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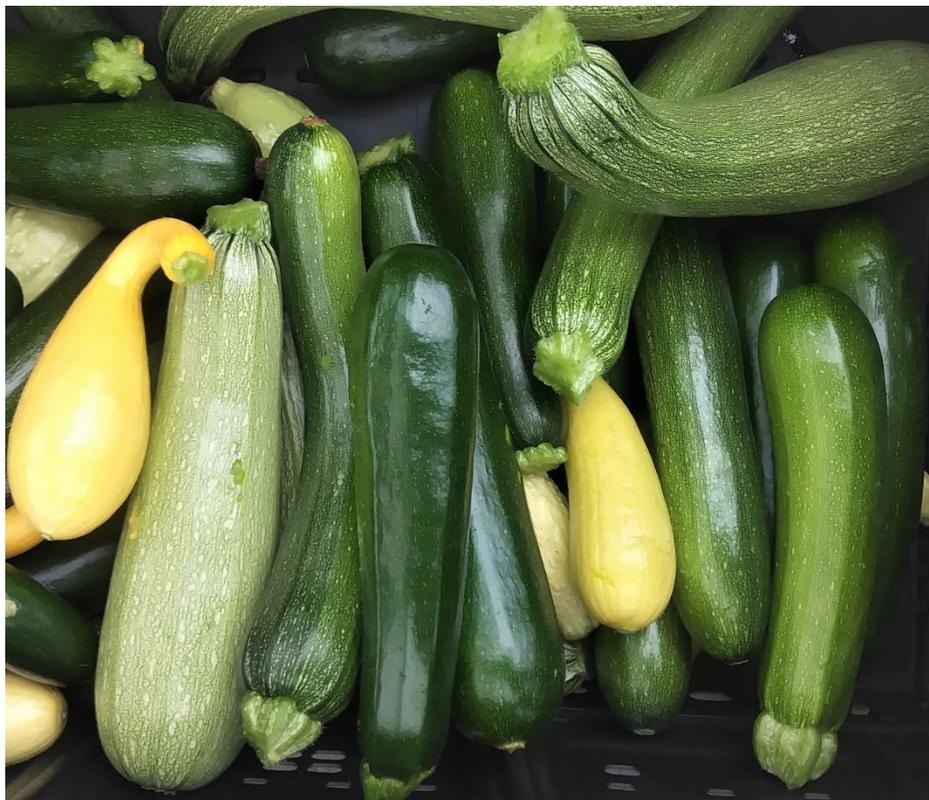
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## **The Relationship between Greenhouse and Field Performance of Nine Summer Squash Cultivars Grown Under Moisture Stressed Conditions in Northern Colorado**



Colorado State University  
Specialty Crops Program  
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The Relationship Between Greenhouse and  
Field Performance of Nine Summer Squash  
Cultivars Grown Under Moisture Stressed  
Conditions in Northern Colorado

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*Abstract.* Drought stress caused by reduced water availability poses a major threat to the global food supply, and most commercial vegetable growers lack cultivar-specific information that would allow them to adopt best management practices to limit the impact of drought stress. Summer squash (*Cucurbita pepo* L.) is an annual vegetable crop in the Cucurbitaceae family that is commonly grown and consumed in the United States. Cultivars including both heirlooms and modern hybrids with reports of “drought tolerance” are currently available on the market, but concomitant irrigation management recommendations are lacking. We conducted a greenhouse dry-down study on nine summer squash and zucchini cultivars, and sustained deficit irrigation (SDI) field trials on a selected seven among them in Colorado’s Front Range in 2018 and 2019. The objective of this study was to determine if crop characteristics identified in the greenhouse studies would align with season-long field success under a minimum 50% sustained moisture deficit (as compared to published irrigation recommendations [p.8]), and moreover if these experimental outcomes would align with reported cultivar characteristics. Colorado-bred conventional hybrids without reports of drought resistance were used as control cultivars in both studies and were hypothesized to exhibit a more drought-sensitive response than heirlooms and modern hybrids described as drought resistant.

Parameters evaluated in the greenhouse dry-down study included: days to death, percent soil moisture at death, root:shoot ratio, and root system morphology. Squash field studies were conducted in a retractable-roof/-sides structure for precipitation exclusion. Soil moisture and environmental conditions were monitored, and yield and quality measures were collected in both years. Photosynthetic activity was also evaluated. Our results revealed that greenhouse performance was not indicative of field performance, and that all squash cultivars produced marketable yield even under severe water deficits in the field. Cultivars with reports of drought resistance did not necessarily out-perform hybrids or open-pollinated cultivars without such

reports. By imposing a sustained deficit  $\geq 50\%$  below recommended season-long rates, we identified four best-performing, and currently available, cultivars of summer squash that experience a yield penalty (reduction) of  $\leq 30\%$  under moisture stressed conditions, which included ‘HYS-03-849’, ‘Jasper’, ‘Dark Star’, and ‘Desert F1’.

## Introduction

Water limitation is one of the single largest threats to agricultural production and the global food supply (Farooq et al., 2009). Therefore, the future of global food security depends at least in part on the identification and breeding of crop species and cultivars that can produce acceptable yields with reduced irrigation. The need for conserving the resources of the Colorado River, which supplies irrigation water for seven of the 17 Western states has recently received greater public attention (Elliott, 2019). In response to these known water limitations, extensive research has been conducted in the interest of reducing water use in agronomic crops and breeding drought-resistant grain crop cultivars around the world. However, such experiments and breeding in annual horticultural food crops remains relatively limited, particularly in the United States (Jiang et al., 2019; Kuşçu et al., 2015; Mashilo et al., 2018; Yuan et al., 2006). Summer squash (*Cucurbita pepo*) has been studied less frequently under reduced irrigation than other members of the Cucurbitaceae family, though this vegetable continues to gain popularity and contains morphological diversity that could contribute to successful drought stress responses (USDA AMS, 2019; Kirnak and Demirtas, 2006; YuJue et al., 2010; Singh et al., 2019). A renewed interest in dry farming techniques has led to research that has begun to reveal the cultivar-dependent success of summer squash and zucchini grown on Oregon farms without supplemental irrigation, which warrants further investigation (Nebert and Garrett, 2019).

Irrigation recommendations for fruit and vegetable crops, including summer squash, are typically generalized on a state-wide basis and fail to take precipitation into account, while at the same time likely over-estimating the true water needs of a crop in an effort to avoid advising growers to reduce irrigation below what is necessary for optimal yields (Masabni, n.d.; Molinar et al., n.d., Singh et al., 2019). The high cosmetic and quality-related standards included in the USDA grading system, in addition to those imposed by produce buyers, makes any degree of crop stress potentially economically harmful (Agricultural Marketing Service, 2016). Texas A&M University recommends summer squash be given 7 to 10 inches (178-254mm) of irrigation at a uniform rate throughout its life cycle, and the University of California Small Farms Program (UCSFP) recommends a minimum of 18 inches (457mm) of irrigation for summer squash crops, adjusted based on evapotranspiration rates (ET) (Masabni, n.d.; Molinar et al., n.d.). More generous recommendations from the UCSFP estimate summer squash water needs at 30 inches (762mm) per season (Molinar et al., n.d.). The estimated mean ET rates in California between the years 1971-2000 ranged from zero to 28 inches (700 mm), depending on the county, limiting the applicability of statewide irrigation recommendations (Sanford & Selnick, 2013).

Under ideal moisture conditions, summer squash yields are estimated by the UCSFP to average 6.8 lbs (3.1 kg) of squash per plant during a growing season lasting from March until August (Molinar et al., n.d.). Similarly, in a regulated deficit irrigation study of summer squash conducted under field conditions in Turkey, a well-watered treatment yielded 6.4 lbs (2.9 kg) per plant with a total water application of 22.7 inches (Kuslu et al., 2014). Therefore, for the purposes of this study it is assumed that 6.6 lbs (3.0 kg) per plant is the standard expected yield for summer squash and zucchini grown under optimal conditions.

Supplemental irrigation is required to produce acceptable yields of fruit and vegetable crops in semi-arid regions, including on the Front Range of Colorado where annual precipitation

averages 16.1 inches per year (Climate Fort Collins, 2019). However, only rain that falls during the growing season of a crop and directly benefits the crop is considered “effective precipitation”. The average effective precipitation for warm season crops in Northern Colorado is just 6.5 inches (409mm), less than half of the average estimated needs for summer squash. Studies have revealed that in moisture stressed conditions, typical drought-sensitive responses in cucurbit crops include a decrease in photosynthetic rates, leaf chlorophyll content, water use efficiency, biomass accumulation and yield (Sure, 2011; YuJue et al., 2010; Proietti et al., 2008). For this reason, supplemental irrigation is essential to produce summer squash, as well as many other fruit and vegetable crops in this region (Schneeckloth and Andales, 2017).

To ensure irrigation needs are met accurately, utilizing evapotranspiration (ET) rates is commonly recommended. This method of calculating water use results in irrigation management regimes adapted to each region and its precipitation rates. However, other factors are more commonly considered by crop producers when making irrigation decisions. For example, watermelon growers in Colorado’s Arkansas Valley irrigate watermelons based on a target total application of 12 inches per season (Bartolo pers. comm., 2019). Agronomic crop producers in Utah were found to make irrigation management decisions based on a variety of factors, including crop development stage, evidence of plant stress, and the behaviors of neighboring farms (Andriyas, 2012). In addition, cultural management strategies, such as the use of plastic mulch, may be effective at reducing drought stress without increasing irrigation volumes, which would reduce the accuracy of standard ET estimations under such management conditions (Bartolo pers. comm., 2019; Kirnak and Demirtas, 2006). While estimates made based on total inches per season or volume of water per plant can be less precise, this straightforward approach can be adjusted based on rainfall, cultural management, and observed crop needs to be more readily adopted by small-scale diversified vegetable growers.

Summer squash is a moderately deep-rooted crop, with an estimated rooting depth of between 36-48 inches (91-122 cm) (Maynard et al., 2007). Having a deep root system that develops rapidly during the seedling stage and is characterized by a high proliferation of roots with a fine average root diameter has been previously associated with increased crop success under drought conditions (Anjum et al., 2011; Comas et al., 2013). Cultivar-specific differences in root system distribution under drought in a field setting has been documented in melons, and in watermelons grafted to cucurbit rootstocks (Miller et al., 2013; Sharma et al., 2018). However, to date, cultivar-specific differences in root system development in summer squash in relation to drought stress has not been investigated in a field or greenhouse setting.

While controlling moisture conditions is relatively simple within a controlled-environment greenhouse, in a field setting rain out shelters are commonly used to prevent the variability in drought stress induction which can occur due to inconsistent rainfall patterns from year to year (Blum, 2010; Sharma et al., 2018). These structures provide more control over the moisture applied, but often restrict the experimental plot size due to infrastructure limitations (Blum, 2010). For this reason, rain exclusion is still a relatively uncommon method of studying irrigation management in field-grown horticultural crops (Yuan et al., 2006). Greenhouse drought studies allow more environmental control than field studies, require less space, and can be completed at any time of year, but are typically conducted at the seedling stage and therefore results are not consistently applicable to the behavior of mature plants in a field setting (Zhang et al., 2011; Hameed et al., 2010).

A wide array of terms is used to describe the responses of crop plants to low moisture conditions. Often, seed companies have described cultivars as “drought tolerant” and “drought resistant” interchangeably. True drought tolerance involves a variety of complex cellular and molecular mechanisms that allow a crop to be successful under drought conditions. Unless

specifically observed, drought resistance is a more appropriate and general term to describe any of a variety of adaptations that would lead to increased success under drought conditions.

Therefore, drought resistance here is used to refer to cultivars with reported success in low-water conditions unless reports of true drought tolerance are specifically made. Based on the available research, we hypothesized that currently available cultivars of summer squash appropriate for Northern Colorado Front Range growing conditions may undergo differing yield penalties under drought conditions, which have not yet been fully elucidated. We proposed that seedling root system development will contribute to survivability in these cultivars, and that this response will be observable in a greenhouse setting and can serve as an indicator for season-long success under drought stress in field conditions. Furthermore, our objective was to measure the responses of cultivars reported to be drought resistant and compare them to those bred for production in non-stressed conditions when both are subjected to an irrigation reduction below 50% of recommended rates. Defining these differences in terms of expected yield penalty (reduction) can assist growers in managing irrigation reductions, modifying cultural practices, and selecting successful cultivars.

## Materials and Methods

*2.1 Overview and Cultivar Descriptions.* Greenhouse studies were designed to evaluate the morphological traits of squash seedlings under induced moisture stress in 2018 and 2019. These potential indicators of drought resistance were then compared to season-long field performance in the same years. Heirlooms and modern cultivars were selected based on seed companies' reports of drought resistance, a record of performance with reduced irrigation, and demonstrated success in dryland (i.e. non-irrigated) systems. Control cultivars were bred in for conventional growing conditions in Lamar, Colorado, which has similar annual precipitation

rates to the target environment of the Northern Colorado Front Range (“Weather averages Lamar, Colorado,” n.d.) (Table 1). Heirlooms and hybrids with unique physical characteristics were evaluated due to farmer’s market customers’ interest in unique produce, and growers’ desire to have access to both open-pollinated and hybrid cultivars (Bond et al., 2006). Field trials were conducted using sustained deficit irrigation (SDI), a specific pattern of deficit irrigation that involves supplying uniform application of water throughout the season so that the crop undergoes an increasing moisture deficit as it reaches maturity, giving the plant time to adapt to increasingly severe drought stress (Ferreles and Soriano, 2007).

Nine squash cultivars with a range of physical traits and adaptations were chosen for inclusion in a greenhouse seedling dry-down study (Table 1). ‘Jasper’, ‘Obsidian’, HZS-03-849’, and ‘Daisy Mae’ were all selected from a Colorado-based vegetable breeder (Hollar Seed, Lamar, CO) and used as control cultivars. These cultivars were not described as drought resistant and were demonstrated to yield well under optimal conditions. These control cultivars were zucchini types, apart from ‘Daisy Mae’ (Daisy), a yellow crookneck summer squash (NE Seeds, n.d.). ‘Early Summer Crookneck’ (Crook) was another yellow summer squash chosen for its earliness, which is a trait that can contribute to drought escape (Terroir Seeds, 2019; Basu et al., 2016). ‘Rugosa Friulana’ (Rugosa), a yellow summer squash with an irregular, bumpy rind, was selected based on its inclusion in dry-farming trials conducted by the Oregon State University (OSU) Dry Farming Collaborative (DFC) (Nebert and Garrett, 2019; Baker Creek Heirloom Seeds, 2019). ‘Genovese’ (Geno), a gray or light green Italian summer squash, was also selected on this basis (Adaptive Seeds, 2018; Seeds from Italy, 2019). ‘Dark Star’ (DkStar) is an organic, open pollinated zucchini reported to be “vigorous” by seed companies and successful in OSU DFC trials (Nebert and Garrett, 2019; Siskiyou Seeds, 2019). ‘Desert F1’ (Desert) was included

in this study because it is the only currently available organic hybrid zucchini specifically reported to be “drought tolerant” (High Mowing Organic Seed and Gardens, 2019) (Table 1).

**Table 1. Summer squash cultivar information for greenhouse and sustained deficit irrigation field studies in Northern Colorado, 2018-2019.**

Cultivar	Seed Source	Fruit Type	Days to Maturity	Seed Company Description	Additional Notes	Environment/ Year(s)
'Daisy Mae'	NE Seed	Yellow crookneck	40-45	High yielding	Colorado-bred, control cultivar	Greenhouse/ 2018-2019
'Dark Star'	Siskiyou Seeds	Zucchini	50	"Remarkably vigorous"	Organic OP, OSU DFC	Greenhouse, Field/ 2018-2019
'Desert F1'	High Mowing Organic Seed + Gardens	Zucchini	50	"Drought-tolerant"	Organic hybrid	Greenhouse, Field/ 2018-2019
'Early Summer Crookneck'	Terroir Seeds	Yellow crookneck	42-60	"Early squash"	Selected in AZ	Greenhouse/ 2018-2019, Field/ 2018
'Genovese'	Adaptive Seeds, Seeds from Italy	Gray/light green	55	Seed produced in Oregon	OSU DFC	Greenhouse, Field/ 2018-2019
'HZS-03-849'	NE Seed	Zucchini	40-45	High yielding	Colorado-bred, control cultivar	Greenhouse, Field/ 2018-2019
'Jasper'	NE Seed	Zucchini	40-45	High yielding	Colorado-bred	Greenhouse/ 2018-2019, Field/ 2019
'Obsidian'	NE Seed	Zucchini	45-50	High yielding	Colorado-bred	Greenhouse/ 2018-2019
'Rugosa Friulana'	Baker Creek Heirloom Seeds	Yellow crookneck, irregular	60	Long-season	OSU DFC, long season comparison	Greenhouse, Field/ 2018-2019

*2.2 Horticulture Center Greenhouse Experiments.* A lack of established methods for optimally studying drought response and root systems in annual fruit and vegetable crops led to our adaptation of methods similar to those used in agronomic crop species (Becker et al., 2015). Greenhouse dry-down studies were conducted to investigate the root system development of squash cultivars under increasingly drought stressed conditions. Seeds were first germinated under controlled greenhouse conditions in rock wool plugs to ensure seedling uniformity. Once their first true leaves had developed, seedlings were transplanted into 4 × 4 × 12in (10 × 10 × 30 cm) pots filled with Profile® Greens Grade™ (Profile Products, Buffalo Grove, IL) growing medium that had been fully saturated with a 1.5 tbsp/gal (6 ml/L) fish emulsion (Alaska, 5-1-1,

Pennington Seed Inc.) and water solution. The pots were drained to container capacity before transplanting. Seedlings, pots, dry medium, and dry medium with fish emulsion solution were all weighed so the gravimetric soil moisture content could be determined for each pot. Experimental units were defined as one plant of one cultivar in one pot. Pots were arranged in racks that fit 9 pots per stand (one of each cultivar) in a randomized complete block design. Six replications (n=6) of each cultivar were planted, except in cases where germination rates limited the sample size; a minimum of three replications were included in these cases. The dry-down studies began on 2 February 2018, and on 23 May 2019. In 2018, greenhouse conditions were set to a minimum temperature of 11°C (52°F), a maximum temperature of 72°F (22°C), and 72% humidity. In 2019, the minimum temperature of 67°F (19°C) 67°F, the maximum temperature was 77°F (25°C) (77°F), and 50% relative humidity (RH) was maintained. No additional irrigation or fertility was applied for the duration of the study, and the growing medium gradually dried down. Data was collected on each pot daily until total desiccation (plant death) was reached. Days to death, gravimetric soil moisture at death, and dry weight of above-ground biomass were all recorded at the end of each experiment.

Once desiccation occurred, roots were washed and carefully collected for later analysis. Roots were preserved in a 18% ethanol solution and stored in a 4°C cooler until they were scanned (Smit et al., 2013, p.200). An EPSON Expression 11000XL scanner was used to capture images of the root system of each plant in the dry-down study. Roots were suspended in deionized water for imaging and then re-collected for dry weight determination. Images of the roots were then analyzed using WinRHIZO software (Regent Instruments Inc. Quebec, Canada 2013) to determine total length of fine (0.0-0.5mm) roots and total root length. Above and below ground biomass was dried in an oven at 65°C for up to one week and weighed. Using the root

and shoot dry weights, root:shoot ratio was determined for each cultivar by dividing root dry weight by shoot dry weight.

*2.3 Field Studies.* Field studies were conducted in Fort Collins, Colorado at Colorado State University's Agricultural Research, Development, and Education Center, South (ARDEC South) (40.610012, -104.993979, Elevation: 1523 m). Squash was grown in a retractable-roof/sides A-frame rain-out structure (CRAVO Equipment Ltd., Brantford, Ontario, Canada). Plots were managed using inputs approved for certified organic farms by the Organic Materials Review Institute (OMRI). Soil test results determined the soil type to be sandy clay loam, containing 2.4-3.0% organic matter. In year one, soil in the field and in the rain-out structure was amended with the addition of a one-inch layer of compost. Plots were fallow in the winter and rototilled in the spring prior to planting in both years. The growing area was kept level as opposed to being formed into beds, as recommended by the OSU DFC (Nebert & Garrett, 2019).

Transplants for field studies were grown in a greenhouse with a minimum temperature of 18°C (65°F), a maximum temperature of 27°C (80°F), and an average RH of 50% using Berger OM Series growing medium (Berger, Saint-Modeste QC) mixed with three gallons of vermicompost, three cups of Down to Earth Fish Bone Meal (3-16-0) and three cups of Down to Earth Blood Meal (12-0-0) incorporated into each 3.8 cubic-foot bag of soilless potting mix. Seeds were planted at 0.5-1 in (1.3-2.5 cm) depth in plastic six-pack inserts and watered daily as needed. Starts were transplanted to field conditions after hardening under shade cloth two to three weeks between 24-May and 6-June in both years. Plots were fertilized with fish emulsion (Alaska, 5-1-1, Pennington Seed Inc.) by fertigation every three to four weeks following crop establishment in accordance with product label directions. Insect and disease pressure were monitored weekly throughout the season.

Squash were sown in an 8 × 24 m (25 × 80') A-frame rain-out structure (CRAVO Equipment, Ltd.) with a retractable roof and sides, similar to rain-out structures described by Blum (2010) (Figure 1). The roof and sides were left open to maintain ambient environmental conditions except in cases of rain or hail. The rain-out structure was closed to exclude all precipitation during the treatment interval (5 July 2018-14 Sept. 2018; 28 June 2019-12 Sept. 2019). Drip irrigation was installed using Irritec P1 Ultra 5/8in drip tape with an emitter flow rate of 1.2 L per hour (0.33 gph) and plants were spaced on 61cm (24in) centers, aligned with 61cm (24in) spaced emitters (1 emitter/plant). Beds were spaced three ft (1 m) apart within treatments and four ft (1.3 m) apart between irrigation treatments. Landscaping fabric was used for weed suppression and to limit soil moisture losses to evaporation. A total of six cultivars were used, and three irrigation treatments applied in a split-plot design with three blocks (n=3) and 4-6 experimental units per cultivar per block. Data from each experimental unit was averaged across each plot.



**Figure 1: Summer squash planted in a rain-out structure structure with sides and roof partially closed and resistance soil matric potential moisture sensors installed.**

Soil moisture sensors (Irrrometer WaterMark Technology, Riverside, California) were installed at 8-12 in (20- 30 cm) and 36 in (91 cm) in both years to monitor soil matric potential (centibars). Watermark sensors were attached to ½in (1.3 cm) schedule 200 PVC pipe with PVC glue and a drainage hole was drilled above the attachment site. Sensors were installed by removing soil cores with a 1/2in (1.3 cm) soil corer and pouring a soil/water slurry into the hole to ensure good soil contact. A total of 36 sensors were installed, with one sensor per depth in each treatment/cultivar combination within block two. 21 out of 36 sensors were connected to dataloggers (Irrrometer WaterMark Monitor, Riverside, California) and calibrated using connected soil temperature sensors. The remaining fifteen sensors in the plot were hand checked three times weekly using a FieldScout Soil Sensor Reader (Spectrum Technologies; Aurora, Illinois). HOBO 4-channel external data loggers (Model U12-008, Onset Computer Corporation, Bourne, MA) were installed to log canopy temperature inside and outside of the rain-out structure to verify that environmental conditions were not impacted by the structure itself.

Irrigation treatments in the field study began after a well-watered establishment period that lasted from transplanting until first flowering. Irrigation treatments began between 28-June and 5-July. Treatments were defined as control (Ctrl), deficit (Def), and drought (Drt). Irrigation applications were made on a recurring schedule, taking into account readings from WaterMark sensors, visible evidence of crop stress, and a target reduction of at least 50% from average recommended irrigation rates in the Western states, which is 16 acre-inches for summer squash (Masabni, n.d.; Molinar et al, n.d.). Drought treatment plots received the same amount of water as the control at each irrigation event, but with two weeks between irrigations as opposed to the one week between irrigation events in the control treatment, which led to the Drt treatment plots receiving 50% of the water that the control did during the treatment interval (Table 2). Water was delivered through the system at 22-24 psi in accordance with drip line capacity to maintain a

0.33 gph (1.2 L per hour) flow rate. Reduced irrigation treatments (Drt, Def) were applied, and yields compared to that of typical commercial crops to quantify yield penalties incurred. The deficit treatment received irrigation at the same time as the control treatment, but in half the control volume, which was accomplished by reducing run time by half at each irrigation event (see Table 3). Total inches of water applied were divided by total yield in kg per plant to calculate an estimate of squash harvested per inch of water applied.

**Table 2. Summer squash irrigation and rainfall amount in rain-exclusion structure in 2018 and 2019.**

Year	Treatment	Pre-treatment <sup>z</sup>		Treatment <sup>y</sup>		Season Total	
		Inches <sup>x</sup>	GPP <sup>w</sup>	Inches	GPP	Inches	GPP
2018	Control (1)	4	14.8	1.5	5.6	5.5	20.4
	Deficit (2)	4	14.8	0.7	2.6	4.7	17.4
	Drought (3)	4	14.8	0.8	3	4.8	17.8
2019	Control (1)	4.6	17.1	1.6	6	6.2	23.1
	Deficit (2)	4.6	17.1	0.9	3.2	5.5	20.3
	Drought (2)	4.6	17.1	0.8	3	5.4	20.1

<sup>z</sup> Pre-treatment interval lasted from transplanting to flowering and was a non-stressed period of crop establishment (four weeks) when rainfall was not excluded.

<sup>y</sup> Treatment interval began at 50% flowering and continued through the end of the growing season (eleven weeks). Rainfall was excluded during this interval by closing the roof and sides of the rain-out structure.

<sup>x</sup> Inches of water include rainfall (pre-treatment) and irrigation (pre-treatment and treatment). Irrigation was converted from gallons per plant (GPP) to inches using a 6ft<sup>2</sup> effective crop area. All rainfall values taken from CoAgMet weather station website.

<sup>w</sup> GPP: gallons per plant of irrigation water (pre-treatment and treatment) plus rainfall (pre-treatment). Rainfall values in inches were converted to gallons per plant using a 6ft<sup>2</sup> effective crop area.

**Table 3. Summer squash irrigation treatment duration, frequency, and volume during the treatment interval<sup>z</sup> averaged across 2018-2019.**

Irrigation Treatment	Duration	Frequency	Volume Applied <sup>y</sup>	Inches applied	Total Volume Applied	Total Inches Applied
1 <sup>x</sup>	1 hour	1x/week	0.33 gal	0.06	5.8gal	1.6
2	0.5 hours	1x/week	0.165 gal	0.03	2.9gal	0.8
3	1 hour	1x/2weeks	0.33 gal	0.06	3gal	0.8

<sup>z</sup> Treatment interval began at 50% flowering and continued through the end of the growing season (eleven weeks). Rainfall was excluded during this interval by closing the roof and sides of the rain-out structure.

<sup>y</sup> Based on a growing area of 3' x 3' (9 ft<sup>2</sup>) per plant.

<sup>x</sup> Control is designated here as treatment 1, Deficit is designated as treatment 2, and Drought is designated as treatment 3.

*2.4 Field Study Data Collection.* Squash fruits were harvested three times per week from the first harvest (7 July 2018, 28 June 2019) through the end of the growing season (14 Sept. 2018, 11 Sept. 2019) for a total of 33 harvests in each year. Number of marketable and unmarketable fruits from each plot were counted at each harvest, and weights recorded. Marketability in the squash crop was visually assessed based on the presence or absence of physical defects, fruit shape (uniformity of pollination), size, firmness, and dullness/luster. Fruits were considered ripe, following pollination and once they reached the desired size based on cultivar, typically 13-18 centimeters (5-7 inches). Overripe fruits that were too large, firm, and/or dull were classified as unmarketable. Squash firmness was assessed using an analog penetrometer (firmness meter Model FM-30, probe diameter = 1.1cm [7/16"], Agricultural Specialty Company Inc., Hyattsville, MD) over the course of four consecutive mid-season harvests between 29 July and 29 Aug. in each year. Firmness of each cultivar and treatment was compared to the control cultivar in the control treatment. Data was collected over multiple harvests to include multiple representatives of each plot (n=9).

Photosynthetic parameters were measured in all squash plots both mid-season (8-10 Aug. 2018; 2 Aug. 2019) and late-season (24-29 Aug. 2018; 15-16 Aug. 2019) using a PhotosynQ MultispeQ v1.0. Main measures of interest were relative chlorophyll (SPAD), quantum yield of photosystem II ( $\Phi_2$ ), light lost to non-photochemical quenching ( $\Phi_{NPQ}$ ), and photochemical quenching ( $\Phi_{NO}$ ).  $\Phi_2$ ,  $\Phi_{NPQ}$ , and  $\Phi_{NO}$  are the three categories of use of incoming light and are measured as a ratio of total incoming light. The youngest fully expanded leaf in full sun was selected from each sampled plant for measurements from 11 am-2 pm. Two plants were measured per plot at each time point (n=6).

*2.5 Statistical Analysis.* All data were analyzed using R version 3.6.1 in R Studio (R Core Team, 2019). Outliers were identified in each model using the outlierTest function. A Bonferroni

adjusted p-value for the data points with the largest residuals was generated to determine outlier status. Outliers were removed from the model if detected. Two-way analysis of variance (ANOVA) was used to identify the significance of main effects of cultivar and irrigation treatment. Interactions between treatment and cultivar were also evaluated and reported when present. The emmeans package was used to compare adjusted marginal means, and the ggplot2 package was used for data visualization. Standard errors were calculated, and error bars added to bar plots. Results from both years are combined and analyzed together when similar, with year added into the model as an additional blocking variable.

## Results

*3.1 Horticulture Center Greenhouse Results.* Cultivar was the primary predictor of days to death in both years of the greenhouse studies. ‘Rugosa’ lived longer than three other cultivars in 2018, (48 days vs. 37 days) and could be differentiated from all other cultivars in 2019 (93 days vs. an average of 62 days). All squash lived longer, on average, in 2019 even though greenhouse set points were slightly warmer and humidity was lower than in 2018. Shoot dry weight (SDW) was also much greater in 2018 than 2019, meaning that the seedlings grew more vigorously and died more quickly in the first year of the experiment. In 2018, ‘Genovese’ had a heavier dry weight than all other cultivars besides ‘Early Summer Crookneck’ and ‘Jasper’. However, in 2019, ‘Early Summer Crookneck’ had the lightest biomass dry weight and was different from ‘Genovese’ in addition to multiple other cultivars (Table 4).

**Table 4. Greenhouse Dry-Down Study Results in 2018 and 2019, including days to death (DTD), percent soil moisture (%SM), total root length (TRL), average root diameter (ARD), root:shoot ratio (R:S), and shoot dry weight (SDW).**

*Greenhouse Dry-Down Study Results*

2018						
Cultivars	DTD <sup>u</sup>	%SM <sup>v</sup>	TRL <sup>w</sup>	ARD <sup>x</sup>	R:S <sup>y</sup>	SDW <sup>z</sup>
'Daisy Mae'	45.0 <sup>ab</sup>	26.4 <sup>ab</sup>	6872 <sup>ab</sup>	0.184 <sup>ns</sup>	0.143 <sup>ns</sup>	1.27 <sup>b</sup>
'Dark Star'	40.2 <sup>ab</sup>	27.0 <sup>a</sup>	6344 <sup>b</sup>	0.204 <sup>ns</sup>	0.164 <sup>ns</sup>	1.38 <sup>b</sup>
'Desert F1'	42.1 <sup>ab</sup>	25.2 <sup>ab</sup>	6511 <sup>b</sup>	0.187 <sup>ns</sup>	0.141 <sup>ns</sup>	1.37 <sup>b</sup>
'Early Summer Crookneck'	43.0 <sup>ab</sup>	26.7 <sup>a</sup>	6846 <sup>ab</sup>	0.18 <sup>ns</sup>	0.127 <sup>ns</sup>	1.4 <sup>ab</sup>
'Genovese'	38.0 <sup>b</sup>	26.9 <sup>a</sup>	6981 <sup>ab</sup>	0.209 <sup>ns</sup>	0.152 <sup>ns</sup>	1.6 <sup>a</sup>
'HZS-03-849'	42.5 <sup>b</sup>	24.7 <sup>ab</sup>	5840 <sup>b</sup>	0.197 <sup>ns</sup>	0.153 <sup>ns</sup>	1.36 <sup>b</sup>
'Jasper'	37.5 <sup>b</sup>	26.3 <sup>ab</sup>	7867 <sup>a</sup>	0.189 <sup>ns</sup>	0.166 <sup>ns</sup>	1.42 <sup>ab</sup>
'Obsidian'	43.0 <sup>ab</sup>	25.2 <sup>ab</sup>	5721 <sup>b</sup>	0.212 <sup>ns</sup>	0.162 <sup>ns</sup>	1.26 <sup>b</sup>
'Rugosa Friulana'	47.7 <sup>a</sup>	23.4 <sup>b</sup>	6900 <sup>ab</sup>	0.181 <sup>ns</sup>	0.154 <sup>ns</sup>	1.34 <sup>b</sup>
2019						
Cultivars	DTD	%SM	TRL	ARD	R:S	SDW
'Daisy Mae'	82.8 <sup>b</sup>	19.1 <sup>c</sup>	2399 <sup>a</sup>	0.187 <sup>ab</sup>	0.147 <sup>ns</sup>	0.57 <sup>ab</sup>
'Dark Star'	66.8 <sup>c</sup>	22.2 <sup>bc</sup>	2035 <sup>ab</sup>	0.211 <sup>a</sup>	0.153 <sup>ns</sup>	0.51 <sup>ab</sup>
'Desert F1'	65.7 <sup>c</sup>	21.1 <sup>b</sup>	2704 <sup>a</sup>	0.194 <sup>ab</sup>	0.137 <sup>ns</sup>	0.6 <sup>a</sup>
'Early Summer Crookneck'	78.4 <sup>b</sup>	21.3 <sup>bc</sup>	1271 <sup>b</sup>	0.169 <sup>b</sup>	0.111 <sup>ns</sup>	0.4 <sup>b</sup>
'Genovese'	61.5 <sup>c</sup>	23.7 <sup>ab</sup>	2032 <sup>ab</sup>	0.195 <sup>ab</sup>	0.12 <sup>ns</sup>	0.59 <sup>a</sup>
'HZS-03-849'	63.3 <sup>c</sup>	22.6 <sup>ab</sup>	2489 <sup>a</sup>	0.205 <sup>a</sup>	0.128 <sup>ns</sup>	0.64 <sup>a</sup>
'Jasper'	61.5 <sup>c</sup>	23.6 <sup>ab</sup>	2524 <sup>a</sup>	0.19 <sup>ab</sup>	0.127 <sup>ns</sup>	0.56 <sup>ab</sup>
'Obsidian'	62.7 <sup>c</sup>	23.7 <sup>a</sup>	2064 <sup>ab</sup>	0.214 <sup>a</sup>	0.133 <sup>ns</sup>	0.58 <sup>a</sup>
'Rugosa Friulana'	92.5 <sup>a</sup>	17.5 <sup>d</sup>	2017 <sup>ab</sup>	0.190 <sup>ab</sup>	0.141 <sup>ns</sup>	0.55 <sup>ab</sup>

<sup>u</sup> DTD is the number of days to death from the beginning of the dry-down study (2 Feb, 23 May).

<sup>v</sup> %SM is the volumetric percent soil moisture present at plant death determined by gravimetric soil moisture measurements

<sup>w</sup> TRL is the total root length of the root system in centimeters, measured from scanned images using WinRHIZO

<sup>x</sup> ARD is the average root diameter in centimeters, measured from scanned images using WinRHIZO

<sup>y</sup> R:S is the root:shoot ratio, calculated by dividing root dry weight by shoot dry weight

<sup>z</sup> SDW is the shoot dry weight in grams

Letters denote differences in statistical significance at  $\alpha \leq 0.05$ . The absence of a letter indicates a lack of statistically significant difference.

Percent soil moisture (%SM) values at plant death, determined through gravimetric soil moisture measurements, were comparable in both years (Table 4). 'Rugosa Friulana' withstood the lowest soil moisture conditions on average in both years (23.4% in 2018, 17.5% in 2019), and 'Genovese', 'Jasper', 'Obsidian', and 'HZS-03-849' died at the highest soil moisture levels in both years (25.2-26.9% in 2018, 22.6-23.7% in 2019), which was considered a more drought-

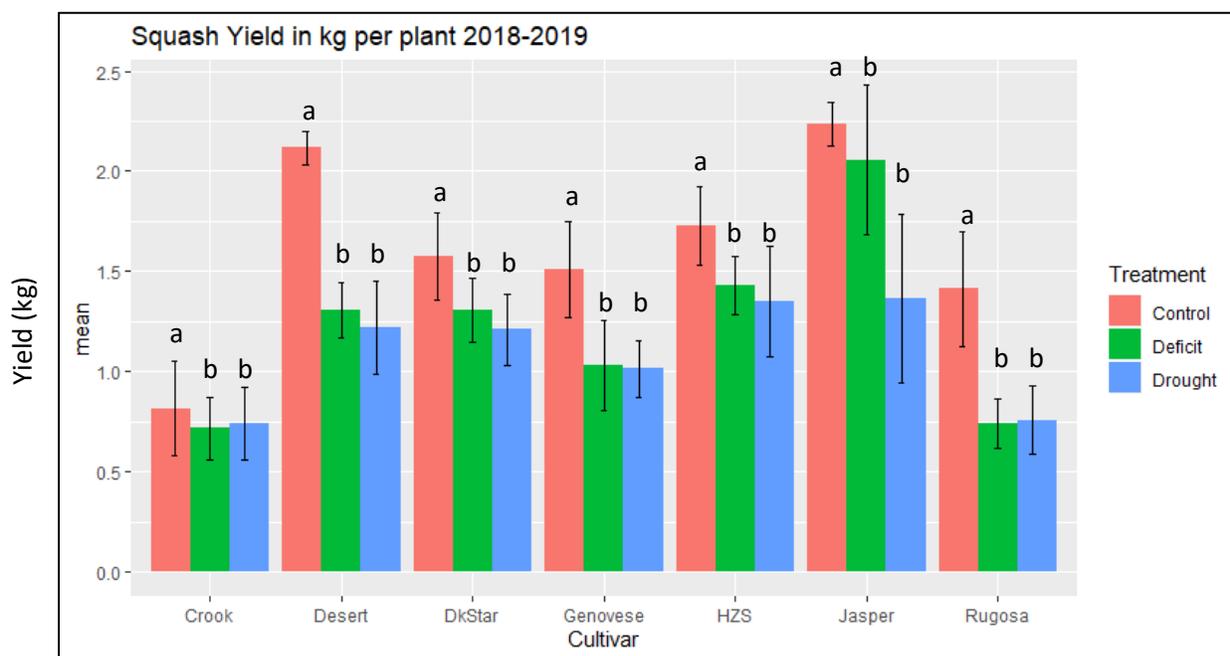
sensitive response that reduced survivability. No differences were found between root:shoot ratio (R:S) in squash cultivars in 2018 or in 2019 (Table 4).

Fine root length varied significantly between cultivars in 2018, following the same trend as total root length (TRL). Only total root length results are presented (Table 4). In 2018, ‘Jasper’ had significantly longer TRL than ‘Dark Star’, ‘Desert F1’, ‘HYS-03-849’, and ‘Obsidian’. In 2019, ‘Jasper’ still had relatively extensive root growth, but this cultivar along with ‘HYS-03-849’, ‘Desert F1’, and ‘Daisy Mae’ could only be differentiated from ‘Early Summer Crookneck’, the cultivar with the shortest TRL. Cultivar was a significant predictor of average root diameter (ARD) in 2018 and 2019, but pairwise comparisons in 2018 were not significant. The cultivar with the finest ARD, ‘Early Summer Crookneck’, was less successful than other cultivars evaluated in the greenhouse study based on all other response variables measured.

*3.2 Field Studies.* The main effects of cultivar and treatment were significant for yield per plant in 2018 and 2019 with no interactions. Therefore, pairwise comparisons were made between treatments within each cultivar (Figure 2). The adjusted marginal mean of all cultivars in the control plot was significantly higher than the yields of the deficit and drought plots, which were similar to one another. For all cultivars, the irrigation reduction from the control application resulted in a yield penalty (reduction) of 25-30%. Cultivars did have significantly different yields from one another, with the lowest yielding cultivar ‘Early Summer Crookneck’ or “Crook” having a mean yield of only 0.5 kg/plant across treatments, and the highest yielding cultivar (‘Jasper’) having a mean yield of 2.1 kg/plant across treatments.

A similar trend was apparent between the firmness of squash cultivars in both years. Cultivar differences were highly significant at ( $P < 0.00001$ ). The control cultivar, ‘HYS-03-849’ had an average firmness of 82 kPa or 11.9 pounds per square inch (psi). ‘Genovese’, ‘Dark Star’,

and ‘Jasper’ had a similar mean firmness, and ‘Early Summer Crookneck’ was punctured at a lower psi and as such was much less firm than the other cultivars, but still firm enough to be considered “fairly firm” in accordance with USDA guidelines (2019). ‘Desert F1’, and ‘Rugosa Friulana’ were significantly firmer than the control cultivar. According to the Agricultural Marketing Service (2016), a lack of firmness is considered a defect in squash, but having increased firmness is not formally considered a characteristic that signifies a reduction in quality.



**Figure 2: Summer squash yield from seven cultivars in kilograms per plant in 2018 and 2019 at ARDEC South in Fort Collins, Colorado (n=6). Pairwise comparisons made between cultivars within each treatment. Different letters indicate statistical significance. Error bars on bar plots indicate standard errors.**

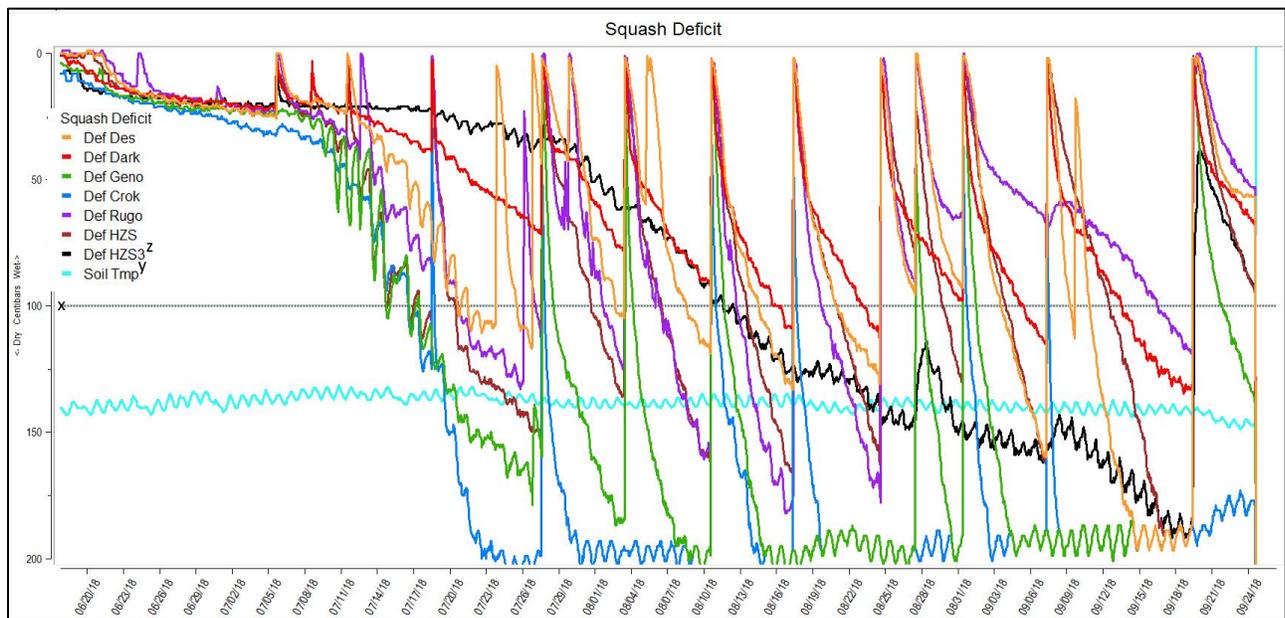
There were no clear trends in Phi2, PhiNO, or PhiNPQ in 2018 or 2019, though there were isolated instances of detectable differences (data not shown). Squash had similar photosynthetic responses to reduced irrigation across treatments and cultivars, both mid and late season, in 2018 and 2019. In 2018, cultivar was the significant predictor of relative chlorophyll, a unitless measure of “greenness”, both mid and late season (Table 5).

**Table 5. Mid-season relative chlorophyll values (SPAD) of six summer squash cultivars in the 2018-2019 field trials measured with a handheld photosynthetic measurement system (MultispeQ). Treatment-level differences were not significant (ns) in 2018.**

*Mid and late-season summer squash leaf relative chlorophyll content.*

Cultivars	2018		2019	
	Mid	Late	Mid	Late
'Dark Star'	48.1 <sup>d</sup>	42.9 <sup>c</sup>	52.4 <sup>b</sup>	52.6 <sup>b</sup>
'Desert F1'	52.7 <sup>ab</sup>	48 <sup>a</sup>	58.1 <sup>a</sup>	55.5 <sup>ab</sup>
'Early Summer 'Crookneck'	44.2 <sup>cd</sup>	40.5 <sup>c</sup>	N/A	N/A
'Genovese'	54.3 <sup>a</sup>	47.1 <sup>ab</sup>	59.2 <sup>a</sup>	56 <sup>a</sup>
'HYS-03-849'	48.7 <sup>bc</sup>	47.5 <sup>ab</sup>	57.6 <sup>a</sup>	55.3 <sup>ab</sup>
'Jasper'	N/A	N/A	56.7 <sup>a</sup>	54 <sup>abc</sup>
'Rugosa Friulana'	45.8 <sup>d</sup>	43.6 <sup>bc</sup>	52.7 <sup>b</sup>	51.1 <sup>c</sup>
Treatments				
Control	ns	ns	53.6 <sup>b</sup>	51.5 <sup>c</sup>
Deficit	ns	ns	57.2 <sup>a</sup>	54.2 <sup>b</sup>
Drought	ns	ns	57.5 <sup>a</sup>	56.5 <sup>a</sup>

Soil moisture readings in centibars from the WaterMark sensors revealed cultivar-level differences in dry-down pattern (Figure 5). The red line showing “Def Dark”, which stands for ‘Dark Star’ in the deficit treatment reveals a much more gradual dry-down curve that does reach lower than the recommended irrigation thresholds (-100 centibars) until late in the season. Each sensor reading returned to zero when they were re-hydrated during weekly irrigation application in this treatment (Figure 3). The black line shows data collected at 36in (91cm) deep in the ‘HYS-03-849’ control cultivar. Soil at this depth was hydrated during the non-stressed establishment period and dried down slowly throughout the rest of the study. Irrigation events during the treatment interval were insufficient to re-wet the soil at this depth, but the soil did not reach total desiccation (-200 centibars) until the end of the growing season. Similar trends were observed in both study years and in all treatment plots.



**Figure 3: Soil moisture in centibars at 30 cm (12in) depth in the deficit squash plot in 2018. “Def HZS3” soil moisture sensor buried at 90cm depth instead of 30cm depth in ‘HZS-03-849’. “Soil Tmp” soil temperature sensor buried at 30cm depth and used to calibrate soil moisture readings. The black dotted line at -100 centibars represents the highest recommended threshold for irrigating in a heavy clay soil.**

## Discussion

As small and large-scale growers alike face dwindling water resources, additional tools and information are needed to inform irrigation reduction decisions. Squash is an ideal crop for the exploration of drought resistance potential in currently available cultivars, both due to the wide variety of genetic resources available, and due to these crops’ popularity among farmers and consumers in Colorado and throughout the United States. Direct markets are increasingly important to both growers and consumers and provide opportunities to introduce unique cultivars and more sustainable management practices on a smaller scale (Bond et al., 2006). Sustained deficit irrigation practices can more readily be followed by small-scale local growers than irrigating based on ET in these crops and is more closely aligned with the methodology of irrigation decisions and current infrastructure on some farms. Currently available literature has

informed us of what to expect from drought sensitive cucurbits but has not fully revealed the range of responses in the diverse summer squash cultivars that are currently on the market.

In this series of experiments, discrepancies were identified between cultivar reports from seed companies, overall cultivar performance in the greenhouse, and yield success under sustained deficit irrigation in the field trials. Among the summer squash cultivars, the organic hybrid ‘Desert F1’ zucchini was the only cultivar claimed to be “drought tolerant”. ‘HZS-03-849’ served as a conventional hybrid zucchini, had reports of high yield potential, but no claims related to drought response.

‘Rugosa Friulana’ was more successful than all other squash cultivars in the greenhouse trials in terms of the number of days it survived. This cultivar also had the greatest ability to extract moisture from the substrate and to persist in low moisture conditions. However, this survivability did not correspond to greater overall root growth. Two of the cultivars with the most extensive (longest) root systems in the dry-down study (‘Jasper’ in both years, and ‘HZS-03-849’ in 2019) tended to die faster (37 days in 2018, 62-63 days in 2019) than ‘Rugosa Friulana’ (48 days in 2018, 93 days in 2019), and had a significantly higher percent soil moisture at death in 2019. There appeared to be a tradeoff between survivability and root system development, as ‘Jasper’ and ‘HZS-03-849’ had better yield in the field studies than ‘Rugosa Friulana’. This was not always the case, though, as ‘Genovese’ had similar root growth and survivability in the greenhouse studies but comparably low yields in the field studies. Though ‘Rugosa Friulana’ exhibited strong survivability traits, this cultivar had one of the lowest yields in the field studies, and ‘Jasper’, a cultivar with weak survivability traits but extensive root system development, had the highest yield averages overall.

Since our objective was primarily to compare standard cultivars with those having reported drought resistance under SDI conditions, the Control irrigation treatment plots received

an average of 5.9 inches of water per season, and the drought and deficit treatments received an average of 5.1 inches of water. This difference of 0.8 inches was enough to result in yield differences in all cultivars due to the two-month period that the treatment interval lasted. Only between 0.7-1.6 inches of water were applied based on treatment over the course of drought-sensitive period of flowering and reproductive growth. The relative success of ‘Dark Star’ compared to ‘Rugosa Friulana’ aligned with outcomes from the OSU Dry Farming Collaborative trials (Nebert and Garrett, 2019). Across all cultivars, additional reductions in irrigation from the control amount did not reduce the proportion of marketable yield or unmarketable yields in any treatments or between any cultivars in 2018 or 2019. Using ‘Jasper’ as an example, the average 5.4 of water applied to each plot yielded 2.1 kg/plant, which translates to 2.6 inches of water applied per kilogram of squash harvested. If we compare this to Kuslu et al. (2014), where 22.7 inches of water were applied to harvest a yield of 3.0 kg/plant, we see that in this study 7.6 inches of water were applied per kilogram of squash harvested. This indicates that ‘Jasper’ in particular was able to convert moisture applied into harvestable yield more efficiently than other summer squash and zucchini.

While many of the soil moisture sensors reached the driest reading measurable with this sensor, without resulting in crop loss, WaterMark sensors can lose soil contact in clay-dominant soils that become very dry and shrink, and therefore may not be ideal for drought studies in such conditions. Studies were conducted in a rain-out structure which was used for rain and hail exclusion, and inside and outside canopy temperature data reveal that the use of the rain-out structure did not lead to differences in environmental conditions and therefore is a good choice for future studies on drought response and deficit irrigation.

These results demonstrate that the most successful cultivars of summer squash in these experiments, which included ‘Jasper’, ‘Desert F1’, ‘HZS-03-849’ and ‘Dark Star’, experience an

approximate yield penalty (reduction) of 30% from the expected 3 kg/plant in conditions of more than 50% water reduction from average recommended rates. While a yield penalty was incurred, no significant changes in quality or marketability were observed, making these cultivars ideal candidates for production scenarios with reduced irrigation inputs.

### Conclusion

These results indicate that more summer squash cultivars than originally hypothesized have the potential to produce acceptable levels of marketable yield with drastically reduced irrigation. We demonstrated that cultivars without claims of drought resistance need to be evaluated on a case-by case basis in field trials, as cultivar greenhouse outcomes did not always align with field trial outcomes. Strong drought-resistant traits may exist in cultivars that have already been bred for overall vigor and high yields, such as in the open-pollinated ‘Dark Star’ and hybrid ‘Jasper’ zucchinis. While selective breeding for drought resistance would likely give us new cultivars that are successful with severe water deficits, other cultivars already on the market may have undiscovered resilience in these conditions.

The difference in total root growth and average days to death between the 2018 and 2019 greenhouse studies reaffirms the importance of consistent environmental conditions (light, temperature, humidity) in greenhouse studies. However, the sensitivity of these studies to environmental conditions makes it even less likely that they will produce results that align with season-long field performance. Neither year of the greenhouse study produced results that were consistent with both seed company reports of drought resistance and field outcomes, however total root length was a better indicator of field success than metrics related to survivability. Because of the weak relationship between cultivars that were successful in greenhouse trials and those that yielded highest in field trials, it is important to continue to search for reliable indicator

traits in the greenhouse and in the meantime, to rely on field studies to identify crop cultivars with season-long success under drought.

Prior to planting, growers may have limited information on how much water will be available to them throughout the growing season, and while ideal irrigation amounts may vary from year to year depending on rainfall and average temperatures, crop producers do not necessarily have an extra supply of irrigation water to respond to these changing conditions. Growers may be able to reduce irrigation in summer squash crops beyond what was applied in this study by not excluding rainfall during growing season. Growing summer squash cultivars such as ‘Jasper’, producing 2.1 kg/plant or ‘Genovese’, ‘Desert F1’, ‘HZS-03-849’, and ‘Dark Star’, producing between 1.2-1.5 kg/plant can help ensure growers that they will still harvest marketable yields and predictable overall yields, even in years of low precipitation or limited irrigation water availability using only 19.9 gallons (5.4 inches) of water per plant.

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