THESIS

WATER-LIMITED COMPETITION AND THE YIELD-DENSITY RESPONSE IN DRYLAND MAIZE (*ZEA MAYS)*: AN ECOLOGICAL AND ECONOMIC ANALYSIS

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Caroline Dewey

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Master's Committee:

Advisor: Meagan Schipanski
Co-Advisor: Louise Comas

Troy Ocheltree

ABSTRACT

WATER-LIMITED COMPETITION AND THE YIELD-DENSITY RESPONSE IN DRYLAND MAIZE (*ZEA MAYS)*: AN ECOLOGICAL AND ECONOMIC ANALYSIS

The plant dynamics of biomass production under competing resources are commonly understood through the empirical generalization of Constant Final Yield (CFY). This law has considerable utility for crop management decisions that often center on altering resources and planting density to maximize plant productivity. Dryland producers are uniquely vulnerable to variability in climactic conditions and precipitation patterns. However, most studies on yield-density relationships have focused on well-watered conditions for maize (*Zea mays*). In this thesis, I investigated the hypothesis that the yield-density relationship in dryland maize will approximate CFY, with the point of plateau determined by water availability (Chapter 1). This concept was tested by planting maize at a range of stand densities (20, 30, 40, 50 thousand plants/ha) under four water regimes in a semi-arid region in Colorado, USA. Plant productivity increased under greater water availability as the planting density increased. A quadratic plateau model best fit the yield-density relationship. Treatments with less water availability did not exhibit yield-limiting thresholds at the densities included. Plant functioning in terms of chlorophyll fluorescence, grain N uptake and proportional allocation to grain (i.e., harvest index) remained relatively unaffected by resource availability to the plants. Results of the study indicate dryland maize systems can reach a maximum yield while forgoing significant physiological stress. The pattern of CFY was approximated, with water availability corresponding to a higher asymptotic point at a greater population density. As a next step, a partial budget analysis was

conducted to assess net returns associated with varying seeding rate and soil moisture in dryland maize cropping system (Chapter 2). Data was selected from the experimental study outlined in Chapter 1. Benefits were calculated in terms of maize grain yield. Cost estimations for each treatment included the cost of seed, representative field operations and management. Results showed that net returns responded positively to high evapotranspiration (ET) conditions. Under low ET conditions a decrease in seeding rate was more profitable. Improved soil moisture improved net returns among both seeding rates. The increase in revenue from grain yield under high ET conditions was greater than any additional costs, even though materials and services costs generally increased. Dryland producers should approach increased seeding with caution if seeking to maximize grain yield at low soil moisture.

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CHAPTER 1: CAN THE LAW OF CONSTANT FINAL YIELD BE USED TO DELINATE PLANT PRODUTIVITY BY COMPETITION FOR WATER?

Introduction

The Law of Constant Final Yield (CFY) describes our general understanding of how resource competition shapes plant productivity in both natural and managed ecosystems. However, this law has been mainly tested under mesic conditions where light is predominately the limiting resource and competition is asymmetric (Weiner & Freckleton, 2010). This is although changing climactic conditions, such as water scarcity, rising temperatures, and changing precipitation patterns, have direct and complex effects on plant resources (Schmidhuber & Tubiello, 2007; Nelson *et al.,* 2014). Semi-arid and arid areas will potentially have to adapt to predictions of higher evapotranspiration and lower soil moisture (Schmidhuber & Tubiello, 2007). These increasing environmental pressures, necessitate a more complex understanding of population- and community-level patterns in drier environments in order to produce prognostic outcomes.

The generalization of plant dynamics, referred to as "Constant Final Yield" (CFY) is a function of plant genetics, resource levels, and spatiotemporal conditions under which the population is measured (Fibich *et al.* 2014; Weiner & Freckleton, 2010). The general assumption is that CFY reflects size asymmetric competition (Weiner & Freckleton, 2010). Asymmetric interspecific competition, or the tendency of variation in plant size to affect plant performance, primarily occurs due to limited light availability (Crawley, 1990). Larger plants shade the smaller sized plants. This competition can impact biomass and reproductive biomass, limiting the total standing biomass of a plant community. At low densities, when resources are abundant, the total biomass is limited by population density. However, when there are more individual plants

than available resources, size distributions are affected and resource limitations are met, leading to an asymptotic density-productivity relationship (Yahuza, 2011). CFY is not universally followed. Exceptions to the CFY have been seen in cases where resource competition is not the primary interaction among plants (Weiner & Freckleton, 2010).). Specifically, the best model of the plant yield-density relationship in row crops has been debated, with some exhibiting a parabolic pattern. A few exceptions have exhibited an over-compensating density dependence effect (Li *et al.,* 2016). Resources have a reported impact on model fit, with water deficit shifting the yield-density model. (Assefa *et al.,* 2016).

This understanding of plant population ecology, specifically the dynamics of growth in response to environmental factors and resources, and intraspecific competition, is directly applicable to managed systems. In particular, agricultural production seeks to maximize reproductive biomass, or crop yield, by altering population density and resource inputs. Planting at optimal population densities is one strategy that can increase yields when water availability is not limiting plant growth (Zhang *et al.,* 2021; Mylonas *et al.,* 2020). The definition of optimal population density can vary with stakeholder priorities; in this paper, optimal population density will refer to the lowest planting density at which the greatest crop yield is attained. This can be understood as the point of asymptotic plateau in a system following CFY.

The staple food crop maize (*Zea mays*) has been a focal point of researchers seeking to accelerate yield increases (Hammer *et al*., 2009, Grote *et al.,* 2021). Yield potential can be increased by altering seeding rate and resource levels, which increase competition (Allen, 2012). However, indiscriminate increases in these factors can decrease resource efficiency, a key concern in closing the efficiency gap and improving sustainability (Zhou & Duan, 2021). There has been considerable research done evaluating the relationship between grain yield and plant

population under different conditions (Haaroff & Swanepoel, 2018). Greater planting density tends to result in a greater rate of grain yield increase (Van Roekel & Coulter, 2011). One study found that an increase in plant density did not result in an increased competition for light, water, and N, but rather a downregulation of photosynthetic capacity in response to competition. Variability in competition models suggest response to crowding and competition may be species-specific. It is proposed these species-specific differences are due to enzyme regulation and plant behavioral attributes such as growth, resource allocation and usage, etc. (Clay *et al.,* 2009).

Producers have struggled with inconsistent grain yields from year-to-year with few publications to turn to regarding optimal planting densities for dryland maize in arid/semi-arid regions like the Central Great Plains. While the relationship between total and harvestable biomass and planting density has been extensively studied in historically wet environments, we lack an understanding of the yield-density response in water-limited environments. Most research on the topic in the United States has been conducted in the Corn Belt and southeast, where precipitation is not the most limiting factor (Norwood & Curie, 2013). Population recommendations in the Corn Belt tend to be higher than in more arid areas. Grain production in arid and semi-arid regions is predominately limited by soil water (Haaroff & Swanepoel, 2018). Some studies conducted in more arid areas found a lower population produced the highest yield (Norwood, 2000). To further increase the understanding of ecological principles in dryland systems, incorporate more adaptive and sustainable agronomic practices, and increase resiliency, we must better understand how plant growth dynamics respond to shifting resources and competition.

The aim of this research was to assess the yield-density relationship of maize with varying external factors in a dryland environment. We conducted a field density experiment of

Zea mays over the course of a season to (1) determine the effects of water availability and population density on plant biomass and yield, and (2) quantify the form of these relationships, identifying any interacting effects.

We hypothesized that harvestable biomass in water-limited treatments would follow the pattern of CFY, plateauing at a point beyond which biomass will no longer increase in response to planting density. And, as water availability increases, we hypothesized that the point of plateau would occur at a greater maximum attainable yield and at higher planting densities (Fig. 1.1).

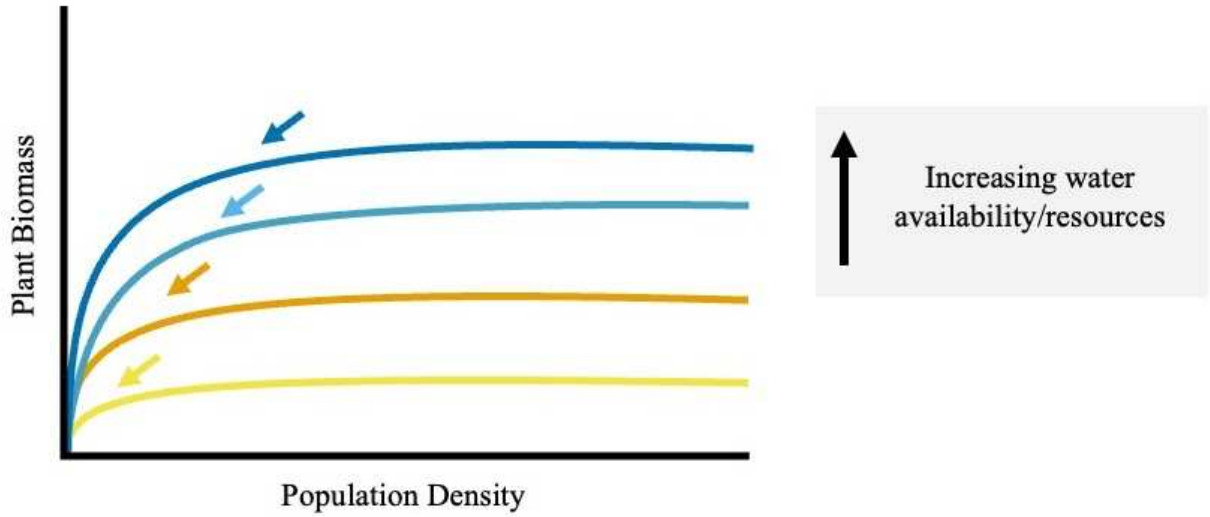

Figure 1.1. Conceptual figure displaying hypothesized yield-density diagrams. Arrows indicate the approximate point of constant final yield. Color differentiates between degree of water availability/resource, with blue being the greatest relative water availability.

Methods

Site and Crop Management

This study was conducted at the USDA ARS, Central Great Plains Resources Management Center in northeastern Colorado during the growing season of 2021. The farm was located in Akron, Colorado (40.15’ N, -103.14’ W). The soil includes Rago silt loam and Weld silt loam with a 0-3% slope (USDA taxonomy). Water holding capacity was 1.67 mm per cm.

Organic matter was approximately 1.8%. Soil information was gathered using the SSURGO database.

The daily average temperature throughout the growing season of 2021 was 18.26 degrees. Monthly mean temperature throughout the growing season of 2021 ranged from 12.8 to 23.4 degrees. Daily relative humidity ranged from an average minimum of 25.8% to a maximum of 87%. In Akron, average annual precipitation is 326 mm (Colorado Agricultural Meteorological Network, 2021). The average annual rainfall in 2021 was 325 mm with approximately 173 mm falling during the growing season. Most rainfall occurred early in the season, with over 50% of the seasonal rainfall occurring in May during the 2021 season. This was a negative deviation from historical trends of average seasonal rainfall of 261 mm. The 229 mm irrigation treatment most closely approximated long term average seasonal precipitation.

Experimental Design and Treatment

The experiment was a split-plot design with four replicate blocks. Four levels of water application were randomized within each replicate block as a whole plot treatment, with four levels of plant density randomized in sub-plots. Three plots were excluded from analysis due to severe wind damage. The excluded plots affected the 20,000 and 30,000 plants ha^{-1} populations of the 0 mm water treatment, as well as the 49,000 plants ha^{-1} population for the 229 mm water treatment. Sub-plots comprised six rows of 25.6 m row lengths. Plots were separated by a two-row buffer. A twelve-row buffer was placed in the center of the site to allow for sprinkler wheel track access.

Maize (*Zea mays*) was planted using a John Deere 1700 MaxEmerge Planter. Maize variety was a DKC 47-47RIB Brand blend. This is a broadly adaptable product in stressed

environments, including drought tolerance. It is engineered to have strong late season health and standability. This is a flex-ear variety, meaning kernels per ear will vary with plant population. Row spacing was 0.762 m. Four planting densities were targeted: 20,000, 30,000, 40,000, and 50,000 plants ha^{-1}. The field rotation/stubble prior to this maize experiment was a limited irrigated winter wheat, harvested in 2020. On the day of planting, 83.5 L ha^{-1} of 10-34-0 liquid ammonium polyphosphate and 93.5 L ha^{-1} of 32-0-0 urea liquid ammonium nitrate were applied, totaling 12.3 kg of N. This field has been managed with no-till for greater than 10 years. Weeds were controlled using herbicides.

Irrigation was applied using a Valley 3 tower linear system with sectional controls. This consisted of flat spray heads on a 1.5 m spacing with drops to 30 cm above ground. Water applications, totaling 0, 76, 152, and 229 mm, were applied as a supplement to rainfall to create four levels of water availability (Fig. 1.2). The 0 mm treatment received 25 mm of irrigation on July 27th, 2020, due to human error, but will still be referred to as "0 mm" here on out. Water additions were applied between July 8th and August 31st, 2021, roughly coinciding with the late vegetative through grain filling stage of maize development, because there was a full soil moisture profile early in the season**.** The evapotranspiration calculations were done using a water

balance approach, utilizing neutron attenuation monitoring. Evapotranspiration determination was in line with water budget methods (Bowman & King, 1965).

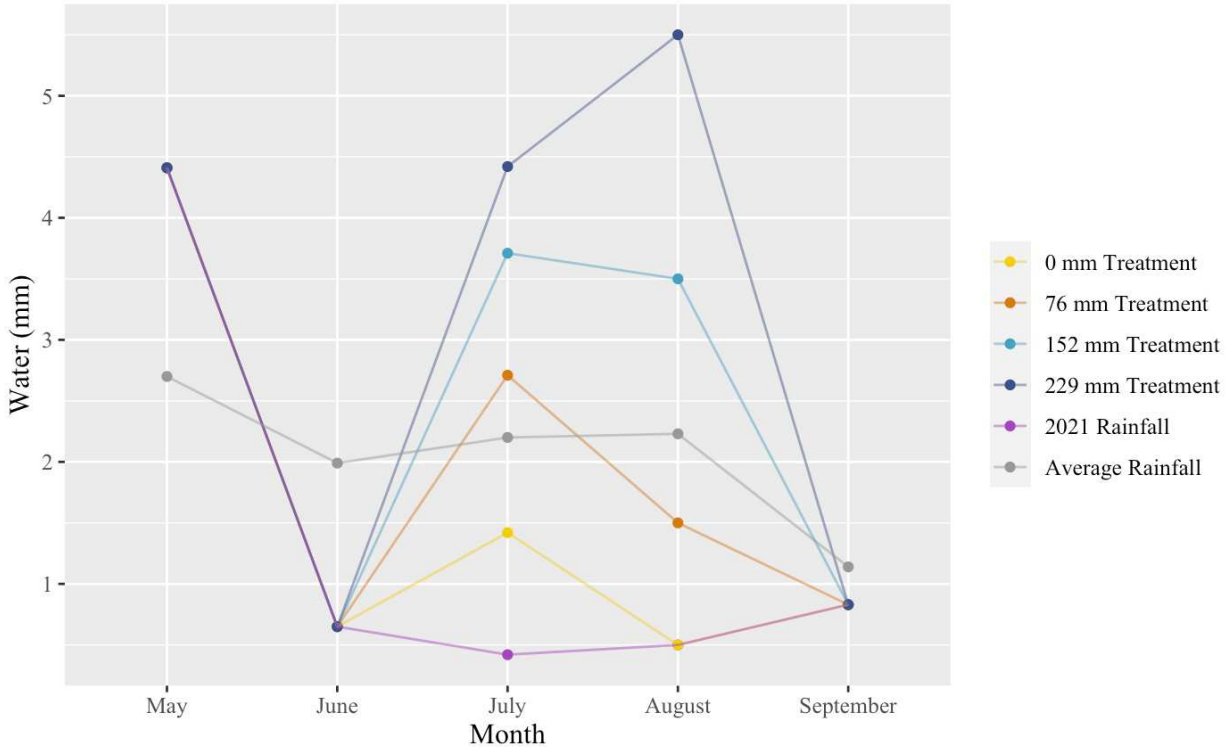

Figure 1.2. Graph comparing the water additions for each treatment with seasonal precipitation trends in 2021 along with average rainfall for the 1992-2021 period recorded by the AKR02 CoAgMet Station. Displayed treatment values include 2021 rainfall in addition to irrigation amounts.

Data Collections

A section of 5 consecutive plants at physiological maturity (R6) in each sub-plot were collected on September 27, 2021. Row length and ear counts were recorded. Sections were chosen adjacent to the neutron probe. Representativeness of stand was also considered in choosing sampling locations. Plants were separated by stalks, leaves, and ears, placed into paper bags, and dried at 60 C. Leaves were dried for 24 to 48 hours. Stems and cobs were dried for 3 to 5 days. The ears were fully dried, shelled through an Agriculex SCS-2: Single Corn Sheller and

weighed. The separated shoot dry matter was weighed and recorded. The grain was placed into paper bags and dried in an oven at 30 C until moisture content reached < 5%.

Grain was then ground using a UDY Cyclone Sample Mill and tested for percent C and N. Total C and N were determined through a LECO CN928 combustion analyzer (LECO Corporation, St. Joseph, MI, USA). Harvest Index (HI) was calculated using the aboveground biomass collected as the proportion of harvested material (grain) to total aboveground biomass.

Maize ears were manually harvested from 3.0 m sections in neighboring rows from each sub-plot on October 15, 2021. The ears were shelled using a plot combine. Grain moisture content was taken using GAC500 XT (DICKEY-John Corp., Minneapolis, MN, USA). Yield is reported at dry weight (0% moisture content).

Leaf Area Index (LAI) was measured using a Licor LAI-2200 between 11:00 and 14:00 h on clear days at a biweekly schedule from July to September. Five positions were selected at equal intervals within a 3 m section, moving diagonally across the row. The sensor was held level.

The fluorescence parameter used here was the light-adapted fluorescence or Y(II). This parameter was also calculated as $\Delta F/Fm'$ or $((Fm'- F_S)/ Fm')$. This was measured using a OS5p+ system (Opti-Sciences, INC., Hudson, NH, USA) between 11:00 and 14:00 h on July 21st and August 10th. All measurements were taken on clear days under exposure to photosynthetically active light- i.e., steady state conditions. Light adapted measurements were taken with a PAR clip positioned halfway longitudinally along the leaf and halfway between the leaf midrib and the edge of the leaf. Five maize plants were randomly selected within a 3m section, alternating between the two rows. Leaves with visible damage were excluded from sampling. Measurements taken within the designated plot area were averaged prior to statistical tests. Standard deviation

and error were calculated across plots grouped by their treatment (n = 4 apart from the treatments with damaged plots). Comparison throughout this experiment is made relative to measurements in the same plot using ratios of change, reducing any error from heterogeneity of optical properties (Maxwell & Johnson, 2000; Murchie & Laweson, 2013).

Profile soil moisture was measured to a depth of 1.8 m using a neutron attenuation (CPN Hydroprobe) via access tubes (InstroTek, INC., Research Triangle Park, NC, USA). The access tube was placed within rows 5 and 6. Readings were centered at 15, 45, 75, 105, 135, and 165 cm. Readings were taken 8 times over the season at the start of the month: three times on a weekly basis in June, one time in July, three times on a weekly basis in August, and once in October.

Data Analysis

Data was analyzed in R Statistical Software (v3.5.0; R Core Team, 2022). Mixed models were created using the car (v.3.0.12), pbkrtest (v.0.5.1), and effects (v.4.2.1) R packages. The split-plot design was captured with block and replication set as multiple random-effect terms. Data visualization was done using the tidyverse (v.1.3.1) package. A two-factor ANOVA analysis with Kenward-Roger approximation for mixed models was utilized to test the main effect of the response variables. Repeated measures on the same sub-plot were considered in the model when applicable. Water, ET, and planting density were considered continuous data for ease of interpretation and predictions.

Mixed models were created with grain yield, harvest index, or LAI as the response variable and the interaction between planting density and water treatment as fixed effects. A quadratic approximation was included in the interaction, as it better fit the relationship when

compared to a linear model. The model exhibited a normal distribution of residuals. The Q-Q plot of residuals were assessed, and variables were transformed as needed to meet model assumptions. For harvest index, the Q-Q plot of residuals approximately followed the reference line with two clear deviations. For LAI, the Q-Q plot of residuals approximately followed the reference line with one clear deviation. Analysis was continued as normal, keeping this slight deviation in mind. Analysis was done on data from the last three sampling dates (3 Aug 2021, 11 Aug 2021, 19 Aug 2021), when vegetative growth has reached its maximum and canopy area has plateaued.

For ET, a mixed model was created with grain yield as the response variable and the interaction between planting density and ET as fixed effects. A quadratic approximation was included in the interaction. The model exhibited a normal distribution of residuals. For fluorescence, a mixed model was created with the July fluorescence values as the response variable. The distribution of residuals was normal. The Q-Q plot of residuals followed an approximately straight line.

Results

Grain Yield

Average grain yield ranged from 5209 to 8643 kg ha^{-1} among all treatments (Fig 1.2). Greater water availability resulted in greater yield productivity overall (Table 1.1). Plant productivity remained the same as plant density increased. From lowest to highest plant

densities, the 0 mm water application grain yields did not change, while yields increased with greater water applications across increasing planting density.

Grain yields followed different responses to planting density depending on water availability (Table 1.1). The range of differences was approximately 1,773 plant ha^{-1} and 3,4343 plant ha^{-1} at the lowest and highest density treatments, respectively. The grain yield response to planting density was a quadratic plateau at greater water availability. Lower water availability treatments exhibited a more linear response (Fig. 1.3). The linear regression slope varied among water treatments. The 299 mm water level slope ($R^2 = 0.86$) was nearly 8x that of 76 mm ($R^2 = 0.35$). The two-way interaction between planting density and water availability significantly affected grain yield (*P = 0.01147)*.

Table 1.1. Analysis of variance with Kenward-roger approximation for mixed models. First column indicates response variable in each respective model. Note: F indicates F value; P indicates P value.

		Water (W)	**Population (P)**	**P x W**
Grain Yield	F	0.244	0.398	6.945
	P	0.624	0.531	0.011
Harvest Index	F	0.477	0.073	0.246
	P	0.493	0.788	0.622
Leaf Area Index	F	7.523	75.905	1.686
	P	**0.007**	**2.269E-15**	0.196
Evapotranspiration	F	15.759	0.662	1.356
	P	**0.002**	0.420	0.250
Fluorescence	F	1.400	0.600	4.496
	P	0.242	0.443	0.039
Nitrogen	F	0.717	0.181	2.109
	P	0.399	0.672	0.149

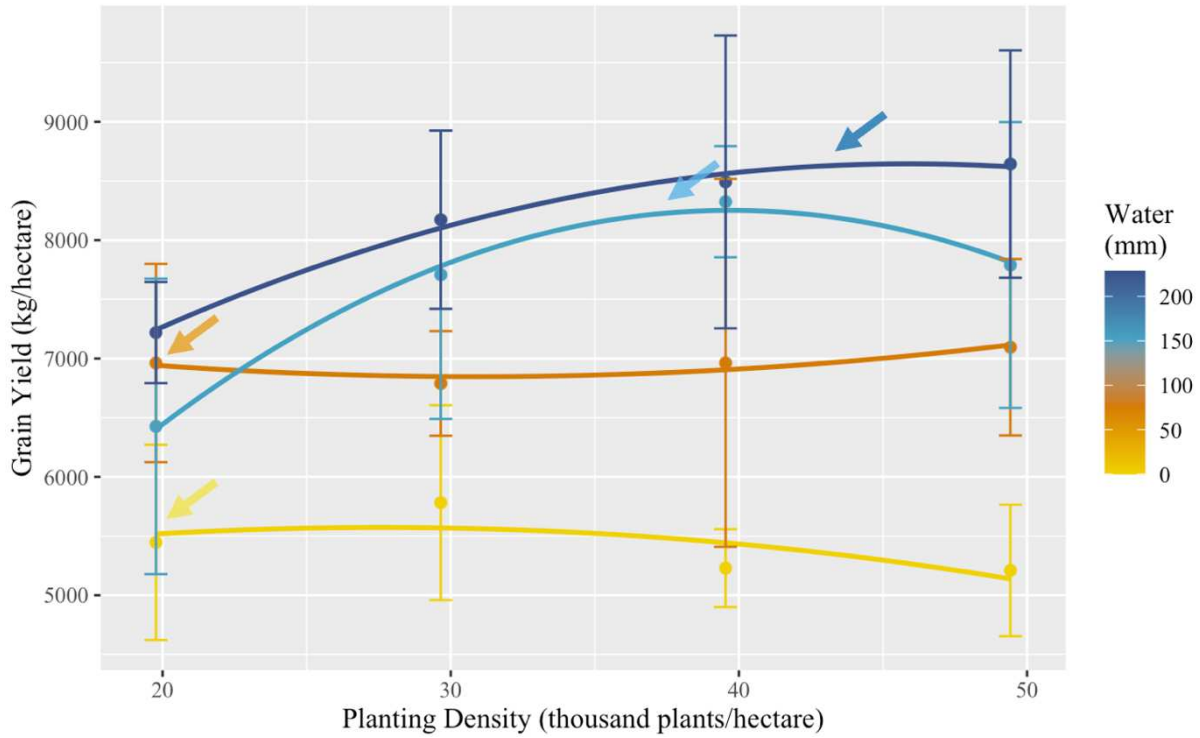

Figure 1.3. The relationship between grain yield (0% moisture content) and planting density under different water levels (0, 76, 152, 229 mm). Each data point represents the average of four plots. Lines are polynomial (quadratic) regression fits of the yield-density linear mixed model. Arrows indicate the approximate point of plateau, or a zero-slope.

Harvest Index

Mean harvest index ranged from 0.55 to 0.61 across all treatments. There were no differences in harvest index in response to population density or water availability nor was there an interaction between these two effects (Fig. 1.4, $P > 0.10$).

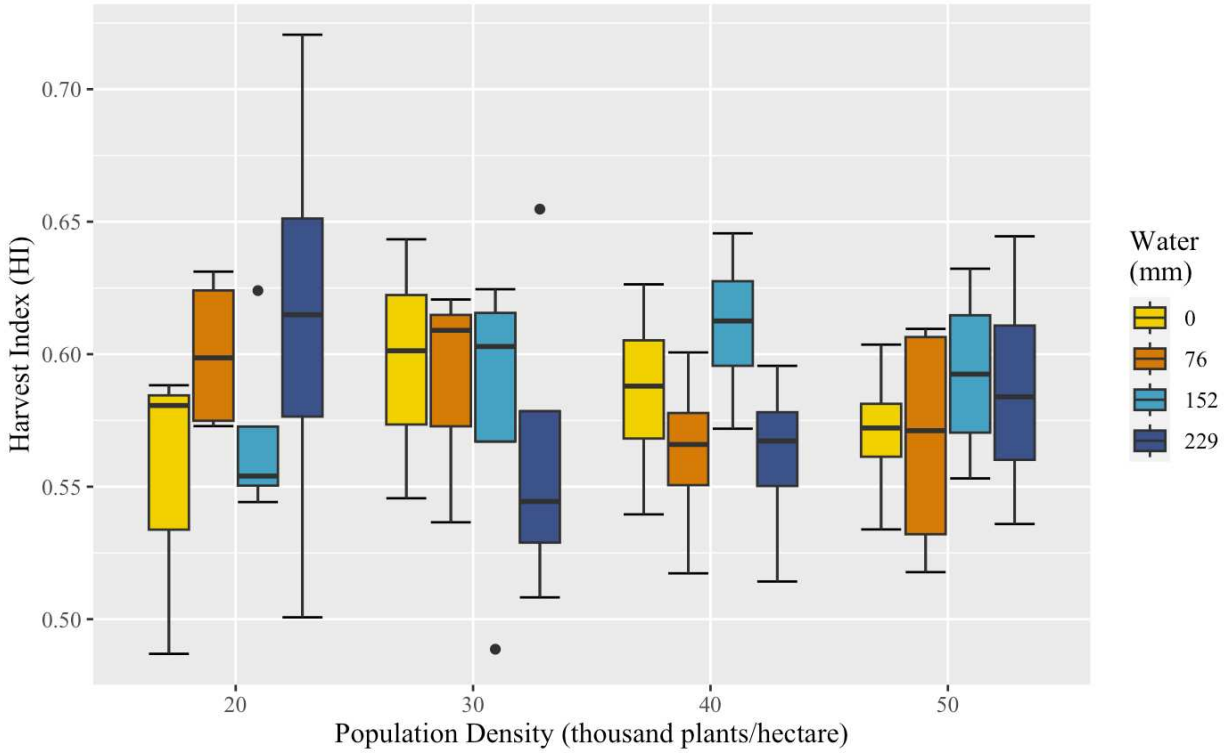

Figure 1.4. Boxplot comparing mean harvest index under different water levels across planting densities.

Leaf Area Index

Mean LAI ranged from 1.39 to 2.82 at final canopy, with the lower values corresponding to the 20,000 and 30,000 plant ha^{-1} and 0 mm treatments (Fig. 1.5). There was no significant interaction effect of the population density and water availability on LAI (Table 1.1). Planting density and water availability had a significant main effect on LAI ($P < 0.01$). Overall, planting density ($P < 0.01$) had greater evidence of a significant impact on leaf area index than water availability. Using data collected on August 3rd, an increase from 20,000 to 50,000 plant ha^{-1} resulted in a 27.2 % increase in LAI, whereas an increase from 0 to 229 mm increased LAI by 20.0%

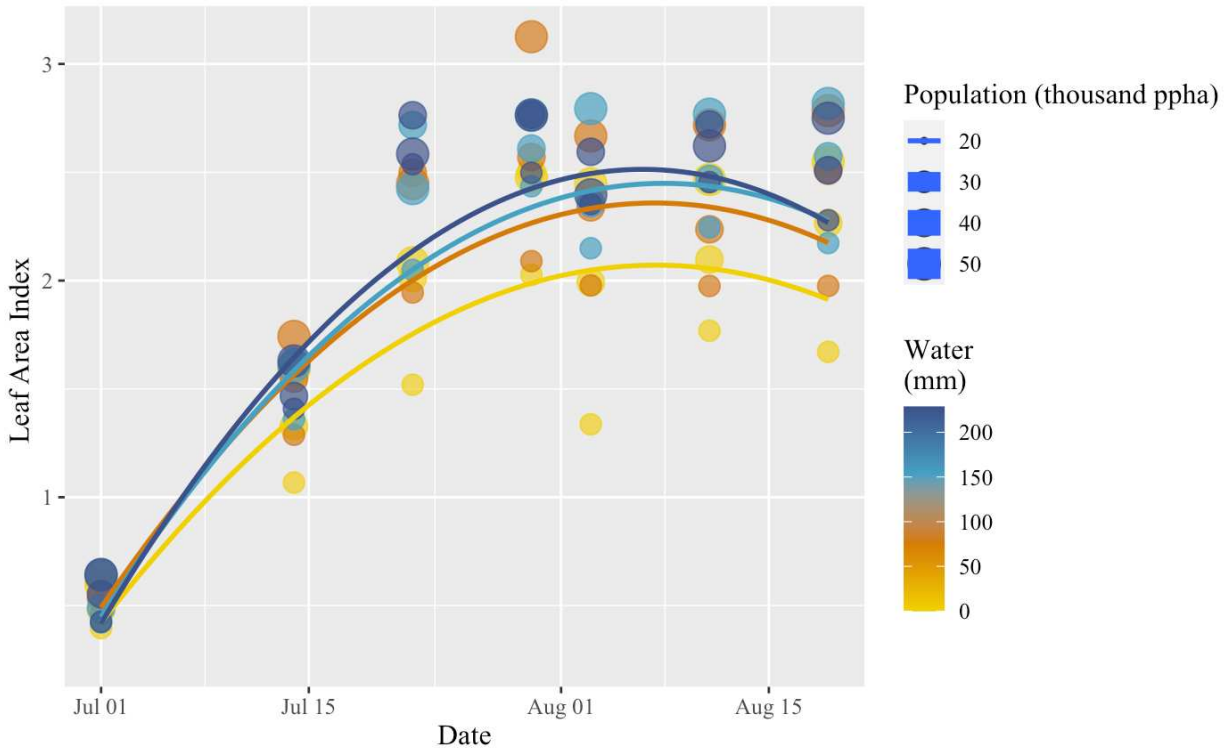

Figure 1.5. Leaf area index across the season under different water levels (0, 76, 152, 229 mm) and planting densities (20,000, 30,000, 40,000, 50,000 ppha). Lines are polynomial (quadratic) regression fits of the LAI-density:water linear mixed model.

ET

Mean ET ranged from 304 to 449 mm among all treatments. The relationship between evapotranspiration (ET) and grain yield exhibited a quadratic relationship (Fig. 1.6). The fit of line decreased with greater water availability such that there was less variability explained by the model than with the 0 mm water treatment ($R^2 = 0.53$).

There was no significant interaction effect of the population density and water availability on ET (Table 1.1). Water availability had a significant main effect on ET ($P < 0.01$). Population density and ET and the interaction effect of the two did not explain a significant proportion of the variability in grain yield (Table 1.2, $P > 0.05$). However, treatments with greater water availability generally exhibited a greater ET and grain yield.

Table 1.2. Analysis of variance with Kenward-roger approximation for mixed model with Grain Yield as the response variable for the model. Note: F indicates F value; P indicates P value.

		Evapotranspiration (ET)	Population (P)	P x E
Grain Yield	F	1.797	1.0011	1.2898
	P	0.1857	0.3220	0.2617

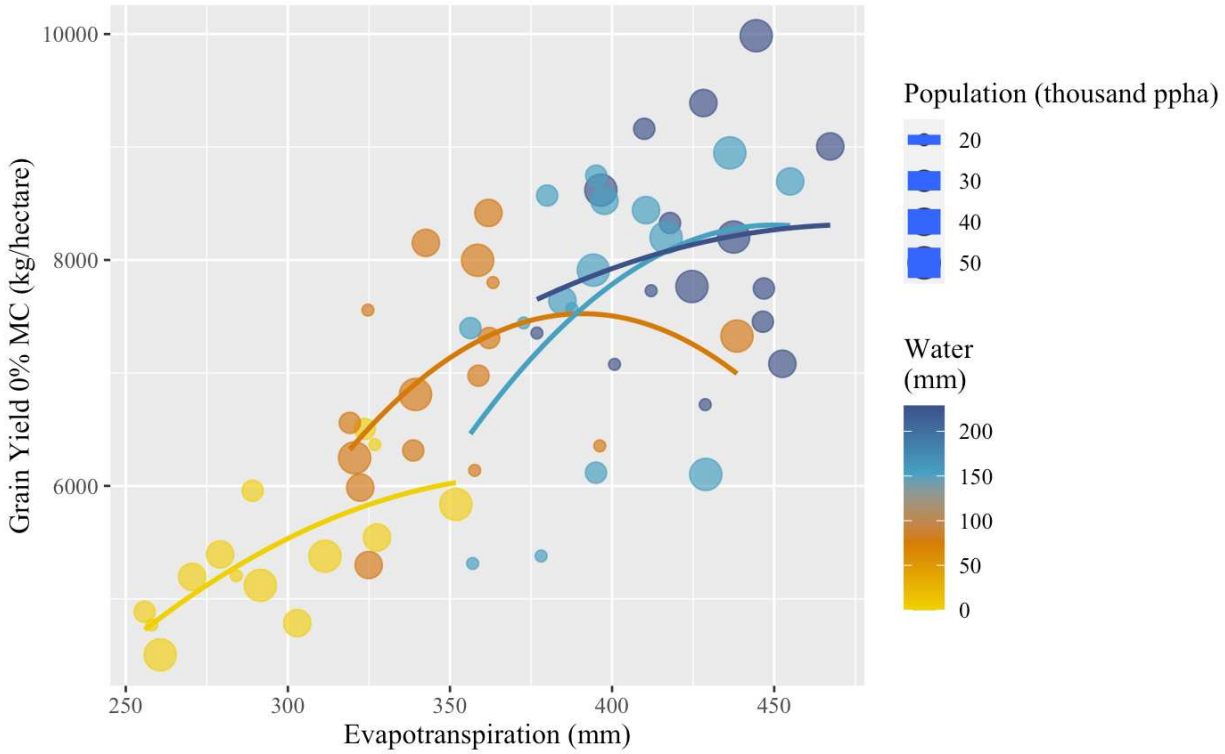

Figure 1.6. The relationship between grain yield (0% moisture content) and evapotranspiration (ET) under different water levels (0, 76, 152, 229 mm) and planting densities (20, 30, 40, 50 thousand ppha). Lines are polynomial (quadratic) regression fits of the grain.

Fluorescence

Apart from water availability of 152 and 229 mm at 30,000 plants ha^{-1}, chlorophyll fluorescence increased over time, indicating a potential increase in photosynthetic efficiency (Fig. 1.7). The greatest increase over time was measured for the 0 mm and 50,000 plants ha^{-1}

treatment. There was an interaction between planting density and water availability in July fluorescence readings (Table 1.1, $P = 0.039$). This interaction effect was less strong in August readings (Table 1.1, P = 0.099).

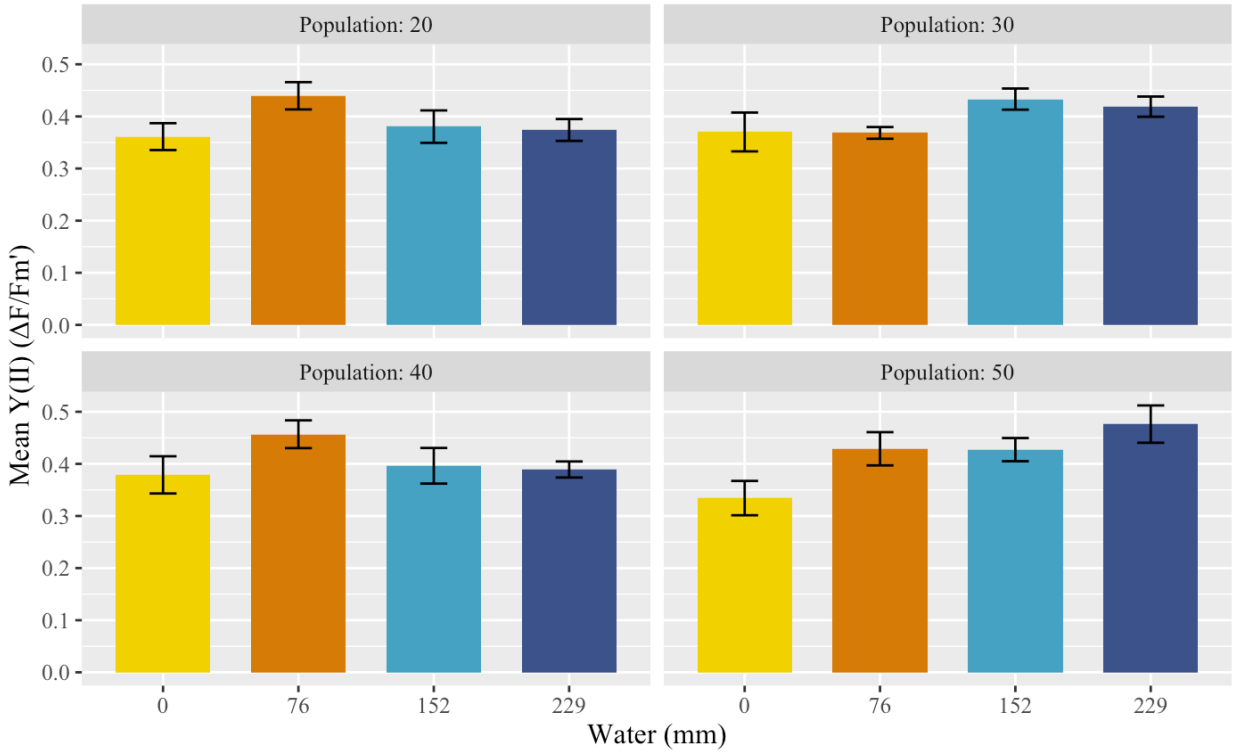

Figure 1.7. Mean chlorophyll fluorescence taken in July for the four water levels (0, 76, 152, 229 mm) at each of four plant densities (thousand plants/ha). The vertical bars at top of bar graph are standard error bars.

Nitrogen

Mean grain N content by area ranged from 11.8 to 13.20 kg N/ha across all treatments (Table 1.3). There was no significant difference in grain N concentration in response to population density and water availability, nor the interaction (Table 1.1, $P = 0.15$). However, there was a tendency for a greater grain N content value found at the 76 mm water level and 40,000 plant ha^{-1} density.

Table 1.3. Mean grain N concentration by area (kg/ha) for the four water levels (0, 76, 152, 229 mm) at each of the four planting densities (thousand plants/ha) for the 2021 experiment.

Planting Population (thousand plants/ha)	**Water** (mm)			
	0	76	152	229
20	12.7	12.5	12.9	12.7
30	12.3	12.7	12.5	12.4
40	12.6	13.2	11.8	12.4
50	12.4	12.3	12.4	11.9

Discussion

The quadratic plateau shape of the grain yield-density relationship found in our study was consistent with previously documented models (Weiner & Freckleton, 2010; Overman & Scholtz, 2011). The planting density at which maximum grain yield was achieved varied depending on water availability. The relationship between grain yield and plant water consumption became more variable when water was not limiting, but planting density did not affect ET. Results indicated plant performance was not limited by light interception, nitrogen availability, or stressed photosynthetic activity. Proportional grain yield per plant, or harvest index, was relatively unchanged, suggesting crowding stress and any subsequent developmental allocation may not have been a factor. Biomass allocation to the ears did not respond to varied planting densities.

In our study no overall yield reduction above maximum yield was seen among treatments. At higher planting densities none of the grain yield responses exhibited a down-turn. It is likely the tested densities were not surpassing the critical population, often referred to as supra-optimal, to where competition would result in self-thinning or density-dependent mortality (Averbeke & Marais, 1992; Hashemi *et al.,* 2005; Weiner & Freckleton, 2010; Assefa *et al.,*

2016). Following the pattern of CFY, the point of maximum yield in drought conditions may occur at a lower stand density than the tested range.

In line with previous research, resource availability determined the strength of the yield-density relationship (Assefa *et al.,* 2016). The near-zero slope of the yield-density relationship at lower water levels (Fig. 2) suggests water availability limited the yield gain from additional planting. This relationship between planting density and grain yield at water-limited conditions has been reported in other experiments primarily based out of regions of Argentina (Hernández *et al.,* 2020). At higher densities plant biomass is constrained, either limited by resources or competition. The implication for producers is that seeding past this maximum point will not be able to overcome a limiting effect on additional biomass. It also suggests that the CFY threshold occurs at a lower planting density than was included in this study for low water availability (0 and 76 mm).

It is generally expected that greater planting densities will be more impacted by size-asymmetric competition as resources are not accessed uniformly, increasing variability. This can have an established effect on biomass allocation and reproductive efficiency, thus grain yield per plant. It is important to note size-asymmetric competition does not necessarily reduce total biomass production (Weiner & Freckleton, 2010). We found the harvest index or grain allocation efficiency of maize was uniform across all treatments, and thus unaffected by resources or competition in this study. With the use of the hybrid variety planted, it was expected that greater crowding and competition would impact flex ear size. However, several studies have indicated that moderate levels of stress do not affect harvest index due to compensation of factors affecting resource capture (Tollenaar *et al.,* 2006; Asefa, 2019). Abiotic factors have had a historically weak effect on harvest index, precluding severe stress. Genetics heritability is the predominant

determinate of harvest index in some cases (Asefa, 2019). Given that more ideal growing conditions (greater water resources) did not improve relative crop productivity (reproductive biomass/total biomass), it is likely our precipitation levels and planting densities did not approach stress levels capable of having a negative effect on harvest index. At this range of resource levels, yield challenges must be met with increasing overall biomass, through a combination of increased population density and water availability. An increase in water conditions alone will not change harvest index per our findings.

The generalization of CFY has many postulated mechanisms, including population density as a limiting factor behind resource utilization. At lower densities with more abundant resources than the population can use, the maximum yield is thought to be limited by the number of plants to use said resources. Whereas at higher densities, resource uptake is independent of population density (Weiner & Freckleton, 2010). There is some evidence to support this proposed mechanism of density-limiting the maximum yield in our study. The most abundant water treatment saw a positive relationship with planting density up to 40,000 plants/ha where an asymptotic yield is approximated from densities onward. Treatments with less water availability exhibiting little to no increase with density implies the resource limitation was the greatest determinant of productivity at that point. To further corroborate this mechanism a greater range of lower densities must be tested, as well as a broader range of water availability from dry to wet conditions. The significant interaction of precipitation and density does give weight to the idea that both are determinants of grain yield.

ET-yield relationships did not differ with population density. A lack of ET shift in response to population density adds to a multitude of works with varied results (Hernández *et al.,* 2020). The findings in this study contrast with the basis that population density, affecting canopy

cover and thus solar radiation, can reduce soil moisture evaporation and affect ET. High planting densities can result in a higher canopy cover that subsequently reduces the amount of solar radiation received by the soil surface (Zhang *et al.,* 2021). A lack of planting densities at high values reaching canopy closure could be a reason for this response. Additionally, ET has been well-documented to closely relate to LAI (Panda *et al.,* 2014). The LAI values we found, although with a clear trend among density treatments, were within a typical range. Maize LAI values can range from 0 to 6 (Gitelson *et al.,* 2003). It is possible solar radiation interception or light interception was not significantly different among treatments to alter soil water evaporation. The soil water evaporation may have also been reduced by soil crusting through a higher surface reflectance and lowered soil temperature (Bolan *et al.,* 2023).

Solar radiation interception is frequently studied in resource-based competition (Tilman & Wedin, 1991). Light interception has been found to be affected by population density, with the parameter LAI exhibiting a positive relationship with density (Zhang *et al.,* 2021). None of the treatments resulted in LAI values that would imply competition resulting in light-dependent suppression. It is unlikely that the reaching of a constant final yield was limited by light availability in these communities. Our findings support a positive relationship between population density and LAI (Fig. 1.5). LAI was also reduced by our water availability gradient. This finding is reinforced by other studies in which water deficiency reduced LAI (Timlin *et al.,* 2014). The lack of a significant interaction between population density and water suggest abiotic stress was not a large determinate of the leaf area development with population density and vice versa.

Chlorophyll fluorescence can be used to indicate damage to PSII, commonly the first signifier of leaf stress (Murchie & Lawson, 2013). There were differences in the functioning of

PSII recorded in the July measurements. These early season readings align with research that has found high density to affect photosynthetic efficiency (Li *et al.,* 2020; Ahmad *et al.,* 2021). Higher planting densities were more sensitive to water stress and the subsequent impact on fluorescence. The evidence of environmental stress affecting the photosynthetic apparatus alleviated throughout the season as water stress decreased. Water additions were primarily applied between July 8th and August 31st, 2021. Readings across the span of such water additions exhibited an improvement in photosynthetic capacity. Plants were still able to operate at a relatively unaffected photosynthetic efficiency following the seasonal simulated precipitation.

This introduces the possibility of reaching the point of maximum yield without lasting stress to the max operating efficiency of PSII. The observation of a yield maximum, in this case, cannot be attributed solely to stressed photosynthetic activity, but other factors at play. As aforementioned, we speculate that planting densities were not high enough to observe the negative effects of competition. This has great implications for producers who may be able to approximate a maximum yield without significant mortality costs, and thus greater economic costs.

N availability can have a significant effect on a multitude of plant characteristics. There are numerous influences on canopy characteristics including but not limited to development, light interception, and leaf area (Timlin *et al.,* 2014). It has also been found to impact photosynthetic efficiency, leaf senescence, and subsequently, grain yield (Ahmad *et al.,* 2021). In line with our findings regarding photosynthetic efficiency and leaf area, N levels of the grain indicate yield limitations observed were likely not attributable to an insufficient nitrogen supply. Grain N did not significantly differ by treatments, leading us to infer the potential mechanisms behind the maximum yield are not due to N. It is possible that the optimal N application had a

mitigating effect on the potential inhibition of photosynthetic efficiency and leaf senescence (Luo *et al.,* 2018; Su *et al.,* 2020). All water levels received the same N application, and our results suggest that N was sufficient for the higher water and population treatments and lower yielding treatments were likely overfertilized.

Conclusion

Although much is known about resource competition and growth dynamics in monocultures, there is a need for better understanding of these generalizations and dynamics in dryland environments. These results are promising for the attainment of a maximum yield while considering water-saving efforts, as many projects in the state of Colorado strive for. Pathways for more limited resource use in monocultures need not come with significant drawbacks to producers or plant communities and can be aided by generalizations like the Law of Constant Final Yield. There is a lower risk than presupposed for reaching a maximum grain yield in dryland monocultures and thus great promise for management shifts in response to global change. Future research should explore the potential of further reduced planting densities in water-limiting conditions producing comparable grain yields.

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CHAPTER 2: PARTIAL-BUDGET ANALYSIS OF VARIABLE SEEDING RATE AND SOIL MOISTURE IN DRYLAND CORN

Introduction

Dryland agriculture, or rainfed-dependent agriculture in semi-arid and arid regions, plays a considerable role in the world's food grain production (Parr *et al.,* 1990). Food security is becoming increasingly threatened by water scarcity, rising temperatures, and changing precipitation patterns. Such changing climactic conditions have the potential to affect agricultural production, impacting viable farmland and crop yields (Schmidhuber & Tubiello, 2007; Nelson *et al.,* 2014). These changing abiotic factors, coupled with a rising world population and subsequent food demands, requires boosts in crop yields under increasingly variable growing conditions. Concurrently, however, there are pressures to limit field inputs such as fertilizer use to lessen agriculture's environmental impacts. Increasing water scarcity concerns and water pumping costs in some regions have led to a growing interest in or need for potential dryland expansion (Rodrigues *et al.,* 2013; Elliott *et al.,* 2013). This is particularly pertinent for regions facing depleting water resources such as the Ogallala or High Plains Aquifer (Deines *et al.,* 2020). Although the scope of dryland expansion with changing climactic conditions is under debate, the need for resource optimization remains for both environmental and economic impacts (Deines *et al.,* 2020, Berg & McColl, 2021). This balance of environmental goals and economic returns is particularly challenging for dryland producers with constrained options for input manipulation.

In addition to limited management decisions, dryland producers are vulnerable to fluctuations in weather. Variability in climactic conditions and precipitation patterns can impact

grain yields and yield estimates (Ray *et al.,* 2015). This contributes to the uncertainty in revenue producers face. Climate-related challenges for these systems make management even more challenging. Producers seeking stable economic conditions look to means of optimization of crop production.

Optimizing crop management often centers around optimizing yield through altering abiotic and biotic factors such as seeding rate and fertilizer. (Allen, 2012). Inputs involved in crop management often face uncertainty in pricing (Lawrence *et al.,* 2018). Seeding rate is an especially costly and crucial element of agricultural management (McNunn *et al.,* 2019). Historically, seeding rate determination has been based upon site yield trends, with higher yield years resulting in more seed being planted the following season. However, this approach is not always transferable to dryland systems, which experience high yield variability due to limited and variable rainfall. There has been in a growing interest in taking a systems-approach, considering many variables such as soil, topography, and yield productivity, to determine an optimal seeding rate (Licht *et al.,* 2017). This systems-based approach is further supported by the non-linear relationship between grain yield and planting density, referred to as Constant Final Yield (Weiner & Freckleton, 2010). The yield-density relationship typically follows an asymptotic pattern as size distributions and resource limitations are met at higher densities. The overlying assumption for this leveling off seen in yield potential at high densities is that interspecific competition for resources is at play (Crawley, 1990). Management decisions, such as planting density (seeding) and resource availability (water, fertility), can take this relationship into account to minimize losses. Across seasons and varying levels of precipitation, the optimal seeding rate can vary, presenting a unique challenge to dryland producers.

Farmers are limited in their ability to adapt to stressors depending on the equipment they have and their ability to adopt new practices. Producers are primarily driven by economic returns and frequently face increasing demands for outputs (Lemos *et al.,* 2104, Morandin *et al.,* 2016). In particular, dryland agriculture, subject to seasonal rainfall trends and timing, faces variable yields and thus financial risk exposure (Mauget *et al.,* 2020). This necessitates the incorporation of economic valuation in management decisions, specifically those manipulating costly inputs such as seed and fertilizer rates. One method of evaluating the economic effects of crop management strategies is through a Partial-Budget Analysis.

Partial-budget analysis is a tool that compares the potential costs and benefits of specific changes to existing farm management practices while assuming that other farm budget components do not change. It weighs the many factors involved in shift to alternative technology, such as additional production resources, additional costs, and resulting revenue (Alimi, 2000; Schipanski *et al.,* 2014). Although the definition of optimal seeding rate can vary with stakeholder priorities, a partial-budget analysis will help inform the most profitable cropping scenario. Considering the non-linearity of the yield-density response, there is a strong potential that the most economically beneficial seeding rate involves relatively less inputs. To further understand the yield-density relationship and increase resource-use efficiency one must consider the environmental and economic nexus.

Using a cropping systems model generated from a field experiment conducted in eastern Colorado and detailed in Chapter 1, we assess economic returns of varying combinations of evapotranspiration and seeding rates. These economic estimates will be used to discuss the net benefits of management decisions. We aim to determine whether reduced planting can result in a gain or loss of investment for dryland producers in Akron, Colorado. The main objective of this

study is to determine the economic optimum maize seeding rates for varying soil moisture availabilities and predicted rainfall using partial budget analyses.

Methods

Site Characteristics

This assessment utilized data from a study conducted at the USDA ARS, Central Great Plains Resources Management Center in northeastern Colorado during the 2021 growing season, respectively. The site was located in Akron, Colorado (40.15' N, -103.14' W). The field was a limited irrigation winter wheat-maize rotation. It has been managed with a no-till method for more than a decade. Maize was manually harvested as is outlined in Chapter 1. Yield is reported at 15.5% moisture content.

Crop evapotranspiration (ET_C) for each experimental plot was determined using a water balance approach in line with water budget methods from neutron probe readings across the season (Bowman & King, 1965). Neutron attenuation measurements were measured down to a depth of 1.8m using a neutron attenuation (CPN Hydroprobe) via access tubes (InstroTek, INC., Research Triangle Park, NC, USA). The access tube was placed within the planted row of one of the two central rows of the plot. Readings were centered at 15, 45, 75, 105, 135, and 165 cm.

Partial Budget Analysis

A partial budget analysis was conducted to determine the seeding rates that optimized maize system returns. We manipulated two factors, seeding rate and grain yield, as primary determinants of profitability in this scenario under two levels of water availability. Comparison was done across conditions of relatively low and high crop ET for 8,000 and 16,000 plants/acre,

"low" and "high" identifying an ET less than or greater than 15 inches, respectively. The summary statistics of the 0" and 9" irrigation treatment data indicated an ET boundary of 15 inches was a suitable distinction between the groupings. These treatments represent the greatest deviations from average rainfall in the experimental study (Fig. 1.2). The seeding rates were selected to represent the lower and higher end of management decisions for this site that producers may make. The base scenario for comparison had the conditions of a 16,000 plants/acre seeding rate and the lower ET grouping, to approximate standard practice in a dryland management context (Lyon, 2012; Schneekloth & Andales, 2017). The analysis will be made relative to these base conditions. The management practice shifts that will be tested include a decrease in seeding rate to 8,000 plants/acre at the same ET grouping, a decrease in seeding rate at the high ET grouping, and an unchanged seeding rate at the high ET grouping. We assumed all other inputs and management would remain unchanged for the different maize seeding rates and corresponding grain yields, given that the experiment was conducted as such.

We used existing density-yield models based off the experimental data to approximate expected grain yield values. The model only considered the data points that received 0" and 9" irrigation treatments, in line with the goal of maximizing distinctions in operating costs, which correspond with an estimated seasonal precipitation of x and y. The irrigation treatments also followed a pattern of an ET less than or greater than 15 inches, complying with the 0" and 9" additions (Table 2.1). We fit linear regressions to the data: $y = 120 - 1.2x$ and $y = 120 + 2.1x$ for low and high-ET groupings, respectively (Table 2.2). Grain yield values were calculated using the regression lines from the experimental data (Figure 2.1). Linear regression was chosen for ease of interpretation and calculation.

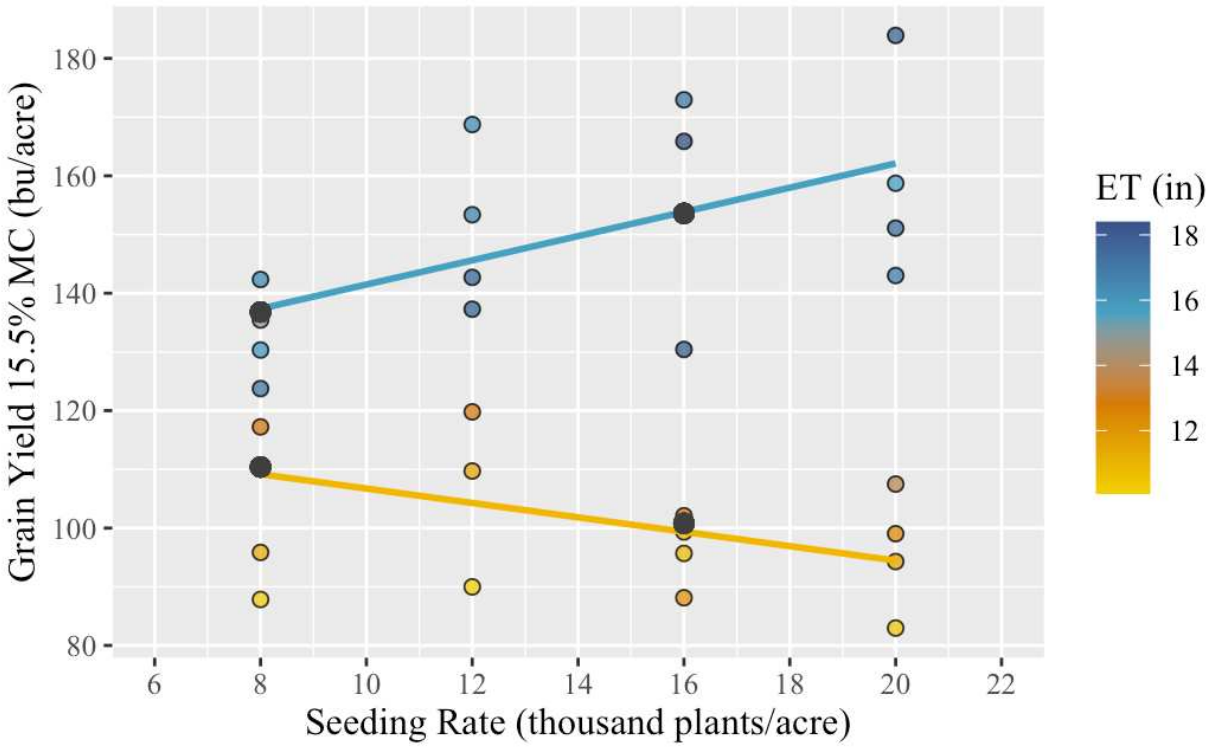

Figure 2.1. The relationship between grain yield (15.5% moisture content) and evapotranspiration (ET) under a range of planting densities (8, 12, 16, 20 thousand plants per acre) and simulated precipitations (0 in, 9 in). Simulated precipitations are irrigation amounts in addition to rainfall. Points marked in dark gray are those selected for partial budget analysis. Lines are linear regression fits of grain yield-density linear model, grouped by data with an ET greater than 15 inches and less than 15 inches.

Table 2.1. Summary statistics of experimental data grouped by ET.

ET Group	n	Mean ET (in)	SD ET (in)
< 15	15	11.84	1.4
> 15	14	16.91	0.82

Table 2.2. Coefficients for two-way ANOVA model with interaction, fitted using a linear model function.

Term	Estimate	SE	Statistic	p
Intercept	118.990903	12.170498	9.7769951	5.04471E-10
Population	-1.226352	0.819047	-1.4972911	0.1468378
factor(ETGroup)	1.872251	17.839849	0.1049477	0.9172548

Population:factor(ETGroup)	3.288347	1.195988	2.7494811	0.01092733

Prices and inputs were estimated based off the University of Nebraska-Lincoln 2023 (EC872) crop budgets. This source used 2021 data for material prices (Klein & McClure, 2022). UNL Agricultural Budgets were chosen given that the variable costs are budgeted separately, rather than using custom rates. The crop budget was selected for complementary characteristics with the experimental data. The crop budget assumes a cropping system of corn with the following characteristics: Bt, ECB, RR2, LL, & RIB dryland, southwest, ecofallow, follows wheat, two crops in three years. Abbreviated characteristics mean the cropping system is assumed to use Bt corn with transgenic traits for weed and insect activity including European corn borer (ECB), glyphosate tolerance or Roundup Ready 2 (RR2), glufosinate tolerance or Liberty Link (LL), and refuge-in-bag or a mix of Bt protected seed (RIB) (DiFonzo, 2023). The net change in income per acre was calculated as the total gain – total loss of the proposed change relative to a 16,000 seeds/acre rate under low ET conditions. Input costs that were varied included seed, at an applied price of $3.50 per thousand. This cost is per the University of Nebraska material seed price of $280.00/bag, obtained using 2021 data. The total seed costs in the scenarios below were $56.00/acre and $28.00/acre for 16,000 and 8,000 seeds/acre, respectively.

Yield was the only revenue source that was varied. Revenue changes were calculated as the change in projected grain yield using the marketing year average price per bushel generated from the Colorado Agricultural Statistics 2021. Partial budget tables show the differences in field operations and materials and services from the respective scenarios. Overhead costs, such as real estate, liability insurance, accounting, etc. are not included. “Haul Grain Bushels” is the cost of transporting corn from a farm to alternative location. This cost has an applied price of

$0.13/bushel. “Dry 2 Points” is the loss associated with on-farm handling during drying. This cost has an applied price of $0.08/bushel. Repair costs were estimated using the Agricultural Engineer’s Yearbook according to the Nebraska Crop Budgets. Cart machinery repair costs were calculated as $0.0002/bushel for power source and $0.008/bushel for implement costs. Cart machinery ownership costs were $1.45/bushel for power source and $1.59/bushel for implement costs. Cart machinery was assumed to have a diesel use of 3.00 per hour and an annual use of 440k bushels. Dryland combine header had a labor cost of $0.0212/bushel and a fuel cost of $0.0356/bushel. Dryland combine header machinery repair costs were calculated as $0.0287/bushel for power source and $0.0051/bushel for implement costs. Combine machinery ownership costs were $0.1598/bushel for power source and $0.0595/bushel for implement costs. Dryland combine header was assumed to have a diesel use of 10.50 per hour and an annual use of 1,000 acres.

Data Analysis

Data was analyzed in R Statistical Software (v3.5.0; R Core Team, 2022). Graphing was done using the tidyverse (v.1.3.1) package. A linear model was created using the effects (v.4.2.1) R package. The model was fit using grain yield as the response. The interaction between planting density and ET grouping was the predictor. ET and planting density were analyzed as continuous data.

Results

Results are condensed into three partial budgets relative to a typical dryland precipitation year for Akron, Colorado, and 16,000 seeds/acre: (1) unchanged seeding rate at a high soil

moisture (ET); (2) lowered seeding rate at a high soil moisture (ET); (3) lowered seeding rate at an unchanged soil moisture (ET). The partial budget analyses based on the grain yield data and seeding rate under the three scenarios are illustrated in table form. The base scenario has an estimated grain yield of 100 bushels/acre.

Scenario 1: High Seeding Rate at a High ET

The partial budget for an unchanged maize seeding rate of 16,000 seeds/acre at an increased or high ET indicated a net economic gain of $226.88 per acre (Table 2.3). The largest cost driver was additional ownership costs. A shift in ET is projected to result in an additional 54 bu/acre corn yield, which using the 2021 CO Agricultural Statistics information, would result in an increase in crop revenues of $253.8/acre. This negates the increase in costs, $19.47/acre and $7.45/acre, associated with a higher crop yield and thus more labor, hauling, etc. This increase in revenue, greater than the additional costs, results in a net economic gain.

Table 2.3. A partial budget analysis for the production of maize. Change in variable costs and benefits are calculated between the scenario of 16,000 seeds/acre at high ET and the base scenario of 16,000 seeds/acre at low ET.

Partial Budget: 16,000 seeds/acre increasing soil moisture - low to high ET			
Reduced Costs	**Additional Costs**		
	Field Operations		
None	Labor @ $25.00/Hr		1.59
	Fuel @ $3.83 and Lube		2.14
	Repairs		2.26
	Ownership		13.48
		Subtotal:	**19.47**
Materials and Services	**Materials and Services**		

Seed	-	Haul Grain Bushels		7.02
		Dry 2 Points Removed		0.43
			Subtotal:	**7.45**

Added Income		**Reduced Income**
Yield Projection: increase of 54 bushels @ $4.70	**253.80**	None

Total annual additional costs and benefits: $226.88/acre

Scenario 2: Low Seeding Rate at a High ET

The partial budget for lowering the maize seeding rate from 16,000 seeds/acre to 8,000 seeds/acre at an increased ET indicated a net economic gain of $183.47 per acre (Table 2.4). There were reduced costs associated with lower density seeding. Seeding at this lower rate is a cost reduction of $28.00/acre. Corn yield was projected to increase by 37 bushels, resulting in an increase in crop revenues of $173.90/acre. Field operations and materials and services increased because of the projected higher yield, $13.32/acre, and $5.11/acre respectively. The reduced seeding cost alone outweighs the additional management costs associated with a greater yield.

Table 2.4. A partial budget analysis for the production of maize. Change in variable costs and benefits are calculated between the scenario of 8,000 seeds/acre at high ET and the base scenario of 16,000 seeds/acre at low ET.

Partial Budget: High Soil Moisture decreasing from 16,000 seeds/acre to 8,000 seeds/acre	
Reduced Costs	**Additional Costs**

			Field Operations		
None			Labor @ $25.00/Hr		1.09
			Fuel @ $3.83 and Lube		1.46
			Repairs		1.53
			Ownership		9.24
				Subtotal:	**13.32**
Materials and Services			**Materials and Services**		
			Haul Grain		
Seed		**28.00**	Bushels		4.81
			Dry 2 Points Removed		0.30
	Subtotal:	**28.00**		***Subtotal:***	**5.11**
Added Income			**Reduced Income**		
Yield Projection: increase of 37 bushels @ $4.70		**173.90**	None		

Total annual additional costs and benefits: $183.47/acre

Scenario 3: Low Seeding Rate at a Low ET

The partial budget for lowering the maize seeding rate from 16,000 seeds/acre to 8,000 seeds/acre at low ET indicated a net economic gain of $70.02 per acre (Table 2.5). A decrease of 8,000 seeds/acre would result in an additional $28.00/acre. Corn yield was projected to increase by 10 bushels, resulting in an increase in crop revenues of $47.00/acre. Field operations and materials and services increased because of the higher projected grain yield. These additional costs, $3.60/acre and $1.38/acre, are associated with a higher crop yield and thus more labor,

hauling, etc. This increase in revenue and reduced seeding cost outweighs the additional costs associated with a greater yield.

Table 2.5. A partial budget analysis for the production of maize. Change in variable costs and benefits are calculated between the scenario of 8,000 seeds/acre at low ET and the base scenario of 16,000 seeds/acre at low ET.

Partial Budget: Low Soil Moisture decreasing from 16,000 seeds/acre to 8,000 seeds/acre			
Reduced Costs		**Additional Costs**	
		Field Operations	
None		Labor @ $25.00/Hr	0.30
		Fuel @ $3.83 and Lube	0.39
		Repairs	0.42
		Ownership	2.49
		Subtotal:	**3.60**
Materials and Services		**Materials and Services**	
		Haul Grain	
Seed	**28.00**	Bushels	1.30
		Dry 2 Points Removed	0.08
Subtotal:	**28.00**	***Subtotal:***	**1.38**
Added Income		**Reduced Income**	
Yield Projection: increase of 10 bushels @ $4.70	**47.00**	None	
Total annual additional costs and benefits: $70.02/acre			

Discussion

The partial budget analyses in this study serve as an evaluation of the net economic returns to increased seeding rates at different soil moisture levels in dryland maize in Akron, Colorado. The analysis found that cost reduction was only present under Scenarios 2 and 3, due to a reduced seeding rate. All scenarios had an added income from a projected grain yield increase. The additional costs associated with this grain yield increase were not greater than added income or reduced seeding costs when it applied.

This projected increase in grain yield with reduced seeding at low ET is in line with research. Water-limiting conditions have been found to reduce yield and affect resource uptake (Teixeira *et al.,* 2014). The greater water availability associated with a high ET resulted in a greater grain yield, even when seeding was reduced by 8,000 seeds/acre. Underseeding in a "wet year" is more productive and profitable than a high seeding rate in more water limiting conditions. Net returns were less favorable per acre when under low soil moisture conditions, Scenario 3 being the least profitable.

The analysis of the economic benefits of decreasing seeding rate at low soil moisture, in this case ET serving as a proxy for soil moisture, projected a positive net change. The grain yield projection was higher for the 16,000 seeds/acre application at high ET, meaning a seeding rate increase will have a greater effect on added income at high soil moisture. The highest revenue increase of the three scenarios was the high seeding rate with a "wet year" occurrence. Seeding at high soil moisture conditions was more productive and profitable than any of the lower soil moisture equivalents. With less significant water-limitations, the increased seeding rate prompted a greater grain yield. This is likely due to the constraints of population density on grain yield in

ideal growing conditions. When resource limitations are not prevalent, the primary determinant of grain yield is seeding rate (Weiner & Freckleton, 2010). In more water-limiting conditions, increased seeding cannot overcome a negative effect on resource uptake and grain yield.

Certainly, there are many factors to consider when employing different crop management strategies. This method is an estimate of possible financial impact. Each farming operation is unique and should employ practices best attuned to their site. Assumptions made in this analysis will not be universal to all partial-budget analyses or farming operations. Market conditions and the inherent uncertainty involved with price fluctuations, costs, and the economy, can impact results as well. These results assume precipitation trends as seen in the season of 2021, with the "high" ET grouping assuming rainfall much greater than average trends for late in the season. Rainfall was considerably higher at the start of growing season when compared to seasonal trends. In addition to the amount of rain, there is a timing component incorporated in the experimental data utilized.

The returns we have estimated may serve as a base for dryland producers in the eastern Colorado area looking to maximize their return on investment. The benefits of higher seeding are generally thought to maximize yield, and thus the return on investment, however the partial budget analysis in this study suggests the contrary under low ET conditions. Additionally, depending on farm-specific decisions regarding fertilizer application with seeding rate, grain yield increases may result in no significant annual benefit to producers. Fertilizer, like seed, is another substantial operating cost that may lessen the impact of added income and add complexity to the cost-benefit calculation.

Conclusion

Although it is a commonly held belief that increased seeding results in an increased grain yield and subsequent revenue, this is not necessarily the case in dryland systems. When approaching dryland agriculture productivity, seeding rate is a less consequential factor on maize grain yield compared to irrigated crop production. The reduced supply expenditures associated with a low seeding rate will benefit producers facing low soil moisture conditions. These findings are meant to serve as a resource for producers implementing optimal seeding rates, however given the variable nature of rainfall in semi-arid and arid environments, this limited dataset from Akron, Colorado should serve as one of many variables to consider.

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