Traits associated with winter wheat grain yield in Central and West Asia

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Research Article

Abstract Improved adaptation of winter wheat (*Triticum aestivum* L.) to drought and heat may be influenced by days to heading, plant height, biomass, canopy temperature (CT) at grain filling, and rate of senescence. This study shows that, under supplemental irrigation or rainfed conditions, days to heading and plant height together explain up to 68% of grain yield (GY) variation, and these associations were further confirmed in several locations across West and Central Asia. Days to heading can be slightly reduced below that of check line Karahan to further improve GY while avoiding the effect of late frosts. Plant height has been decreased in recent germplasm, but further reductions below that of check line Karahan could still improve GY in a wide range of environments. However, in Iranian sites, taller genotypes showed better adaptation with higher biomass and increased reserves for grain filling. Canopy temperature and rate senescence were not associated with GY. A normalized difference vegetation index, used to estimate biomass (Feekes stages 4–5), had intermediate heritability across environments and correlated positively with GY under low plant density and should be explored further as a tool for early selection.

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INTRODUCTION

In rainfed areas of West and Central Asia, where winter wheat predominates (Portmann et al. 2010), improving adaptation to drought is a high priority due to low or uneven rainfall during the crop cycle. Several traits have been identified for improving drought and heat adaptation in both spring (Reynolds and Tuberosa 2008; Lopes et al. 2012a) and winter wheat (Foulkes et al. 2007). One of the first steps in incorporating a new physiological trait (PT) into a crossing program is to determine how consistent its association is with grain yield (GY) in elite material. This study set out to evaluate priorities for breeding winter wheat adapted to the rainfed areas of West and Central Asia.

Plants exposed to stress at sensitive stages of plant development generally display a disproportionately weak agronomic performance (Worland 1996; Donmez et al. 2001). For example, water stress at key reproductive stages consistently reduces GY (Fischer and Maurer 1978). Several traits associated with GY and providing adaptation to stresses are described below. An increased capacity to extract water from depth can result in improved GY under drought by reducing plant water deficit in cases where water is available in deeper soil layers. Furthermore, the capacity to extract water from deep soil through improved root systems is associated with canopy temperature (CT), which can be easily measured with an infrared thermometer (Lopes and Reynolds 2010). Strong relationships have been found between biomass and GY, which show the importance of vegetative growth before anthesis in increasing the plant's ability to supply carbohydrates for grain filling (Donmez et al. 2001; Villegas et al. 2001). Dry matter accumulation prior to anthesis is particularly important in Mediterranean areas, because grain filling generally takes place under hot and dry conditions that limit photosynthesis, and yield depends greatly on translocation of pre-anthesis assimilates to the grain (Villegas et al. 2001). Under heat stress, which often occurs in dry environments, a lower rate of senescence (RS), corresponding to slower losses of chlorophyll, is associated with increased GY (Lopes and Reynolds 2012).

This study evaluated the expression of several PTs in elite winter wheat germplasm in West and Central Asia to determine their association with GY. Traits tested included: timing of floral initiation or days to heading (DH), plant height (PH), CT at grain filling (CTgf), and estimated biomass (Feekes stages 4–5) with normalized difference vegetation index (NDVI), RS, and GY. Specifically, this study aimed to: (i) determine the traits primarily associated with improved yields in the Central and West Asia region so as to set priorities for their continued introgression into current germplasm; (ii) test interactions between physiological and agronomic traits across environments; and (iii) identify high-throughput PTs for use in progeny selection.

RESULTS

Contributions of agronomic and PTs to GY in two environments in Turkey and two water regimes

Trial A

Trial A was sown with a plant density of 500 plants/m² using 30 historical (old to modern) varieties under rainfed and

supplemental irrigation in two locations in Turkey (Eskisehir and Konya) during the 2011–2012 crop cycle. Eskisehir had 374.6 and 474.6 mm of water in rainfed and supplemental irrigation trials, respectively, with maximum temperatures of 34.2 °C during grain filling and average temperature across the crop cycle of 8.2 ± 10.0 °C; Konya trials were conducted with 306.1 and 406.1 mm of water for the rainfed and supplemental irrigation trials, respectively. Supplemental irrigation of 100 mm was required for soil saturation in both environments. In Konya, maximum temperatures of 39.2 °C during grain filling and average temperature across the crop cycle of 10.3 ± 9.9 °C were registered. For more information on long-term weather and geographical information data, see Tables S1, S2. Table 1 shows heritability, means, for Trial A with ANOVA, least significant difference (LSD), and correlations of the various traits with GY and estimated biomass (biomass) measured between Feekes stages 4 and 5, using means of each genotype across two environments (E) × two water regimes (WRs). For reference, Karahan (check variety without Rht-B1b and -D1b) showed intermediate (near average) PH and DH (93.3 cm and 145 d, respectively) in Trial A. The traits with the highest heritability were DH and PH. Intermediate heritability was displayed by GY, NDVI measured at pre-booting stages (NDVIpb) and after booting (NDVIab) and estimated biomass (Feekes stages 4–5). Rate of senescence and CTgf showed low heritability (Table 1). All traits showed significant genotypic effects, except RS and CTgf. Furthermore, genotype by environment (G × E) interactions were significant for GY, DH, PH, and CTgf (genotype means at each environment are shown for these traits in Table S3), however, genotype by WR effects were not significant (Table 1) in all traits. Environment by water regime (E × WR) effects were significant for all traits tested (Table 1), but quantitative interactions (non-cross-over) were observed (Table S3 for means in each environment and WR). The rainfed WR decreased yield, DH, PH, biomass, and RS, but increased CTgf in the two tested environments (Table S3). The NDVIpb increased in the rainfed WR in both Eskisehir and Konya (Table S3). The NDVIab decreased in rainfed Eskisehir and Konya as compared to the supplemental irrigated WR (Table S3).

Associations between DH and GY, and between PH and GY, were significantly negative and explained approximately 40% of GY variation (Table 1). The NDVIpb was not significantly correlated with GY; however, the NDVIab was negatively associated with GY and positively associated with biomass (Table 1). Biomass was not significantly associated with GY in Trial A (Table 1).

Trial B
Trial B was conducted with lower plant densities (200 plants/m²) using 75 advanced breeding lines only in Konya (2011–2012 crop season) under rainfed and with supplemental irrigation with the same conditions described for Trial A in Konya. For reference, in Trial B, Karahan showed above average PH and intermediate DH (92.5 cm and 149 d, respectively). Heritability (Table 2) was highest for DH and NDVIab, and intermediate for GY, PH, NDVIpb, and biomass (Feekes stages 4–5) and genotype means at each environment are shown for biomass in Table S4. Heritability was low for days to maturity (DM), RS, and CTgf (Table 2). Significant genotypic effects were observed for all traits (except CTgf, Table 2). G × WR was significant only for biomass (Table 2). Under the rainfed WR, GY, DM, NDVIab,

and RS were decreased as compared to the supplemental irrigation WR (Table S4) but no significant effects were observed for DH and PH between the two WR. However, NDVIpb, biomass, and CTgf were increased under rainfed as compared to supplemental irrigation WR (Table S4). The highest and most significant correlations with GY were observed for biomass (positive association; Table 2), DH, and DM (negative associations; Table 2). The NDVIpb measurements were positively associated with GY; however, the NDVIab did not correlate significantly with GY (Table 2). Significant associations were not reported for GY with PH in Trial B (Table 2).

Associations of agronomic traits with winter wheat GY in different environments and sets of winter wheat germplasm: DH and PH
Multiple and simple regressions were calculated in Trials A and B (Table 3) for DH and PH as explanatory variables of GY. In Trial A, the ability of DH and PH to predict GY was particularly significant, under rainfed conditions (average GY was 2.2 T/ha), explaining up to 68.5% of GY variation (Table 3). In Trial B, DH was significantly correlated with final GY, explaining up to 68.4% (Table 3) of GY variation in Konya rainfed (average GY was 2.9 T/ha). However, PH was not significantly associated with GY. To further show how important DH and PH are for improving GY, data from international nurseries for semiarid regions (see Tables S1, S2 for information on the sites), released every year by the International Winter Wheat Improvement Program (IWWIP) based in Turkey (2007 through 2011 seasons, Table 4), were analyzed. Significant associations between DH and GY were always negative; associations were particularly significant in the most arid and warm conditions, but there were little or no effects in more favorable environments, as shown by higher Pearson correlation coefficients between GY and DH in low-yielding environments (Table 4). For PH, negative associations with GY were observed in high-yielding environments, whereas positive associations were observed in low-yielding environments, particularly in Iranian environments (Table 4). To further determine optimal levels of DH and PH across several environments, bi-plot analysis was performed in two different sets of germplasm: (i) Trial A (Figure 1) including a historic set of bread wheat varieties; (ii) data collected from IWWIP international trials in 2010 which contained modern breeding material where PH has been optimized (Figure 2). In both sets of germplasm (Trial A and IWWIP international trials), a common check was used (Karahan) not possessing Rht-B1b or -D1b, (highlighted in both Figures 1, 2 with an arrow and shown as K). Overall, Karahan had intermediate phenology (DH) as represented by its position near the bi-plot origin within both sets of germplasm (historical group and modern advanced lines, see Figures 1B, 2B). However, Karahan had intermediate PH among the historical lines as shown by its position near the bi-plot origin in Figure 1C, whereas it showed high PH among the modern advanced lines as shown by its position on the right side of the panel (Figure 2C). On average across all environments in Trial A, varieties 6, 14, and 28 had the highest GY (Figure 1A). Varieties 6 and 24 were earlier than check line Karahan (Figure 1B), whereas varieties 14 and 24 (Figure 1C) were shorter than check line Karahan. Variety 28 was earlier and shorter then Karahan and variety 6 was similar to Karahan in terms of PH as shown by

Table 1. ANOVA and basic statistical analysis of Trial A with 30 winter wheat varieties grown in Eskisehir and Konya under supplemental irrigation and rainfed conditions

VAR	H²	LSD	MAX	MIN	AVG	G	E	WR	G × E	G × WR	E × WR	G × E × WR	r (GY)	r (BIOM)
df						29	1	1	29	29	1	29		
GY (Kg/ha)	0.68	623	3,695	1,965	2,953	<0.005	<0.005	<0.005	<0.05	0.56	<0.005	0.26	NA	−0.13
GY$_{ESKIRR}$	0.60	1,474	5,366	2,492	4,116	<0.05	NA	NA	NA	NA	NA	NA	NA	−0.21
GY$_{ESKRAF}$	0.52	857	4,246	2,344	3,343	<0.05	NA	NA	NA	NA	NA	NA	NA	−0.19
GY$_{KONIRR}$	0.33	1,319	4,182	1,777	2,938	0.10	NA	NA	NA	NA	NA	NA	NA	0.08
GY$_{KONRAF}$	0.82	453	2,222	868	1,518	<0.005	NA	NA	NA	NA	NA	NA	NA	0.07
DH (d)	0.97	1.326	149	138	144	<0.005	0.06	<0.05	<0.005	0.71	<0.005	0.69	**−0.63**	0.13
DH$_{ESKIRR}$	0.95	2.2	153	138	145	<0.005	NA	NA	NA	NA	NA	NA	−0.30	0.11
DH$_{ESKRAF}$	0.94	1.9	148	138	143	<0.005	NA	NA	NA	NA	NA	NA	**−0.51**	0.21
DH$_{KONIRR}$	0.85	2.7	149	138	145	<0.005	NA	NA	NA	NA	NA	NA	−0.32	0.1
DH$_{KONRAF}$	0.90	2	147	137	144	<0.005	NA	NA	NA	NA	NA	NA	**−0.79**	0.08
PH (cm)	0.96	4.76	98.1	87.9	87.9	<0.005	0.06	<0.05	<0.005	0.71	<0.005	0.69	**−0.6**	0.21
NDVIpb	0.53	0.04	0.25	0.20	0.23	<0.005	<0.005	<0.005	0.40	0.61	<0.005	0.78	−0.36	0.36
NDVIab	0.71	0.05	0.72	0.56	0.63	<0.005	<0.005	0.81	0.51	0.77	<0.005	0.79	**−0.67**	**0.74**
Biomass[a]	0.70	0.0003	0.0061	0.0049	0.0056	<0.005	<0.005	<0.05	0.30	0.80	<0.005	0.65	−0.15	NA
RS[b]	0.20	0.0001	−0.0005	−0.0008	−0.007	0.34	NA	<0.005	NA	0.13	NA	NA	0.31	−0.3
CTgf (°C)	0.00	1.6023	35.1158	32.0803	33.4642	0.33	<0.005	<0.005	<0.05	0.82	<0.005	0.57	−0.22	0.12

Heritability (H^2), least significant difference (LSD at $P < 0.05$), maximum and minimum (MAX and MIN), average (AVG) for each trait, ANOVA with degrees of freedom (df), probabilities associated with genotype (G), environment (E), water regime (WR), genotype by environment (G × E), and genotype by water regime (G × WR) interactions, and genotype by environment by water regime interactions (G × E × WR) are presented. Pearson correlation coefficient of each trait with grain yield (r (GY)) and with biomass (r (BIOM)) are presented. Traits: grain yield (GY), days to heading (DH), plant height (PH), normalized difference vegetation index (NDVI) measured at pre-booting stages (NDVIpb) and after booting (NDVIab), estimated biomass (Biomass) measured between Feekes stages 4 and 5, rate of senescence (RS) and canopy temperature at grain filling stages (CTgf). GY and DH are also shown for each environment separately in Eskisehir with supplemental irrigation (ESKIRR) or rainfed (ESKRAF), in Konya with supplemental irrigation (KONIRR) or rainfed (KONRAF). Significant correlations (with $P < 0.05$ using $n = 30$ genotypes means across two environments and two WRs) are shown in bold. [a](NDVI GDD^{-1}). [b]Calculated from trials conducted in Konya with supplemental irrigation and rainfed but not available for Eskisehir (NDVI GDD^{-1}). GDD, degree days; NA, not available or applicable.

Table 2. ANOVA and basic statistical analysis of Trial B with 75 winter wheat modern advanced lines grown in Konya under supplemental irrigation and rainfed conditions

Trait	H^2	LSD	MAX	MIN	AVG	G	WR	G × WR	r (GY)	r (BIOM)
df						74	1	74		
GY (Kg/ha)	0.77	653	2,837	700	1,842	<0.005	<0.005	0.19	NA	**0.62**
GY$_{KONIRR}$	0.51	1213	3,721	1076	2,194	<0.05	NA	NA	NA	**0.58**
GY$_{KONRAF}$	0.89	417	2,420	546	1,496	<0.000 5	NA	NA	NA	**0.68**
DH (d)	0.95	2.9	160.2	142.4	149.8	<0.005	0.56	0.96	**−0.80**	**−0.62**
DH$_{KONIRR}$	0.85	5.2	160.0	142.3	149.9	<0.005	NA	NA	**−0.66**	**−0.62**
DH$_{KONRAF}$	0.93	3.4	160.5	142.0	149.6	<0.005	NA	NA	**−0.83**	**−0.64**
DM (d)	0.5	5.3	190.5	178.1	183.6	<0.005	0.35	0.97	**−0.76**	**−0.55**
PH (cm)	0.88	8.36	102.64	65.19	87.02	<0.05	<0.005	0.99	0.10	0.11
NDVIpb	0.82	0.04	0.30	0.13	0.20	<0.005	<0.005	0.96	**0.54**	**0.93**
NDVIab	0.91	0.08	0.64	0.40	0.51	<0.005	<0.005	0.22	0.20	0.02
Biomass[a]	0.82	0.001	0.0007	0.003	0.004	<0.005	<0.005	<0.05	**0.62**	NA
RS[b]	0.39	0.003	−0.009	−0.019	−0.015	<0.005	<0.005	0.24	−0.01	**−0.34**
CTgf (°C)	0.02	2.13	34.51	30.22	32.67	0.52	<0.005	0.41	**−0.28**	−0.09

Heritability (H^2), least significant difference (LSD at $P < 0.05$), maximum and minimum (MAX and MIN), average (AVG), ANOVA with degrees of freedom (df), probabilities associated with genotype (G), water regime (WR) and genotype by WR interaction (G × WR) effects, Pearson correlation coefficient of each trait with grain yield (r (GY)) and with biomass (r (BIOM)) are shown. Traits included in the analysis: grain yield (GY), days to heading (DH), days to maturity (DM), plant height (PH), normalized difference vegetation index (NDVI) measured at pre-booting stages (NDVIpb) and after booting (NDVIab), estimated biomass from NDVI measurements (Feekes Stages 4–5) (Biomass), rate of senescence (RS), and canopy temperature at the grain filling stages (CTgf). GY and DH are also shown for each environment separately with supplemental irrigation (KONIRR) or rainfed (KONRAF). Significant correlations (with $P < 0.05$ and $n = 75$ genotypes means across two WRs) are shown in bold. [a](NDVI GDD^{-1}). [b](NDVI GDD^{-1}). GDD, degree days; NA, not available or applicable.

its position near the bi-plot origin (Figure 1C). Using data from International trials (Figure 2), three clear groups of environments were observed in terms of GY: high-yielding environments (>4 T/ha) consisted of AZB03, RUS01, ROM01, and AFG13; intermediate-yielding environments (between 1.5 and 4 T/ha) consisted of AZB01, IRN11, and IRN07; and low-yielding environments (<1.5 T/ha) consisted of IRN04, IRN09, and KAZ02 (Figure 2A). Overall, lines 9, 17, 23, 24, and 25 were among the best performing lines across several environments. However, lines 28 and 30 were more adapted to the Iranian sites, but local checks (removed from analysis because these were different at each environment) had the highest GY.

Karahan had intermediate DH (Figure 2B) and high PH among all other advanced lines (Figure 2C), as explained above. Overall the best performing advanced lines with GY above average in most sites (9, 17, 23, 24, and 25) had lower DH and PH than Karahan. However, advanced lines 17 and 25 showed similar DH to Karahan but were shorter. In summary, very late and very tall advanced lines (shown on the right side of bi-plots in Figures 1, 2) were the lowest yielding in most environments. In Iranian environments, local checks were the tallest lines in the set and were the highest yielding; however, these were not included in the analysis due to them being different in each environment as explained above.

Table 3. Multiple and simple regression of days to heading (DH) and plant height (PH) with grain yield in two environments (ENV) and two water regimes (WR) using means of each variety or advanced line in Eskisehir (ESK) and in Konya (KON) with supplemental irrigation (IRR) or rainfed (RAF)

ENV/WR (Trial)	n	R^2 (%)	P	r (DH)	r (PH)	Bo	$B_{(DH)}$	$B_{(PH)}$	Res
ESK IRR (A)	30	**29.3**	<0.001	−0.30	**−0.53**	4,407 ± 4,990	24.0 ± 39.9	−37.8 ± 13.6	539
ESK RAF(A)	30	**25.8**	<0.001	**−0.51**	−0.27	**16,202 ± 4,469**	−91.2 ± 34.9	2.4 ± 11.5	405
KON IRR (A)	30	16.1	<0.10	−0.32	−0.37	11,066 ± 6,969	−47.0 ± 51.6	−14.1 ± 10.6	515
KON RAF (A)	30	**68.5**	<0.0001	**−0.79**	**−0.61**	**17,028 ± 2,528**	**−98.8 ± 18.9**	**−12.1 ± 5.6**	208
KON IRR (B)	75	**43.6**	<0.0001	**−0.66**	0.07	**15,159 ± 1,725**	**−86.5 ± 11.5**	NA	464
KON RAF (B)	75	**68.4**	<0.0001	**−0.83**	−0.04	**13,537 ± 957**	**−80.5 ± 6.4**	NA	256

(A) Correspond to a set of 30 historical winter wheat varieties where DH and PH both correlated significantly with yield and therefore multiple regressions were used; (B) correspond to a set of 75 winter wheat advanced lines where only DH correlated significantly with yield and therefore simple regression was used. Significant multiple or simple regressions and estimates with standard deviations, coefficients of determination (R^2) and associated probabilities (P), Pearson correlation coefficients of grain yield with DH (r (DH)) or with PH (r (PH)) are shown in bold when correlations are significant (at $P < 0.05$); estimates of each parameter and standard deviations for origin (Bo), DH ($B_{(DH)}$), PH ($B_{(PH)}$), and residuals of the model (Res) are shown. NA, not applicable.

Table 4. Precipitation (PREC), maximum temperature (MAX T), average temperature (AVG T), grain yield (GY), minimum grain yield (MIN GY), maximum grain yield (MAX GY), average days to heading (AVG DH), and correlation with yield (rGY_DH) with associated probabilities (P <), average plant height (AVG PH) and correlations with yield (rGY_PH) with associated probabilities (P <) measured in several environments (ENV, see Tables S1,S2) and years (Y)

ENV	Y	PREC (mm)	MAX T (°C)	AVG T (°C)	GY	MINGY (T/ha)	MAXGY (T/ha)	AVGDH (d)	rGY_DH	P<	AVGPH (cm)	rGY_PH	P<
IRN11	2007	293	36	13	3.2	1.9	4.2	151	−0.5	0.001	67	0.4	0.05
UZB02	2007	NA	NA	NA	5.3	4	6.6	131	−0.4	0.1	95	0.2	NS
IRN11	2008	155	31.4	10.6	0.9	0.6	1.1	160	−0.7	0.001	45	0.6	0.01
TAJ01	2008	NA	NA	NA	2.3	0.5	3.7	NA	NA	NA	93	0.2	NS
UZB02	2008	NA	NA	NA	4.6	3	6.4	126	−0.2	NS	113	−0.1	NS
IRN07	2009	324	39	11.8	2.6	1.9	3.3	159	−0.7	0.0001	71	0.5	0.001
IRN09	2009	262	37	11.4	0.9	0.4	1.6	155	−0.8	0.0001	55	0.8	0.0001
IRN11	2009	220	34.6	11.8	2	1.5	3.4	167	−0.8	0.0001	61	0.5	0.01
TAJ01	2009	NA	NA	NA	4.4	2	5.9	NA	NA	NA	62	0.4	0.03
UZB06	2009	NA	NA	NA	3.2	2.3	3.8	110	−0.1	NS	97	−0.1	NS
AFG13	2010	NA	NA	NA	4.4	3.1	5.7	107	−0.57	0.001	103	−0.2	NS
AZB01	2010	NA	NA	NA	2.9	1.7	5.1	133	−0.05	NS	103	0.05	NS
AZB03	2010	NA	NA	NA	4.6	3	7.2	139	−0.06	NS	118	−0.1	NS
IRN04	2010	NA	NA	NA	0.95	0.5	1.4	153	0.15	NS	82	0.14	NS
IRN07	2010	NA	NA	NA	2.6	1.9	3.3	159	−0.66	0.001	71	0.51	0.01
IRN09	2010	NA	NA	NA	0.9	0.4	1.6	155	−0.75	0.0001	55	0.75	0.0001
IRN11	2010	NA	NA	NA	2	1.5	3.4	167	−0.75	0.0001	61	0.47	0.01
IRN14	2010	NA	NA	NA	1.4	1	1.9	152	−0.51	0.001	56	0.22	NS
KAZ02	2010	NA	NA	NA	0.8	0.7	0.9	133	−0.09	NS	70	0.47	0.01
ROM01	2010	NA	NA	NA	4.9	3.1	6.5	139	−0.27	NS	103	−0.42	0.05
RUS01	2010	NA	NA	NA	4.4	1.9	7.3	140	0.12	NS	117	−0.41	0.05
TUR09a	2011	474.6[a]	34.2	8.2	3.3	2.3	4.2	144	−0.51	0.0001	94	−0.27	NS
TUR09b	2011	375	34.2	8.2	4.3	3.1	5.2	146	−0.3	NS	96	−0.5	0.01
TUR13a	2011	406.1[a]	39.2	10.3	2.9	1.7	4.2	144	−0.32	0.1	96	−0.37	0.05
TUR13b	2011	406.1[a]	39.2	10.3	2.2	1.1	3.7	150	−0.66	0.0001	87	0.2	NS
TUR13c	2011	306	39.2	10.3	1.5	0.5	2.4	150	−0.8	0.0001	87	0	NS
TUR13d	2011	306	39.2	10.3	1.5	0.8	2.2	145	−0.79	0.0001	94	−0.61	0.001
TUR13e	2011	306	39.2	10.3	1.5	0.5	2.4	150	−0.83	0.0001	87	−0.04	NS

Meteorological data represent the specific year when each trial was conducted. [a]With known supplemental irrigation. NA, not available; NS, non-significant.

NDVI and estimated biomass calculated from NDVI (Feekes stages 4–5) as an adaptive trait in winter wheat

Overall, some degree of association was observed between NDVI measurements and DH and/or PH (Figure 3). In Trial A, grown at higher plant densities, NDVI at the pre-booting stage was not significantly associated with DH and PH, only at the post-booting stage were these correlations evident. In both Eskisehir and Konya (with supplemental irrigation and rainfed), average NDVI measured after booting stage was positively associated with DH and PH (Figure 3A, B). Furthermore, in Trial A, DH (11 d range of variation across 30 varieties) and PH (37 cm range of variation across 30 varieties) explained 23%–68% of NDVI variation by multiple regression in different environments during grain filling (data not shown). In Trial B, grown at lower plant densities, NDVI was associated with DH but not with PH (Figure 3C). At the pre-booting stages, in Trial B, average NDVI was negatively associated with DH, however, after booting stage, this association became positive (Figure 3C).

Estimated biomass calculated from NDVI, measured at initial stages of plant development (Feekes stages 4–5), was positively associated with G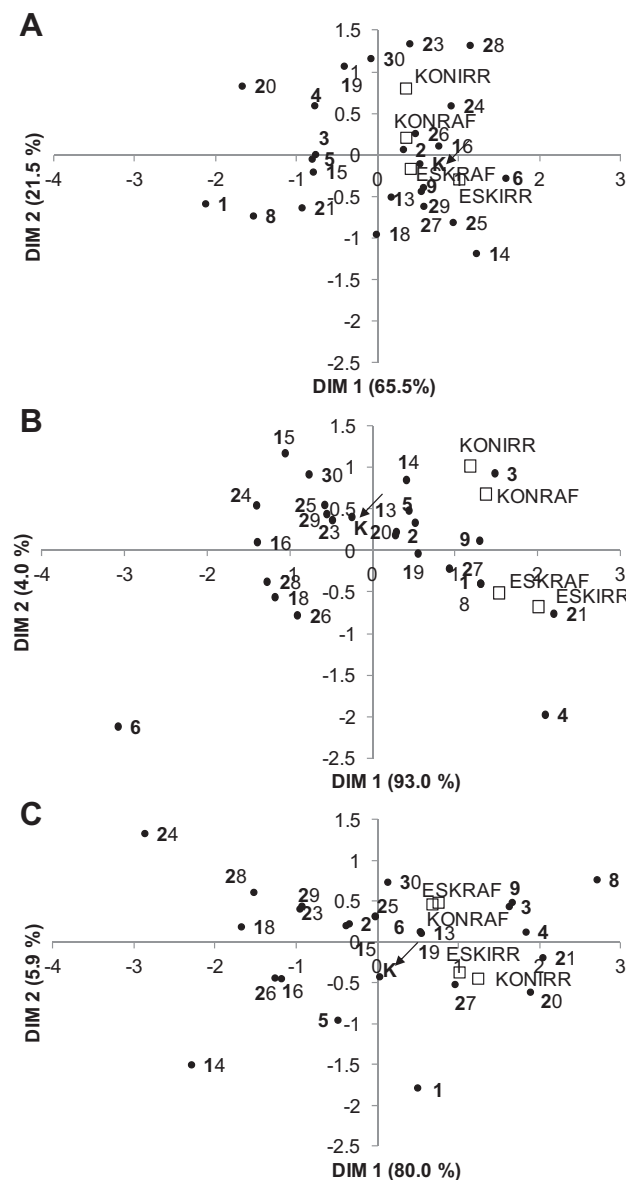Y in Trial B in both supplemental irrigation and rainfed conditions (Figure 4A; Table 2), explaining up to 52% of GY variation. Moreover, estimated biomass was negatively correlated with DH in Trial B (low-density planting) with supplemental irrigation and rainfed growth conditions (Figure 4B). Estimated biomass explained a higher proportion of GY variation in the supplemental irrigation WR (47%) than in the lower yielding rainfed environment (34%) (data not shown). In Trial A (high-density planting), estimated biomass did not contribute to final GY and it was not associated with either DH or PH (Table 1).

DISCUSSION

Associations of agronomic and PTs with winter wheat GY under supplemental irrigation and rainfed conditions

We demonstrated that, in winter wheat trials conducted in Konya and Eskisehir, DH and PH can together explain up to 68% of variation in GY in very low-yielding environments (1–2 T/ha). This indicates that improvement of GY in winter wheat for very low-yielding environments is highly related to earliness and adequate PH. For intermediate environments, other traits also may be useful to further improve yields. For example,
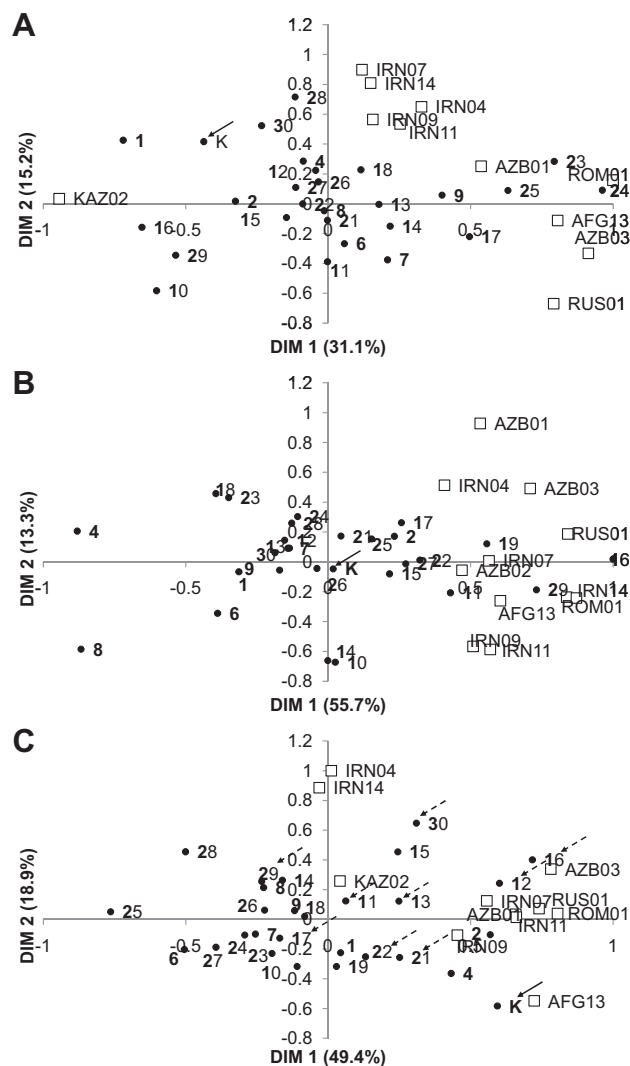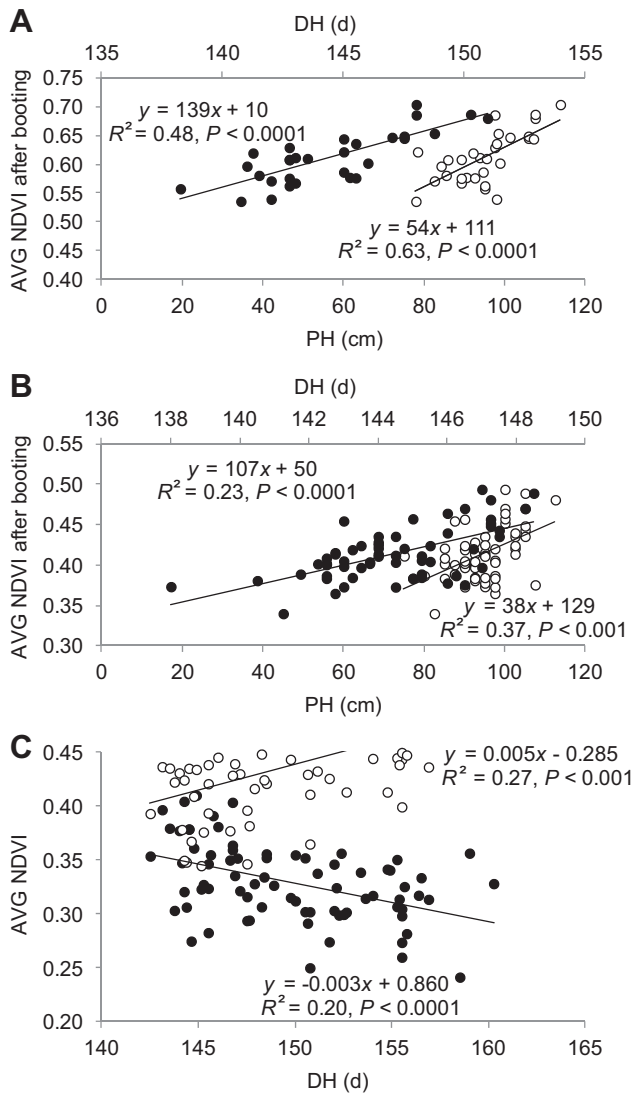
Figure 1. Bi-plot analysis of grain yield (A), days to heading (B), and plant height (C) against environments of Trial A in Eskisehir and Konya rainfed (ESKRAF and KONRAF, respectively) and with supplemental irrigation (ESKIRR and KONIRR, respectively) with 30 varieties, to determine optimal levels of expression of plant height and days to heading to maximize grain yield
Check line, Karahan (K) is highlighted with an arrow (not containing Rht-B1b or -D1b). In the bi-plot analysis, treatments (genotype, dark circles) were used as variables and environments (open squares) as units.

Figure 2. Bi-plot analysis of grain yield (A), days to heading (B), and plant height (C) against 11 environments of international nursery International Winter Wheat Improvement Program (IWWIP) data (http://www.iwwip.org) collected during the 2010–2011 season in a set of modern advanced breeding lines
Check line, Karahan (K) is highlighted with a black arrow (not containing Rht-B1b or -D1b) and taller advanced lines without Rht genes are indicated with dashed arrows. In the bi-plot analysis, treatments (genotype, dark circles) were used as variables and environments (open squares) as units.

estimated biomass calculated from NDVI measurements at early stages of development (Feekes stages 4–5) was positively associated with GY under low plant densities in a set of 75 advanced breeding lines (modern germplasm only), but did not contribute to GY at high plant densities in the historic group of 30 varieties (see Tables 1, 2). Further, biomass
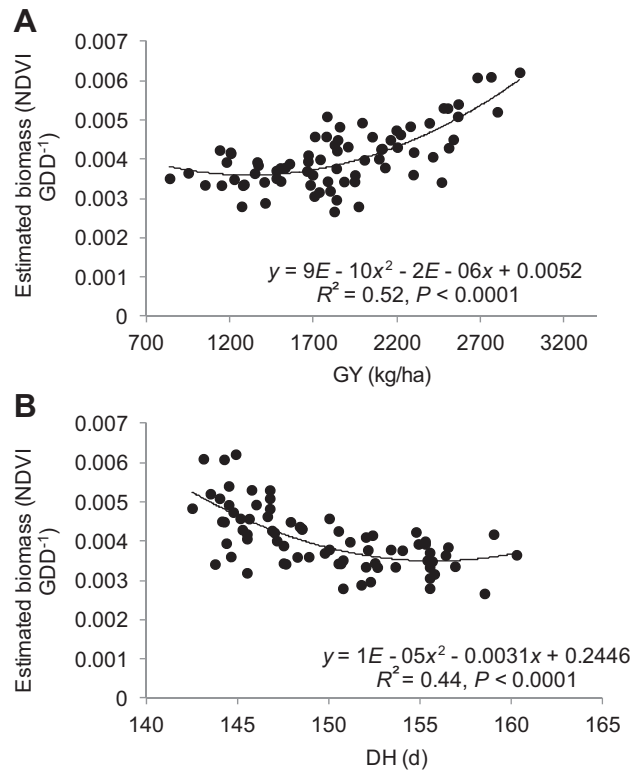
in the low plant density Trial B was greatly controlled by DH (see Figure 4), but this was not the case in Trial A (data not shown). Trade-offs, interactions with different sets of germplasm, and best conditions for screening should be studied before starting to use biomass estimated with the NDVI widely in breeding. For example, one such case where caution must be practiced when using NDVI is when measurements are taken after the post-booting stage: isolated NDVI measurements after booting were consistently correlated (positively) with DH, as shown by significant associations

A

$y = 139x + 10$
$R^2 = 0.48$, $P < 0.0001$

$y = 54x + 111$
$R^2 = 0.63$, $P < 0.0001$

B

$y = 107x + 50$
$R^2 = 0.23$, $P < 0.0001$

$y = 38x + 129$
$R^2 = 0.37$, $P < 0.001$

C

$y = 0.005x - 0.285$
$R^2 = 0.27$, $P < 0.001$

$y = -0.003x + 0.860$
$R^2 = 0.20$, $P < 0.0001$

Figure 3. Associations between normalized difference vegetation index (NDVI) measurements and phenology (DH) or plant height (PH) for Trial A grown in Eskisehir (A) and in Konya (B); and for Trial B in Konya (C)
Panels **(A)** and **(B)** show associations between average NDVI measured at the post-booting stage in Trial A with DH (dark circles) and PH (white circles) taken as an average of each wheat variety ($n = 30$) in both experimental conditions tested (rainfed and with supplemental irrigation). Panel **(C)** shows associations between average NDVI measured at the pre- (dark circles) and post-booting (white circles) stages in Trial B with DH taken as an average of each wheat advanced line ($n = 75$) in both experimental conditions tested (rainfed and with supplemental irrigation). Regression equations, coefficients of determination (R^2), and associated probabilities ($P<$) are shown.

between these two traits in all trials tested (see Figure 3). Hence, these NDVI measurements after booting are not related to biomass but instead with greenness (Lopes and Reynolds 2012) and this may confound selection. Specifically,

A

$y = 9E - 10x^2 - 2E - 06x + 0.0052$
$R^2 = 0.52$, $P < 0.0001$

B

$y = 1E - 05x^2 - 0.0031x + 0.2446$
$R^2 = 0.44$, $P < 0.0001$

Figure 4. Associations between estimated biomass (Feekes stages 4–5) and grain yield (GY) (A), and days to heading (DH) (B)
Regression equations, coefficients of determination (R^2), and associated probabilities ($P<$) are shown for 75 wheat advanced lines (Trial B) as a mean of two replications in two experimental conditions (rainfed and with supplemental irrigation).

when selecting for high NDVI measured after booting, late flowering wheats will be selected and therefore low-yielding genotypes will be selected. Several studies have highlighted the importance of assessing NDVI in winter wheat between Feekes Physiological Growth stages 4 and 5 to provide a reliable prediction of GY, biomass, and N uptake (see Raun et al. 2001 and references therein). Our results confirm that to use NDVI as a tool for selection of high biomass genotypes, measurements must be taken at Feekes stages 4–5. We conclude that heritability of biomass (Feekes stages 4–5) was intermediate, can be measured at early stages of development, and therefore is a very promising tool for selecting high GY under low plant densities (generally caused by water stress). Canopy temperature at grain filling has previously been used to detect genotypes with cooler canopies under stress conditions, usually related to improved root systems and water extraction capacity at depth (Lopes and Reynolds 2010). We observed a very low heritability for CTgf in the two environments (Konya and Eskisheir) tested (Tables 1, 2), but this was most likely due to rather high wind speed experienced almost every day, though water was present at depth, at least up to 1.5 m (data not shown). Rate of senescence showed significant genotypic effects only in Trial B, though significant associations

with GY were not observed (see Tables 1, 2). However, in Trial B, we identified a negative association between RS and estimated biomass (Feekes stages 4–5), in agreement with the theory that higher biomass results in lower RS (Lopes and Reynolds 2012). Despite the observed moderate to low heritability, RS may have limited effects on GY in the conditions and germplasm tested here; furthermore, decreased biomass and possible sink limitations may mimic the favorable effects of low RS (Derkx et al. 2012); therefore, further data may be required under different growth conditions and in different sets of germplasm. Other strategies and tools are available for testing to improve and strengthen breeding programs, such as carbon isotope discrimination (Xu et al. 2007) though costs are still high for this technique; furthermore, wide crosses are a source of new genetic diversity yet to be exploited in winter wheat with successful genotypes available with good sources of water use efficiency and nutrient utilization efficiency (Huang et al. 2007).

DH and PH as priority traits for introgression

Earliness (low DH) has been associated with drought avoidance in spring wheat in environments subjected to severe early season drought stress, for example, in northern Mexico and the Great Plains (Fischer and Maurer 1978; Donmez et al. 2001). Gouache et al. (2012) proposed earliness and heat tolerance as high priorities for wheat research and breeding in France, and highlighted the potential use of modeling in evaluating adaptive strategies to those conditions. There is currently no available data on the role of earliness in drought or heat escape in Central and West Asia winter wheat rainfed systems, but this study shows that, in this region, significant associations between DH and GY were negative in 17 out of 28 environments (see Table 4). Further, these associations were more significant in the most arid conditions with lower precipitations and low yields (see Table 4). These results reveal the importance of using earliness as a priority trait during selections to improve GY in low-yielding environments, where drought and heat are highly probable events, but without compromising winter wheat GY in more favorable years. For example, available data for IRN11 (with <300 mm of total precipitation, see Table S1) for four consecutive seasons indicated that in this region associations between GY and DH were always negative. Most Iranian winter wheat areas have more than 50% probability of having less than 300 mm of total annual precipitation and in Turkey, these probabilities are considerably low in most areas, but years with less than 300 mm are possible in Konya and to a lesser extent in Eskisehir (see Tables S1, S2) and earliness should be a target to improve GY in these regions. Our results showed that the check variety Karahan had intermediate DH among old and modern advanced lines in the two sets of germplasm tested (Figures 1, 2), showing that since Karahan was released in 1999, heading date has been stable and accordingly not optimal. These results suggest that the material tested here is still quite late in terms of DH; however, a threshold for earliness has to be defined to avoid negative effects in high-yielding regions or years. In fact, Lopes et al. (2012b) have shown in spring wheat, that in warm well-irrigated environments in Sudan, correlations between GY and DH were positive, probably due to biomass production limitations in very early material and this threshold has to be clearly identified in winter wheat.

Evaluation of DH extremes is required to define optimal levels of DH and representative checks of early, intermediate, and late DH expression must be included in all evaluations of germplasm. Moreover, knowledge of the underlying genes controlling flowering time in winter wheat, and clear identification of genes that can be easily manipulated for earliness, is imperative (Griffiths et al. 2009). Facultative types with relatively lower vernalization requirements than winter wheat but with strong photosensitivity to long days can be one option to obtain earliness, but manipulation of other genes requires evaluation. Furthermore, it is expected that strong photosensitivity to long days can lead to a less variable heading date.

Dwarfing genes Rht-B1b and Rht-D1b in wheat reduce height and shoot biomass but do not reduce root length or weight, root system depth or water uptake compared with tall near isogenic lines (Richards 1992; Miralles et al. 1997). Rht-B1b and -D1b, where most beneficial in comparatively tall back-grounds, and in near optimum environments where PH is maximized (Flintham et al. 1997; Chapman et al. 2007). Identification of ideal PH by region and conditions is required for two main reasons: (i) GY of tall plants is reduced due to low harvest index and increased lodging (Flintham et al. 1997; Berry et al. 2004) and (ii) extreme dwarfism is associated with reduced biomass and GY (Austin 1999). Flintham et al. (1997) identified a target PH range for maximizing yield and demonstrated that the effects of reduced height alleles (Rht) on GY of near isogenic lines depend on the stature of their tall backgrounds at particular locations. Chapman et al. (2007) tested a set of isogenic pairs of wheat cultivars across a global range of water-limited environments and concluded that, in almost all instances, shorter lines outperformed their taller counterparts.

We used the IWWIP dataset to also analyze the contribution of PH to GY in winter wheat, and found both negative (nine of 28 environments) and positive associations (10 of 28 environments) between the two traits. Negative associations between PH and GY in higher yielding environments with higher precipitation and lower temperatures can be at least partially explained by the association between biomass and lodging, as described above (Flintham et al. 1997; Austin 1999; Berry et al. 2004). Positive associations between PH and GY in lower yielding environments (particularly in Iranian sites) with decreased precipitation and higher temperatures (see Tables S1, S2) possibly may be partially explained by reduced water availability at depth. Iranian soils are known for reduced depth (Hajabbasi 2005) and an extra advantage of higher shoot biomass wheats and resources for grain filling in tall types in contrast to shorter types would result in increased GY in these environments where water availability for photosynthesis and sugar production during grain filling is restricted. Despite this specific response, for the range of PH variation in the germplasm included in our study, the best performers had lower PH than that of check variety Karahan in several locations (as depicted in the bi-plot analysis), showing that the average PH of germplasm is not yet ideal and can be further decreased. Further, the overall superiority of shorter wheat types is in agreement with results shown by Mathews et al. (2006) in spring bread and durum wheat supporting the idea that "short talls" may be useful in marginal environments (yield <3 Mg/ha). Moreover, nearly, all Turkish cultivars

released after 1967 were bred directly and/or indirectly from materials provided by the IWWIP, but although the IWWIP exploited both Rht-B1b and -D1b, the percentage of Rht-B1b and -D1b is still remarkably small (Yediay et al. 2011). For example, the set of germplasm released by the IWWIP in 2010, contains less than half of the advanced lines with either Rht-B1b or -D1b (http://www.iwwip.org) and only one had two Rht genes (advanced line 28 in Figure 2C). However, there has been some effort to reduce PH in the IWWIP, for example, we have shown that Karahan had intermediate PH among old varieties, but higher PH among modern advanced lines. Overall, with the exception of Iranian environments, the results presented in this study suggested that by decreasing PH further below Karahan, GY can still be improved.

Implications for winter wheat breeding in Central and Western Asia

Days to heading and PH can still be optimized in terms of adaptation to a wide range of environments, but limits for earliness and PH must be clearly identified in future studies. Overall, DH and PH can be further decreased below that of check line Karahan, and this was observed in trials conducted in Turkey (Eskisehir and Konya). These results were further confirmed by significant negative correlations between DH and GY in a wide range of environments, years and sets of winter wheat germplasm tested. The same negative associations between PH and GY were observed, however, in Iranian regions, taller germplasm (with more biomass and more reserves for grain filling) will be of advantage during grain filling probably due to decreased soil depth and water availability. Another important trait, estimated biomass (Feekes stages 4–5), had intermediate heritability, can be measured at early stages of development, and therefore is a very promising tool for selecting high GY under low plant densities (e.g. caused by early water stress).

Based on phenotypic data interpretation of the relations between DH and PH with yield, it seems a relatively straightforward task to manipulate these two traits in new germplasm for optimal expression. The empirical approach (visual observation during phenotypic selection) towards optimization of these two traits is still the most preferred method of introgression and it has been successfully applied during and since the "green revolution". However, knowledge of genes or markers with large additive effects and their adaptation to the environment, particularly those that also maximize the increase in GY, will facilitate targeting introgression via marker-assisted selection (Griffiths et al. 2012) and strategic crossing. It is well known that some height-reducing alleles are better than others in promoting yield due to different levels of pleiotropy (Griffiths et al. 2012). It is also likely that multiple genes controlling DH are similarly pleiotropic in effect. Only when the isolated effect of each of these genes is evaluated will manipulation of PH and DH be possible with some degree of confidence.

MATERIALS AND METHODS

Plant material and environments

In order to test physiological and agronomic traits, we conducted trials during 2011–2012 in Turkey, using a set of 30 historical (old to modern) winter wheat (*Triticum aestivum* L.) varieties (Trial A conducted in Konya and Eskisehir), and another set of 75 modern advanced lines (Trial B conducted only in Konya) from the IWWIP in Turkey using a well-adapted variety, Karahan, as a check in both trials. Two trials (with two different WRs) were set up at each environment: one rainfed and one with supplemental irrigation of approximately 100 mm given at booting stage in Eskisehir and Konya. All trials were sown late October (in Eskisehir Oct. 25 and in Konya Oct. 30). Soils in Eskisehir had 1.3% organic matter and 2 p.p.m. nitrate with pH of 7.6. Soils in Konya had 1% of organic matter and 2.5 p.p.m. nitrate with pH of 7.7. Appropriate fertilization and weed control were implemented to avoid yield limitations. Nitrogen fertilization was applied at soil preparation and on Mar. 15 with 150 kg/ha split in two halves. Weeds were controlled with herbicide in spring using DuPont Harmony Extra. The experimental design was a randomized block design with two replications in 5 m long and 1 m wide plots with an inter-row distance of 0.25 m, consisting of six rows with plant rates of approximately 500 plants/m² for Trial A and approximately 200 plants/m² for Trial B.

To further confirm the impacts of DH and PH on GY in a wide range of environments in West and Central Asia, results from international nurseries released by IWWIP (data available online at http://www.iwwip.org/) were used in correlation analyses. The sets of germplasm evaluated also contained Karahan as a check line. Environmental and long-term weather data are shown in Tables S1, S2 and environments were classified according to stresses. High-temperature sites were considered as places with at least above 0 probability of having temperatures above 35 °C (35 °C threshold has been used in Porter and Semenov 2005) and drought sites were considered as such when receiving less than 300 mm of rainfall as indicated in Gornall et al. (2010).

Yield and physiological traits

We determined GY using standard protocols (Sayre et al. 1997). Days to heading was taken as the point when more than 50% of plants were displaying heads starting from emergence date (Zadocks Stage 59, Zadoks et al. 1974), and CT was measured at the grain filling stage (CTgf) using a portable infrared thermometer (Mikron M90 Series, Mikron Infrared Instrument, Oakland, NJ, USA) between 11:00 and 13:00 hours. Physiological maturity (measured only in the Konya trials) was measured as the time when 50% of the spikes in a plot showed a total loss of green color, corresponding to Zadoks stage 89 (Zadoks et al. 1974). Plant height was determined by measuring the distance from the base of the stem to the top of the spike, excluding awns. Biomass at several stages of development was estimated using NDVI and calculated using measurements taken at approximately 660 and 770 nm $((R770 - R660)/(R770 + R660))$ (http://www.ntechindustries.com/lit/gs/GS_Vegetation_Indices.pdf). All NDVI measurements were taken with a GreenSeeker sensor (Optical Sensor Unit; 2002 Ntech Industries, Ukiah, CA, USA). The instrument records the reflectance in one plot at a frequency of 30–50 times/plot; the distance between the GreenSeeker and the plot was kept constant at approximately 50 cm.

Measurements started shortly after winter cold temperatures (Feekes Physiological Growth stages 4 and 5) and continued every 1 or 2 weeks up to physiological maturity in

Konya (a total of 13 measurements were taken on Mar. 26; Apr. 2, 9, 16, and 24; May 2, 7, 16, and 25; and June 4, 11, 21, and 28), but ended at the mid-grain filling stages in Eskisehir (a total of seven measurements were taken on March 28; April 5, 12, and 25; May 9 and 22; and June 5). Estimated biomass (Feekes stages 4–5) was calculated as shown in Raun et al. (2001), using the sum of NDVI at the first 2 weeks after dormancy divided by degree days (GDD) between the two dates (GDD = $(T_{min} + T_{max})/2$), with T_{min} and T_{max} (maxima and minima temperature) recorded from daily temperature data. Rate of senescence was determined only in Konya, using the last five NDVI measurements after heading (for further details on the calculations, see Lopes and Reynolds 2012).

Statistical analysis

To determine the significance of genotypic, environmental (Konya and Eskisehir), WR (irrigated and rainfed) and genotype by environment and WR interaction effects, ANOVA was performed using the PROC MIXED from SAS considering all effects as crossed and fixed (SAS Institute, Cary, NC, USA). The Bartlett test indicated unequal variances for the two environments and for this reason the PROC MIXED was used together with the Satterthwaite approximation method after the MODEL statement to calculate the effective degrees of freedom of a linear combination of independent sample variances. All observations having the same level of the factor entered on the GROUP option (environment) of the REPEATED statement had the same estimated variance.

Means were compared by applying the LSD test and, in Trial A, environment by WR interactions were evaluated by least squares means computed for each effect using the LSMEANS statement in SAS and the PDIFF option to deliver *P*-values for differences (5%) of the LSMEANS. Trait reproducibility across environments was assessed with broad sense heritability as:

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_{ge}^2/e + \sigma^2/re}$$

where *r*, number of repetitions; *e*, number of environments; σ^2, error variance; σ_g^2, genotypic variance; and σ_{ge}^2, genotype by environment interaction variance.

Phenotypic correlations were calculated using the CORR procedure (SAS Institute) for each genotype average across locations or in each location. Simple and multiple regressions were used to detect how well GY and NDVI could be predicted from DH and PH using Microsoft Excel (Microsoft, Redmond, WA, USA) and add-in POPTOOLS (Hood 2010).

Bi-plot analysis was used to study genotype × environment effects according to Samonte et al. (2005) for GY, DH, and PH with the objective of finding optimal expression of DH and PH to maximize GY in two different sets of germplasm: Trial A which included old and modern varieties and data collected from IWWIP international trials with modern advanced lines in 2010–2011 crop cycle only; data available at http://www.iwwip.org/, file 13IWWYT-SA-REPORT.xlsx but with data from local check line (a different variety in each location), removed from the analysis. In the bi-plot analysis, treatments (genotype) were used as variables and environments as units. For better visualization of genotype effects, bi-plot scores have been multiplied by four. A bi-plot is a scatter plot of scores of treatments (genotypes or varieties) and environments of the first dimension against the scores of treatments and environments of the second dimension. The treatment and environment scores are represented as vectors in a 2-D space. Both treatment and environments vectors are drawn from the origin (0.0) to the end-points determined by their scores. An angle less than 90° or larger than 270° between a treatment vector and an environment vector indicates that the treatment has a positive response in that environment. A negative treatment response is indicated if the angle is between 90° and 270°. The site regression analysis can identify the subsets of treatments based on effects of treatment per se and treatment by interaction simultaneously, which means that the size of each vector is directly proportionate to its trait value.

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SUPPORTING INFORMATION

Table S1. Long-term weather data in several sites in West and Central Asia

Average spring to summer temperature, average winter temperature (between Nov. 1 and Mar. 31); total annual precipitation; average across number of years where data was available (# years); probability of observing days with temperatures above 35 °C ($P > 35$ °C) in the summer (between Apr. 1 and July 31); temperatures below -17 °C during the winter ($P < -17$ °C); probability of observing less than 300 mm ($P < 300$ mm) of annual precipitation are all shown. NaN, data not available

Table S2. Sites in West and Central Asia used for germplasm evaluation and corresponding latitude (LAT), longitude (LONG), and altitude. NA, not available

Table S3. Means, standard error of difference (SED), and least significant difference (LSD) of 30 varieties (Trial A) grown in Eskisehir and Konya with supplemental irrigation and under rainfed conditions (analysis of variance is shown in Table 1)

Means of all varieties in each environment and water regime are also shown: Eskisehir with supplemental irrigation (ESKIRR) or rainfed (ESKRAF), in Konya with supplemental irrigation (KONIRR) or rainfed (KONRAF). (t) after SED, LSD, and degrees of freedom (df) corresponds to total analysis, with all genotypes, environments, and water regimes. Means, SED, LSD, and df of traits showing significant genotype by environment interactions are displayed for each environment separately (GY, DH, PH, and CTgf). Significant differences ($P < 0.05$) between pairs of water regimes are shown in bold. SED and df is also shown for environment by water regime interactions

Table S4. Means and standard error of difference (SED) of 75 advanced lines (Trial B) grown in Konya with supplemental irrigation and under rainfed conditions (ANOVA is shown in Table 2)

Means of all advanced lines in each environment and water regime are shown: in Konya with supplemental irrigation (KONIRR) or rainfed (KONRAF). (t) after SED, least significant difference (LSD), and degrees of freedom (df) corresponds to total analysis, with all genotypes, environments, and water regimes. Means, SED, LSD, and df of biomass are shown separately for each water regime due to significant genotype by environment interactions. Significant differences ($P < 0.05$) between pairs of water regimes are shown in bold. SED and df is also shown for environment by water regime interactions.