RESEARCH

Breeding for Yield Potential has Increased Deep Soil Water Extraction Capacity in Irrigated Wheat

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ABSTRACT

The global wheat (*Triticum aestivum* L.) growing area under irrigation has risen to approximately 20%. However, future availability and quality of irrigation water is likely to decline due to competition from the needs of the expanding population combined with the effects of climatic change. Recent genetic improvements of the yield of irrigated spring wheat lines reported by CIMMYT have been associated with significantly higher biomass, suggesting that either crops are becoming more water use efficient or are extracting more water from their environment. Water uptake characteristics of eight CIMMYT spring bread wheat cultivars—released during the period between 1950 and 2009—were measured in three contrasting irrigation regimes in northwestern Mexico during 2009/2010 and 2010/2011 and compared with crop growth. Increases in yield and biomass of genotypes were associated with additional water uptake in all environments whilst the water use efficiency for yield and biomass production was unchanged across cultivars but increased as a main effect of reduced water supply. Modern cultivars showed increased ability to extract moisture from deeper soil profiles (60–120 cm) especially during grain filling, associated with higher stomatal conductance in the fully irrigated environment and lower canopy temperatures in all environments. Expression of C isotope discrimination was progressively lower with increasing water stress. Results indicated increased water uptake by roots especially from deeper soil profiles allowing greater water harvest.

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Abbreviations: CHL, chlorophyll content of the flag leaf; CID, C isotope discrimination; CIDg, C isotope discrimination of the harvested grain; CT, canopy temperature; CTgrf, canopy temperature during grain filling; CTveg, canopy temperature during booting; DD, degree days; DM, dry mass; DRT, drought; GNO, grains per square meter; GRF, grain filling; Gs, stomatal conductance; HI, harvest index; IRR, full irrigation; RED, reduced irrigation; REP, reproductive; TE, transpiration efficiency; TGW, thousand grain weight; TWU, total water uptake; VEG, vegetative; WSC, water soluble carbohydrate; WU, water uptake; WUE, water use efficiency; WUE_B, water use efficiency of biomass; WUE_Y, water use efficiency of yield; YEAR, site–season.

Wheat is grown on over 200 million ha of land worldwide and provides approximately one-fifth of the total calorific input of the world's population (Braun et al., 2010). Presently approximately 20% of the global wheat growing area is irrigated (Mekonnen and Hoekstra, 2010), with the area under irrigation especially high in developing countries such as India and China where at least 75 to 80% of the area is irrigated (Reynolds et al., 2008), and expansion of the irrigated area has been a major driver of cereals production in recent decades (Araus et al., 2008). Agriculture presently uses approximately 80% of the world's usable water (Molden, 2007) and increasing amounts of water will be required to drive productivity (Falkenmark and Rockström, 2004) to supply the continued global demand for cereals consumption (Rosegrant and Agcaoili, 2010). However, simultaneous demand from growing domestic, municipal, industrial, and

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environmental needs of the expanding population will increase competition for usable water, which combined with changing rainfall patterns associated with climatic change and declining water resources in some regions will reduce the amount and predictability of supplies (Easterling, 2007; WWAP, 2009).

Water availability has already become the main abiotic factor limiting crop productivity in several regions of the world, and despite being relatively well adapted to drier environments—being grown widely throughout the world in semiarid areas such as North Africa, Central Asia, and Australia—the growth and yield of wheat is severely compromised by reduced water supply (Araus et al., 2002, 2003). Increasingly, therefore, water availability will be one of the fundamental limitations to the expression of yield potential in high input agricultural systems while productivity will become less predictable under low irrigation or rainfed environments—the primary means of food production for most farmers in developing countries—further adding to the challenge for global food security. The future of irrigated agriculture will therefore take place under increasing water scarcity, and substantially more water use efficient crop production—the use of less water to achieve high yield—must be a major objective of agricultural research (Richards et al., 2002; Araus, 2004).

In high yielding irrigated environments, where water is not a major limitation to productivity, increases in yield associated mainly with increased harvest index (HI) (e.g., Sayre et al., 1997) would not necessarily require more water since total biomass has not changed. However, more recently, increased yield potential has been associated with increased biomass in irrigated situations (see Reynolds et al., 2009) raising the question, therefore, of whether that this is a result of cultivars using water more efficiently or extracting more water from the environment. Even in studies comparing cultivars that show genetic gains in yield independently of biomass, different estimates of transpiration efficiency (TE)—including stomatal conductance (Gs), canopy temperature (CT), and C isotope discrimination (CID)—suggested that superior cultivars were in fact extracting more water from the soil during grain filling (Fischer et al., 1998).

Although TE (defined as the amount of biomass produced per millimeter of water transpired; Condon et al., 2004) typically increases under water deficit due to the conservative response of stomata to reduced water availability in the soil, it is widely accepted that genetic gains in most water-stressed environments have and will continue to come from increased capacity to extract water from the environment (Blum, 2009). An important exception is in environments where water is not available at soil depth and hence genetic variation in TE has been shown to be associated with performance (Condon et al., 2002). In spring wheat, the association between water uptake (WU) and performance under drought was demonstrated in a mapping population by measuring the association of cooler canopies with yield (Olivares-Villegas et al., 2007), common quantitative trait loci for yield and CT were shown (Pinto et al., 2010), and the association of deeper roots and the ability to extract more water from soil profiles below 0.5 m were shown in contrasting sister lines from the same population (Lopes and Reynolds, 2010).

The objectives of the current study were to compare a set of spring wheat genotypes representing breeding progress from 1950 to 2009 under different levels of irrigation to (i) determine whether progress in breeding was associated with increase water use efficiency (WUE) or increased WU, (ii) compare water use patterns of the genotypes at discrete soil profiles down to 1.2 m to determine whether genetic effects are consistent at different depths, (iii) compare water use patterns of the genotypes at different crop stages to establish how phenology may interact with differences in WU or WUE, and (iv) examine the relationships of WU and WUE with other physiological and agronomic traits to determine potentially useful interventions in genetic improvement protocols.

MATERIALS AND METHODS

Plant Material

Eight spring bread wheat cultivars were selected to represent genetic progress in yield potential of CIMMYT cultivars released between 1950 and 2009 (Table 1). Genotypes were selected to span CIMMYT's spring wheat breeding history starting with a tall landrace as a baseline, including five hallmark semidwarf cultivars, and two of the most recent lines with good expression of yield and biomass. There was no prior knowledge of relative WU or WUE of these lines.

Environments

Two field trials were conducted in Mexico (CIMMYT Obregon Experimental Station), Yaqui valley, Sonora, northwestern Mexico (27°20′ N, 109°54′ W, and 38 m above sea level) during the field seasons 2009/2010 and 2010/2011 (henceforth referred to by the year of harvest: 2010 and 2011, respectively). The soil type is an aridisol type, a heavy clay loam low in organic matter (0.76%) and slightly alkaline (pH 7.7) with a plant-available water holding capacity of about 200 mm. At Obregon, semidry, stable environmental conditions are dependent on irrigation. The site is a high radiation, irrigated environment for which meteorological data are summarized in Table 2. A prophylactic program of insecticides, fungicides, and herbicides was applied to control pests, diseases, and weed infestations, and accordingly there were no significant incidences in the experiments. Lodging of the tallest cultivar, Yaqui_50, was prevented by fixed wires, and consequently no lodging was observed in either trial.

Plants were sown on raised beds (described by Limon-Ortega et al., 2000) spaced at 80 cm intervals, each with two crop rows (24 cm between rows) with three contrasting irrigation regimes. The plot size, seed rate, and irrigation regime varied between treatments: (i) for full irrigation (IRR) the

Table 1. Cultivar characteristics.

Cultivar	Cultivar name	Year of release	Pedigree
Yaqui_50	Yaqui_50	1950	NEWTHATCH/MARROQUI-588
SieteCerros_66	SieteCerros	1966	PENJAMO T 62/GABO 55
Seri_82	Seri	1982	KAVKAZ/BUHO//KALYANSONA/BLUEBID
Bacanora_88	Bacanora	1988	JUPATECO F 73/BLUEJAY//URES T 81
Attila_90	Attila (PBW 343)	1990	NORDDEPREZ/VG9144//KALYANSONA/BLUEBIRD/3/YACO/4/VEERY $^{\#}$5
Tacupeto_01	Tacupeto	2001	URQUIZA/3/BONZA/4/TORIM F 73/5/ALDAN/6/SERI M
Navajoa_07	Navajoa	2007	ATTILA/PASTOR
Croc_09	Croc_1/AeSquarrosa(205)//Borl95/3/Prl/Sara/Tsi/Vee $^{\#}$5/4/Fret2	2009	CROC_1/AE.SQUARROSA (205)//BORLAUG M 95/3/PARULA/ICTA SARA 82//TESIA F 79/VEERY $^{\#}$5/4/FRET2

Table 2. Mean monthly weather data for 2009/2010 (2010) and 2010/2011 (2011) growing seasons and long-term mean (LTM) (2001–2010). Temperature values shown are the monthly average of the minimum or maximum air temperatures.

	Minimum air temperature (°C)			Maximum air temperature (°C)			Monthly solar radiation (MJ m^{-2})			Monthly rainfall (mm)		
Month	2010	2011	LTM	2010	2011	LTM	2010	2011	LTM	2010	2011	LTM
Nov.	12.9	10.0	12.4	29.9	29.3	29.8	478	533	468	3	0	4
Dec.	8.0	8.4	7.8	23.9	26.5	24.4	426	459	422	1	0	6
Jan.	7.6	5.8	7.3	24.8	24.4	24.5	474	496	469	19	0	25
Feb.	8.0	4.9	7.8	24.3	24.5	24.9	557	574	518	9	0	12
Mar.	8.4	8.5	8.5	27.1	29.3	27.4	752	787	730	0	0	1
Apr.	10.9	11.7	10.9	29.1	30.7	30.4	798	824	772	0	0	1

plot area was 3.2 by 12.0 m (four beds per plot) with 192 g per plot seed rate and five irrigation events during the plant growth cycle, applied when approximately 50% of the available soil moisture in the 0 to 120 cm profile was depleted, (ii) for reduced irrigation (RED) the plot area was 3.2 by 6.0 m (four beds per plot) with 97 g per plot seed rate and two irrigation events during the plant growth cycle, at sowing and at the start of booting, and (iii) for drought (DRT) the plot area was 1.6 by 3.5 m (two beds per plot) with 70 g per plot seed rate and only one irrigation at sowing.

Plots were sown in a total randomized block design with three replicates for the IRR and RED treatments (giving a total of 24 plots) and two replicates for the DRT treatment (giving a total of 16 plots). The IRR treatment was duplicated to provide additional data for yield and harvest biomass. Experiments were surrounded by buffer plots of durum wheat (*Triticum durum* Desf.) to reduce edge effects. The experiments were sown on 27 Nov. 2009 (DRT) and 2 Dec. 2009 (IRR and RED) and 22 Nov. 2010 (DRT and RED) and 29 Nov. 2010 (IRR) and harvested in April the following year. This corresponded with the spring wheat season in the region. Irrigation was gravity-fed flood irrigation in the IRR treatment and drip irrigation in the RED and DRT treatments. Total water available under IRR, RED, and DRT treatments, averaged across cultivars and years, was 559, 300, and 197 mm, respectively.

Agronomic and Physiological Measurements

The date and success of emergence was judged by estimating the number of plants contained within a quadrat sample when 50% of seedlings had emerged. Starting from this date of emergence, days to booting was determined when 50% of fertile stems were in the swollen boot stage (GS45) (Zadoks et al., 1974; Tottman and Broad, 1987), days to anthesis was determined when 50% of the spikes had half of the florets with anther extrusion (GS65), and days to maturity were recorded when 50% of the peduncles showed total loss of green color (GS87). For the IRR treatment, five samples of plant material were taken: at 40 days after emergence (approximately GS30), GS45, GS65 plus 7 d, GS65 plus 27 d, and GS92 ("harvest"); for the RED treatment, three samples of plant material were taken: at GS45, GS65 plus 7 d, and GS92; and, for the DRT treatment, one sample of plant material was taken, at GS92. In the IRR and RED treatments, the outer beds of the plot were not sampled, and for all treatments a buffer of at least 50 cm was left between successive samples areas and at the plot ends.

For preharvest growth stages, a sample of plant material was taken for growth analysis from each plot at defined growth stages in IRR and RED. Plant samples were cut at ground level using a quadrat of 0.80 m^2 (0.50 by 1.6 m) and the material transferred to the laboratory and analyzed on the day of collection. A subsample of the plant material was then dried until constant mass (i.e., 80°C for 72 h) and weighed for biomass determination. At harvest, a grab sample of 100 fertile stems was taken from each plot for the determination of HI (grain weight/biomass); nonfertile stems were not included in the HI calculations. The grab sample was dried and weighed, the dry spikes were cut from the grab sample and counted (to determine spikes per square meter), spikes were then threshed, and the grain was redried and weighed. The straw and chaff weight was determined by the difference between dry grain weight and dry grab sample weight. The remaining plot was cut by a plot combine harvester and dried to constant weight for yield determination, excluding the outer beds and 50 cm borders of each plot in the IRR and RED treatments. Plot biomass was estimated from yield/HI. Yield components were calculated using standard protocols (Pask et al., 2012). The thousand grain weight (TGW) (mg) was determined by weighing two samples of 200 randomly chosen dried whole grains. From these data the number of grains per spike and grains per square meter (GNO) were calculated and expressed per square meter of ground area.

Physiological measurements were made of all cultivars using standard protocols (see Pask et al., 2012): plant height during early grain filling, canopy temperature during booting (CTveg) and canopy temperature during grain filling (CTgrf), chlorophyll content of the flag leaf (CHL) at around anthesis, stem water soluble carbohydrate (WSC) content and stem WSC per square meter at anthesis plus 7 d, and CID (Δ^{13}C) of the harvested grain (CIDg) (data collected in 2010 only). In addition, for the IRR treatment, CID of the newest leaf taken at the three-leaf stage (i.e., GS13) and Gs were measured during heading and, for the DRT treatment, relative water content, leaf water potential, and morphological traits: flag leaf, peduncle and spike glaucousness and pubescence, and flag leaf rolling all measured during early grain filling.

Available soil water (from irrigation plus rainfall) was estimated by direct measurement of the gravimetric water content and converting to volumetric soil water content at the following profile depths: 0 to 30, 30 to 60, 60 to 90, and 90 to 120 cm in each plot immediately after biomass sampling and after irrigation. Values of soil bulk density of 1.3 and permanent wilting point of 20% of volumetric soil water were assumed for the calculation of water availability (expressed in mm of water), based on previous samplings at the same locality (Reynolds et al., 2007). Soil cores of 42 mm width and 120 cm length were extracted (using a hydraulic soil corer) (Giddings Machine Co.) from four (IRR and RED) or two (DRT) locations between the paired rows of the bed in each plot before irrigation and several randomly selected "check plots" after irrigation. The cores were separated into the four profiles and bulked according to profile. A sample of soil from each profile was weighed, dried at 105°C for 48 h, and reweighed. Changes in available soil water below 120 cm depth were considered to be negligible based on previous studies in these soils (Reynolds et al., 2007).

Determination of Water Use Efficiency of Yield and Biomass

Water use efficiency of yield (WUE_Y) (g mm^{-1}) is defined as the grain dry mass (DM) production (yield) per unit of water taken up from the soil from both irrigation and precipitation (WU) (i.e., yield/WU). Water use efficiency of biomass (WUE_B) (g mm^{-1}) is defined as the biomass DM production (biomass) per unit of water taken up from the soil from both irrigation and precipitation (i.e., biomass/WU). Water use efficiency of biomass for each phase of crop growth was calculated by using the total water extracted by each cultivar during a defined phase and the amount of biomass accumulated for that phase. No estimate was made for direct evaporation from the soil surface in these experiments and so WU and WUE will be systematically over- and underestimated, respectively. However, full ground cover was reached within a few days of each other in all genotypes (data not shown) so confounding genetic effects of ground cover on WU and WUE would be highly unlikely.

Statistical Analysis

Statistical analysis of data was performed using GENSTAT version 12.1 (VSN International, 2009). Data are presented in the results at three irrigation treatments across the two site–seasons. Standard ANOVA procedures were used to calculate treatment means, standard errors, and significant differences between treatments. A cross-site–season ANOVA was applied for three irrigation treatment levels (IRR, RED, and DRT) to analyze treatments effects across experiments and the interaction with site–season (YEAR), assuming irrigation treatments were fixed effects and replicates and YEARs were random effects. A probability value of 0.05 or less ($P \leq 0.05$) was taken to be statistically significant although values between 0.05 and 0.10 may receive comment in the text. Where there was a significant effect of year of release (RELEASE), polynomial (POL) regressions were fitted across RELEASE (i.e., POL(RELEASE;3) × YEAR) to test the form of the relationship (i.e., linear, quadratic, or cubic).

RESULTS

Growing Conditions

Minimum and maximum temperature, total rainfall, and total solar radiation during the growing season were recorded for each trial and compared to the long-term mean (Table 2). For all treatments, conditions were typical of a high radiation, irrigated, spring wheat environment with solar radiation and temperatures increasing from stem elongation through grain filling. There was a small amount of rainfall during the 2010 growing season before the start of booting (28.6 mm) whilst no rain fell during the 2011 growing season. Consequently, the RED and DRT trials resulted in gradually intensifying moisture stress levels as water from booting and seeding irrigations was depleted, respectively. Average monthly minimum and maximum temperatures in all stages were recorded. The period between anthesis and physiological maturity experienced the highest mean maximum air temperatures of, on average, 28.0, 28.3, and 27.5°C in the IRR, RED, and DRT treatments, respectively. Average CTs measured in the same time frame were observed to increase with DRT treatment at, on average, 24.1, 26.7, and 27.9°C in respective treatments. In 2011 minimum night temperatures for 3 to 5 February (during mid stem extension) fell to between −1 and −2°C with slight frost tipping of the uppermost leaves observed.

Crop Growth and Development

The growth cycle averaged 1068, 1234, and 1956 degree days (DD) from crop emergence to heading, anthesis, and physiological maturity, respectively, in the IRR treatment (equivalent to 73, 84, and 124 d). In comparison with IRR, in RED the DD to anthesis and physiological maturity were reduced, on average, by 30 (2.4%) and 159 DD (8.1%), respectively, and in DRT by 52 (4.2%) and 246 DD (12.6%), respectively.

For the purposes of quantifying WU patterns and its association with growth, the growing period was divided into three phases: vegetative (VEG), reproductive (REP), and grain filling (GRF). The REP phase was defined by a period of 30 d (average of 470 DD in IRR) around anthesis (averaged across all genotypes), determined with 20 d (average of 313 DD in IRR) before and 10 d (average of 157 DD in IRR) after the date of anthesis; the VEG phase was defined by the period from emergence to REP (average of 923 DD in IRR); and the GRF phase from REP to physiological maturity (average of 563 DD in IRR). The relative duration of GRF as a fraction of growing period was 0.29, 0.24, and 0.22 for IRR, RED, and DRT, respectively.

Crop Yield, Harvest Biomass, and Yield Components

Crop yield (g m^{-2}) increased significantly with year of release in all three treatments, and harvest biomass (g m^{-2}) increased significantly with year of release at IRR and RED with a trend for an increase in DRT and with a significant interaction between year of release and irrigation treatment for yield (Table 3). Yield in the IRR treatment ranged from 376 g m^{-2} for Yaqui_50 to 722 g m^{-2} for Croc_09, with a large increase of 204 g m^{-2} between Yaqui_50 and SieteCerros_66. Yield under RED and DRT was reduced, on average, by 45 and 68%, respectively, in comparison with IRR. While all treatments showed different genotypic patterns in yield, Yaqui_50 was always the lowest yielding and Croc_09 was always the highest yielding. Regression analysis between year of release and yield suggested that the relationship deviated significantly from linearity ($P < 0.01$ for quadratic and cubic effects); however, this deviation appeared entirely due to the inclusion of Yaqui_50 (associated with low HI). A linear regression fitted to yield (but excluding Yaqui_50) showed an average increase in yield since 1966 of 2.85, 0.91, and 2.23 g m^{-2} yr^{-1} (0.49, 0.27, and 1.49% yr^{-1}) for IRR, RED, and DRT, respectively. Effects were consistent across seasons but slightly larger in 2011. Harvest biomass in the IRR treatment ranged from 1256 g m^{-2} for Yaqui_50 to 1727 g m^{-2} for Croc_09 and under RED and DRT was reduced, on average, by 33 and 50%, respectively. All treatments showed a different genotypic pattern in biomass; Seri_82 had the lowest biomass in RED and DRT and Croc_09 had the highest (IRR and DRT) or second highest (RED) biomass. A linear regression fitted to biomass (including Yaqui_50) showed an average increase of 7.37, 4.16, and 2.81

Table 3. Crop yield, harvest biomass, harvest index (HI), and yield components—thousand grain weight (TGW), grains per square meter (GNO), and grains per spike (GPS)—for each cultivar. Data shown averaged across the two seasons. Significance of the analysis is shown.

	Yield[†]			Biomass			HI			TGW			GNO			GPS		
Cultivar[‡]	IRR	RED	DRT	IRR	RED	DRT	IRR	RED	DRT	IRR	RED	DRT	IRR	RED	DRT	IRR	RED	DRT
		g m^{-2}			g m^{-2}						g							
Yaqui_50	376	220	145	1,256	896	724	0.30	0.25	0.20	34.3	27.1	30.8	10,948	8,333	4,601	34	30	23
SieteCerros_66	580	359	169	1,424	992	707	0.44	0.37	0.23	35.3	27.6	29.9	16,222	13,266	5,429	51	45	26
Seri_82	613	336	162	1,388	892	668	0.47	0.38	0.23	39.2	28.8	30.0	15,657	11,643	5,219	54	45	27
Bacanora_88	702	338	166	1,593	946	714	0.47	0.36	0.23	35.3	25.0	27.0	19,673	13,800	5,975	53	44	26
Attila_90	659	367	232	1,580	1,018	762	0.44	0.36	0.30	37.7	26.9	29.3	16,248	14,264	7,681	47	43	30
Tacupeto_01	638	360	225	1,574	1,162	796	0.43	0.32	0.27	44.6	31.0	37.9	13,764	11,678	5,552	50	39	27
Navajoa_07	708	387	232	1,696	1,104	819	0.44	0.35	0.27	41.5	28.6	33.1	16,128	13,943	6,681	46	43	28
Croc_09	722	390	266	1,727	1,146	925	0.45	0.34	0.28	43.3	28.9	33.0	15,041	13,721	7,895	45	40	30
Mean	625	345	200	1,530	1,019	764	0.43	0.34	0.25	38.9	28.0	31.4	15,460	12,581	6,129	47	41	27
SED G	19.6	11.9	17.9	50.3	47.0	84.5	0.011	0.008	0.025	0.50	0.70	1.10	620.3	505.7	644.9	1.5	1.4	2.5
P[§] G	***[¶]	***	***	***[¶]	***	ns	***	***	*	***	***	***	***	***	**	***	***	ns[#]
P G × T		***			ns			***			***			***			ns	

*Significant at the 0.05 probability level.

**Significant at the 0.01 probability level.

***Significant at the 0.001 probability level.

[†] IRR, full irrigation; RED, reduced irrigation; DRT, drought.

[‡] G, genotype; SED, standard errors of differences of means; T, irrigation treatment.

[§] P, probability. Degrees of freedom for G are IRR and RED is 28 (64[¶]) and DRT is 14.

[#] ns, not significant.

g m^{-2} yr^{-1} (0.59, 0.48, and 0.42% yr^{-1}) for IRR, RED, and DRT, respectively.

Harvest index, TGW, and GNO all increased significantly with year of release in all three treatments. In the IRR treatment all three components were lowest for Yaqui_50 at 0.30, 34.3 g, and 10,948, respectively, while Bacanora_88 had the highest HI and GNO at 0.47 and 19,673, respectively, and Tacupeto_01 had the highest TGW at 44.6 g. Harvest index showed little difference between 1966 and 2009 (range 0.43 to 0.47) with Seri_82 and Bacanora_88 showing the highest HI. In comparison with IRR, HI under RED and DRT was reduced, on average, by 21 and 42%, respectively. The RED treatment showed a similar genotypic pattern in HI while DRT showed lower HI for pre-1990 released cultivars and higher HI for post-1990 released cultivars, with an average of 0.22 and 0.28, respectively. In the IRR treatment, TGW showed an average increase of 0.16 g yr^{-1} (0.48% yr^{-1}) between 1950 and 2009 and was highest for Tacupeto_01 at 44.6 g, with all post-2000 released cultivars showing values >40 g. In comparison with IRR, TGW under RED and DRT was reduced, on average, by 28 and 19%, respectively. In both the RED and DRT, Tacupeto_01 again had the highest TGW and Bacanora_88 had the lowest TGW. In the IRR treatment, differences in GNO between 1966 and 2009 did not show a consistent increase with year of release, in the range 13,764 to 19,673, with Bacanora_88 showing the highest GNO. In comparison with IRR, GNO under RED and DRT was reduced, on average, by 19 and 60%, respectively, and in RED and DRT the highest GNO was shown by Attila_90 and Croc_09, respectively, while Yaqui_50 had the lowest GNO in all treatments.

Crop Water Uptake

Total water uptake (TWU) from emergence to physiological maturity for the soil profile from 0 to 120 cm increased significantly with year of release in IRR, with a trend for an increase in RED and DRT (Fig. 1), the interaction between year of release and irrigation treatment was not significant. In the IRR treatment TWU ranged from 522 mm for Yaqui_50 to 597 mm for Croc_09. Under RED and DRT, TWU was reduced on average by 46 and 65%, respectively. All treatments showed a different genotypic pattern in TWU; Seri_82 had the lowest TWU under both RED and DRT while Tacupeto_01 and Navajoa_07 had the highest TWU in respective treatments. A linear regression fitted to TWU showed an average increase of 1.02 mm yr^{-1} (0.20% yr^{-1}) for IRR while the RED and DRT treatments showed smaller nonsignificant annual increases of 0.35 and 0.17 mm yr^{-1} (0.12 and 0.09% yr^{-1}), respectively.

Total water uptake was summarized into four depth profiles: 0 to 30, 30 to 60, 60 to 90, and 90 to 120 cm (Fig. 2). Linear regressions were fitted to the WU at each depth profile on the TWU for the combined soil profile. In the IRR treatment there was no change in WU in the upper profile (0–30 cm) whilst the three deeper profiles (30–60, 60–90, and 90–120 cm) showed increases in WU of 0.26, 0.23, and 0.50 mm mm^{-1} of TWU, respectively. Similar trends were observed in the RED and DRT treatments (data not shown), with the two deepest profiles (60–90 and 90–120 cm) showing the largest effect on TWU in all treatments. Furthermore, for the IRR and RED treatments TWU was calculated for the three crop growth phases (VEG, REP, and GRF) by interpolation (Fig. 2; data not shown for RED). Linear regressions were fitted for WU of each phase on TWU across all crop stages. Results showed increases in WU at all crop growth phase, which was greater for VEG and then REP and GRF at 0.44, 0.30, and 0.26 mm mm^{-1} of TWU for IRR and 0.52, 0.32, and 0.16 mm mm^{-1} of TWU for RED treatments.

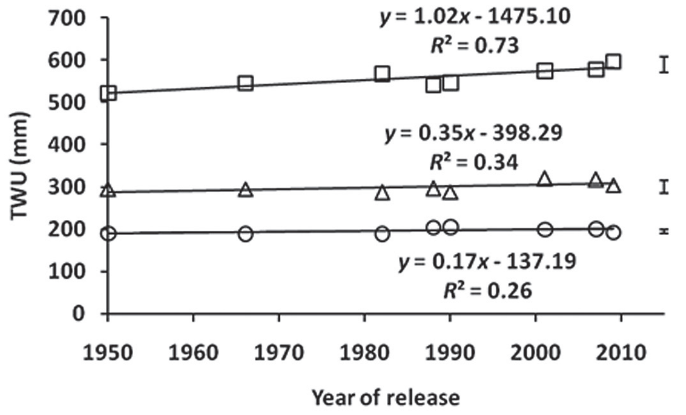

Figure 1. Total water uptake (TWU) (mm) (i.e., water uptake for all crop growth and for the whole soil profile) for eight cultivars as a function of year of release (1950–2009) and irrigation treatments: full irrigation (□), reduced irrigation (△), and drought (○). Fitted lines to each treatment, with standard errors of differences of means (SED) genotype (G) × year (Y) bar (df = 28, 21, and 14).

Crop Water Use Efficiency

Water use efficiency of yield showed no change with year of release for IRR and RED treatments (excluding Yaqui_50) but a significant increase for DRT was observed (Fig. 3) giving a significant interaction between year of release and irrigation treatment. Water use efficiency of yield in the IRR treatment ranged from 0.78 g m^{-2} mm^{-1} for Yaqui_50 to 1.37 g m^{-2} mm^{-1} for Bacanora_88, with a large increase of 0.32 g m^{-2} mm^{-1} between Yaqui_50 and SieteCerros_66. Averaged across cultivars but excluding Yaqui_50, WUE_Y was, on average, 1.17 g m^{-2} mm^{-1} for cultivars released between 1966 and 2009. A similar trend was observed in RED, with an average of 1.22 g m^{-2} mm^{-1} between 1966 and 2009. The DRT treatment showed lower WUE_Y for pre-1990 released cultivars and higher HI for post-1990 released cultivars, with an average of 0.85 and 1.22 g m^{-2} mm^{-1}, respectively, and a significant annual increase of 0.0086 g m^{-2} mm^{-1} (1.37% yr^{-1}).

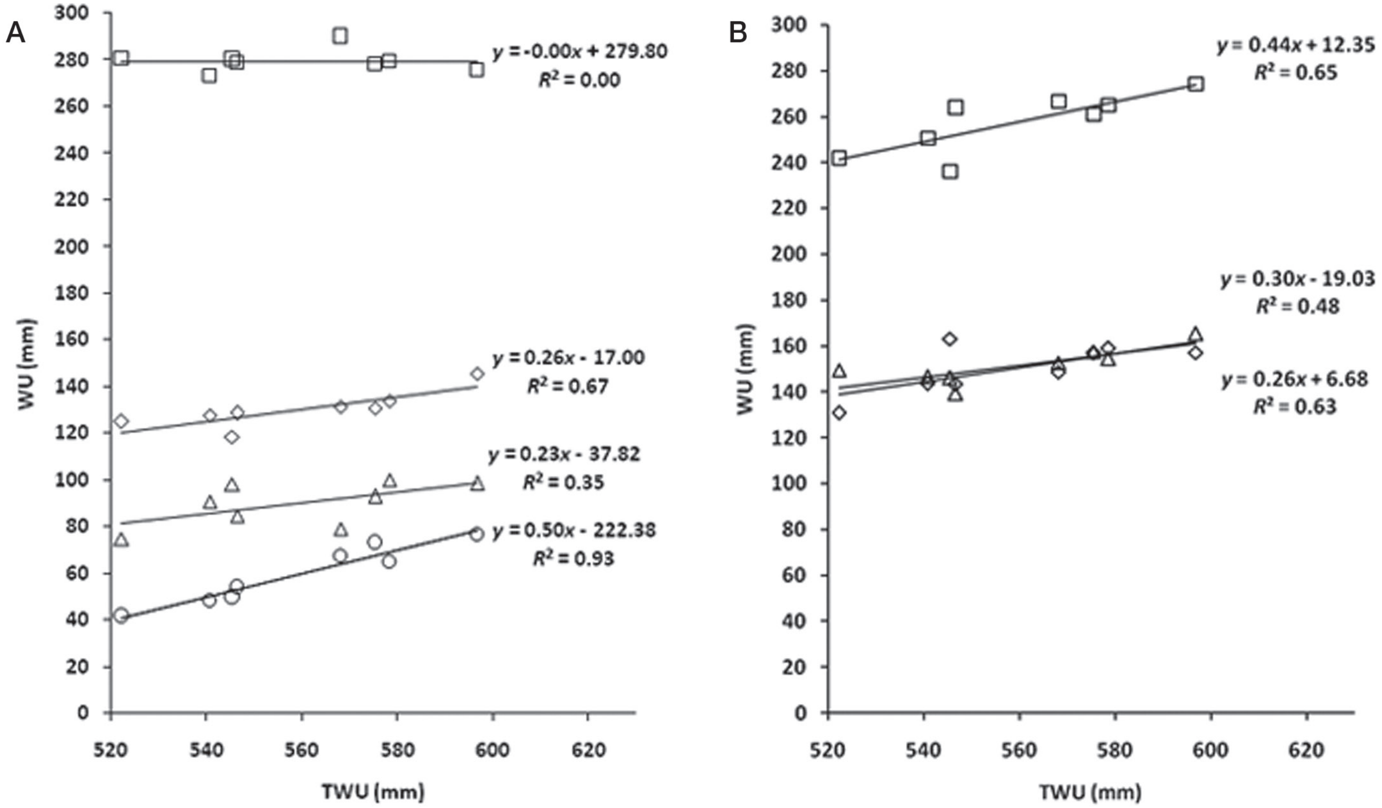

Figure 2. Water uptake for the full irrigation treatment: (A) Total water uptake (TWU) (mm) for all crop growth summarized into four depth profiles: 0 to 30 (□), 30 to 60 (◇), 60 to 90 (△), and 90 to 120 (O) cm. (B) Water uptake (WU) (mm) summarized into three crop growth phases: vegetative (□), reproductive (◇), and grain filling (△) versus total water uptake (mm) (i.e., for all crop growth) for eight cultivars (released 1950–2009). Fitted lines to each soil depth profile and crop growth phase, respectively.

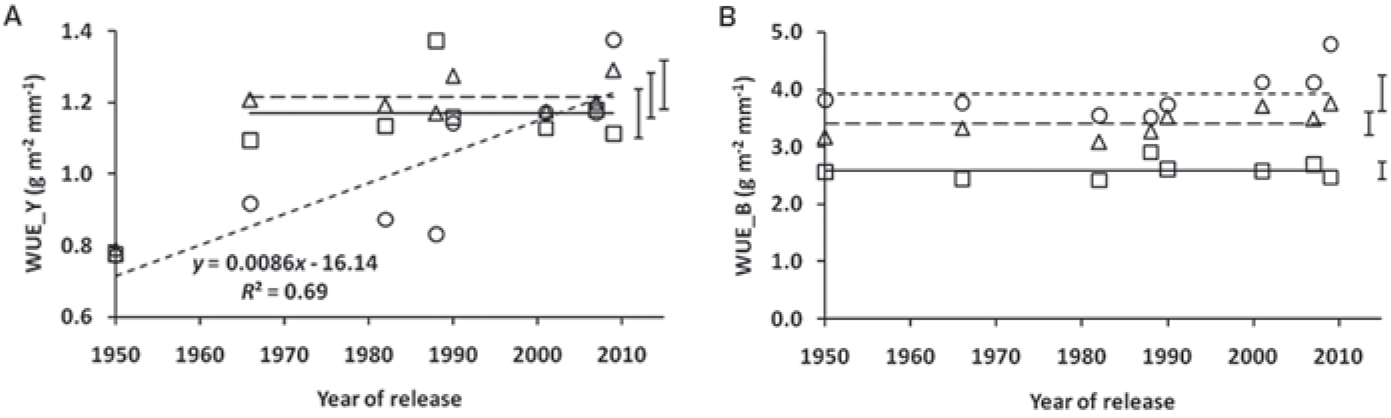

Figure 3. (A) Water use efficiency of yield (WUE_Y) (g m^{-2} mm^{-1}) and (B) water use efficiency of biomass (WUE_B) at harvest (g m^{-2} mm^{-1}) for eight cultivars as a function of year of release (1950–2009) and irrigation treatments: full irrigation (□), reduced irrigation (△), and drought (O). Fitted lines to each treatment (full irrigation ——, reduced irrigation – – –, and drought - - - - -), with standard errors of differences of means (SED) genotype (G) × year (Y) bar (df = 24, 18, and 14, respectively, for WUE_Y and df = 28, 21, and 14, respectively, for WUE_B).

Water use efficiency of biomass did not show a significant systematic trend with year of release in any treatment (Fig. 3), and the interaction between year of release and irrigation treatment was not significant. Water use efficiency of biomass in the IRR treatment ranged from 2.42 g m^{-2} mm^{-1} for Seri_82 to 2.91 g m^{-2} mm^{-1} for Bacanora_88, with an average across cultivars of 2.59 g m^{-2} mm^{-1}. Water use efficiency of biomass was larger under RED and DRT by 32 and 52%, respectively. In both the RED and DRT treatments there was a trend for an increase in WUE_B for cultivars released post-2000; for RED the values of WUE_B were 3.27 and 3.65 g m^{-2} mm^{-1} for pre-2000 and post-2000 cultivars, respectively, and for DRT values were 3.68 and 4.35 g m^{-2} mm^{-1}, respectively.

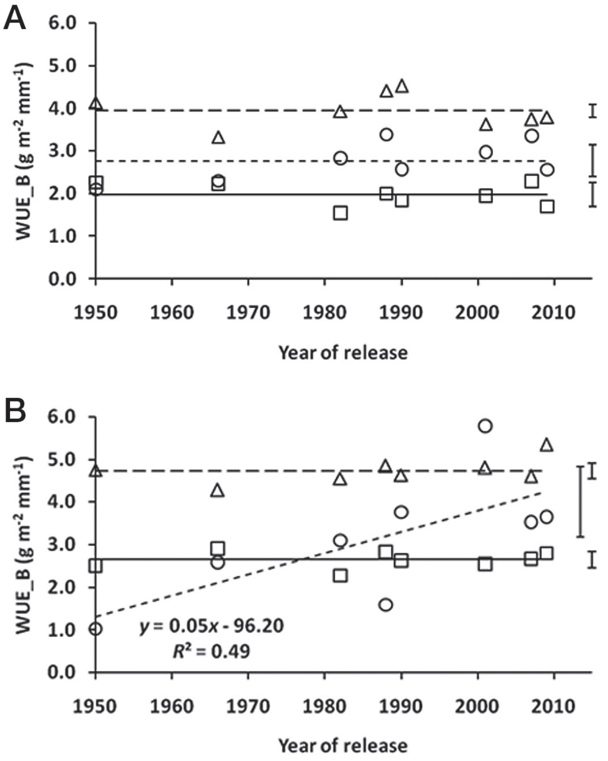

Figure 4. Water use efficiency of biomass (WUE_B) (g m^{-2} mm^{-1}) summarized into three crop growth phases, vegetative (□), reproductive (△), and grain filling (○), for eight cultivars as a function of year of release (1950–2009) and irrigation treatments: (A) full irrigation and (B) reduced irrigation. Fitted lines to each crop growth phase (vegetative ———, reproductive – – –, and grain filling - - - -), with standard errors of differences of means (SED) genotype (G) × year (Y) bar (df = 28 for full irrigation and df = 21 for reduced irrigation).

For the IRR and RED treatments WUE_B was calculated for three crop growth phases (VEG, REP, and GRF) by interpolation of data between sampling dates (Fig. 4). For both IRR and RED, WUE_B was highest in the REP and lowest in the VEG growth phases; exact values for IRR were 1.98, 3.94, and 2.76 g m^{2} mm^{-1} for the VEG, REP, and GRF growth phases, respectively; for RED values were 2.65, 4.73 and 3.13 g m^{2} mm^{-1}, respectively. Linear regressions were fitted for WUE_B at each growth phase on year of release. The only significant systematic trend was for the GRF phase in the RED treatment, which showed an average increase of 0.05 g m^{-2} mm^{-1} yr^{-1} (3.84% yr^{-1}) and ranged from 1.04 g m^{-2} mm^{-1} for Yaqui_50 to 5.79 g m^{-2} mm^{-1} for Tacupeto_01; cultivars released pre-2000 and post-2000 showed WUE_B values of 2.42 and 4.33 g m^{-2} mm^{-1}, respectively.

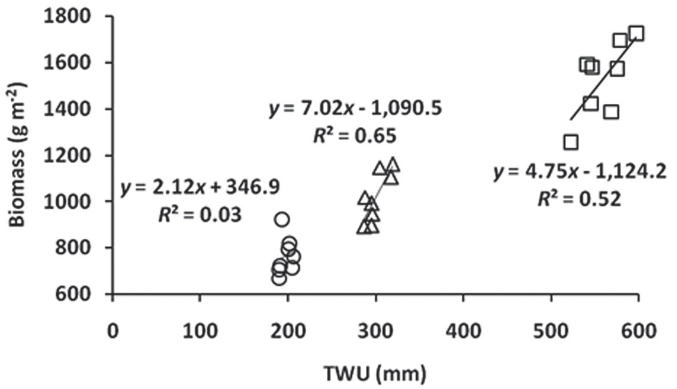

Figure 5. Harvest biomass (g m^{-2}) versus total water uptake (TWU) (mm) for eight cultivars (released 1950–2009) and irrigation treatments: full irrigation (□), reduced irrigation (△), and drought (○). Fitted lines to each treatment. WU, water uptake.

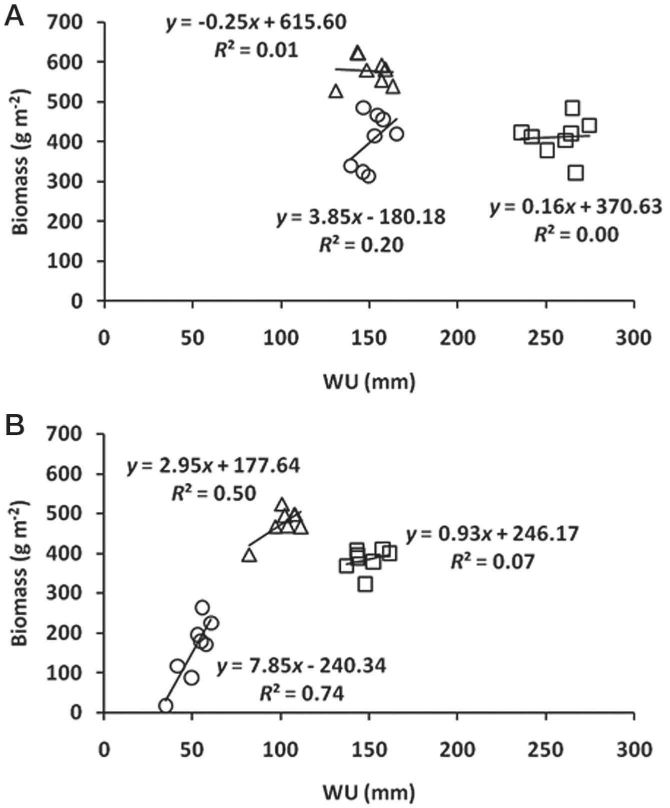

Figure 6. Biomass (g m^{-2}) versus water uptake (WU) (mm) summarized into three crop growth phases, vegetative (□), reproductive (△), and grain filling (○), for eight cultivars (released 1950–2009) and irrigation treatments: (A) full irrigation and (B) reduced irrigation. Fitted lines to each crop growth phase.

Crop Water Use for the Production of Biomass

Biomass at harvest showed a positive trend with increasing TWU in all three treatments (Fig. 5). A linear regression fitted to these data showed an average increase of 4.75, 7.02, and 2.12 g of biomass per millimeter of TWU for IRR, RED, and DRT, respectively. For the IRR and RED treatments the biomass accumulated and water taken up was summarized for each crop growth phase (VEG, REP, and GRF) by interpolation between samplings (Fig. 6). Results for both environments showed that in the VEG and REP phases there was no increase of biomass accumulation with increased WU whereas in the GRF phase there was a positive increase of biomass accumulation

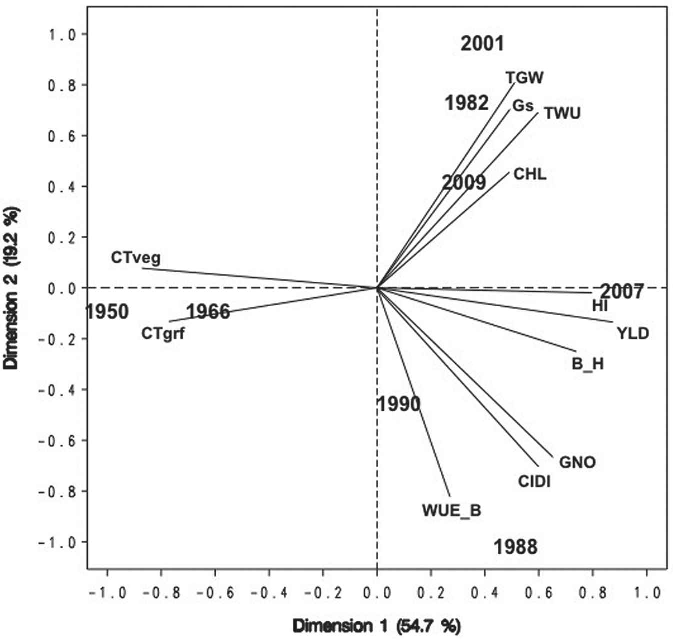

Figure 7. Biplot of yield versus crop characteristics for the full irrigation treatment for eight genotypes (released 1950–2009). B_H, biomass at harvest; CHL, chlorophyll content of the flag leaf (at around anthesis); CIDI, C isotope discrimination of leaf tissue during tillering; CTgrf, canopy temperature during grain filling; CTveg, canopy temperature during booting; GNO, grains per square meter; Gs, stomatal conductance; HI, harvest index; TGW, thousand grain weight; TWU, total water uptake; WUE_B, water use efficiency of biomass; YLD, grain yield.

with WU, with the linear regression of biomass on WU showing an average increase of 3.85 and 7.85 g m^{-2} mm^{-1} for the IRR and RED treatments, respectively.

Canopy Temperature, Stomatal Conductance, and Carbon Isotope Discrimination

The physiological measurements CTveg and CTgrf, Gs at heading, CHL at around anthesis, and CID of leaf tissue during tillering were included in a biplot analysis for IRR with the agronomic traits yield, biomass, yield components (HI, TGW, and GNO), and WU and use efficiency (Fig. 7). Canopy temperature during booting, CTgrf, and CIDg were negatively related to TWU, yield, and biomass; TWU was positively related to yield and biomass and to Gs and CHL.

Canopy temperature measured during grain filling showed a strong negative trend with increasing WU from the deepest soil profile (90–120 cm) in all three treatments (Fig. 8A). In the IRR treatment CTgrf ranged from <24°C for Navajoa_07 and Croc_09 to >25°C for Yaqui_50. Averaged across cultivars, growth stages, and time of measurement (11 AM to 2 PM), CTgrf was 24.1, 26.7, and 27.9°C for IRR, RED, and DRT, respectively. A linear regression fitted to CTgrf showed an average decrease in CT with increasing WU of –0.032, –0.034, and –0.150°C mm^{-1} of WU for IRR, RED, and DRT, respectively.

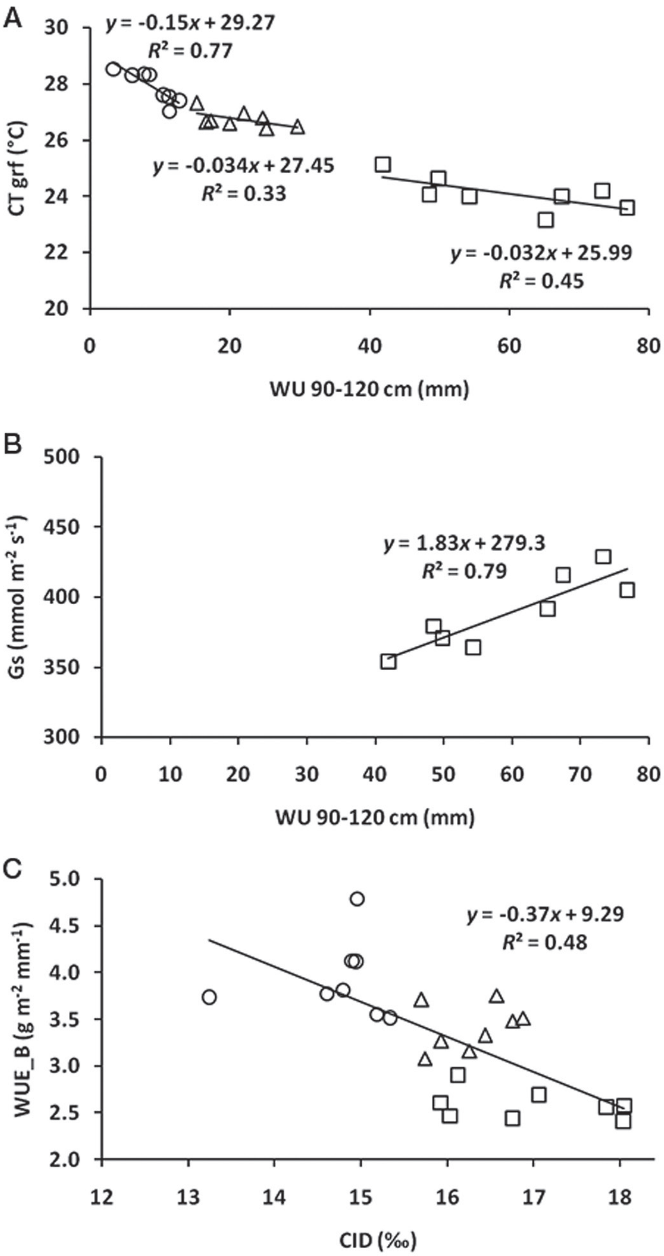

Figure 8. (A) Canopy temperature at grain filling (CTgrf) (°C) versus water uptake from the deepest soil profile (WU 90–120 cm) (mm) for irrigation treatments, full irrigation (□), reduced irrigation (△), and drought (○), for eight cultivars (released 1950–2009). Fitted lines to each treatment. (B) Stomatal conductance (Gs) (mmol m^{-2} s^{-1}) versus water uptake from the deepest soil profile (WU 90–120 cm) (mm) for the full irrigation (IRR) treatment (□) for eight cultivars (released 1950–2009). Fitted line to IRR treatment. (C) Carbon isotope discrimination of the harvested grain (CIDg) (‰) versus water use efficiency of biomass (WUE_B) (g m^{-2} mm^{-1}) for irrigation treatments, full irrigation (□), reduced irrigation (△), and drought (○), for eight cultivars (released 1950–2009). Fitted line to all three treatments.

Stomatal conductance—measured in the IRR treatment only—showed a strong positive trend with increasing WU from the deepest soil profile (90–120 cm) (Fig. 8B). A linear regression fitted to these data showed increased conductance of 1.83 mmol m^{-2} s^{-1} mm^{-1} of WU.

Analysis of grain tissue showed a main effect of environment with respect to discrimination against fixation of the heavier ^{13}C isotope, CID decreasing with water deficit as expected and averaging 17.0, 16.3, and 14.7‰ for IRR, RED, and DRT, respectively (Fig. 8C). Carbon isotope discrimination measured on the leaf tissue in IRR showed positive trends with yield and biomass and a negative trend with CTgrf. However, CID measured on leaf and grain tissue did not show consistent trends with WUE_B in any environment.

DISCUSSION

Responses under Full Irrigation

Genetic yield gains reported here are in broad agreement with other comparable studies (Waddington et al., 1986; Sayre et al., 1997), and the gains in both yield and biomass reported for the more recent cultivars used in the current study are also in agreement with a comprehensive 3-yr study (Aisawi, 2011). Total water uptake also showed genetic gains at a rate of 1.02 mm yr^{-1}. Cultivars released post-2000 took up >575 mm of available soil water compared with 522 mm for Yaqui_50, an increase of >10%. Analysis of WU from individual soil profile depths showed that the majority of the increase in TWU came from the deeper soil profiles (60–120 cm). In particular, WU from the deepest soil profile (90–120 cm) increased the most with year of release, at 0.50 mm mm^{-1} of TWU, and accounted for the majority of the increase in TWU (47%) between Yaqui_50 and Croc_09. This would suggest that the more modern cultivars have greater root proliferation at depth in the soil profile, permitting increased water harvest rather than allowing as much water to drain beyond the root zone or be left in the soil profile at harvest.

Dividing TWU between the three crop growth phases showed that the majority of water was taken up during the VEG phase with a similar amounts taken up during REP and GRF (on average at 46, 27, and 27%, respectively) and that although WU increased with year of release in all growth phases, the greatest increase was observed during the VEG phase (0.44 mm yr^{-1}). However, as VEG was longest phase, at on average 943 DD (compared with 470 and 563 DD for REP and GRF, respectively), then the rate of WU per DD suggests a more comparable value between growth phases. In fact, the rate of WU per DD was highest during REP and similar for VEG and GRF, overall at 0.32, 0.28, and 0.27 mm per DD, respectively. The increase in the rate of WU with year of release was greatest in REP and then VEG, with little difference amongst cultivars during GRF. Cultivars released post-2000 took up water faster in REP and VEG (at 0.29 and 0.34 mm per DD) than older cultivars (at 0.27 and 0.31 mm per DD). Conversely during GRF both pre- and post-2000 cultivars averaged 0.27 mm per DD, except for the most recent cultivars that took up more water associated with a longer duration of the GRF phase.

Responses under Reduced Irrigation

Moderate water stress (RED) and severe water stress (DRT) resulted in yields of approximately one-half and one-third of those under full irrigation (IRR). Genetic progress in yield was apparently greatest—in this small set of cultivars—under severe water stress (DRT) with results showing that modern varieties performed relatively better under water stress than older varieties; progress was higher in fact than findings of Perry and D'Antuono (1989), who found genetic gains of 0.57% in 28 wheat varieties in severely water-limited environments in Western Australia. However, the findings are in agreement with those of Manès et al. (2012), who looked at trends of the CIMMYT international nursery Semi-Arid Wheat Yield Trial between 1994 and 2010 over several hundred sites worldwide and found yield gains during this period to average 1%. The decrease in yield under water deficit was the consequence of a reduction in both biomass production and its partitioning to yield, as crop water deficit developed particularly during reproductive and grain-filling growth stages. Effects on yield components showed a large decrease in GNO explained mainly by reduced spike fertility and a reduction in TGW attributed to earlier senescence. A high proportion of grain in RED were small and shriveled as too many grains had been set for the water available postanthesis whilst under severe water stress the TGW was increased slightly as plasticity in grain number improved the source–sink balance and grains were consistently smaller but bolder.

Total water uptake (mm_uptake) was reduced with decreasing irrigation, by a half under moderate water stress and two-thirds under severe water stress, but demonstrating an increasing efficiency of extraction of available soil moisture (mm_available) (i.e., in terms of mm_uptake/mm_available). Results showed that genetic progress in TWU under RED and DRT was similar to that in the IRR treatment. Since it has been reported in some studies that under water stress crop plants tend to increase the proportion of biomass allocated to the roots—increasing rooting depth and density and distribution—to capture more moisture (Barraclough et al., 1989; Palta and Gregory, 1997), estimates of total biomass and therefore HI may be subjective although not all studies have shown increased root to shoot ratio (Reynolds et al., 2007). Results again showed a trend for genetic gains in TWU and with WU from the deeper soil profiles (60–120 cm) contributing most to the annual progress in both moderately (56%) and severely (89%) water-stressed environments. Present results, however, contradict studies that suggested that total WU has not significantly increased in modern wheats in Australia under mild water limitation (Siddique et al., 1990b) or has decreased slightly (Siddique et al., 1990a).

The superior performance of the more modern cultivars in water-stressed environments attributable to their ability to extract significantly more water from the deeper soil layers confirms earlier studies (Hattendorf et al., 1988; Angadi and Entz, 2002; Lopes and Reynolds, 2010). Furthermore, dividing TWU across growth phases in the moderately water-stressed environment again showed that the majority of water was taken up during the VEG phase (49%) and by far the least during GRF (17%). The VEG phase also showed the largest increase in WU with year of release (0.52 mm yr^{-1}) although the rate of WU was fastest during REP (0.22 mm per DD) and comparing across cultivars the greatest increase in the rate of WU with year of release was in GRF—allowing more modern cultivars to increase productivity and HI under water stress.

Responses of the Efficiency of Water Use for Yield and Biomass Production to Year of Release and Environment

In the IRR environment, the efficiency with which water was used to produce both yield and harvest biomass remained unchanged with year of release, with effects generally similar across all irrigation treatments. Results showed that WUE_Y was constant at, on average, 1.17 g m^{-2} mm^{-1} between 1966 and 2009—Yaqui_50 excluded from the linear regression due to the confounding effects of HI—and WUE_B was constant at, on average, 2.59 g m^{-2} mm^{-1}. Water use efficiency of yield and WUE_B are strongly linked as both are the product of crop growth whilst WUE_Y is also determined by the partition of biomass to the grain. These values are consistent with those reported by Siddique et al. (1990b) of 1.58 g m^{-2} mm^{-1} for WUE_Y and by Reynolds et al. (2007) of 2.24 to 5.74 g m^{-2} mm^{-1} for WUE_B for wheat grown in similar environments. Results show that high productivity and yield potential under conditions of high water demand are generally associated with unchanged or even reduced WUE_B (e.g., Muñoz et al., 1998) mainly because of nonconservative high water use. Results for CID of leaf material indicated that there was no intrinsic difference in WUE_B between cultivars (Condon et al., 2002) and Richards et al. (1993) also observed that WUE_B seemed to be similar between old and modern cultivars; however, relatively little work has been conducted on how WUE_B has changed with breeding practice to the present day.

Calculating WUE_B for individual crop growth phases showed large differences: the highest efficiency of water use was during REP and then GRF and VEG at, on average, 3.94, 2.76, and 1.98 g m^{-2} mm^{-1}, respectively. The higher efficiency observed during the mid phase of crop growth may be explained by a more conservative yet productive use of water by the crop, as the demand for water from the canopy exceeded supply causing temporary water limitation whilst the overall productivity of the canopy remained high. Efficiency decreased during GRF as the vapor pressure deficit—the difference between the water vapor concentration of the intercellular spaces and the atmosphere—increased, resulting in a high rate of transpiration due to high evaporative demand from the atmosphere but a low ratio of photosynthesis to transpiration (Condon et al., 2002). During both the REP and GRF phases direct evaporation from the soil surface was reduced by complete canopy cover, and the largest part of soil water was therefore transpired. Conversely, during VEG the supply of water exceeded demand by the crop and large quantities of water may have been lost by direct evaporation from the soil surface—studies show that up to 40% of total soil water may be lost by evaporation in wheat (Loss and Siddique, 1994; Zhang et al., 1998)—without taking part in transpiration and thereby reducing WUE_B. No difference in WUE_B between cultivars was observed for individual growth phases while it could be assumed that evaporative losses from the soil were approximately the same across cultivars.

Linear correlation between biomass and TWU showed an increase at, on average, 4.75 g m^{-2} mm^{-1}, with the additional 75 mm of water taken up by Croc_09 equating to 471 g of biomass compared to Yaqui_50. It appears that genetic advances in biomass were therefore driven by modern cultivars being able to take up more water, particularly from deeper soil profiles. Similar associations with high crop biomass production (and often final yield) and high crop water use have been observed in many studies (e.g., Hanks, 1983; Hsiao, 1993) since plant production is dependent on WU in high radiation, high vapor pressure deficit environments. Present results (not shown) also suggest that even in IRR crops were mildly water limited and theoretically would have responded to greater water supply—although this would have increased the risk of soil waterlogging and lodging (see Dodd et al., 2011, which shows that irrigation benefits winter wheat yields even in the relatively wet U.K. climate). When divided between growth phases, results showed that the majority of this effect occurred during the GRF phase at, on average 3.85 g m^{-2} mm^{-1} while increased WU amongst cultivars during the VEG and REP phases had little effect on biomass production as plants may have been limited by radiation interception and radiation-use efficiency, respectively. During GRF, cultivars released post-2000 took up more water when compared with cultivars released pre-2000, at on average 159 and 147 mm, respectively (+8.4%), and consequently continued to produce more biomass (+19.1%) through an extended duration of this phase when the products of photosynthesis go directly towards filling the grain, with lower respiratory or other costs, and were expressed as higher grain weight for these cultivars. This is consistent with other studies (e.g., Kirkegaard et al., 2007).

In comparison with the IRR environment, WUE_Y increased slightly in the moderately water-stressed environment and remained unchanged with year of release at, on average, 1.22 g m^{-2} mm^{-1}—again with Yaqui_50 excluded. In the severely water-stressed environment WUE_Y showed a significant increase with year of release, with genotypes released post-1990 showing higher values than those released pre-1990 at, on average, 1.22 and 0.85 g m^{-2} mm^{-1}, respectively—the more modern cultivars therefore showing similar values to those observed in IRR and RED. This difference can be explained by a greater stability in partitioning to yield under severe drought by the more modern cultivars, expressed as higher grain per square meter—both greater GPS and spikes per square meter—and as higher TKW. These cultivars had only a slightly longer postanthesis period (+7 DD) as a result of the increased water supply, which may not fully explain the 15% increase in TKW and therefore may have physiological advantages to drive greater partitioning. Araus et al. (2002) also observed improved WUE_Y in modern cultivars through increased HI driven by more assimilates to the grain in addition to drought-resistance advantages such as faster development, earlier flowering, and improved canopy structure (Siddique et al., 1990b). The upper limit of WUE_Y in well-managed spring bread wheat grown in water-limited conditions is typically 2.0 g mm^{-1} (Angus and van Herwaarden, 2001; Passioura, 2006).

Water use efficiency of biomass increased with increasing water limitation at, on average, 3.41 and 3.93 g m^{-2} mm^{-1} for RED and DRT, respectively, and has long been known to increase with increasing DRT stress and reduced water supply (e.g., Myers et al., 1984). The reduction in soil moisture and hence plant WU moderates growth rates leading to a reduction in transpiration and higher WUE_B compared to IRR. In addition, losses of soil moisture by direct evaporation (and probably subsoil drainage) are reduced in low irrigation conditions leading to apparent increases WUE_B. Although WUE_B was not effected by year of release, in both environments cultivars released post-2000 showed a trend for increased WUE_B compared with cultivars released pre-2000, by 12 and 18%, respectively. It is likely that this increase in WUE of biomass production is due to physiological mechanisms that are discussed in the following section. In the RED environment, the division of WUE_B by growth phase again showed that there were no differences between cultivars in the VEG and REP phases, with WUE_B again considerably higher in the REP phase than in the VEG phase at, on average, 4.73 and 2.65 g m^{-2} mm^{-1}, respectively. However, WUE_B during GRF showed a significant increase with year of release, with cultivars released pre-1990 showing approximately half the efficiency of those released post-1990 at, on average, 2.08 and 4.19 g m^{-2} mm^{-1}, respectively.

Correlations between biomass and TWU for the RED and DRT environments showed that there was again a linear relationship with a trend for biomass production to be driven by WU, rather than by changes in WUE_B at, on average, 7.02 and 2.12 g m^{-2} mm^{-1} for respective environments. These results indicate that the marginal return for capturing water in moderately water-stressed environments is higher than in IRR but with overall growth severely limited by water deficit especially in DRT. When divided between growth phases in RED, results showed that the majority of this effect again occurred during the GRF phase at, on average 7.85 g m^{-2} mm^{-1}—twice the value of IRR—while increased WU amongst genotypes during the VEG and REP phases had little effect on biomass production. The relative water stress during GRF in the RED environment would have been high due to the large crop canopy developed during the lower water stress VEG and REP phases and overall perhaps physiologically as high as that in DRT where the crop had developed more in tune with severe limitation. Under water-stress conditions, therefore, more modern cultivars are have both a higher capacity to extract more water from the soil profile—especially at depth—and are able to use this water more efficiently during GRF for biomass production. It is very likely that a similar effect occurred in DRT accounting for the increase in WUE_B for these cultivars.

Physiological Processes of Water Use in Productive and Efficient Crops

Results showed a strong association between stomatal conduction and increased WU—especially from the deeper soil profiles—and with the more productive cultivars, released post-2000, showing higher stomatal conductivity values than older cultivars at, on average, 410 and 377 mmol m^{-2} s^{-1}, respectively. High Gs indicates that photosynthesis and transpiration rates are potentially high and over time allows greater C fixation per unit land area and response to high sink demand (Fischer et al., 1998). Transpiration from the surface of the canopy results in evaporative cooling, and hence the surface temperature can also give an indication of the photosynthetic rate (Reynolds et al., 1994; Fischer et al., 1998). Canopy temperature values during GRF decreased with increasing WU from deeper soil profiles (60–120 cm) at –1°C per 42 mm, with cultivars released post-2000 showing lower CT—indicating increased leaf transpiration—than older cultivars at, on average, 23.6 and 24.4°C, respectively. These results further indicate that the more modern cultivars have a superior ability to capture water at depth and more water in total. Additionally, the increase in WU, particularly during GRF, extended the duration of green crop canopy as delayed senescence or “stay-green” and was associated with increased productivity during this phase in the more modern cultivars—most likely increasing grain filling and yield.

Although rooting traits were not directly measured in this study—given the difficulty of phenotyping roots—measurements of Gs and CT both provide indirect indicators of increased root WU capacity due to the active regulation of stomatal aperture. The increase in WU capacity and ability to extract moisture from the deepest two soil profiles and during the GRF phase may suggest that the more modern cultivars have increased root length density—essential for the effective uptake of soil moisture in the rooting zone—at depth, combined with continued postanthesis root growth, which is not uncommon (e.g., Barraclough, 1984), especially deeper in the soil profiles (Gregory et al., 1978). Studies have shown that root activity continues until close to physiological maturity (Gregory et al., 1978), and as a consequence the longer duration of the GRF phase of the more modern cultivars may be associated with greater root activity during this phase and vice versa.

Under water-limited conditions, the same cultivars experienced contrasting environmental pressures. Reduced water availability lowered Gs and transpiration, with the need to maintain functional water status of the leaves. This is supported by an increase in CTgrf values measured for RED and DRT, on average, at 26.7 and 27.9°C, respectively, with CT again showing strong correlation with WU from depth in each environment. Further evidence of a reduction in stomatal conduction—especially during GRF—can be seen from CID values measured in the grain, compared across environments, which show a reduction in discrimination against fixation of the heavier isotope of C (Rebetzke et al., 2002; Condon et al., 2002, 2004) at, on average, 17.0, 16.3, and 14.7‰ for IRR, RED, and DRT environments, respectively. However, as Gs decreases and leaf temperature increases, the efficiency of gas exchange increases (Condon et al., 2002) leading to increased TE at the leaf level (i.e., the proportion of WU that is transpired) and higher WUE_B (Muñoz et al., 1998)—accounting for the effects observed both between environments and between growth phases under water stress.

With increasing water limitation, cultivars demonstrated smaller plant size, shorter leaf length and/or smaller leaf area, and shorter crop growth duration (data not shown), features that reduce the interception and use of solar radiation and so are associated with low productivity and yield potential. However, these ascribe higher WUE_B as they reduce water use and slow crop growth rate. Under RED—where high yield potential can contribute to yield—water stress effectively emerged at around the end of anthesis and was most significant during the GRF phase. In this environment, reduction of plant size—and hence photosynthetic area—was through reduced peduncle elongation and a smaller flag leaf while spike length was unchanged but held fewer viable grains. Under DRT, water stress effectively emerged during stem elongation and the plant size, flag leaf length, and spike length was further reduced, allowing plants to be more in tune with water stress. Severe water stress postanthesis induced premature senescence reduced green canopy area, with senescence observed to start at the least productive lower leaves, so further reducing water use in this environment.

Under severe water stress, all cultivars showed phenotypic plasticity by reducing leaf size to reduce water use (data not shown). Exposure to a drying soil has been shown to promote root plasticity—morphology and growth—increasing partitioning to the root mass (root:shoot ratio) with deeper rooting systems (Gregory et al., 1995) and more branched seminal roots and a higher total root length to total leaf area (Morita et al., 1997). This therefore increases the ability of the plant to extract soil moisture from deeper soil profiles (Reynolds et al., 2007), which is particularly important when the crop depends on stored water. Spring wheat rooting depth in the Mediterranean type environment was found to be between 60 cm (Gregory et al., 1992) and 80 cm (Siddique et al., 1990a; measured in Australian spring wheat cultivars) in soil depth while results from the present study showed WU in the deepest soil profiles for all cultivars. However, more modern cultivars demonstrated increased TWU through WU from the deepest two soil profiles (60–120 cm) indicating great prioritization—through partitioning and/or activity—of rooting system at depth. More WU from deep soil profiles has found to be synonymous with better performance under DRT (Lopes and Reynolds, 2010) and the more modern cultivars in this study were able to maintain a cooler canopy and be more productive in the DRT environment, a trait that shows good association with yields under DRT (Olivares-Villegas et al., 2007).

CONCLUSIONS

The genetic progress in yield observed in the well-irrigated environment can be attributed to an increased capacity of modern cultivars to take up water, especially from the deeper soil profiles and during grain filling, allowing greater Gs and transpiration rates and consequently driving biomass production. The ability to extract more water from deeper in the soil profile and more water in total is probably explained by deeper, more vigorous root systems. However, high productivity requires nonlimiting water supplies for nonconservative use, and cultivars in the present study had been empirically selected in optimal environments without selection for efficiency of water use. Water use efficiency of biomass was observed to have remained constant with year of release and higher during the reproductive and grain-filling phases than during the vegetative phase but again unchanged amongst cultivars. Similar trends were observed in water-limited environments where breeding for increased yield potential realized higher yields and biomass from increased water harvest and with higher WUE_B observed with increasing water stress as a function of more conservative water use and reduced growth rates than of a net improvement in plant production biochemistry of assimilation (Blum, 2005).

In 2000, Norman E. Borlaug, 1970 Nobel Peace Prize laureate, called for a "blue revolution" in agriculture to mitigate against the coming impacts of water scarcity on food production. Water availability is already the most limiting factor to the expression of yield potential for wheat yields—even in irrigated environments—globally, and in the coming decades there will be less usable water available for irrigation as ground and surface water sources rapidly decline in wheat growing areas around the world. Further expansion of the area under irrigation is therefore not expected, and there is a need to ensure that water harvest is maintained or even improved. Detrimental effects of climate change—with higher temperatures increasing evapotranspiration losses—are likely to be most devastating where irrigation water is not available to compensate for decreased rainfall. The current study indicates that breeding for yield potential in irrigated environments has improved water harvest through increasing TWU, especially at depth, and that this is also associated with increased TWU and performance in drier environments (Table 3).

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