introgressions of *Thinopyrum ponticum* 7AgL chromosome segments, spanning 23%, 28% and 40% of the distal end of durum wheat 7AL arm, were previously shown to contain multiple beneficial gene(s)/QTL for yield-related traits, in addition to effective disease resistance (*Lr19, Sr25*) and quality (*Yp*) genes. In the present study, durum wheat near isogenic recombinant lines (NIRLs), harbouring each of the three introgressions, were included for the first time in multi-location field trials, to evaluate general and environment-specific effects of the alien chromatin on 26 yield-related traits. Results from nine different trials across contrasting environments of Italy, Morocco and South Australia over four years revealed that the overall impact of 7AgL introgressions into the tetraploid wheat background did not incur, except in one environment, a major yield penalty. The effect of the three 7AgL segments on individual yield-contributing traits resulted in significant increases of biomass m^{-2} (+9%), spike number m^{-2} (+13%), grain number m^{-2} (+11%) and spikelet^{-1} (+8%), as well as a significant decrease in grain weight (−8%). When the separate NIRLs were analysed, each of the three 7AgL segments were associated with specific yield component variation. The effects of the 40%-long segment proved to be the most stably expressed across environments and involved significant increases of spike and grain number m^{-2} (13% and 15%, respectively), grain number spike^{-1} (10%) and spike fertility index (46%), though accompanied by a significant decrease in thousand grain weight (−23%). In spite of this trade-off between grain number and grain weight, their interplay was such that in four trials, including drier environments, a grain yield advantage was observed. This evidence, and comparison with the two other NIRLs, substantiates the hypothesized existence of major gene(s)/QTL for grain number in the most proximal 28–40% 7AgL region, exclusive to the 40%-long 7AgL introgression. The present study represents an important validation of the use of chromosomally engineered genetic stocks for durum wheat improvement, targeting not only disease resistance and quality traits but also relevant yield components.

1. Introduction

Due to the continuing need to enhance crop productivity to feed a burgeoning world population, amidst climate changes that will further add to the pressure of availability of land and water, the goal of significantly increasing yield of staple crops such as wheat is becoming more challenging than ever (Ray et al., 2013; Liu et al., 2016; Zhao et al., 2017). To mitigate against these ongoing challenges, crop species

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Abbreviations: NIRL, near isogenic recombinant line; HI, harvest index; SNM2, spike No. m^{-2}; BM2, biomass m^{-2}; GYM2, grain yield m^{-2}; GNM2, grain No. m^{-2}; TGW, 1000 grain weight; GYS, grain yield spike^{-1}; GNS, grain No. spike^{-1}; GNSP, grain No. spikelet^{-1}; SPN, spikelet No. spike^{-1}; PH, plant height; HD, days to heading; SDWA, spike dry weight at anthesis; TDWA, tiller dry weight at anthesis; SIA, spike index at anthesis; SDW, spike dry weight at harvest; TDW, tiller dry weight at harvest; CHAFF, chaff dry weight at harvest; SL, spike length; SFI, spike fertility index; FLW, flag leaf width; FLL, flag leaf length; FLA, flag leaf area; CHLZ75, chlorophyll content at Zadoks 75; CHLZ77, chlorophyll content at Zadoks 77; CHLZ79, chlorophyll content at Zadoks 79; GLM, general linear model

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are already undergoing a 'migration' from their conventional growing regions (Chapman et al., 2012). Durum wheat (*Triticum durum* var. *durum*, 2n = 4x = 28, genomes AB), cultivated on approximately 8% of the world's wheat area (Mediterranean basin, North America's Great Plains, Mexico, Australia, Russia, Kazakhstan, India, Ethiopia and Argentina; Bassi and Sanchez-Garcia, 2017; Royo et al., 2014), exemplifies this migration phenomenon, with its progressive displacement from traditional cultivation areas (Ceoloni et al., 2014a). To develop durum wheats with improved yield and adaptation, understanding and dissecting the multi-layered genotype × environment interaction is crucial if we are to close the gap between actual and attainable yields (Bassi and Sanchez-Garcia, 2017; Dodig et al., 2012; Maccaferri et al., 2011; Marti and Slafer, 2014; Parent et al., 2017; Slafer et al., 2014; Tardieu and Tuberosa, 2010; Zaïm et al., 2017).

A powerful strategy to enhance the genetic potential and plasticity of cultivated germplasm resides in the exploitation of the ample and still largely untapped variability present in wild wheat relatives (Zaïm et al., 2017; Ceoloni et al., 2014b, 2017a; Dempewolf et al., 2017; Prohens et al., 2017; Zhang et al., 2017). Targeted and precise introgression of useful alien genes is readily possible through efficient sexual means, foremost the cytogenetic methodologies of "chromosome engineering" (Ceoloni et al., 2005, 2014a, 2014b, 2015). This approach, integrated with continuously developing techniques of genome and chromosome analysis (e.g. marker-assisted selection, association mapping, next generation sequencing, *in situ* hybridization), represents a unique platform for creation of novel and breeder-friendly genetic stocks.

In the majority of cases, alien genes transferred into cultivated *Triticum* species have enhanced biotic and abiotic stress tolerance, thus indirectly contributing to yield improvement (Ceoloni et al., 2014a). Use of wild relatives for direct improvement of wheat yield components has instead been sporadic, as their productivity is poor, and conspicuous effects on wheat yield rarely observed (Ceoloni et al., 2015; Dempewolf et al., 2017; Zhang et al., 2017). Nonetheless, noteworthy examples do exist in the widely cultivated bread wheat, where there appears to be a higher buffering ability when chromosomes are manipulated vs. tetraploid durum wheat (reviewed in Ceoloni et al., 2014a, 2015; Mondal et al., 2016). One such example concerned the transfer of a portion from the group 7 chromosome arm (=7AgL or $7el_1L$) of the decaploid perennial species *Thinopyrum ponticum* (Popd.) Barkworth & D. R. Dewey (2n = 10x = 70, genomes $E^eE^eE^xStSt$, see Ceoloni et al., 2014b) onto the 7DL arm of bread wheat. The sizeable 7AgL translocation, named T4 (~70% of the recipient 7DL arm, harbouring the *Lr19+Sr25+Yp* genes), led to increased grain yield (5–35%), biomass (6–31%) and grain number (10–18%) across a number of non-moisture stress environments, and in different backgrounds of CIMMYT germplasm (Monneveux et al., 2003; Reynolds et al., 2001; Singh et al., 1998; Tripathi et al., 2005; Miralles et al., 2007).

The *Lr19+Sr25+Yp* gene package is considered particularly valuable for durum wheat breeding, due to the high efficacy of *Lr19* and *Sr25* resistance genes towards main rust diseases of the crop (Gennaro et al., 2009; Ceoloni et al., 2014a), and the contribution to increase carotenoid pigmentation and semolina colour of the *Yp* gene (Gennaro et al., 2007). Of several durum wheat-*Th. ponticum* recombinants obtained through chromosome engineering (Ceoloni et al., 2005), three, carrying 23%, 28% and 40% of the recipient 7AL arm replaced by homoeologous 7AgL segments (corresponding to distal portions of the T4 introgression), were employed in development of near-isogenic recombinant lines (NIRLs) into the background of cv. Simeto. The three NIRLs, evaluated for yield performance across four years in one rain-fed locality of Central Italy, showed increases in grain yield (1–36%), biomass (2–38%) and grain number (3–39%) associated with presence of 7AgL chromatin (Kuzmanović et al., 2014, 2016). Furthermore, detailed phenotyping of the NIRLs for several yield-contributing traits enabled the structural-functional dissection of 7AgL chromatin incorporated onto 7AL, with assignment of yield-contributing *Th. ponticum* genes/alleles (previously associated to the entire T4 segment) to specific 7AgL sub-regions (Kuzmanović et al., 2014, 2016).

With no information from other environments on the expression of 7AgL and its effects on yield in durum wheat, the aim of the present work was to assess the yield performance of the same three durum wheat-*Th. ponticum* NIRLs across an array of rain-fed environments, and to evaluate possible environment/7AgL segment-specific associations with final yield and individual yield-related traits, ultimately in view of using these recombinants across environments or in site-directed breeding programs.

2. Materials and methods

2.1. Plant materials

Three durum wheat-*Th. ponticum* NIRLs, named R5-2-10, R112-4 and R23-1 (hereafter referred to as R5, R112 and R23, respectively), developed in the background of cv. Simeto by repeated backcrossing (BC) (Ceoloni et al., 2005), were used across four years and three countries. Simeto (pedigree: selection from Capeiti 8 x Valnova) is a variety released in 1988, well adapted to the Italian growing conditions. The NIRLs have portions of *Th. ponticum* 7AgL chromosome arm replacing 23%, 28% and 40% of their distal 7AL arm, respectively, and all three lines include the alien *Lr19+Sr25+Yp* genes in the sub-telomeric region. Similarly to the plant material described in Kuzmanović et al. (2016), each of the genotypes analysed, corresponding here to $BC_5F_{5\text{-}9}$ (R5 and R112) and $BC_4F_{5\text{-}9}$ (R23) progenies, was represented by either being a homozygous carrier ("+") or non-carrier ("–") of the given 7AgL segment. Each "+" and "– "NIRL included two families originating from sister lines.

2.2. Field experiments

A total of nine rain-fed field trials were carried out over four years and four locations where durum is typically cultivated (two in Italy, one in Morocco and in one Australia) and used for the multi-environment yield assessment. Details on all trials are reported in Table 1. Years and locations were combined and hereafter referred to as environments, with a specific acronym assigned in Table 1. Two of the nine trials have been described previously in Kuzmanović et al. (2016) (VT12 and VT13), from where a subset of traits was considered in the present analysis. In eight environments, all three NIRLs with respective controls were used, while in AUS14, only R5 and R112 were analysed. Sowing densities applied were those commonly used in each of the experimental locations (Table 1). In all field experiments, complete randomized block designs with three replicates for each sister line was used, resulting in a total of 24 plots in AUS14 and 36 plots in the other eight environments (2 per each sister line, i.e. 6 per each +/– NIRL). Meteorological data during the growing seasons for daily temperatures (minimum, mean and maximum) and rainfall (Table 2) were retrieved from meteorological stations at experimental sites, except for MOR14, for which the data were downloaded from NASA's (National Aeronautics and Space Administration, USA) site for Prediction of Worldwide Energy Resource (http://power.larc.nasa.gov). All trials were managed according to standard local practices including fertilization, weed, pest and disease control, in order to avoid, in particular, leaf rust spreading on *Lr19* non-carrier plants (– NIRLs), hence to eliminate the indirect yield-contributing factor of *Lr19*-carriers (+ NIRLs).

2.3. Measurements of yield-related traits

A list of traits and details on environments in which the materials were analysed, as well as on the sample type and number for each replicated plot, are reported in Table 3. Measurements of all traits were performed as described in Kuzmanović et al. (2016) with some