

Response of Maize Yield Components to Growth Stage-Based Deficit Irrigation

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ABSTRACT

In the face of declining water resources and climatic variability, growth stage-based deficit irrigation may be a feasible approach to enhance agricultural system resilience. A 3-yr experiment was conducted to evaluate the impact of deficit irrigation on maize (*Zea mays* L.) in the late vegetative (Lveg) and maturation (Mat) growth stages, where phenology, dry leaf weight, aboveground biomass, yield, kernel number, 1000 kernel weight, and grain-filling rate were evaluated. Water deficit during the Lveg stage decreased the kernel number and dry leaf weight, thus decreasing the potential grain-filling rate (less photosynthetic tissue). In contrast with deficit during the Lveg stage, deficit during the Mat stage directly reduced the grain-filling rate and duration and thus had the strongest effect on grain yield. A growth stage interaction was evident, such that the reduction in yield associated with water deficit applied during the Lveg stage was exacerbated by water deficit applied during the Mat stage. Yield reduction was proportional with the severity of the water deficit, in all cases. Nevertheless, water deficit applied during the Mat stage had a larger impact on maize yield compared with water deficit applied during the Lveg stage. If farmers have reduced water allocations but seasonal flexibility in the timing of irrigation water application, they will maximize yield by saving water for reproductive and maturation growth stages.

Core Ideas

- Water deficit during the late vegetative stage decreased the kernel number and dry leaf weight.
- Deficit applied during the maturation stage directly reduced the grain-filling rate.
- Yield reduction was proportional with the severity of the water deficit.
- Water deficit during the maturation stage had a larger impact on maize yield compared with that at the late vegetative stage.

AGRICULTURAL WATER resources have been diminished due to drought associated with climate change, declining aquifers, and increased competition for water from municipal, environmental, and industrial uses. In addition to the reduction in total available water, climate change is predicted to increase the variation in mean seasonal precipitation, as well as the distribution of precipitation during the growth season, thus making agriculture production even more unstable (Walthall et al., 2013). In the face of declining water supplies and climatic uncertainty, effective water management strategies are needed to preserve the resilience of agriculture (Walthall et al., 2013).

In semiarid Northern Colorado, maize (*Zea mays* L.) is grown mostly under irrigated conditions. Average annual precipitation in the region (2008–2013) is about 197 mm and average maize crop evapotranspiration (ET) is 666 mm (Trout and DeJonge, 2017); thus, irrigation is imperative during the growing season to meet crop water requirement. When irrigation water supplies are limited, producers must consider alternative water management strategies to maintain economic productivity. Many studies have been conducted on water management strategies that maximize maize production. In addition to improving plant performance, agronomic practices, and irrigation systems, growth stage-based deficit irrigation has also been demonstrated to maintain and enhance the sustainability of maize production under water limitations (Comas et al., 2019; Kirda, 2002; Walthall et al., 2013).

Growth stage-based deficit irrigation represents a feasible option for altering the timing and amount of irrigation in response to a plant's sensitivity to stress during growth stages. However, successful implementation of growth stage-based deficit irrigation requires knowledge of water use, crop growth, and response to water stress during specific growth stages (Geerts and Raes, 2009; Kirda, 2002). For maize, significant yield loss can be expected if deficit irrigation is applied during the most sensitive growth stages—from tassel emergence to the beginning of grain filling (Abendroth et al., 2011). These reductions in yield are caused primarily by the reduction in grain number, resulting

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Abbreviations: AGB, aboveground biomass; DAP, days after planting; ET, evapotranspiration; ET_r, reference evapotranspiration; GDD, growing degree days; GFR, grain-filling rate; K_{num}, kernel number; K_{wt}, kernel weight; Lveg, late vegetative stage; Mat, maturation stage; Rep, reproductive stage; SWD, soil water deficit; VT, end of deficit irrigation.

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from poor synchronization in the emergence of male and female flower components (Bolaños and Edmeades, 1996; Çakir, 2004; NeSmith and Ritchie, 1992a; Saini and Westgate, 2000). Water stress occurring during emergence to tasseling (but before tasseling occurs) has significant impact on crop height and leaf size, but less impact on grain yield (Abrecht and Carberry, 1993; Çakir, 2004). Deficit irrigation or irrigation omission during the grain-filling period could reduce yield by 20 to 40%, with kernel weight being the most affected yield component (Çakir, 2004; NeSmith and Ritchie, 1992b). Previous research on maize has mainly focused on the impact of water deficit during a single growth stage (Bolaños and Edmeades, 1996; Çakir, 2004; Otegui et al., 1995). By studying the crop water use as well as crop yield under deficit irrigation in the late vegetative and maturation stages, Comas et al. (2019) suggested that higher water use efficiency (yield/ET) can be achieved by applying deficit at the late vegetative stage rather than maturation stage. Here we studied the response of maize growth to water deficit applied during the late vegetative (V8–VT) and maturation growth stage (R4–R6), using measures of leaf dry weight, aboveground biomass, crop phenology, kernel number, grain-fill process and yield, and the causality relationships among them.

MATERIALS AND METHODS

Study Site and Experiment Management

The field experiment was conducted on maize (cv. Dekalb DCK52-04) at the USDA-ARS Limited Irrigation Research Farm (LIRF) in Greeley, CO (40°26'57" N, 104°38'12" W, elevation 1427 m asl). The farm is located within a region of irrigated farmland that surrounds the farm. The alluvial soils of the study field are sandy and fine sandy loam of Olney (fine-loamy, mixed, superactive, mesic Ustic Haplargids) and Otero series (coarse-loamy, mixed, superactive, calcareous, mesic Aridic Ustorthents). The experimental results shown here are from the 2012, 2013, and 2015 seasons; 2014 was omitted from analysis due to excessive seasonal precipitation.

The experimental field was divided into two equal sections, and maize was grown in rotation with sunflower (*Helianthus annuus* L., Syngenta sunflower hybrid 3495 Ns/CL/DM) with the same irrigation treatment design). Each section was divided into four replicate blocks, and each block was divided into 12 plots (9 × 43 m) containing 12 crop rows oriented north–south (with 0.76-m spacing), to which 12 irrigation treatments were randomly assigned. All measurements were taken from the middle 6 (of 12) rows to avoid edge effects.

Irrigation water from a groundwater well was delivered to the end of each plot through underground PVC pipe and applied to each crop row through surface drip irrigation tubing with 30-cm in-line emitter spacing (1.1 L h⁻¹ per emitter). The tubing was installed each year after emergence and removed before harvest. Quantities of irrigation were measured independently for each treatment with turbine flowmeters (Badger Recordall Turbo 160 with RTR transmitters, Badger Meter, Milwaukee, WI), which were calibrated and cross-calibrated to ensure accuracy and consistency. Irrigation applications were controlled by and recorded with Campbell Scientific CR1000 data loggers (Campbell Scientific, Logan, UT). A constant-pressure water supply controlled with a variable-frequency drive booster pump, low pressure loss in the delivery system, and relatively flat topography

resulted in predicted water distribution uniformity among and within plots exceeding 95% (Trout and DeJonge, 2017). Maize was planted on 30 April/1 May, 15 May, and 1 June in 2012, 2013, and 2015, respectively, at a seeding rate of 80,000 to 84,000 seeds ha⁻¹. Plants emerged on 14 May, 23 May, and 10 June and plant stand assessment was evaluated for each treatment plot and the final population were 80,496 in 2012, 77,665 in 2013, and 82,570 in 2015. Fertilizers were applied at planting and in-season with the irrigation water to avoid nutrient deficiencies on all treatments. Total applied N ranged between 266 and 349 kg ha⁻¹ in 2012, 230 to 294 kg ha⁻¹ in 2013, and 242 to 290 kg ha⁻¹ in 2015, depending on the treatment. A liquid starter N of 41 kg ha⁻¹ was applied at planting each year with approximately 170 kg ha⁻¹ applied as fertigation over four irrigation events in 2012, 160 kg ha⁻¹ applied over five irrigation events in 2013 (Comas et al., 2019), and 167 kg ha⁻¹ applied as fertigation over four irrigation events in 2015 in July prior to tasseling. The remainder of N (97–175 kg ha⁻¹ in 2012, 74–127 kg ha⁻¹ in 2013, 38–120 kg ha⁻¹ in 2015) was applied through the season with the well water used for irrigation, which contained high nitrate content (approximately 25 mg kg⁻¹ N).

The 12 irrigation treatments with varying levels of deficit irrigation (Table 1, Column 1) were arranged in a randomized block design with four replications. Deficit irrigation was applied during the late vegetative (Lveg, V8–VT) (Abrecht and Carberry, 1993) and/or maturation growth stage (Mat, R4–R6). Each treatment was targeted to meet a percentage of potential non-stressed crop ET (Allen et al., 1998, 2005) during Lveg and Mat stages (e.g., 100/50 treatment would indicate a target of 100% of maximum ET during the late vegetative stage and 50% of maximum ET during the maturation stage). All treatments received 100% ET_c from planting through V7, and from VT to R4. Treatment 80/50 (T80/50) in 2012 and 2013 was replaced with T40/80 in 2015 to further investigate the effect of water deficit during the maturation stage. The sum of actual irrigation amount for each treatment by growth stage is shown in Table 1.

A Colorado Agricultural Meteorological Network (CoAgMet; <http://www.coagmet.com>) automated ET weather station (GLY04) is located on a 0.4-ha irrigated grass lawn adjacent to the research plots. Hourly weather data was used to calculate ASCE Standardized Penman–Monteith alfalfa reference evapotranspiration (ET_p) (ASCE-EWRI, 2005). The ET_c was determined using the FAO-56 dual crop coefficient method (Allen et al., 1998) with basal crop coefficients adapted from Table E-2 in Jensen and Allen (2016) and adjusted for measured crop canopy cover and senescence (Allen and Pereira, 2009). Precipitation was measured with a tipping bucket rain gauge at the weather station and two tipping bucket gauges within the plots (Trout and DeJonge, 2017).

The average weather conditions, growing degree days (GDD), accumulated ET_c, and precipitation for each growth period at the experimental field during the 3 yr are shown in Table 2. Seasonal rainfall was less in 2012 than 2013 and 2015 (89, 188, and 137 mm, respectively). A total of 11 rainfall events occurred during the 2012 growing season from planting to harvest, totaling 89 mm. In 2013, there were 22 rainfall events and a total of 188 mm, most occurring during the Mat growth stage. Rainfall in 2015 totaled 137 mm and 25 events, where most rainfall occurred in the early season.

Table 1. Total irrigation amount (mm) for each treatment in different growth stages in 2012, 2013, and 2015 where Lveg is late vegetative, Rep is reproductive, and Mat is maturation growth stages.

Treatment†	2012			2013			2015		
	Lveg	Rep	Mat	Lveg	Rep	Mat	Lveg	Rep	Mat
T100/100	236	138	201	185	162	80	166	151	164
T100/50	243	139	48	185	114	35	166	90	33
T80/80	186	147	155	142	144	63	126	120	134
T80/65	187	147	73	142	136	50	126	116	69
T80/50	185	146	46	142	120	35	–	–	–
T80/40	185	145	42	142	116	10	126	110	0
T65/80	146	152	146	101	165	63	84	136	134
T65/65	146	151	72	100	157	50	84	112	69
T65/50	144	152	57	101	141	35	85	112	24
T65/40	143	151	41	101	138	10	85	114	0
T50/50	108	157	61	78	149	35	54	113	24
T40/40	83	156	42	60	146	10	40	113	0
T40/80	–	–	–	–	–	–	40	136	124

† Treatment: %vegetative ET/%maturation ET.

Field Measurements

Soil Water Deficit

Soil water content at the soil surface (0- to 15-cm layer) was measured by a portable time domain reflectometer (MiniTrase, Soilmoisture Equipment Corp, Santa Barbara, CA). At subsequent deeper depths, neutron attenuation (neutron moisture meter, CPN-503 Hydroprobe, InstroTek, San Francisco, CA) was used to measure soil water content at 30-cm depth increments to 2 m, in the middle row of each plot. Both measurements were taken before and/or after irrigation two or three times a week, from the Lveg stage to the end of the growing season. Field capacity was estimated for each soil layer from previously observed soil water content measurements on this site following large rainfall or irrigation events and allowing for drainage. Soil water deficit (SWD) of each layer was calculated as (field capacity volumetric water content minus current volumetric water content) × depth of layer. Because there was no evidence of water uptake from deeper soil layers, the total SWD in each plot was calculated as the sum of deficits of each layer from the 0- to 1050-mm depth. All measured SWD in Lveg and Mat stages were calculated to represent the mean SWD for Lveg and

Mat, respectively, and used for further studies. More detailed information about soil water measurement, SWD calculation, and crop evapotranspiration calculation using soil water balance can be found in Trout and DeJonge (2017).

Maize Growth and Yield Measurements

Maize phenology was measured every 3 to 7 d during the growing season, from 5 plants in each plot, or a total of 20 plants for each treatment. Aboveground biomass was measured at the beginning of deficit irrigation (ca. V7), end of vegetative deficit irrigation (VT) stage, and end of the growing season. In each biomass sampling, leaves, stems, ears, and grain were measured separately for each of the five plants collected from each plot. All biomass samples were oven-dried to constant mass at 60°C. Grain was removed from the ear after being dried and then both grain and cob were re-dried and weighed. The dry weight sum of leaves, stems, cob, and grain was considered the total aboveground biomass and was calculated for each plot.

Once grain moisture in the plots fell to approximately 16%, grain yield was collected by hand harvesting the ears from the center 23 m of the middle four rows of each plot. Ears were fed through a stationary thresher (Wintersteiger Classic ST,

Table 2. Meteorological information for T100/100 in each growth stage in 2012, 2013, and 2015. ET_c , cumulative crop evapotranspiration (mm); GDD, cumulative growing degree day units (°C), sum of temperature $[(T_{max} + T_{min})/2 - 10]$ in each stage; P , total precipitation (mm); T_{mean} , daily average temperature (°C); R_s , daily cumulative solar radiation ($MJ\ m^{-2}$); VPa , actual vapor pressure (kPa); u , daily average wind speed ($m\ s^{-1}$); Evveg, early vegetative stage; Lveg, late vegetative stage; Rep, reproductive stage; Mat, maturation stage; #T30, number of days with maximum temperature higher than 30°C; AveT30, average daily maximum temperature when it was higher than 30°C.

Stage	2012				2013				2015			
	Evveg 1 May–15 June	Lveg 16 June –21 July	Rep 22 July–9 Aug.	Mat 10 Aug.–3 Oct.	Evveg 15 May –26 June	Lveg 27 June –27 July	Rep 28 July –22 Aug.	Mat 23 Aug.–1 Oct.	Evveg 3 June –5 July	Lveg 6 July –2 Aug.	Rep 3 Aug. –27 Aug.	Mat 29 Aug. –2 Nov.
ET_c	107	308	135	220	93	208	174	168	84	187	153	192
GDD	313	527	254	454	396	392	256	346	393	280	273	334
P	37	37	3	12	20	30	33	105	66	10	23	38
R_s	24	26	23	19	26	23	21	18	22	24	25	16
T_{mean}	17	24	23	18	19	22	20	19	21	22	22	15
u	2.8	2.0	1.7	1.5	3.0	2.2	1.4	1.5	2.2	1.6	1.3	1.5
VPa	0.8	1.3	1.4	1.0	0.9	1.5	1.5	1.4	1.5	1.4	1.4	1.0
#T30	13	31	18	23	18	19	13	16	14	17	17	16
AveT30	32.0	35.2	34.0	32.8	32.8	33.6	32.2	33.7	33.0	32.9	32.4	31.4

Table 3. Average measured soil water deficit (mm) in different growth stages for each treatment in 2012, 2013, and 2015.

Treatment	2012			2013			2015		
	Lveg	Rep	Mat	Lveg	Rep	Mat	Lveg	Rep	Mat
	mm								
T100/100	37de†	36bc	40e	37de	21a	29f	26cde	42ab	40e
T100/50	28e	30c	81b	35e	20a	61ab	13e	34b	81ab
T80/80	35de	34bc	52de	47de	22a	34 ef	24de	44ab	45de
T80/65	40cde	33bc	69bc	44de	19a	46 cde	34bcd	57ab	70bcd
T80/50	39cde	36bc	76b	49cde	16a	54abc	28cde	47ab	85ab
T80/40	51b	46ab	103a	47cde	21a	63a			
T65/80	47bcd	40bc	53cde	55bcde	22a	27f	33bcd	59a	48de
T65/65	50bc	39bc	67bcd	56bcde	22a	37def	44ab	52ab	54cde
T65/50	49bc	41bc	75b	59bcd	22a	49bcd	40abc	49ab	75abc
T65/40	49bcd	41bc	85ab	70abc	25a	62a	36bcd	59a	95a
T50/50	71a	57a	86ab	73ab	25a	55abc	46ab	64a	85ab
T40/40	73a	58a	90ab	81a	28a	63a	52a	57ab	84ab
T40/80							52a	64a	37e

† Means followed by a different letter within a column are significantly different at $P = 0.05$ according to the Tukey-Kramer HSD range test.

Wintersteiger AG, Ried, Austria). Grain was bagged, weighed, and subsampled for moisture content determination with a DICKEY-John GAC500-XT Moisture Tester (DICKEY-John Corp, Auburn, IL). Grain yield was computed with adjustment to 15.5% grain moisture. The weight of 1000 kernels of oven-dried grain were measured and the average kernels per ear were estimated from grain yield per plant based on plant population and kernel weight. Growing degree day during each maize growth stage was calculated as the sum of temperature difference between daily average temperature and base temperature (assuming 10°C). The grain-filling rate (GFR, mg °C⁻¹) during the Mat stage was estimated by dividing grain weight gain per plant by GDD in the Mat stage (MGDD).

Statistical Analysis

The relationships and their interaction among observations—such as SWD at Lveg (SWD_{veg}) and Mat stage (SWD_{mat}), dry leaf weight at the end of Lveg stage (L_{wl}), kernel weight (K_{wl}), kernel number (K_{num}), GFR, phenology, and yield—were compared using simple linear regression model, which is lm function in R, and the difference between treatments were examined by

ANOVA in the R_{misc} package in R statistical software (R Core Team, 2013).

RESULTS AND DISCUSSION

Effect of Deficit Irrigation on Soil Water Deficit

The average measured SWD values for different growth stages are summarized in Table 3. In the Lveg stage, SWD increased with decreasing irrigation amount (Table 3). For example, Lveg SWD was approximately 33 mm in the 100%, 41 mm in the 80%, 49 mm in the 65%, and 72 mm in 40 and 50% treatments in 2012. The 40 and 50% treatments had highest SWD values. During the Rep stage, all treatments were treated with full irrigation. The SWD in 100/100 was maintained at less than about 42 mm in the soil profile throughout the growing season in all years. In the Mat stage, the 40 and 50% treatments also had highest SWD values. In 2015, T40/80 showed stress in Lveg and was brought out of stress in the Mat stage. All treatments in the Mat stage in 2013 did not show the desired level of stress during this growth stage and year. This caused by large rainfall (75 mm) received from 10 to 15 Sept. 2013 so all treatments were brought back to full profile. As such, the targeted

Table 4. Day after planting when maize reached R6 stage (maturity) in each treatment in 2012, 2013, and 2015. Numbers in parentheses are the growing degree days in the maize maturation period (MGDD, R4–R6).

Irrigation treatment†	Maturation stage														
	2012					2013					2015				
	100	80	65	50	40	100	80	65	50	40	100	80	65	50	40
	d after planting														
Late vegetative stage															
100	156 (454)		143 (389)		140 (346)		135 (335)		152 (334)		117 (252)				
80		156 (454)	143 (389)	143 (389)	143 (389)		137 (355)	137 (355)	134 (331)	127 (298)		138 (331)	125 (284)		117 (252)
65			156 (454)	143 (389)	143 (389)		137 (355)	137 (355)	134 (331)	127 (298)		138 (331)	125 (284)	117 (252)	117 (252)
50				143 (389)					134 (331)					117 (252)	
40					143 (389)					127 (298)		134 (320)			117 (252)

† Irrigation treatment: % of ET.

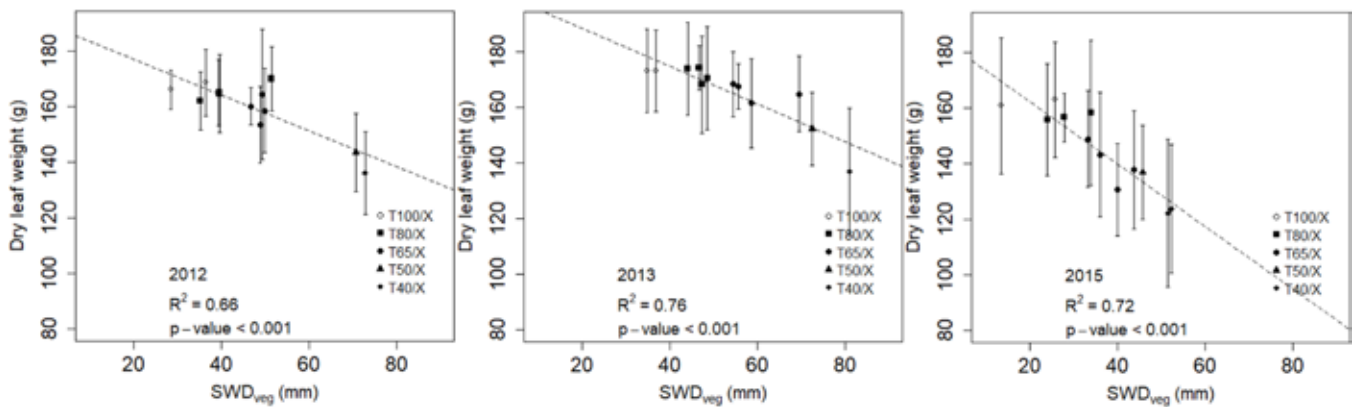


Fig. 1. Relationship between the mean soil water deficit in the late vegetative stage (SWD_{veg}) and dry leaf weight per plant at the end of late vegetative stage in 2012, 2013, and 2015 (error bars represent standard deviation). Each series represents a deficit irrigation treatment applied during the late vegetative stages.

50% treatment actually received 70% of full ET during Mat, as reported by Comas et al. (2019).

Although neutron attenuation is considered the most accurate measurement of soil water content, it is limited in applicability in that it is not a continuous measurement. We have aggregated the SWC measurements by averaging all measurements from all replicates of the same treatment, across the major growth stage (e.g., Lveg). Due to the high frequency of irrigations (two times every 3 wk), the timing of the SWC measurements has potential to bias an averaged value (i.e., before irrigation vs. after irrigation). However, to closely quantify the water balance, this study obtained frequent SWC observations two to three times per week, both before and after irrigations. This measurement frequency is adequate to characterize SWD over a major growth period, and this claim is supported by strong relationships with agronomic and biological measurements as discussed in the sections below.

Effect of Deficit Irrigation on Plant Phenology

Deficit irrigation treatments started at 46, 44, and 33 d after planting (DAP) in 2012, 2013, and 2015, respectively. During the 3 yr, maize in all treatments reached the flowering stage (R1) at the same time within the year (always after the VT stage), which occurred 84 DAP in 2012, 75 DAP in 2013, and 61 DAP in 2015. All treatments also reached R3 at the same time in each year. A difference in phenological development under deficit irrigation was observed in the Mat stage (Table 4). Deficit irrigated

treatments reached physiological maturity (R6) sooner than the fully watered treatment (Table 4). NeSmith and Ritchie (1992b) reported that water deficit applied during the maturation stage shortened the grain-filling period by 8 d due to the early senescence of green leaves. Regardless how much irrigation was given during the Lveg stage, the 50 and 40% treatments required the same amount of time to reach maturity in 2012 and 2015. The 80 and 65% treatments in 2013 required a similar amount of time to reach maturity. T40/80 required more time to reach R6 than treatments with 65% or less of full irrigation. If we assume that grain maturation occurs, indicating seed filling ceases, regardless of whether the seed is completely filled (Çakir, 2004; McMaster et al., 2008; Westgate and Boyer, 1985), it appears that applying water deficit during the Mat stage accelerates senescence, reduces photosynthesis (Comas et al., 2019), and results in the early termination of grain filling (McMaster et al., 2008).

Effect of Deficit Irrigation on Dry Leaf Weight and Aboveground Biomass

There was no significant difference among treatments in dry leaf weight (Lwt) and aboveground biomass (AGB) at the beginning of Lveg. Lveg deficit irrigation started at V8. By the end of Lveg, deficit treatments show significantly reduced Lwt and AGB in all experimental years (Fig. 1 and Fig. 2, $p < 0.001$). As was expected, the most severe effect of water deficit on the dry matter was observed in the 40% treatment. The 40% water stress treatment resulted in decrease in Lwt by 24% in 2012, 27%

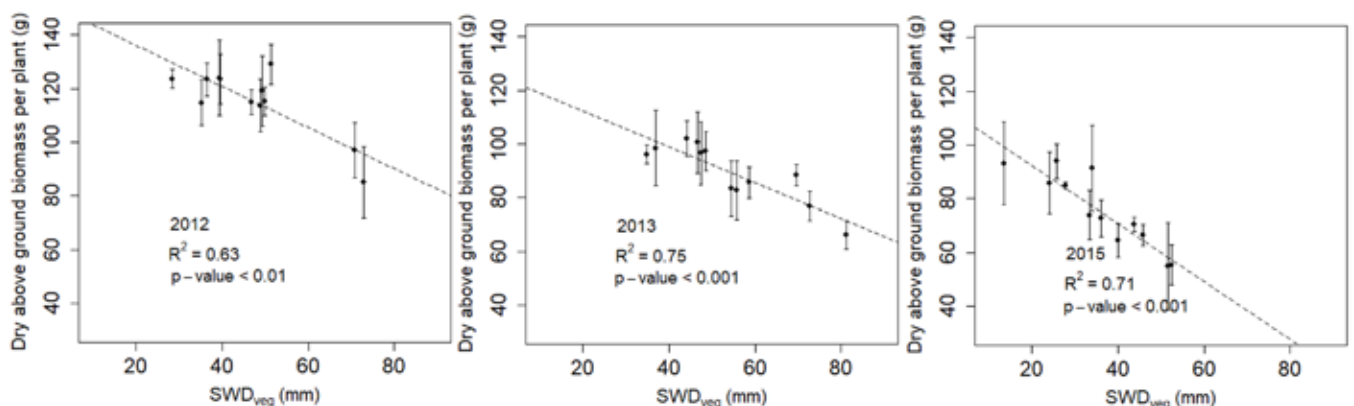


Fig. 2. Relationship between the mean soil water deficit in the late vegetative stage (SWD_{veg}) and aboveground biomass per plant at the end of late vegetative stage in 2012, 2013, and 2015 (error bars represent standard deviation).

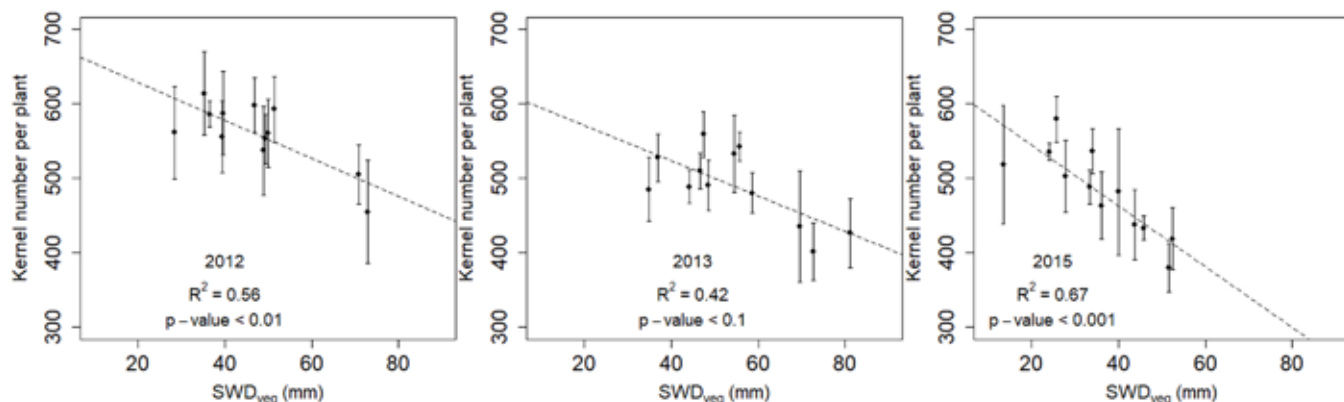


Fig. 3. Relationship between the averaged soil water deficit in the late vegetative stage (SWD_{veg}) and kernel number per plant in 2012, 2013, and 2015.

in 2013, and 32% in 2015. Similarly, AGB in the 40% treatment was reduced by 45% in 2012, 49% in 2013, and 69% in 2015. Previous reports also found reduced height, leaf area, and growth due to deficit irrigation applied during the late vegetative stage (Çakir, 2004; Jama and Ottman, 1993; NeSmith and Ritchie, 1992c).

Comparing treatments with equal target deficits during the Lveg stage, AGB at the end of growing season was significantly decreased ($p < 0.01$) with decreasing irrigation in the Mat stage (Table 5). It is likely that this decline in AGB under water deficit resulted from hydraulic failure (Gleason et al., 2017), and subsequent reductions in photosynthesis (Bolaños and Edmeades, 1996), and earlier leaf senescence during the grain-filling stage (Jurgens et al., 1978, NeSmith and Ritchie, 1992b, Westgate and Boyer, 1985). For treatments with the same target deficit during the Mat stage, AGB decreased with decreasing irrigation applied during the Lveg stage ($p < 0.01$). This could be explained by two reasons: (i) more water deficit during the Lveg stage resulted in smaller plants, thus less leaf weight and AGB carried over to the Mat stage (Fig. 1 and 2), which indirectly inhibited the grain-filling process during the Mat stage (Çakir, 2004) by reducing dry leaf weight and the photosynthetic capacity needed to provide adequate carbohydrate reserves for grain filling; and (ii) plants under deficit during the Lveg stage had fewer stored reserves that could be used for grain filling.

Effect of Deficit Irrigation on Kernel Number Per Plant

Average kernel number per ear (K_{num}) is a critical maize yield component that, together with average kernel weight, defines the yield capacity during the grain-filling stage (NeSmith and Ritchie, 1992b; Ritchie and Hanway, 1989; Tollenaar, 1977). Kernel number ranged from 600 in the fully watered treatment to 400 under severe stress (i.e., T40/40). These results are similar to those reported by (Dağdelen et al., 2009). Figure 3 shows the relationship between K_{num} in each treatment and averaged SWD in the Lveg stage in each of the 3 experimental years. Compared to T100/100, T40/40 reduced K_{num} by 11% in 2012, 24% in 2013, and 24% in 2015. Previous studies reported a reduction in K_{num} when deficit irrigation was applied during both Lveg and Rep stages (Ritchie and Hanway, 1989). Ear size and number of ovules (potential kernels) are likely determined between V12 and V17 stages (Ritchie and Hanway, 1989). Water deficit during the Rep stage reduces the fertilization of ovules (Kiniry and Ritchie, 1985; NeSmith and Ritchie, 1992a; Ritchie and Hanway, 1989), but this was not measured in our experiment because deficit was avoided during the Rep stage in all treatments. Figure 4 shows the relationship between K_{num} in each treatment and averaged SWD in the Mat stage in 3 yr. The data point with low K_{num} and low SWD_{mat} is T40/80 (in 2015, Fig. 4), which had less water stress in Mat stage but had relatively low K_{num} . The data point with high SWD_{mat} and high K_{num} is T80/40 (in 2012, Fig. 4), which had less water stress in Lveg. Thus, based on the response of these two treatments,

Table 5. Measured dry aboveground biomass ($Mg\ ha^{-1}$) at the end of growing season in 2012, 2013, and 2015. Data from 2012 and 2013 was previously published (Comas et al., 2019).

Irrigation treatment†	Maturation stage															
	2012					2013					2015					
	100	80	65	50	40	100	80	65	50	40	100	80	65	50	40	
	$Mg\ ha^{-1}$															
Late vegetative stage																
100	24.2ab‡					20.67ab					25.44a				18.15bcd	
80		24.14ab	21.24abc	18.82cd	21.20abc		22.01a	19.33abc	18.48bcd	16.99cde		20.98 b	19.56bc		16.19cde	
65			24.43a	18.74cd	18.8cd	18.46cd		20.66ab	20.46ab	17.11cd	15.55de		18.76bc	14.84def	14.44def	14.28def
50				18.44cd					16.30cde						13.03ef	
40					15.88d					13.86e			13.75ef		11.51f	

† Irrigation treatment: % of ET.

‡ Means followed by a different letter within a column are significantly different at $P = 0.05$ according to the Tukey-Kramer HSD range test.

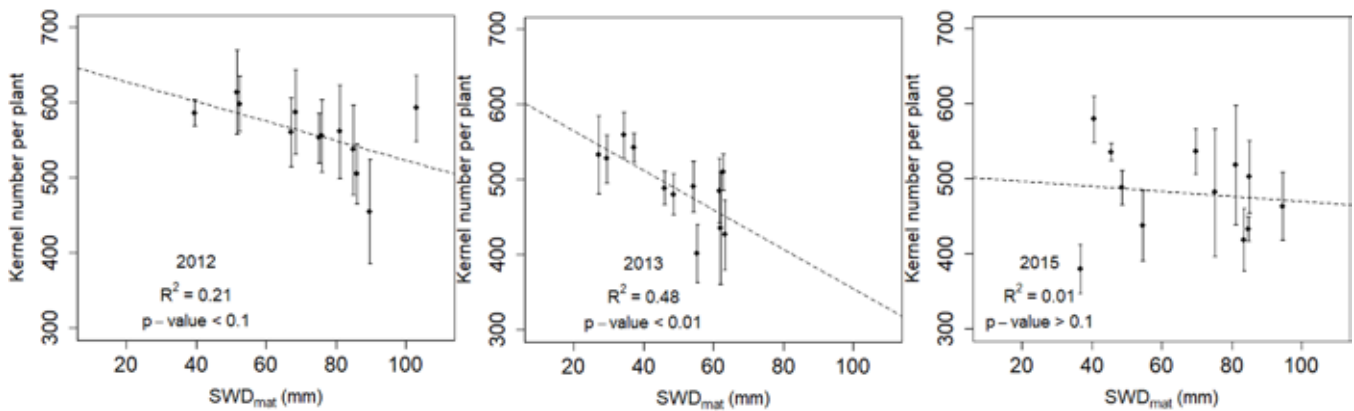


Fig. 4. Relationship between the averaged soil water deficit in the Mat stage (SWD_{mat}) and kernel number per plant in 2012, 2013, and 2015.

T80/40 and T40/80, we could say that water deficit in the Lveg stage had more effect on K_{num} than in the Mat stage.

Effect of Deficit Irrigation on 1000 Kernel Weight

Significant differences in 1000 kernel weight (K_{wt}) were observed between treatments. Kernel weight declined with decreasing target deficits during the Mat stage (Table 6). The SWD_{mat} was negatively correlated with K_{wt} ($R^2 > 0.7$, $p < 0.001$, not plotted). The K_{wt} in T40/40 declined by 17, 24, and 45% compared with T100/100 in 2012, 2013, and 2015, respectively. Other research has indicated that water deficit after R3 (during the grain-filling period) may result in decreased kernel weight due to reduced photosynthesis and early leaf senescence and a shortened grain-filling period (Grant et al., 1989; Mansouri-Far et al., 2010; NeSmith and Ritchie, 1992b). The average K_{wt} in T100/100 in all 3 yr was 288.3 g, which is similar to the maximum 1000 kernel weight for the region (283 g; Çakir, 2004). Çakir (2004) reported that K_{wt} decreased with increasing water deficit during the Mat stage but was also indirectly affected by water deficit applied during the Lveg stage via reductions in leaf area and ovule numbers. The larger leaf area evident in the less stressed treatments (Comas et al., 2019) may have resulted in heavier kernels by providing additional photosynthesis and greater carbohydrate reserves. The T80/80 had greater K_{wt} than T40/80 in 2015, which could be explained by a shorter Mat stage in T40/80 (Table 4). On the other hand, we might expect a tradeoff between K_{num} and K_{wt} whereby greater numbers of kernels are associated with smaller kernels. For example, T100/50 had less K_{wt} than T50/50 in both 2012 and

2013, which could be because T100/50 had larger K_{num} than T50/50 (546 vs. 453 in 2012 and 586 vs. 516 in 2013), given that both treatments had the same maturity duration.

Effect of Deficit Irrigation on Grain-Filling Rate and Yield

Grain-filling rate was calculated by the ratio between the final weight of grains per plant and GDD during the cumulative Mat stage (MGDD) (Table 4). The low MGDD in 2015 resulted from late planting, low daily mean temperature and mite damage during the Mat stage (Table 2). The GFR was influenced by both water deficit in Lveg and Mat (Table 7), and decreased with decreasing irrigation during Mat in treatments with the same MGDD. The GFR also decreased with decreasing irrigation during Lveg in all 3 yr. The mean GFR across years in T100/100 was $0.43 \text{ g}^\circ\text{C}^{-1}$, and the average MGDD was 378°C . NeSmith and Ritchie (1992b), who studied the effect of water deficit in the Mat stage on the grain-filling process, reported that the rate of grain filling was not significantly influenced by water deficit during the Mat stage; however, they did not measure the length of the grain-filling period or MGDD.

Mean grain yield adjusted to 15.5% moisture for the full irrigation treatment over 3 yr examined was 15.27 Mg ha^{-1} , whereas the yield from T40/40 was reduced by 32, 45, and 64% in 2012, 2013, and 2015, respectively (Table 8). Since maize yield is a product of MGDD and GFR, it was influenced by both water deficit in Lveg and Mat. Overall, maize yield in each treatment in 2012 and 2013 was higher than those in the corresponding

Table 6. 1000 kernel weight (g) in response to deficit irrigation during the late vegetative and maturation stage in 2012, 2013, and 2015.

Irrigation treatment†	Maturation stage														
	2012					2013					2015				
	100	80	65	50	40	100	80	65	50	40	100	80	65	50	40
g															
Late vegetative stage															
100	301a‡			246bc		275a			241abcd		290a			207cd	
80		287ab	256abc	238c	247bc		270a	276a	247abc	204d		266ab	244bc		184de
65		288ab	253bc	244bc	241c		268a	257ab	241abcd	222bcd		268ab	217cd	185de	174de
50				254bc					252ab					180de	
40					248bc					207cd		249abc			157e

† Irrigation treatment: % of ET.

‡ Means followed by a different letter are significantly different at $P = 0.05$ according to the Tukey-Kramer HSD test.

Table 7. Grain-filling rate (g °C⁻¹) in 2012, 2013, and 2015.

Irrigation treatment†	Maturation stage														
	2012					2013					2015				
	100	80	65	50	40	100	80	65	50	40	100	80	65	50	40
	g °C ⁻¹														
Late vegetative stage															
100	0.39a‡			0.36ab		0.41abc			0.34bcd		0.50a			0.43abcd	
80		0.39a	0.39a	0.34ab	0.38ab		0.45a	0.38abcd	0.38abcd	0.36abcd		0.43abc	0.46ab		0.37bcdef
65		0.38ab	0.36ab	0.35ab	0.33ab		0.43ab	0.41abc	0.34cd	0.34cd		0.40bcde	0.33cdef	0.35cdef	0.32def
50				0.33ab					0.34cd					0.31ef	
40					0.29b					0.30d		0.30ef			0.27f

† Irrigation treatment: % of ET.

‡ Means followed by a different letter within a column are significantly different at $P = 0.05$ according to the Tukey-Kramer HSD range test.

Table 8. Yield (Mg ha⁻¹) from treatments differing in deficit irrigation during the late vegetative and maturation stage in 2012, 2013, and 2015. Data from 2012 and 2013 was previously published (Comas et al., 2019).

Irrigation treatment†	Maturation stage														
	2012					2013					2015				
	100	80	65	50	40	100	80	65	50	40	100	80	65	50	40
	Mg ha ⁻¹														
Late vegetative stage															
100	15.73a‡			12.67abcd		15.70a			13.08bc		14.39a			10.32bc	
80		14.95ab	13.33abcd	11.27cd	12.81abcd		15.30a	14.85ab	13.07bc	10.6d		11.59ab	12.04ab		8.10cde
65		14.71abc	12.62abcd	12.04bcd	11.64bcd		15.10a	13.90abc	12.12cd	10.90d		12.05ab	8.42cd	7.45cde	7.24de
50				11.38cd					12.06cd					6.70de	
40					10.69d					8.57e		8.52cd			5.13e

† Irrigation treatment: % of ET.

‡ Means followed by a different letter within a column are significantly different at $P = 0.05$ according to the Tukey-Kramer HSD range test.

treatment in 2015, likely resulting from the shorter duration and more severe water deficit of Mat in 2015 (Tables 3 and 5).

CONCLUSIONS

Maize yield was a product of the number of kernels produced per plant and the rate and length of the grain-filling process. Water deficit applied during the Lveg stage was associated with kernel number and leaf weight, and thus, has indirect impact on the kernel mass developed during the Mat stage. This indirect impact became stronger when less water was also applied during the Mat stage. Water deficit during the Mat stage had direct impact on reduced 1000 kernel weight and expedited maturity date of R6. Water deficit applied in the Mat stage had a greater impact on the yield than when water deficit occurred during the Lveg stage. Results here further support that irrigation deficit during maturation is more damaging than deficit during late vegetative stages by limiting kernel development and should be considered when planning irrigation schedules to reduce irrigation use. Modeling the effects of deficits on kernel development in future efforts will likely aid decisions leading to the optimal distribution of irrigation water.

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