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# Positive effects on yield-contributing traits associated with *Thinopyrum ponticum* chromosome segments introgressed into durum wheat

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**Abstract.** As a possible means of coping with the many challenges in today's wheat breeding, widening of the crop genetic basis via exploitation of alien genetic variation from wild relatives is a promising and sustainable approach. Thanks to recent progress in chromosome engineering, through which alien chromosome segments can be transferred to wheat, it is now possible to target even complex traits such as those related to the yield. During the last three seasons, under Mediterranean rainfed conditions, three durum wheat-*Thinopyrum ponticum* near-isogenic recombinant lines with distal portions of their 7AL arm replaced by 23%, 28% and 40% of alien (= 7AgL) chromatin, respectively, containing the *Lr19+Sr25+Yp* genes, were included in field trials with, first, spaced plants (2 years) and then, plots (1 year) for evaluation of 7AgL-associated effects on yield-contributing traits. Overall, the results revealed the involvement of defined 7AgL portions in the increase of traits such as flag leaf width and tiller number/plant (23-28% portion), grain number/m<sup>2</sup> and spike fertility index (28-40% portion), all traits contributing to the observed higher grain yield and biomass. Moreover, parameters measured in the plot trial (phenological phases duration, fertility at anthesis, chlorophyll content), suggested the presence in the 23-28% 7AgL region of loci significantly increasing booting-to-anthesis phase and chlorophyll content during grain filling. Conversely, the 28-40% interval was found to be associated with negative effects on biomass at anthesis and post-anthesis chlorophyll content, hence on grain filling.

**Keywords.** Chromosome engineering – *Triticum durum* – Alien gene transfer – Breeding – Yield QTL.

## **Effets positifs sur les caractères liés au rendement associés aux segments chromosomiques de *Thinopyrum ponticum* introgressés dans le blé dur**

**Résumé.** Afin de faire face aux nombreux défis que pose aujourd'hui la sélection du blé, une option possible est l'élargissement de la base génétique de la culture à travers l'exploitation de la variabilité génétique d'espèces sauvages apparentées, qui semble être une approche prometteuse et durable. Grâce aux récents progrès de l'ingénierie chromosomique permettant de transférer dans le blé des segments de chromosomes étrangers, il est maintenant possible de cibler aussi des caractères complexes tels que ceux liés au rendement. Au cours des trois dernières saisons, trois lignées recombinantes quasi-isogéniques de blé dur *Thinopyrum ponticum*, chez lesquelles les portions distales du bras 7AL ont été remplacées par 23%, 28% et 40%, respectivement, de chromatine étrangère (= 7AgL), contenant les gènes *Lr19 + SR25 + Yp*, ont été utilisées pour des essais sur le terrain, dans des conditions de culture en sec typiquement méditerranéennes. Dans un premier temps, on a mis en place un certain nombre de plantes espacées (2 ans), et ensuite, on a installé des parcelles (1 an) pour l'évaluation des effets associés au 7AgL sur les caractères liés au rendement. Dans l'ensemble, les résultats ont confirmé que les portions définies de 7AgL déterminent un renforcement de certains caractères tels la largeur de la feuille étandard et le nombre de tiges par plante (portion 23-28%), le nombre de grains/m<sup>2</sup> et l'indice de fertilité de l'épi (portion 28-40%), qui contribuent tous à l'augmentation observée du rendement en grain et de la biomasse. En outre, les paramètres mesurés au cours de l'essai en plein champ (durée des stades phénologiques, fertilité à l'anthèse, teneur en chlorophylle), ont permis de conclure à la présence dans la région 23-28% du 7AgL des locus qui augmentent significativement le stade gonflement-anthèse et la teneur en chlorophylle pendant le remplissage du grain. À l'inverse, il a été démontré que la portion 28-40% est associée à des effets négatifs sur la biomasse à l'anthèse et sur la teneur en chlorophylle post-anthèse, donc sur le remplissage des grains.

**Mots-clés.** Ingénierie chromosomique – *Triticum durum* – Transfert de gènes étrangers – Sélection – QTL de rendement.

## I – Introduction

Due to the current ‘bottleneck’ caused by the restricted crop genetic base, coupled with rising climatic and social challenges for wheat production increase of crop yield acquires an even more strategic importance among the goals of today’s breeding programs. After more than 50 years of intensive efforts for agronomic and genetic improvement of this crucial crop for mankind, further increments in its yield are difficult to accomplish without the application of novel breeding strategies. For complex traits such as yield, with a typical multigenic control by several quantitative trait loci (QTL), a relatively low heritability and a significant interaction with the environment, a valid approach contemplates genetic dissection of the trait and effective genotyping and phenotyping of the available natural variation. The search for loci underlying yield-contributing traits can be extended to ‘non-crop’ species, including wild relatives, land races, and other non-adapted genetic materials, which display a wealth of potentially useful traits for crop improvement, along with undesirable ones. Indeed, the ability to transfer only the defined, target alien genes and get rid of unwanted ones is the key to harnessing alien genetic variation, making it an effective way to counter problems of crop genetic erosion.

The wheatgrass genus *Thinopyrum*, belonging to the wheat tertiary gene pool, represents a particularly large reservoir of desirable traits for improvement of cultivated *Triticum* species. The genus includes a large number of perennial diploid to decaploid species, used for more than half a century to enrich cultivated wheat germplasm with an array of genes for disease and pest resistance (e.g., Li and Wang, 2009), for tolerance to abiotic stresses (e.g., Colmer *et al.*, 2006, Li *et al.*, 2008), as well as for processing quality (Liu *et al.*, 2008), and even yield-related traits (Singh *et al.*, 1998; Kuzmanović *et al.*, 2013). A *Thinopyrum* chromosome group turned out to be particularly rich in valuable genes for wheat improvement is the one sharing homoeology with wheat group 7 chromosomes, and perhaps the most extensively targeted is the one belonging to the decaploid *Th. ponticum* (tall wheatgrass,  $2n = 10x = 70$ ), originally named 7Ag (Sears 1973) or 7eI (Sharma and Knott, 1966; Knott *et al.*, 1977).

Thanks to the advances in ‘chromosome engineering’ approaches (Sears, 1972; Ceoloni and Jauhar, 2006) useful genes/QTL from the 7Ag chromosome were successfully transferred into cultivated wheats since the mid 20<sup>th</sup> century. In particular, several major genes or QTL of proved or potential breeding value were found to be concentrated on its long arm. When introduced into wheat cultivars in the form of substitution and translocation lines, 7Ag chromosomes of different *Th. ponticum* accessions revealed the presence of genes controlling resistance to several wheat diseases, including rusts (e.g. *Lr19*, *Sr25*; e.g. Gennaro *et al.*, 2009) and scab (or Fusarium head blight, FHB; see Forte *et al.*, these Proceedings), as well as genes affecting grain pigment content (*Yp*) and even yield (for review see Ceoloni *et al.*, 2013). In general, there is a limited number of examples of wild genes used to improve yield in modern cultivars, due to the narrow or, by chance gained, knowledge of yield potential of wild germplasm.

The existence of loci associated with increase in yield in wheat-*Th. ponticum* genetic stocks was initially reported by CIMMYT, on the basis of results obtained by using near-isogenic lines (NILs) of the original T4 translocation (70% of 7AgL arm inserted into wheat 7DL) into various bread wheat backgrounds (Singh *et al.*, 1998; Reynolds *et al.*, 2001; Monneveux *et al.*, 2003). The effect of 7AgL translocation was found to consist of increased yield, biomass and grain number per ear (10-15%) in all backgrounds studied, and, though not consistently, to be particularly evident under non moisture stress. However, no precise information was available on the position along the large 7AgL segment of the loci underlying such traits. Interestingly, the largely syntenic and colinear 7AL region contains several QTL for yield-contributing traits in both bread and durum wheat (Kuzmanović *et al.*, 2013).

With the primary aim of transferring into durum wheat the *Th. ponticum* *Lr19+Yp+Sr25* linked genes (Ceoloni *et al.*, 2000, 2005; Gennaro *et al.*, 2003), distal portions of the same 7AgL segment

of line T4 were separately introduced into the 7AL arm of durum wheat recombinant lines (Ceoloni *et al.*, 2005). Recent results from analysis of yield and yield-contributing traits on field-grown, spaced plants of three such durum wheat-*Th. ponticum* recombination lines, carrying 23%, 28% and 40% distal 7AgL chromatin on 7AL (Fig. 1), in combination with physical and genetic maps of recombinant 7AL-7AgL chromosomes, led to delineate functional sub-regions within the 40% distal 7AgL to which genes/QTL responsible for the conspicuous increase of flag leaf area, tiller number/plant, seed number/ear, grain yield/plant and above-ground biomass could be associated (Kuzmanović *et al.*, 2013, and Fig. 1). In the first two seasons of agronomic analyses (2009 and 2010), in particular, total productive tiller number per plant was significantly increased in R112-4 (+25%) and R23-1 (+16%) recombinants, in the former recombinant being associated with significant increase in biomass per plant (28%). Of special interest showed to be the increase in R112-4 recombinant of the flag leaf width (11%), together with the increase in 2010 only in grain yield (36%) and seed number (27%) per plant of the same recombinant. Consequently, R112-4 ranked as the best line among the three tested. A stable increase in seed number per plant was also observed across the two years in R23-1 (22%), though accompanied by significant decrease in thousand kernel weight (-20%). In order to validate the expression of these and additional productivity traits in plot trials, a multi-year field experiment with the same 3 durum wheat-*Th. ponticum* recombinant lines was started in Viterbo, Central Italy, and here we report results of the first year analyses.

## II – Material and methods

### 1. Plant materials and growth conditions

Materials employed in the field trial carried out in Viterbo in the 2011-2012 season were derivatives of the 3 durum wheat-*Th. ponticum* recombinant lines represented in Fig. 1. They had been subjected to several backcrosses (BC) to the recurrent cv. Simeto, so to produce near-isogenic recombinant lines (NIRLs). In particular, BC<sub>5</sub>F<sub>8</sub>, BC<sub>5</sub>F<sub>7</sub> and BC<sub>4</sub>F<sub>7</sub> progenies of R5-2-10, R112-4, and R23-1, respectively, were used. Genotypes were represented by homozygous carriers (= HOM+) and non-carriers (= HOM-) of the corresponding 7AgL segment. For each NIRL, HOM+ and HOM- variants were represented by 2 families originating from sister lines, replicated 3 times and randomized, to give a total of 36 plots (1.5 m x 1.5 m each). During the entire growth period, appropriate weed, disease and pest control measures were applied; plants were fertilized according to the standard procedure and grown under rainfed conditions.

### 2. Measurements of yield and yield-related traits and statistical analysis

During vegetative growth, at maturity and post-harvest stages, the following traits were measured: phenological phases – terminal spikelet (TS), booting (BS), heading (HD), anthesis (ANT), grain filling (GF), stem elongation (SE), booting to anthesis (BS-ANT); spike fertility traits (6 data points/plot) – spike dry weight at anthesis (SDW), biomass/shoot at anthesis (BST), fertile floret number/spike at anthesis (FF), spike length (SL), spike index (SI), No. spikelets/spike (SPNE), No. grains/spike (GNS), No. grains/spikelet (GNSP), grain yield/spike (GYS), spike fertility index (SFI); flag leaf traits and plant height (10 data points/plot) – flag leaf width (FLW), flag leaf length (FLL), flag leaf area (FLA), plant height (PH); chlorophyll content (SPAD) at watery ripe, early milk, medium milk and late milk stages of grain filling; productivity traits (25 tillers/plot) - grain yield/m<sup>2</sup> (GYM2), No. grains/m<sup>2</sup> (GNM2), No. spikes/m<sup>2</sup> (SNM2), biomass/m<sup>2</sup> (BM2), biomass/tiller (BTIL), grain yield/tiller (GYTIL), 1000 grain weight (TGW), harvest index (HI). Chlorophyll content was measured on the flag leaf by SPAD meter (Minolta, Japan). General linear model-ANOVA (GLM-ANOVA) was performed with SYSTAT12 (Systat Software Incorporated, San Jose, CA, USA) software package.

### III – Results and discussion

The first plot trial with the durum wheat-*Th. ponticum* NIRLs has given encouraging results. With respect to the previous analyses on the same material (Kuzmanović *et al.*, 2013), mainly focused on observations at maturity and post-harvest stages, the present work included as well analysis of traits at earlier developmental stages, such as biomass and spike fertility recorded at anthesis, and chlorophyll content, recorded from anthesis to ripening. Furthermore, the duration of phenological phases and their potential association with yield-related traits has been analysed. Several significant effects of given 7AgL segments on yield-related traits were confirmed, and new ones highlighted.

As emerged in previous analyses (Kuzmanović *et al.*, 2013), the R112-4 recombinant confirmed to have significantly increased values for several yield-contributing traits due to the presence of its 28%-long 7AgL segment on 7AL. Firstly, compared to its control (HOM-), HOM+ plants of this NIRL showed to have significantly higher (+6%) FLW (Table 1), a trait positively correlated with TGW (not shown). These results support our hypothesis (Kuzmanović *et al.*, 2013) of the location of a genetic determinant for FLW within the 7AgL segment present in R112-4 and absent from R5-2-10 (between 23% and 28% distal 7AgL chromatin on 7AL, see Fig. 1). Since this segment is common to the R23-1 7AgL portion, the lack of expression of this locus, as well as of others putatively assigned to the same region (see below), might be due to the presence of a Segregation distortion (*Sd*) gene(s) in the most proximal part of the R23-1 7AgL segment, negatively affecting a variety of plant traits (Ceoloni *et al.*, 2013).

Secondly, R112-4 recombinant plants also confirmed to produce significantly higher number of spike-bearing tillers (SNM2), without any yield penalty (GYM2, Table 1). The observed 20% increase was highly remarkable, given the conventional sowing density of 350 seeds/m<sup>2</sup> adopted (in previous years, spaced plants showed a similar increase of 25%, see Kuzmanović *et al.*, 2013). Since such a constant increase was unique to the R112-4 NIRL, a putative locus for tiller number appears to be located within 7AgL segment present in R112-4, absent from R5-2-10, and not expressed by R23-1 (see above; Fig. 1). Additionally, measurements performed with SPAD meter during grain filling revealed significantly higher chlorophyll content (+15%) at late milk stage in the R112-4 recombinant compared to its HOM- control and the other HOM+ genotypes (Table 1, Fig. 1). This indicates a potentially higher photosynthetic efficiency of R112-4, which contrasts with the significantly decreased chlorophyll content of R23-1 HOM+ plants throughout ripening (from watery to late milk stage). This, in turn, was probably largely responsible for the lower TGW observed in the latter recombinant (Table 1).

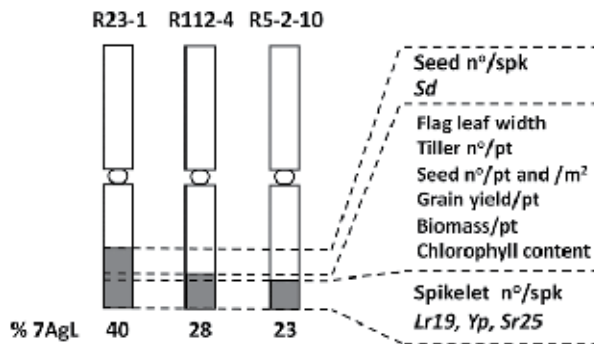


Figure 1. Recombinant 7AL-7AgL chromosomes representing the three durum wheat NIRLs used in the present study, with physical location within the 7AgL segments of main genes and newly identified loci for yield-contributing traits; spk: spike, pt: plant.

**Table 1. Means and standard errors (SE) as from the ANOVA-GLM analyses for yield-contributing traits of the durum wheat 7AgL recombinant lines (HOM+) and their respective controls (HOM-) grown in Viterbo (Central Italy) in the 2011-2012 season**

Trait	R5-2-10 HOM+		R5-2-10 HOM-		R112-4 HOM+		R112-4 HOM-		R23-1 HOM+		R23-1 HOM-	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
TS (N° days*)	125.2	0.71	125.2	0.71	126.0	0.71	124.5	0.71	125.2	0.71	125.7	0.71
BS (N° days)	149.7	0.49	149.7	0.49	150.0	0.49	149.2	0.49	151.7	0.49	151.8	0.49
HD (N° days)	152.3	0.75	152.2	0.75	152.8	0.75	151.8	0.75	155.7	0.75	155.5	0.75
ANT (N° days)	163.3	0.36	161.5	0.36	163.3	0.36	161.0	0.36	165.8	0.36	165.2	0.36
GF (N° days)	56.7	0.36	58.5	0.36	56.7	0.36	59.0	0.36	54.2	0.36	54.8	0.36
SE (N° days)	38.2	0.56	36.3	0.56	37.3	0.56	36.5	0.56	40.7	0.56	39.5	0.56
BO-ANT (N° days)	13.7	0.49	11.8	0.49	13.3	0.49	11.8	0.49	14.2	0.49	13.3	0.49
SDW (g)	0.6	0.02	0.6	0.02	0.6	0.02	0.6	0.02	0.5	0.02	0.6	0.02
BST (g)	4.0	0.10	4.3	0.10	3.9	0.10	4.0	0.10	3.6	0.10	4.1	0.10
FF	29.7	1.41	32.5	1.41	29.8	1.41	29.7	1.41	28.5	1.41	28.8	1.41
SL (cm)	6.0	0.11	6.1	0.11	5.9	0.11	5.8	0.11	6.7	0.11	6.7	0.11
SI	0.6	0.01	0.6	0.01	0.6	0.01	0.6	0.01	0.5	0.01	0.5	0.01
SPNE	16.9	0.35	16.8	0.35	16.5	0.35	16.4	0.35	18.3	0.35	18.0	0.35
GNS	39.1	1.43	39.1	1.43	40.5	1.43	38.7	1.43	50.7	1.43	46.2	1.43
GNSP	2.3	0.06	2.3	0.06	2.5	0.06	2.3	0.06	2.8	0.06	2.6	0.06
GYS (g)	2.8	0.09	2.7	0.09	2.7	0.09	2.7	0.09	2.3	0.09	2.9	0.09
SFI	68.5	3.42	67.1	3.42	71.3	3.42	68.2	3.42	112.5	3.42	81.3	3.42
FLW(cm)	1.6	0.02	1.6	0.02	1.7	0.02	1.6	0.02	1.5	0.02	1.5	0.02
FLL (cm)	12.8	0.48	12.8	0.48	12.5	0.48	12.8	0.48	12.5	0.48	13.6	0.48
FLA (cm <sup>2</sup> )	21.0	0.99	20.8	0.99	21.3	0.99	20.7	0.99	1.0	0.99	20.9	0.99
PH (cm)	82.6	0.81	83.2	0.81	80.0	0.81	78.1	0.81	98.6	0.81	99.7	0.81
GYM2 (g)	408.9	20.52	397.6	20.52	440.7	20.52	428.2	20.52	415.0	20.52	423.2	20.52
GNM2	408.9	20.52	397.6	20.52	440.7	20.52	428.2	20.52	415.0	20.52	423.2	20.52
SNM2	239.8	10.42	241.6	10.42	315.5	10.42	263.8	10.42	299.4	10.42	272.2	10.42
BM2 (g)	974.3	46.62	929.8	46.62	1064.4	46.62	1026.4	46.62	1086.6	46.62	1081.2	46.62
BTIL (g)	6.3	0.20	6.0	0.20	6.0	0.20	6.2	0.20	5.6	0.20	6.5	0.20
GYTIL (g)	2.6	0.06	2.6	0.06	2.5	0.06	2.6	0.06	2.1	0.06	2.5	0.06
TGW (g)	72.0	0.57	71.8	0.57	67.7	0.57	71.0	0.57	48.3	0.57	64.2	0.57
HI	0.4	0.01	0.4	0.01	0.4	0.01	0.4	0.01	0.4	0.01	0.4	0.01
SPAD**	48.2	1.2	45.9	1.2	50.4	1.2	43.7	1.2	41.6	1.2	46.0	1.2

\* from sowing date; \*\* chlorophyll content at late milk stage of grain filling

On the other hand, R23-1 confirmed its ability to produce much higher seed number/spike, as seen from the 30% higher GNM2 accompanied by 38% higher SFI (Table 1). This increment was not exhibited by R5-2-10 nor by R112-4; moreover, no correlation was observed between No. grains/m<sup>2</sup> and No. spike/m<sup>2</sup> (not shown). All these observations suggest that the increase in seed number might be associated with a genetic factor independent of the locus controlling tiller number, and present on 7AgL chromatin exclusive to R23-1 (between 28% and 40% distal 7AgL; Fig. 1). In line with previous results (Kuzmanović *et al.*, 2013), the higher seed number in R23-1 N1RL was not paralleled by an increase in yield, but, instead, accompanied by a much lower TGW (-25%, Table 1). This drawback, probably representing one of the side effects of the *Sd* gene(s), could be associated with the observed lower spike weight at anthesis and lower chlorophyll content of R23-1, as well as with its shorter grain filling period compared to other recombinants (Table 1), negatively correlated with TGW.

R5-2-10 and R112-4 recombinants showed to have slightly later anthesis date (ANT) compared to their respective controls (about 2 days), followed by, as expected, significantly shorter grain filling period (GF, Table 1). R23-1 HOM+ plants did not show significant alteration of the ANT or GF compared to HOM- plants; however, compared to the other HOM+ genotypes they had significantly longer ANT and shorter GF. Anthesis date was positively correlated with GNS and GNM2 (not shown), but it did not result in a significant increase in yield in any of the recombinants (Table 1). Duration of stem elongation phase (SE), known to be essential for spike growth and fertility, was significantly higher in R5-2-10 only, although all recombinants showed a tendency for longer SE compared to their HOM- controls (Table 1). On the other hand, the period comprised between booting and anthesis (BS-ANT), which appears to be the most important phase for nutrient transfer from stem into spike (e.g. Isidro *et al.*, 2011), was significantly longer in R5-2-10 as well as in R112-4 N1RLs. This suggests that also the BS-ANT duration may contribute to the higher yield potential of R112-4.

Field trials, extended to a variety of locations, are being continued. So far, the 7AgL positive attributes expressed by the R112-4 recombinant appear the most readily exploitable in advanced breeding programs for yield improvement of durum wheat. Considering the additional beneficial genes present in the same alien segment (*Lr19+Yp+Sr25*), this represents a particularly demonstrative example of how a knowledgeable use of a suite of alien traits can result in effectively unlocking their great potential for breeding gains. On the other hand, the potentially enhancing yield traits associated with 7AgL chromatin unique to R23-1, primarily No. grains/spike and No. grains/m<sup>2</sup>, might be potentially usable in bread wheat breeding, given the higher tolerance of the latter to sizable alien introgressions and to *Sd* gene effects as compared to durum wheat (Ceoloni *et al.*, 2013 and unpublished). To verify this, and to assess the effect of 7AgL portions smaller than the T4 translocation in a hexaploid background, the 3 durum wheat recombinants described here are being crossed and backcrossed with bread wheat cultivars to create hexaploid N1RLs to be used in future comparative trials.

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