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Drought-Tolerant Barley: I. Field Observations of Growth and Development

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Abstract: An ever-growing challenge to agricultural production worldwide is the reduced availability of water and increased incidence of drought. The development of low-irrigation barley cultivars marks a significant achievement in breeding efforts for drought tolerance, but specific traits conferring adaptation to water stress remain unclear. Here, we report results from two years of replicated field trials comparing yield, phenology, water usage, and rooting characteristics of low-irrigation varieties "Solar" and "Solum" to high-input, semi-dwarf varieties "Kopious" and "Cochise". The objective was to identify differential performance of varieties under high- and low-water conditions through comparison of growth and developmental traits. Rooting characteristics were analyzed by digging in-field root profile walls to a depth of 1.8 m. Varieties were compared under high (877 mm) and low (223 mm) water regimes including irrigation and precipitation. Observed traits associated with improved performance of the low-irrigation varieties under drought conditions included early vigor, early flowering, greater root growth at 40–80 cm depth, and more effective water use exhibited by greater water extraction post-anthesis. The deeper rooting pattern of the low-irrigation varieties may be related to their ability to use more water post-anthesis under water stress, and thus, to fill grain, compared to high input varieties.

Keywords: drought tolerance; low irrigation; barley; root traits; field trial; water use; root profile

1. Introduction

Barley has demonstrated a capacity to thrive in arid and semi-arid climates where drought is a determinant of crop productivity. The projected increase in incidence and severity of drought conditions combined with the predicted decline in water availability has sparked interest in crop production that is less water dependent [1,2]. As a result of the increasing demand for cereal grains, attributable to human and animal consumption, there is an emerging consensus that demand could be better met through the development, dissemination, and adoption of drought tolerant genotypes [3,4].

Major drought tolerance traits assessed in this study relate to crop growth, water use, and yield. Crop growth as measured by biomass is indicative of a crop's ability to retain function in a dehydrated state [5–8]. Greater early-season leaf or shoot biomass, known as early vigor, is another drought adaptive trait. Early season canopy cover reduces evaporation from the soil surface leaving more water available for crop growth [9–11]. Plant height under drought stress compared to under non-stress conditions is also an indicator of crop drought tolerance as is the allocation of carbohydrate reserves to grain filling, expressed by harvest index [12–14].

Harvest index, the ratio of grain to total above-ground biomass, and grain yield in cereals is most affected by terminal drought stress, i.e., stress during the critical reproductive stage of anthesis. Therefore, traits associated with increased water access during grain fill, or changes in crop duration are associated with greater harvest index and grain yield [15,16]. A primary way to increase crop water access is through deeper roots, if subsurface water is available. Water use during this period is critical as photosynthate is allocated to grain growth [17,18]. In association with rooting depth, penetration ability of roots is of interest, as soil hardness generally increases as the soil dries [19,20].

Another means to improve water access is by adapting crop phenology to seasonal moisture availability. Considered one of the most impactful breeding strategies for low-water environments, faster phenological development has led to improved yield of cereals in Mediterranean-type environments characterized by winter precipitation and terminal drought stress [21–23]. Shorter crop duration maximizes growth when temperatures and vapor pressure deficit are lower.

The development and release of one-irrigation barley cultivars marks a significant achievement in breeding efforts for drought tolerance; however, the specific physiological and phenological traits associated with their drought tolerance remain unclear. In an effort to elucidate these traits, two years of replicated field trials were conducted in Tucson, Arizona comparing low-input varieties "Solar" and "Solum" to high-input, conventional varieties "Kopious" and "Cochise". We hypothesize that the low-input varieties will perform better under low water conditions and vice versa at high water conditions due to differences in yield components, phenology, water use patterns, and rooting characteristics.

2. Materials and Methods

2.1. Varietal Information

Development of barley cultivars adapted to water-limited environments was the motivation for a breeding program headed by R.T. Ramage and R. K. Thompson with the Agriculture Experiment Station (AES) of the University of Arizona and the Agriculture Research Service (ARS), USDA. In 1981, Composite Cross XXXIX was released, a population adapted to a single irrigation of 15 cm to 20 cm applied at or before planting (enough to wet the soil profile to a depth of 1.5 m to 1.8 m), with normal seasonal rainfall around 7 cm to 11 cm in Southwest Arizona. Selection criteria included turgid plants at flowering, plump seed, and ability to outcross (male sterility) [24].

Continued breeding efforts using the Composite Cross XXXIX germplasm resulted in the release of six-row "one-irrigation barley" varieties: Solum in 1991 (by the ARS, USDA and Arizona AES) and Solar (by Arizona AES) in 2006. Originating as F6 selections, these varieties were released as spring barleys for winter crop production in low-water-use environments in the Southwestern United States where only one or two irrigations were applied. Variety trials by Arizona AES (2002 to 2004) have confirmed "Solar" has significantly higher yield, test weight, and lodging resistance than its predecessor "Solum" [25].

The conventional varieties included in this study were "Kopious" and "Cochise", derived from Composite Cross XXXII, a short-straw high-input population developed by Ramage et al. [26]. These varieties normally receive 5 to 7 flood irrigations of around 150 mm per irrigation each season.

2.2. Site Characteristics

Field studies were conducted to study barley performance under high- and low-irrigation conditions. Trials were conducted in the years of 2015 and 2018 at the University of Arizona, Campus Agricultural Station in Tucson, AZ located at 32°9′36″ N, and 110°33′36″ W. Soil type was a Gila very fine sandy loam (coarse-loamy, mixed, superactive, calcareous, thermic Typic Torrifluvent). The field was fallow prior to the 2015 and 2018 planting.

2.3. Cultural Methods

The cultural methods were similar each year, with slight variations. For the 2015 trial, planting occurred on 3 December 2014 and was established with sprinkler irrigation from 12 December to 16 December (33 mm). For the 2018 trial, planting occurred on 7 December 2017 and was established with sprinkler irrigation from 12 December to 1 January (51 mm). In both years, the seed was planted into dry, flat soil with a cone planter. The low-input varieties were planted at a seeding rate of 78 kg ha^{-1} (1.24 million seeds ha^{-1}) and the high-input varieties were planted at a seeding rate of 157 kg ha^{-1} (2.4 million seeds ha^{-1}) to reflect the optimum seeding rate for each variety type.

Nitrogen was applied in the form of urea (46–0–0) at a rate of 56 kg N ha^{-1} at planting. During the growing season, an additional 112 kg N ha^{-1} was applied around the tillering stage to both irrigation treatments. Weeds and insects were controlled as needed. Each plot was 7 rows wide with a row spacing of 15 cm and a plot length of 9 m. The experimental design was Latin square with each variety having four reps per treatment.

2.4. Soil Water Measurements

Neutron probe access tubes were installed to a depth of 1.8 m to measure volumetric water content at depth increments of 0.3 m. Soil water was measured approximately once a week and relative to irrigations (0–1 day before, and 3–4 days after irrigation) with a neutron probe (CPN Model 503DR, Campbell Pacific Nuclear International Inc., Concord, CA, USA). The neutron probe was calibrated by regressing volumetric water content against standardized neutron count ratios using multiple paired measurements when soil was wet and dry. Volumetric soil moisture content for the neutron probe calibration was determined from gravimetric water content and bulk density.

Neutron probe counts from 0 m to 1.8 m were used to calculate period water use for each variety by the water balance method, with precipitation and irrigation included and runoff assumed to be negligible. The period water use values were summed at the end of the season for total water use of each variety.

Water use (ET) was estimated from the differences in soil water content between specific time periods plus rainfall. Deep percolation was considered negligible as soil water content was taken at least 3 days after an irrigation when field capacity had been reached and most deep percolation had already occurred. Furthermore, soil water content was measured at 1.8 m, a depth beyond which not much water would percolate. The time periods between soil water measurements were at least 3 days after an irrigation and 0–1 day before the next irrigation, as mentioned above. Water use between soil water measurements before and after an irrigation were estimated by averaging the estimated daily water use before and after the soil water measurements. This daily water use was calculated from the crop coefficient (Kc) multiplied by reference evapotransiration (ET_o). The Kc was calculated from ET/ET_o. Water use between planting and the first soil water measurement was estimated using a Kc of 0.25 multiplied by ETo from the nearby weather station.

2.5. Soil Water Retention Characterization

Soil water characteristics previously reported by Miller and Ottman were used [27]. Soil bulk density was 1.48 g cm^{-3}. Volumetric soil water content was 0.24 m^3 m^{-3} at field capacity (θvFC), 0.085 m^3 m^{-3} at permanent wilting point (θvPWP), and plant-available water (θvPAW) was 0.155 m^3 m^{-3}. The differences in soil water characteristics among depths were small and less than the standard error of these measurements, so values were averaged across depths.

2.6. Irrigation Treatments

The experiment included two irrigation treatments: high and low, hereon referred to as HI and LI respectively (Table 1). In both years, sprinkler irrigation was applied to both treatments until seedling emergence. Sprinkler irrigation was used to germinate the seed as it results in better stand establishment than flooding, where a soil crust often forms inhibiting seedling emergence. Flood irrigation was used during the season after emergence since the soil profile could be saturated with a single flood irrigation, whereas several sprinkle irrigation events would be required to do so to prevent surface runoff. The frequency of flood irrigations in the HI treatment was based on levels of soil water depletion (SWD), with irrigations occurring around 50% depletion or approximately every two weeks during mid-season, totaling 6 irrigations per season. In 2015, the LI treatment only received sprinkler irrigation and no subsequent flood irrigations due to high precipitation in December and January. In 2018, the LI treatment received one flood irrigation following emergence, and an additional flood irrigation at the five-leaf stage. The source of irrigation water was tertiary-treated municipal effluent.

Table 1. Soil water depletion (SWD) and irrigation amounts for barley irrigation trials conducted in Tucson, AZ in 2015 and 2018. The growing season precipitation was 151 mm in 2015 and 55 mm in 2018.

Water Source	Date	High Irrigation Treatment		Low Irrigation Treatment	
	2015	**SWD**	**mm**	**SWD**	**mm**
Sprinkler Irrigation	12–16 Dec. *	n/a	33	n/a	33
Floods	16 Dec. *	n/a	117		
	23 Jan.	0.40	78		
	20 Feb.	0.52	156		
	4 Mar.	0.65	152		
	27 Mar.	0.70	128		
	10 Apr.	0.74	137		
	total		801		33
	2018	**SWD**	**mm**	**SWD**	**mm**
Sprinkler Irrigation	11 Dec *–1 Jan.	n/a	51	n/a	51
Floods	10 Jan.	n/a	53	n/a	52
	9 Feb.	0.49	110	0.49	105
	9 Mar.	0.47	81		
	23 Mar.	0.48	84		
	6 Apr.	0.50	89		
	26 Apr.	0.84	91		
	total		637		208

* Dates in December were in 2014 and 2017 when respective plantings occurred.

2.7. Plant Measurements

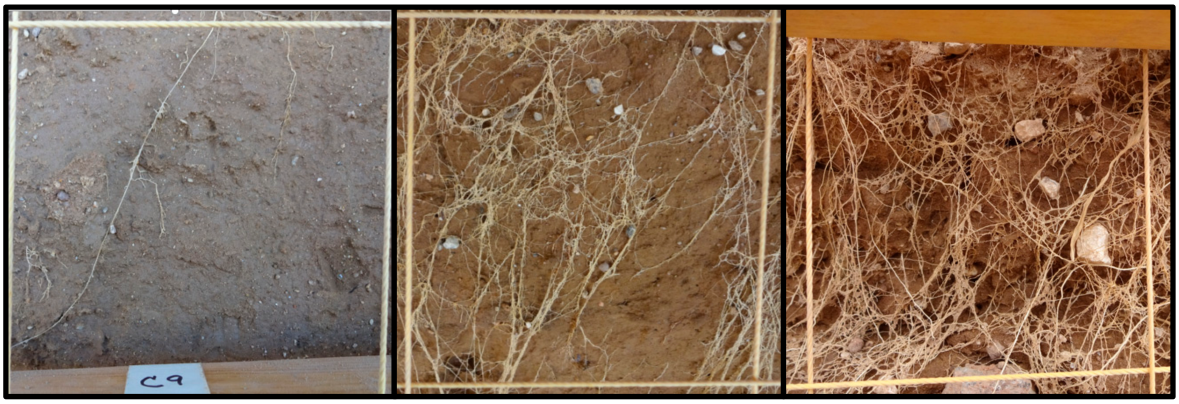
Measurements of plant biomass and interception of photo synthetically active radiation (PAR) were taken throughout the season around five leaf, first node, boot, and flowering stages. Date of heading, flowering, and physiological maturity were recorded. Biomass samples were obtained from an area of two rows by a 45.7 cm cut at the base. Dry weight was assessed after samples had dried at 60 °C for 2 to 10 days depending on growth stage. Intercepted PAR was measured with a Sunfleck Ceptometer (Decagon Devices, Pullman, WA, USA). Measurements were taken within one hour of solar noon on clear days. Three averaged readings were taken at the soil surface within the canopy, along with companion measurements of incident PAR outside the influence of the canopy.

Heading date was recorded when 50% of the heads were past the leaf collar. Flowering date was recorded when 50% of heads had anthers extruded. Maturity date was noted when 50% of heads and peduncle had changed to tan color.

At harvest, biomass yield, height, and lodging were assessed as well as grain yield, test weight, and seed weight. Plant height was averaged from 10 heads. For final biomass yield, 1 m^2 of whole barley plants were hand-harvested and dried at 60 °C. Grain weight was assessed from the 1 m^2 sample. For final grain yield, 5 rows by 1.5 m were hand-harvested and threshed. Clean seed was assessed for test weight and seed weight.

2.8. Method of Root Analysis

Root density at physiological maturity was assessed using the profile wall method. A 1.8-m deep trench traversing the plots was dug with a back-hoe, taking care to create a vertical, flat profile, that was later smoothed with a shovel. The profile wall was washed slowly with water using a fanned spray nozzle to expose the roots. For each variety under both irrigation treatments, the density of roots within 10 cm × 10 cm grids were rated on a scale of 1 to 10 along the total profile (100-cm wide by 180-cm deep). For example, a rating of 1 was given when 1 to 2 roots were present in the grid square, a rating of 5 was given when approximately 50 percent of the grid square was filled with roots, and a rating of 10 was scored when roots filled the majority of the grid square. See Figure 1 for examples of root ratings.



(a) **(b)** **(c)**

Figure 1. Examples of root density ratings from the profile walls: (**a**) rating of 1; (**b**) rating of 5; (**c**) rating of 10.

In 2018, a 6-mm thick plexiglass sheet measuring 1.2 m × 0.85 m was placed flush against each profile wall and buried early in the season. The intention was to have the roots grow up to the plexiglass and be observable without washing, however, washing was still required. Placement of the plexiglass did create a flat soil surface for when the root profile wall was dug and greatly facilitated the process of washing away the soil.

2.9. Statistical Analysis

The data was analyzed by SAS version 9.4 using the PROC GLM procedure, except for water use which was analyzed using the PROC MIXED procedure, and the root profile wall data which was analyzed using SPSS version 25 with the GLM procedure.

2.10. Weather

Weather data was recorded by the Arizona Meteorological Network (AZMET) Campus Agricultural Center weather station, located about 0.5 km from the experimental plots. See Table 2 for growing season temperature, precipitation, and ET_o.

Table 2. Monthly average maximum and minimum temperature, precipitation, and reference ET_o for the 2015 and 2018 growing seasons compared with the 31-year average in Tucson, AZ.

Month	Max. Temperature			Min. Temperature			Precipitation			Reference ET_o		
	2015	2018	31-yr avg.	2015	2018	31-yr avg.	2015	2018	31-yr avg.	2015	2018	31-yr avg.
	°C						mm					
Dec. *	18.9	21.7	18.9	3.3	2.8	1.6	55	8	22	51	69	59
Jan.	19.4	22.8	19.5	3.9	2.2	1.8	57	6	22	61	76	68
Feb.	23.9	21.1	21.0	6.7	3.9	3.4	9	41	18	89	76	84
March	26.1	25.0	24.8	8.9	6.1	6.3	16	0	10	140	130	142
April	28.3	31.1	28.2	9.4	10.6	9.2	6	0	7	180	183	184
May	30.0	33.9	32.8	12.8	13.9	13.5	8	0	3	203	221	228
Mean	24.4	25.9	24.2	7.5	6.6	13.5	-	-	-	-	-	-
Sum	-	-	-	-	-	-	151	55	82	724	754	765

* Month of December shows data for 2014 and 2017 when respective plantings occurred, ET_o was calculated using the standardized Penman–Monteith equation.

3. Results

3.1. Light Interception

Fraction of photosynthetically active radiation (fPAR) intercepted by the crop differed among varieties depending on irrigation treatment and year (Table 3). Under HI in 2015, fPAR was higher for the high-input varieties at first and last sampling, and in 2018 there was no difference between groups. Under LI in 2015, fPAR was also greater for the high-input varieties at all sampling times. Conversely, under LI in 2018, the low-input varieties had higher fPAR at all measurement times. High precipitation during the beginning of the 2015 growing season may explain the improved performance of the high-input varieties under low irrigation conditions for this year. In 2015, in Dec–Jan, there was 122 mm of precipitation, compared to 14 mm in 2018 and the 33-year average of 44 mm at the field location.

Table 3. Effect of irrigation treatment on the fraction of photosynthetically active radiation (PAR) intercepted by barley for trials conducted in Tucson in 2015 and 2018.

Irrigation Treatment	Variety	2015			2018			
		21 Jan.	19 Feb.	16 Mar.	2 Feb.	23 Feb.	20 Mar.	27-Mar.
High	"Cochise"	0.532	0.976	0.996	0.459	0.668	0.911	0.596
	"Kopious"	0.540	0.984	0.996	0.623	0.864	0.973	0.719
	Mean	0.536	0.98	0.996	0.541	0.766	0.942	0.657
	"Solar"	0.312	0.975	0.987	0.534	0.811	0.946	0.652
	"Solum"	0.294	0.975	0.969	0.481	0.752	0.943	0.613
	Mean	0.303	0.975	0.978	0.508	0.781	0.944	0.632
	Variety	ns	ns	**	**	**	**	**
	Variety Adaptation	*	ns	**	ns	ns	ns	ns
	$LSD_{.05}$	ns	ns	0.012	0.069	0.065	0.015	0.052
Low	"Cochise"	0.468	0.989	0.992	0.369	0.626	0.872	0.529
	"Kopious"	0.457	0.990	0.991	0.588	0.856	0.955	0.692
	Mean	0.463	0.990	0.992	0.479	0.741	0.914	0.611
	"Solar"	0.381	0.985	0.988	0.577	0.821	0.955	0.684
	"Solum"	0.305	0.977	0.976	0.607	0.817	0.958	0.706
	Mean	0.343	0.981	0.982	0.592	0.819	0.957	0.695
	Variety	*	**	**	**	**	**	**
	Variety Adaptation	**	**	**	**	**	**	**
	$LSD_{.05}$	0.116	0.007	0.004	0.097	0.067	0.047	0.072

* Significance of variety effect and variety adaptation effect was based on a *p*-values: + < 0.10, * < 0.05, ** < 0.01; while ns = not significant. Least significant difference (LSD) was calculated at the $p < 0.05$ level.

3.2. Plant Growth and Biomass Accumulation

Biomass yield differed among varieties depending on irrigation treatment (Table 4). Under HI in 2015, biomass yield did not differ between nor within groups except at the first sampling time in which the high-input varieties had greater biomass than the low-input varieties. Under HI in 2018, biomass yield did not differ between groups except at the last sampling time in which the low-input varieties outperformed the high-input varieties. Under LI in 2015, the high-input varieties had higher biomass at the first two sampling dates, possibly due to unusually high precipitation, but the low-input varieties had higher biomass at the last sampling date. Under LI in 2018, the low-input varieties had higher biomass at all but one of the sampling times.

Table 4. Effect of irrigation treatment on biomass yield (g m^{-2}) of barley for trials conducted in Tucson in 2015 and 2018.

Irrigation Treatment	Variety	2015			2018			
		21 Jan.	19 Feb.	16 Mar.	7 Feb.	23 Feb.	16 Mar.	27 Mar.
High	"Cochise"	150	1812	3215	90.4	278	963	1656
	"Kopious"	166	1744	2903	141	303	1364	1833
	Mean	158	1778	3059	116	290	1163	1744
	"Solar"	125	1787	3165	134	360	1473	2081
	Solum	114	1729	2921	120	315	1206	2180
	Mean	119	1758	3043	127	338	1339	2131
	Variety	*	ns	ns	+	ns	ns	ns
	Variety Adaptation	**	ns	ns	ns	ns	ns	*
	$LSD_{.05}$	35.9	334	381	41.3	96.8	434	472
Low	"Cochise"	144	1884	2795	68.2	283	911	1196
	"Kopious"	184	1952	2404	162	314	1202	1670
	Mean	164	1918	2600	115	298	1056	1433
	"Solar"	142	1930	2978	157	497	1324	2013
	"Solum"	130	1676	3064	144	407	1330	2365
	Mean	136	1803	3021	151	452	1327	2189
	Variety	**	*	*	**	ns	ns	**
	Variety Adaptation	**	+	**	*	*	ns	**
	$LSD_{.05}$	28.3	186	441	48.7	246	489	618

* Significance of variety effect and variety adaptation effect was based on a p-values: + < 0.10, * < 0.05, ** < 0.01; while ns = not significant. Least significant difference (LSD) was calculated at the $p < 0.05$ level.

3.3. Phenology

All varieties progressed faster under LI (Table 5). As a group, under HI, the low-input varieties flowered five days earlier in 2015, and eight days earlier in 2018 than the high-input varieties. Under LI, the low-input varieties flowered two days earlier in 2015 and four days earlier in 2018 compared to the high-input varieties. Similarly, under HI, compared to the high-input varieties, the low-input varieties reached physiological maturity (PM) eight and nine days earlier in 2015 and 2018, respectively. Under LI, the low-input varieties reached PM nine and six days earlier in 2015 and 2018, respectively.

Another phenological difference observed was time between heading and flowering. Under HI, all varieties flowered one to two days after heading. Under LI, however, the high-input varieties flowered 0 to 1 days after heading while the low-input varieties maintained the one to two-day interval observed under HI. A shortened heading to anthesis interval, observed both years, may be a sign of stress response in "Cochise" and "Kopious".

Table 5. Effect of irrigation treatment on heading, flowering and physiological maturity of barley by date for trials conducted in Tucson in 2015 and 2018.

Irrigation Treatment	Variety	2015			2018		
		Heading	Flowering	Maturity	Heading	Flowering	Maturity
High	"Cochise"	9 Mar.	11 Mar.	1 May	20 Mar.	22 Mar.	6 May
	"Kopious"	9 Mar.	11 Mar.	1 May	22 Mar.	24 Mar.	30 Apr.
	Mean	9 Mar.	11 Mar.	1 May	21 Mar.	23 Mar.	3 May
	"Solar"	5 Mar.	7 Mar.	23 Apr.	15 Mar.	17 Mar.	26 Apr.
	"Solum"	5 Mar.	6 Mar.	23 Apr.	13 Mar.	14 Mar.	23 Apr.
	Mean	5 Mar.	6 Mar.	23 Apr.	14 Mar.	15 Mar.	24 Apr.
	Variety	**	**	**	**	**	**
	Variety Adaptation	**	**	**	**	**	**
	LSD $_{05}$	0	0.4	0	2.2	2.2	0.85
Low	"Cochise"	7 Mar.	7 Mar.	11 Apr.	19 Mar.	19 Mar.	24 Apr.
	"Kopious"	7 Mar.	7 Mar.	10 Apr.	20 Mar.	20 Mar.	23 Apr.
	Mean	7 Mar.	7 Mar.	10 Apr.	19 Mar.	19 Mar.	23 Apr.
	"Solar"	4 Mar.	6 Mar.	3 Apr.	14 Mar.	16 Mar.	19 Apr.
	"Solum"	3 Mar.	4 Mar.	31 Mar.	13 Mar.	14 Mar.	16 Apr.
	Mean	3 Mar.	5 Mar.	1 Apr.	13 Mar.	15 Mar.	17 Apr.
	Variety	**	*	**	**	**	**
	Variety Adaptation	**	*	**	**	**	**
	LSD$_{.05}$	1.6	1.8	1.20	1.51	1.14	1.31

* Significance of variety effect and variety adaptation effect was based on a p-values: + < 0.10, * < 0.05, ** < 0.01; while ns = not significant. Least significant difference (LSD) was calculated at the p < 0.05 level.

3.4. Final Yield Components

Yield and yield components differed among varieties depending on irrigation treatment, variety, and year (Tables 6 and 7). For the HI treatment in 2015 and 2018, high-input varieties had higher total yield and grain yield compared to low-input varieties. Differences between test weight were not significant. Under HI, harvest index was similar between groups in 2015 but higher for the high-input varieties in 2018. In contrast, under LI in 2015 and 2018, low-input varieties had higher grain yield and test weight. "Solar" was the only variety to meet or surpass the minimum test weight (605 kg m^{-3}) to be qualified as Grade 1 barley based on standards set by the Federal Grain Inspection Service of the US [28]. Harvest index was also higher for the low-input group in 2015 but not significantly different in 2018. Total yield did not differ between groups under LI either year; however, "Solar" had the highest and "Cochise" the lowest total yield of all varieties. Kernel weight and plant height were higher for the low-input varieties under both LI and HI treatments in both years. Percent of lodging was higher for the low-input varieties in 2015 under HI and LI. Between the low-input varieties, "Solar" lodged significantly less. In 2018, lodging was minimal. Lastly, under LI the average height of the semi-dwarf varieties (69 cm in 2015 and 59 cm in 2018) was below optimal height for mechanical harvest (typically 76 cm to 86 cm) [29].

Table 6. Effect of irrigation treatment on barley yield and yield components for a trial conducted in Tucson in 2015.

Irrigation Treatment	Variety	Total Yield	Grain Yield	Harvest Index	Test Weight	Kernel Weight	Lodging	Plant Height
		g m^{-2}	g m^{-2}	%	kg m^{-3}	g/1000	%	cm
High	"Cochise"	2490	715	29	623	31.6	31	85
	"Kopious"	3019	813	40	684	42.3	0	86
	Mean	2755	764	34	654	37.0	16	86
	"Solar"	2456	470	31	672	45.0	19	102
	"Solum"	2020	437	35	601	42.5	61	93
	Mean	2238	454	33	637	44	40	98
	Variety	+	**	+	*	**	*	**
	Variety Adaptation	*	**	ns	ns	**	+	**
	$LSD_{.05}$	467	145	7.8	60.1	6.0	38	6.5
Low	"Cochise"	1705	236	20	482	17.3	0	69
	"Kopious"	1565	260	19	470	17.4	0	69
	Mean	1635	248	19	476	17.4	0	69
	"Solar"	1890	335	25	607	25.5	4	104
	"Solum"	1181	262	27	480	26.6	43	95
	Mean	1536	299	26	544	26.1	24	99
	Variety	+	**	+	**	**	**	**
	Variety Adaptation	ns	**	*	**	**	**	**
	$LSD_{.05}$	512	51.9	7.5	29.9	5.8	19	4.3

* Significance of variety effect and variety adaptation effect was based on a *p*-values: + < 0.10, * < 0.05, ** < 0.01; while ns = not significant. Least significant difference (LSD) was calculated at the $p < 0.05$ level.

Table 7. Effect of irrigation treatment on barley yield and yield components for a trial conducted in Tucson in 2018.

Irrigation treatment	Variety	Total Yield	Grain Yield	Harvest Index	Test Weight	Kernel Weight	Lodging	Plant Height
		g m^{-2}	g m^{-2}	%	kg m^{-3}	g/1000	%	cm
High	"Cochise"	1389	620	40	726	30.0	0	83
	"Kopious"	1630	677	38	743	32.6	0	81
	Mean	1509	647	39	734	31.3	0	82
	"Solar"	1347	524	34	810	40.7	3.75	104
	"Solum"	1018	358	32	762	44.3	2.5	100
	Mean	1183	442	33	786	42.5	3.13	102
	Variety	*	*	ns	**	**	ns	**
	Variety Adaptation	*	**	*	**	**	ns	**
	$LSD_{.05}$	409	193	ns	27.5	4.2	ns	7.5
Low	"Cochise"	843	299	32	544	20.6	0	58
	"Kopious"	952	220	20	535	18.4	0	61
	Mean	898	259	27	540	19.5	0	59
	"Solar"	1132	403	32	696	27.3	0	97
	"Solum"	794	274	32	600	27.7	0	93
	Mean	963	339	32	648	27.5	0	95
	Variety	**	*	ns	**	**	-	**
	Variety Adaptation	ns	*	ns	**	**	-	**
	$LSD_{.05}$	134	101	ns	42.0	5.1	-	4.4

* Significance of variety effect and variety adaptation effect was based on a *p*-values: + < 0.10, * < 0.05, ** < 0.01; while ns = not significant. Least significant difference (LSD) was calculated at the $p < 0.05$ level.

3.5. Root Traits

A comparison of root growth by each variety under HI verse LI shows that the high-input varieties had more root growth under HI than they did under LI, especially in the top 0–30 cm (Figure 2). Conversely, the low-input varieties had more root growth under LI than HI especially from 40–80 cm depth. The low-input varieties also had higher average root growth compared to high-input varieties in both years under LI (Figure 3). In 2015, "Solum" had significantly more roots than the other varieties from 0–100 cm and in 2018 "Solar" had significantly more roots than the other varieties from 50–90 cm. Under HI, there was no difference in average root growth between varieties; however, "Kopious" had more roots than the other varieties at 40–50 cm depth in 2015, and in 2018, "Cochise" had more roots than the other varieties at 20–30 cm depth.

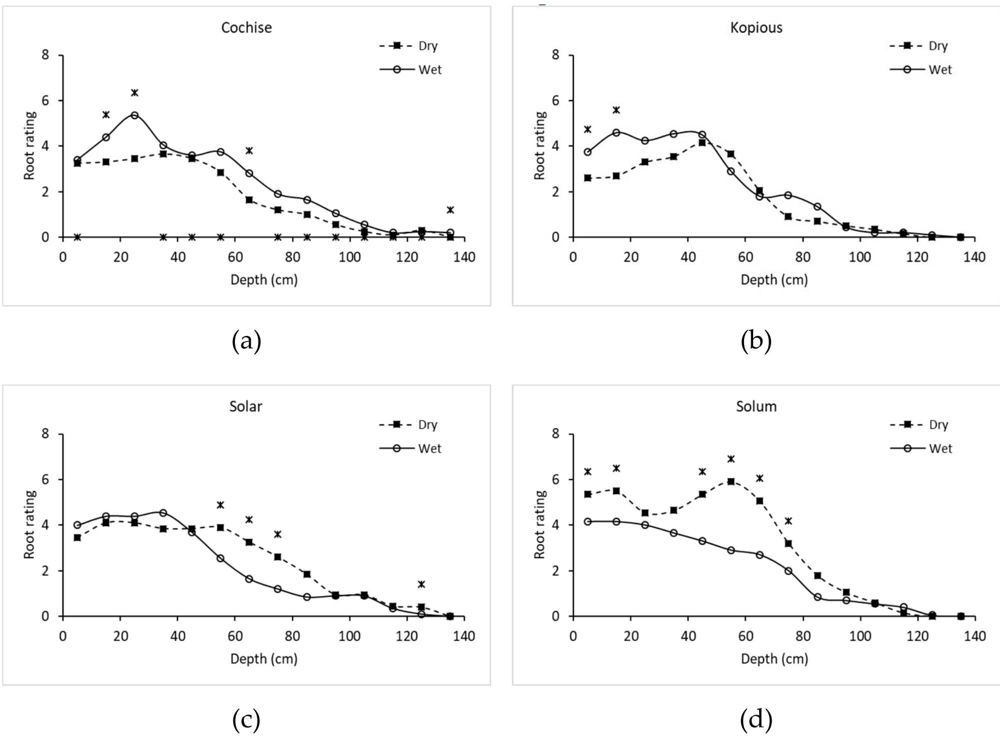
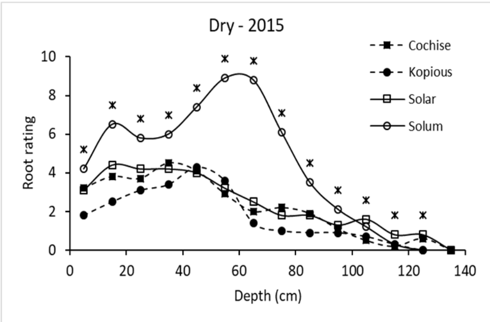
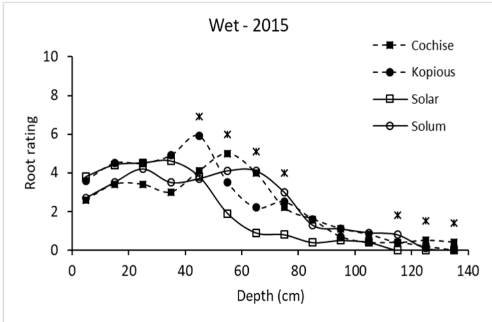


Figure 2. Root density ratings at depths from profile walls dug at physiological maturity under high irrigation (dry) and low irrigation (wet) by variety: (**a**) "Cochise"; (**b**) "Kopious"; (**c**) "Solar"; (**d**) "Solum". Crossmark "×" indicates significant difference in root density at $p < 0.05$.

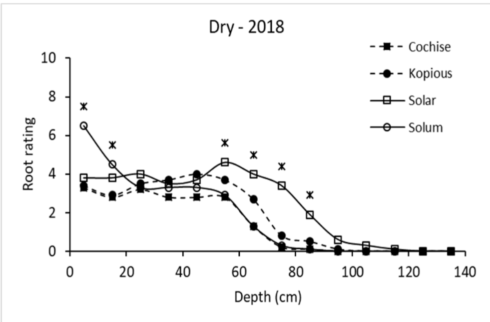
Observations from the root profile showed dramatic differences in rooting between varieties, especially at depth. (Figure 4). The profile also revealed that under LI, "Solar" and "Solum" roots were able to penetrate through a hard caliche layer starting at 70 cm to 80 cm depth (Figure 5). Caliche is a hardened, naturally cemented deposit of calcium carbonate common in the soils of arid regions. In addition, under HI, roots of all varieties generally appeared thinner and less aggregated than roots under LI which appeared thicker and often formed a webbed, mesh-like conglomeration (Figure 6). Roots of the low-input varieties showed this webbed phenotype more often than the high-input varieties; however, as Figure 7 shows, they too sometimes formed this root morphology.



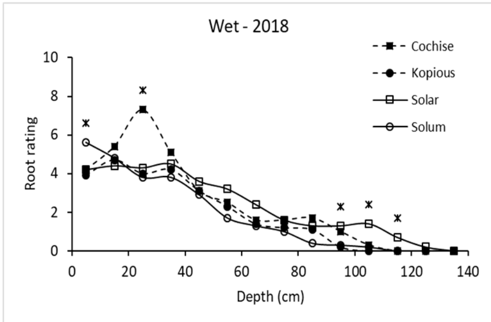
(a)



(b)



(c)



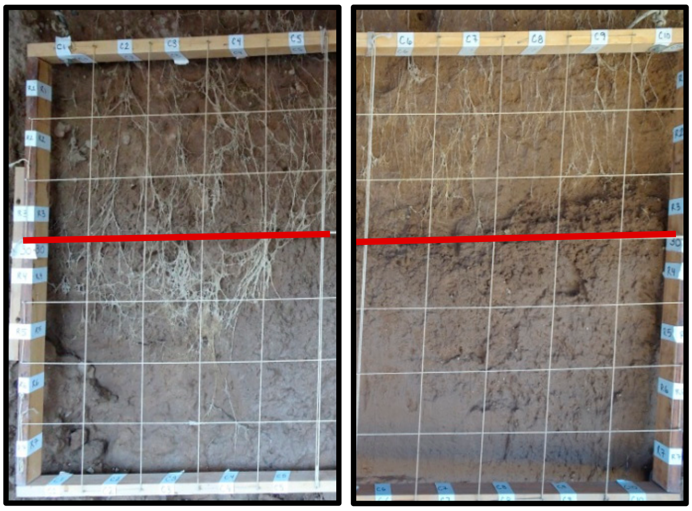
(a)

Figure 3. Root density ratings at depths from profile walls dug at physiological maturity by low irrigation (LI) or high irrigation (HI) treatment and year: (**a**) LI 2015; (**b**) HI 2015; (**c**) LI 2018; and (**d**) HI 2018. Crossmark "×" indicates significant differences in root density at $p < 0.05$.

(a)

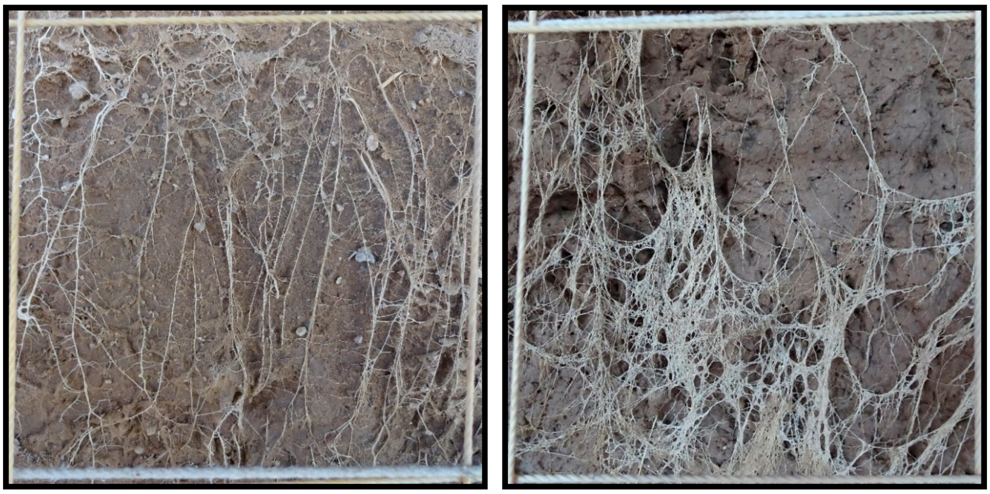
(b)

Figure 4. Roots of physiologically mature barley varieties at 90–100 cm depth when grown under low irrigation in 2018: (**a**) "Solar" roots; (**b**) "Kopious" roots.



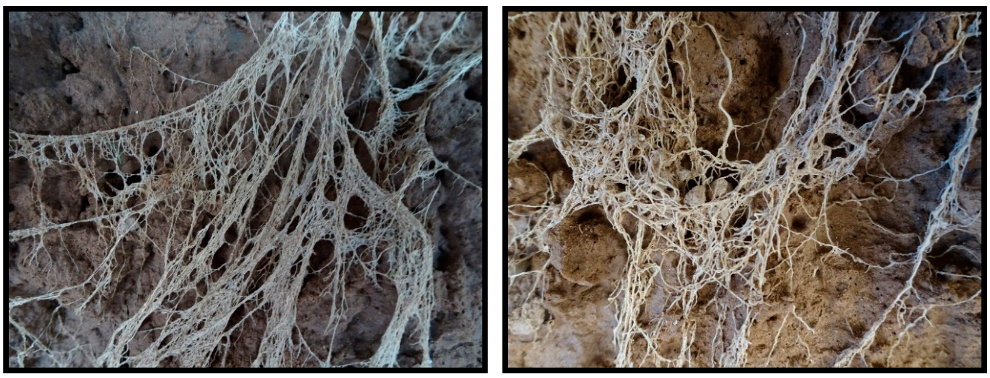
(a) **(b)**

Figure 5. Root profile at physiological maturity (PM) from 50–10 cm under low irrigation treatment in 2018, red line indicates start of caliche layer at 70 cm: (**a**) "Solar" variety at PM with roots growing through caliche; (**b**) "Cochise" variety at PM showing root growth stops at the caliche layer.



(a) **(b)**

Figure 6. Different root phenotypes exhibited under high and low irrigation: (**a**) "Cochise" roots at 30–40 cm under high irrigation; (**b**) "Solum" roots at 30–40 cm under low irrigation.



(a) **(b)**

Figure 7. Webbed root phenotype under low irrigation seen at higher magnification: (**a**) "Solar" roots at 50–60 cm; (**b**) "Kopious" roots at 30–40 cm.

3.6. Water Use

Total cumulative water use was generally similar between varieties under both high and low irrigation in 2015 and 2018, with the exception of "Cochise" under HI in 2018, using significantly more water than the other varieties (Figure 8). "Cochise" began using more water than the other varieties post-anthesis, approximately 100 days after planting. However, general trends of cumulative water use by growth stage, show that the high-input varieties use more water pre-anthesis while the low-input varieties use more water post-anthesis (Table 8).

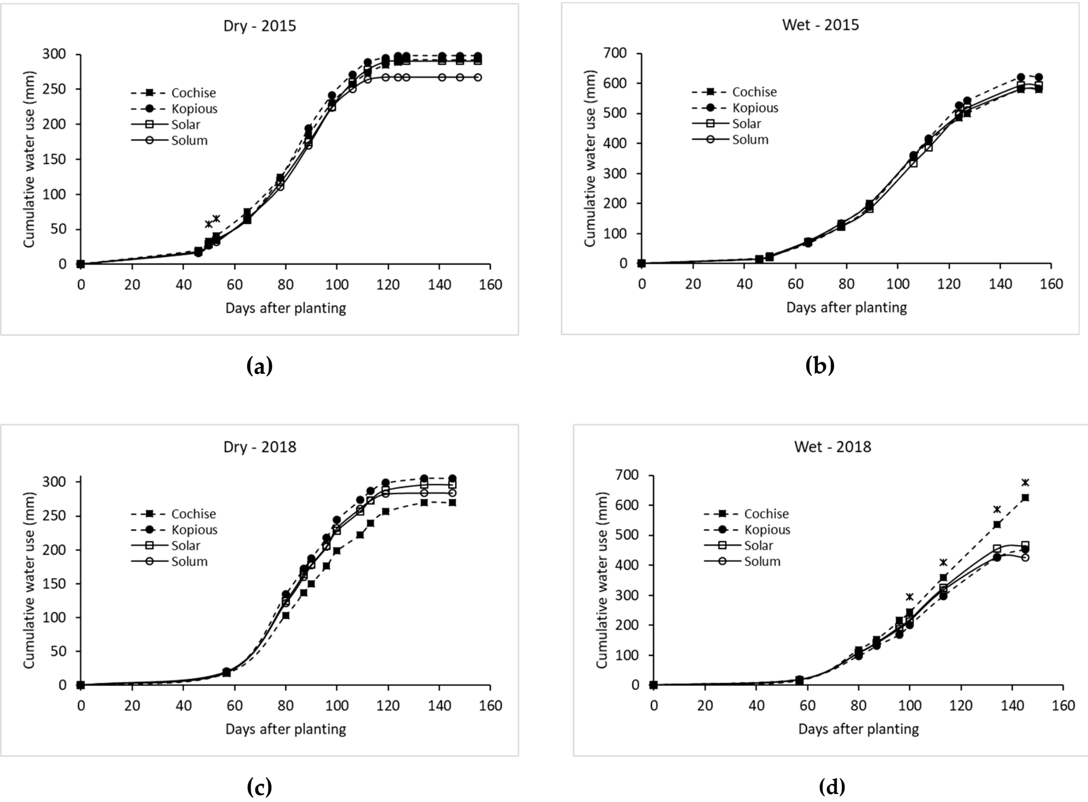


Figure 8. Cumulative water use (mm) since days after planting: (**a**) 2015, high irrigation; (**b**) 2015, low irrigation treatment; (**c**) 2018, high irrigation; (**d**) 2018, low irrigation treatment. Crossmark "×" indicates significant difference at $p < 0.05$.

Table 8. Effect of irrigation treatment on barley water use (mm) for trials conducted in Tucson in 2015 and 2018.

Irrigation Treatment	Variety	Cumulative		Pre-Anthesis		Post-Anthesis	
		2015	2018	2015	2018	2015	2018
High	"Cochise"	581	627	272	244	309	383
	"Kopious"	621	454	271	215	351	241
	Mean	601	540	271	229	330	312
	"Solar"	594	466	209	171	386	293
	"Solum"	581	426	218	151	363	275
	Mean	588	446	213	161	374	284
	Variety	ns	**	**	**	**	**
	Variety adaptation	ns	*	**	**	**	+
	Variety × depth	*	**	ns	**	**	**
	$LSD_{.05}$	ns	52	24	27	35	35

Table 8. *Cont.*

Irrigation Treatment	Variety	Cumulative		Pre-Anthesis		Post-Anthesis	
		2015	2018	2015	2018	2015	2018
Low	"Cochise"	292	270	210	181	82	88
	"Kopious"	298	306	221	231	77	74
	Avg	295	288	216	206	80	81
	"Solar"	290	296	186	197	105	100
	"Solum"	267	284	170	186	97	98
	Mean	279	290	178	192	101	99
	Variety	ns	ns	**	*	**	**
	Variety adaptation	ns	ns	**	ns	**	**
	Variety × depth	ns	ns	ns	ns	**	ns
	$LSD_{.05}$	ns	ns	26	35	15	16

* Significance of variety effect and variety adaptation effect was based on a *p*-values: + < 0.10, * < 0.05, ** < 0.01; while ns = not significant. Least significant difference (LSD) was calculated at the $p < 0.05$ level.

4. Discussion

4.1. Early Vigor

Defined by fast leaf area development and biomass accumulation, early seedling vigor is associated with greater leaf area, and thus, greater incident light interception [30,31]. Our results show higher light interception by the low-input varieties under LI at all sampling times in 2018, but not 2015, which may have been due to high rainfall during the early 2015 season. Higher fPAR at the beginning of the 2018 season suggests early vigor in the low-input varieties under LI when considering fPAR as a proxy for leaf area.

Similar to the fPAR results, biomass was also greater for the low-input varieties under LI at first sampling in 2018. Greater early season growth is particularly useful under drought conditions as ground cover and canopy shading serve to reduce evaporation from the soil surface, increasing available water for transpiration and crop growth [32,33].

4.2. Early Flowering and Maturity

The importance of early flowering/heading as a drought escape mechanism has been extensively reported on, as have positive correlations between earliness and grain yield under drought stress in cereals [34,35]. In this study, early flowering and maturity were observed in the varieties bred for low irrigation conditions and correlated with higher grain yield under LI. Under HI, early maturity was negatively correlated with grain yield.

4.3. Root Length Density, Depth, and Penetration

Greater average root length density and deeper roots of "Solar" and "Solum" under LI correlated with higher grain yield. Similar results have been reported in other studies in which deeper rooted genotypes had higher grain yield under drought stress [36–41]. The observation from the root profile that "Solar" and "Solum" roots were able to penetrate through a caliche layer starting at 70 cm depth is noteworthy. Mechanical impedance is a major limiting factor of root growth [42]. Cereal cultivars better able to penetrate hard pans have been shown to have deeper root growth and better access to water [43–45]. Many of the studies on root penetration ability have been conducted in pot experiments with artificially compacted soil. The use of root profile walls in this experiment allowed for in-field visual documentation of roots growing through hard soil.

4.4. Plant Height and Lodging Resistance

Though dramatic gains in grain yield were achieved through the development of semi-dwarf cereals, in cases of severe water deficit, they may be too short for mechanical harvest, or less economically profitable in areas where straw used as animal feed is an important commodity, e.g., West Asia and North Africa [46]. A multisite study by Silva Lopes et al. [47] found plant height was significantly and positively associated with grain yield in the most low-yielding, rainfed environments. The results from this study found the taller varieties, "Solar" and "Solum" outperformed the semi-dwarf cultivars in grain yield under LI. The low-input varieties were also able to maintain similar plant height under LI as that under HI which is indicative of their drought tolerance [13]. Moreover, under LI the average height of the semi-dwarf varieties (69 cm in 2015 and 59 cm in 2018) was below optimal height for mechanical harvest (typically 76 to 86 cm) [29].

As expected, the semi-dwarf varieties had significantly less lodging than the standard-height varieties, particularly under HI. "Solar" demonstrated significantly less lodging than its predecessor "Solum", as it was bred to do [25]. Bending strength or stiffness has been associated with root penetration of hard soils [48]. The improved lodging resistance of Solar may somehow be related to the ability of Solar roots to better penetrate through drying/hard soil.

4.5. Effective Use of Water

Effective use of water (EUW) describes maximizing soil water capture for assimilate partitioning to reproduction [49]. Effective use of water was demonstrated through early vigor and higher harvest index of the low-input varieties under LI. In addition, under both irrigation treatments cumulative water use over the season was the same between all the varieties tested, indicating those bred for low-water use environments had greater grain yield per unit water use under LI. The observation that the low-input varieties use less water pre-anthesis and more water post-anthesis under drought conditions suggest they may employ a water conservation technique such as early vigor to ensure water is still available during the critical grain filling period or have a means of accessing more water during this period, such as the rooting traits of "Solar" and "Solum". A study by Siddique et al. [50] similarly found early flowering genotypes of wheat exhibiting early vigor had lower rates of soil evaporation early in the season and used a greater ratio of water post-anthesis than pre-anthesis.

4.6. Future Research

Given the extensive time and labor required for root profile analysis, future research could explore how to improve the efficiency, effectiveness, and replicability of this method to better study roots in realistic soil environments. Real time monitoring of water use may reveal interesting patterns undetectable by the neutron probe. Further exploration of differences in root morphology and traits associated with water usage would help to further our understanding of drought tolerance.

5. Conclusions

Though debate exists regarding whether selection under optimal or stress conditions is preferable when breeding for drought tolerance, the results of this study show the varieties bred for low-water conditions had greater grain yield and test weight under LI than varieties bred for high-water-use conditions. Advantageous traits under HI conditions were associated with poorer performance under drought stress, specifically later maturity, shallow root systems, and less water-use post-anthesis. Observed strategies of drought tolerance in this study included early vigor, early flowering, greater root density at depth, and greater water extraction post-anthesis. The root profile pit addressed the need for root studies conducted in realistic environments and revealed insights difficult to capture with other field-based methods.

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