# Reconciling conflicting results regarding climate change effects on plants:
# A case study with wheat

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# Abstract

Anthropogenic climate change will have considerable effects on plants. The extent to which these effects are positive or negative, however, has been controversial as some studies have found climate change to be positive on plants, while others find climate change effects to be detrimental to plants. In this thesis, a fully factorial experiment combining water and temperature over broad ranges (10-90% soil water content under 16°C-40°C), was carried out to address three shortcomings that might help explain the contrasting effects of climate change on plants: testing only one climate variable (e.g., only water or only temperature), failure to account for nonlinear responses to climatic variables, and studying a limited number of response variables. The experiment utilized wheat as the model species and yielded a diversity of outputs in dependent variables, which ranged from individual significant effects, significant interactions, and significant linear and non-linear responses to water and temperature. This study demonstrates that much of the contrasting results about plant responses to climatic variables could arise primarily from simplistic experiments that fail to capture the complex interaction between multiple plant traits and interactive climate conditions.

# Table of Contents

# List of Tables

# List of Figures

# 1. Introduction

Plants, being primary producers, are some of the most important species on earth. Plant biodiversity is critical to maintaining functional ecosystems not only for other plants, but for all organisms globally (Heywood and Iriondo 2003; Cruz-Cruz, González-Arnao, and Engelmann 2013; Medail and Quezel 1997). Plants are also important because humans can eat and digest a wide variety of plants, and have utilized plants as feed for livestock, textile fibers, paper, building materials, and other resources (Giam et al. 2010). Ecosystem functioning and human civilization is dependent upon plants.

Anthropogenic climate change (ACC) will influence many factors that will affect plants, such as temperature and water availability (Parmesan and Hanley 2015; Huntley 1991; Thuiller et al. 2005; Porter et al. 2014). ACC is expected to further raise the average global temperature while still providing cold flashes, alter weather patterns, and shift storm systems (J.E. Olesen et al. 2011; Izaurralde et al. 2011; Solomon et al. 2007) As global temperatures rise, the warmer air will have elevated water retention capabilities, leading to an increase in soil water evaporation (Magrin, Travasso, and Rodríguez 2005; Forster et al. 2007). This increase in evaporation will result in drought in certain areas. Air in other regions that are already humid will not be able to hold as much water, so under increased precipitation these locations will be at increased flood risk (Betts et al. 2007; Gedney et al. 2006; Kooperman et al. 2018). These changes will undoubtedly alter plant growth and productivity.

The influence of ACC on plants has been the root of controversy. Some studies have found that the rise in temperature will expand growing ranges and seasons, leaving countries with more farmable area, while other studies have found the temperature increase is leading to heat stress and cell death for many plants (J.E. Olesen et al. 2011; Bertrand et al. 2008; X. Yang et al. 2015; Clements and Ditommaso 2011; Roux and McGeoch 2008). The changes in global precipitation have also been under investigation, as studies have found some plants will increase in biomass and yield under these shifting patterns, while other plants have dropped in productivity (Hatfield and Prueger 2015; Grosso et al. 2008; Z. Wu et al. 2011; Trenberth 2011). Changes in precipitation will allow for some plants to inhabit areas that has not previously been seen, but contradictory studies have shown precipitation to be the limiting factor in range shifts (Thomey et al. 2011; Zeppel, Wilks, and Lewis 2014; Choat et al. 2012). It is imperative to resolve this controversy to inform the accuracy of climate models, which will in turn aid in proper public perception of ACC, conservation efforts, and potential policy change (Osborne et al. 2007; Bonan et al. 2003; Levis 2010)

There are several factors that could explain the debated effects of ACC on plants. One cause of this debate can be attributed to the climate variables being analyzed. Given the multifactorial nature of the climate, studies that only investigate the effects of one climate variable could contribute to this disagreement. For example, if tested individually, the effects of temperature could give misrepresented results depending on what watering levels the plants are grown with. If water levels are kept consistently high throughout an experiment, the plants with elevated temperature will experience an increase in evapotranspiration, which will allow plants to cope with higher temperatures, whereas if water levels were kept low, higher temperatures might appear harmful (Magrin, Travasso, and Rodríguez 2005). This situation calls for studies to analyze multiple variables and their interactions to be conclusive (Parmesan and Hanley 2015; Yeo 1998; Gray and Brady 2016).

Second, plant performance has been shown to maximize at an optimum level for given climate variables, with decreased performance on either side of that optimum level (Jochner et al. 2016; Peek et al. 2002; J. Wu, Wurst, and Zhang 2016). A consequence of this biological attribute is that the same change in one climate variable could have different responses depending on where they start on either side of the optimum. For instance, one degree of warming could have a positive effect if it occurs in places that are to the left of the optimum range, meaning that they are cooler than the optimum temperatures plants prefer. However, the same temperature increase could lead to negative effects for plants that are on the right side of the optimum temperature spectrum where temperatures are already too hot for plants (Yin 1995; Chen et al. 2019). This possibility could explain many contrasting results on the effects of temperature (Scherm and van Bruggen 1994). Most studies only test ambient temperatures against a limited number of small degree incremental treatments, so there is no possibility to analyze the data nonlinearly. It has been suggested that the dominance of these studies proving climate change is positive for plants is due to many of the studies taking place in temperate zones where a few degrees of temperature increase simply adds a few days to the growing year because it is still within the optimal temperature range (X. Yang et al. 2015; Osland and Feher 2020; Kelly and Goulden 2008; Colautti and Barrett 2013). The bias of experiments in temperate zones can be attributed to the disparity between the higher latitudinal developed countries that fund ample higher education research institutions, and the lack thereof in tropical zones. One way to correct for this knowledge gap is to implement treatments for a given climate variable over a broad range of which a species operates. Evaluating multiple treatments over the range of climate variability allows for the assessment of nonlinear responses.

A final reason that might help to explain this controversy is the set of responses that are measured in the plants when exposed to the given climate variables. It is broadly known that the range of a climate variable in which a species can survive is much wider than the range that the species produces reproductive or food structures (Saini and Westgate 1999; Barnabás, Jäger, and Fehér 2008; Lui, Andersen, and Jensen 2003). Under varying climate manipulations, plants will adjust biomass allocation to alternative parts of their structure (Zhang et al. 2015). Conclusions about the effects of ACC can differ depending on what response variables were collected, as certain measurements can only inform on biomass instead of food production, which is usually the top concern. Experimentally testing these three shortcomings of common experiments is the driving motivation for this thesis.

The purpose of this study is to shed light on the controversy surrounding ACC’s effects on plant productivity. Specifically, this study will be investigating (1) the effects of water availability and temperature to address the interaction between these variables and the multifactorial nature of ACC, (2) testing water and temperature nonlinearly by looking at these variables over a broad range with sufficient treatments, and (3) collect a dozen response variables to measure how the plant responds to these treatments in various parts of its structure. By accomplishing these objectives, this study will determine if these three possible causes for discrepancies in climate change studies on plants are in fact at the root of the controversy, and if so, emphasize the importance of properly designing experiments as to not overlook the importance of these factors.

## 1.1 Species Selection

This study utilized hard red spring wheat (*Triticum aestivum*) as the model species to shed light on the controversy surrounding the effects of ACC on plants. There are many reasons why wheat was chosen. It reaches adulthood quickly so it was convenient timing-wise, but does not grow too large for a lab setting. Seeds are cheap, a necessity when there are hundreds of replicates in the study, and wheat can survive in a large range of conditions, making it acceptable to test extremes on. Wheat is a crop, allowing food producing structures to be observed, and it is one of the most common grains grown globally (Portmann, Siebert, and Döll 2010). It also has distinct structures, which allows for measurements to be taken easily and quickly (see Figures 1a-1c).

Although this study only tested one plant, wheat was used as it is one of the most common crops grown around the world. Wheat is not typically found in many tropical regions, though there are not many crops that cover both temperate and tropical regions equally. This study would not necessarily be useful in the extrapolation of results into much different vegetative species, but crops are one of the top concerns surrounding plants in the face of climate change.

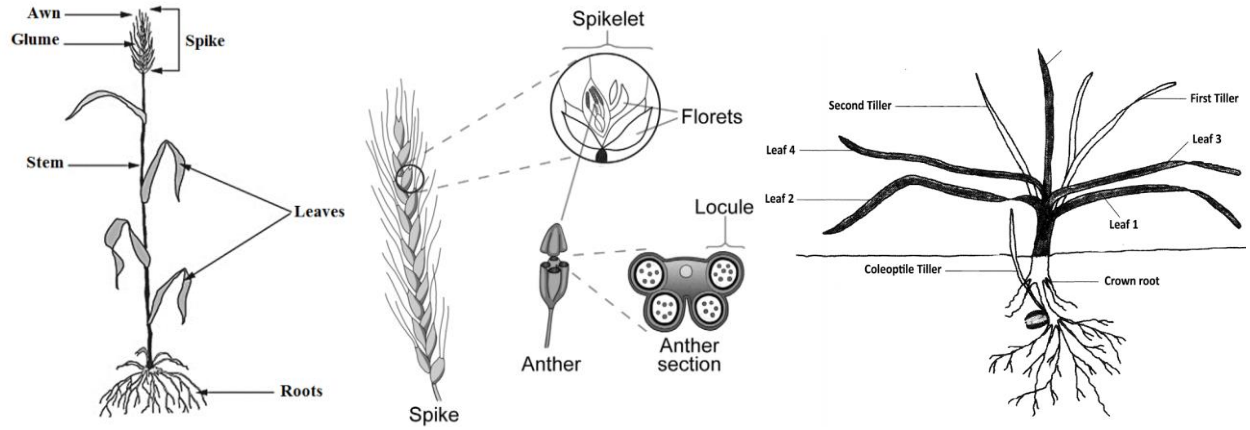

Figure 1: (a - left) Whole wheat anatomical structure (Khan and Mubeen 2012)

(b - middle): Anatomy of wheat spike (Richards et al. 2012)

(c - right): Wheat tiller illustration (Fowler 2018)

# 2. Methods

## 2.1 Experimental Design

The goal for this experiment is to test three main shortcomings found in many studies. These are (1) testing more than one climate variable and their interactions, which was accomplished by experimenting on temperature and soil water content, (2) analyze these variables nonlinearly, which was made possible by having five orthogonal treatment levels, and (3) collect general response variables but also those specifically pertaining food producing structures and changes in biomass allocation. A schematic of this design can be seen in Figure 2.

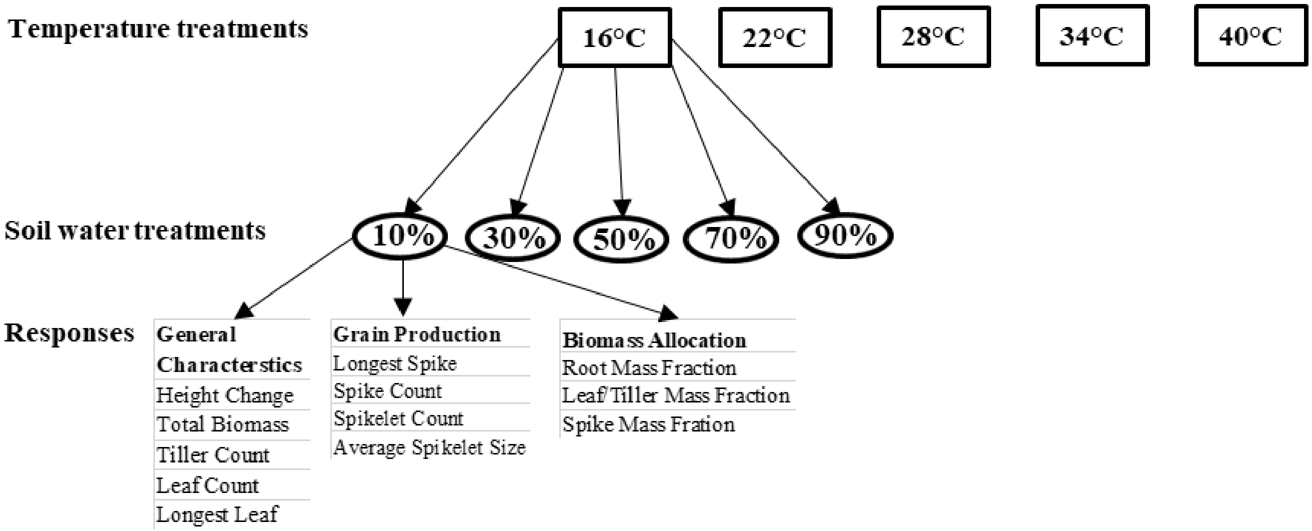

Figure 2: Factorial design of the experiment depicting the five temperature treatments in degrees Celsius, the five watering treatments in percent soil water capacity, and the 12 response variables that were measured in all 450 plants.

### 2.1.1 Chamber Setup

This experiment utilized fully automated plant growing chambers that have the capacity to regulate temperature and watering levels. Each chamber contains 5 rows by 10 columns that can hold a total of 50 pots per chamber. There are 10 chambers, and they are covered with a fabric tent that is lined with 5mm insolation and can be fully sealed to reduce temperature variability. Every chamber is 200cm long, 100cm tall, and 100cm deep. There are two clear viewing windows on each chamber’s tent that allow the experimenter to look inside while keeping the chamber sealed. The windows have a cover that is removable and is also insolated to retain full insolation when the windows are covered. The chambers are kept indoors to provide stable external conditions. Figure 3 exemplifies a simplified schematic of the chamber design.

### 2.1.1.1 Chamber Watering Control

To control water, inside each chamber is a robot that lifts and weighs each pot. The goal weight for every pot is programmed into the robot before the experiment begins, so if the pot is underweight the machine will add water until it reaches the correct weight. The machine is able to complete a watering cycle every six minutes and begins each cycle by calibrating itself against a column of pots filled with sand. This ensures the error is no higher than 0.3g. One limitation that this machine design faces is that as the plant gains weight, the watering program will continue to hold the pot to the original set weight. This did not prove to be a significant error in this study as the total weight of the heaviest plant found in this experiment was 0.4% of the weight of the watering treatment it was grown under. This would suggests that the error induced from this drawback is not enough to significantly affect the results.

### 2.1.1.2 Chamber Temperature Control

To regulate temperature, the chambers have a temperature controller that is external from the chamber. The temperature can be set and adjusted on the controller. Each chamber contains a heater that will flip on to increase temperature, an air conditioning unit that cools the temperature, and a fan that is continually circulating the air inside the chamber. The temperature inside the chamber is regulated to 0.3°C. The desired temperature can be set for every chamber separately, so they could all be run on different temperature, if necessary.

### 2.1.1.3 Chamber Lights

The machines also have the capability to simulate day and night conditions, specifically by reducing the temperature and shutting off the lights. The plant growth lights installed in each chamber emit 200PAR (Photosynthetically Active Radiation) at the level of the leaves. This is within the optimum range, as demonstrated by the plants in this experiment reaching maturity.

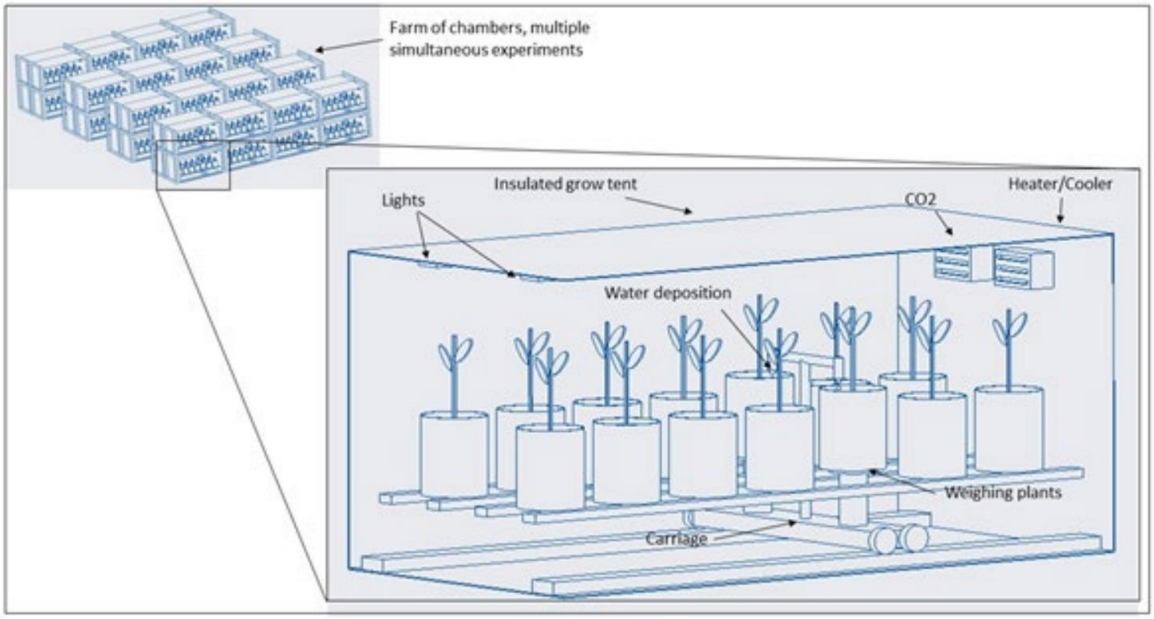

Figure 3: Simplified schematic of the chamber design depicting the rows of plants, the carriage with the robot for watering, and various temperature regulating equipment.

### 2.1.2 Experimental Treatments

Most previous experiments have been too constrained by technical limitations to test multiple treatments of more than one climate variable. With these growth chambers, this type of experiment is now possible. Testing a broad range of treatments was done by implementing five temperature and water treatment levels orthogonally. The five temperature settings were evenly spaced apart by 6°C, ranging from 16°C to 40°C. To account for the cooling effect of nighttime, the temperature between 6pm to 6am was set on a reduced gradient. The highest temperature dropped 10°C at night, the next temperature setting experienced an 8°C reduction, and so on, ending with a 2°C nighttime dip for the lowest temperature. The lights in the chamber were on, simulating sunshine, from 6am-6pm, and the other 12 hours were darkness for night. The five treatments of water were evenly spaced percentages of soil water capacity, ranging from 10% to 90%. For each specific intersection of temperature-watering treatment, there were 18 replicate plants.

## 2.2 Experimental Procedure

### 2.2.1 Seedling Germination

Before the experiment began, the seeds were germinated outside of the chambers. Wheat seeds were placed on plastic trays lined with wet paper towels, with one end of the paper towel hanging over the side of the tray so it could be rewetted via capillarity by dipping that edge in water. Another tray was placed on top to cover the seeds and avoid evaporation. Seeds germinated after two days, but were monitored under these conditions for five days to ensure they were strong enough to handle the planting.

### 2.2.2 Transplanting

Every pot in this experiment was allocated one three-day-old seedling. Each one gallon pot was filled with 550g of dry all-purpose Miracle Gro Potting Mix, then water was added and mixed until 70% soil water content was achieved. A seedling was measured and placed inside the pot with all roots slightly below the surface. The seedlings that were planted in medium were chosen to be about equal height to provide consistency.

After being planted, all of the seedlings in pots were placed inside the chambers and left to acclimate to the transplanting. They were kept at 70% soil water content and ambient day and night temperatures for one week. All plants survived this acclimation period with no signs of obvious stress (e.g., wilting or dying). Following these seven days, the plants were then exposed to specific water and temperature treatments (see Figure 2). All 450 plants in this experiment were transplanted on the same day, and began experimental conditions simultaneously.

### 2.2.3 Harvesting and Processing Samples

After 56 days of experimental conditions, the plants were harvested. The plants must be grown for an equal number of days to remain consistent, though due to the vast number of replicates in this study, all 450 plants could not be harvested to completion in one day. To rectify this, every plants' roots were coarsely rinsed and the whole plant was labeled and frozen on the same day, which pauses the growth process and maintains consistency (Perry 1998; Mazur 1970). All plants were then thawed, measured, cleaned, and left to dry in the following three days. Measurements that were taken are listed as dependent variables in Table 1.

The root washing process was methodical and standardized to maintain quality and consistency. When roots were being washed, they were first dipped and carefully rubbed with bare fingertips in a container of water to loosen all excess soil. Once all possible medium was removed, the roots were placed on a mesh platform in a sink. The sink faucet was modified with a pressure spout, so the roots were effectively power washed. After that, the roots were transferred back into the basin of water for a final hand washing. Once the roots were deemed clean, they were transferred back into their cleaned pot and set in the open chamber to air dry.

Once the plants had air dried, they had to be dehydrated in the ovens. Each plant was cut into sections: the roots were cut at the seed, and the spike (if present) was cut at the base of the lowest spikelet (see atomical structures in Figures 1a and 1b). If no spike was present, the plant was left in two sections. Every plant was labeled on an oven tray as to not mixed them up. The trays were placed inside two ovens, a Fisher Scientific Isotemp Oven Model 630F and a Model 650G, and dried for one hour at 105°C. Additional time was added in increments of 10 minutes if the plant weight continued to reduce, per the methods in Cai et al. (2016). Plant biomass metrics were then measured using a scale that was consistently tested against calibration weights to ensure proper reporting. The drying and weighing process was completed in the five days following the harvesting.

### 2.2.4 Data Collection

A dozen response variables were measured to capture the growth range of the plants' physical responses to water and temperature treatments as they relate to general characteristics, grain producing structures, and biomass allocation changes. All of the variables and the method used to collect them are indicated in Table 1.

Table 1: Describing the specifics of how each dependent variable was measured during data collection.

| **Dependent variable measured** | **Standard measuring procedure** |
|---|---|
| Height change (mm) | Final height (seed to top of spike excluding awns) – starting height recorded on transplanting day |
| Total dry biomass (g) | Dry biomass of entire plant structure |
| Tiller count | Number of tillers including the main stem |
| Leaf count | Total number of leaves per plant |
| Longest leaf (mm) | Longest leaf that was over 75% green |
| Longest spike (mm) | Longest spike from base of the lowest spikelet to the top of the highest spikelet, excluding awns |
| Spike count | Number of spikes an individual plant had |
| Spikelet count | Total number of spikelets per plant, not per spike |
| Average spikelet size (mm) | Three random spikelets were measured for every spike, excluding awns, and all averaged together |
| Root mass fraction ($g\ g^{-1}$) | Root weight / total dry biomass |
| Leaf/tiller mass fraction ($g\ g^{-1}$) | Leaf & tiller weight / total dry biomass |
| Spike mass fraction ($g\ g^{-1}$) | Spike weight / total dry biomass |

## 2.2.5 Data Analysis

All data was analyzed using regression analysis in R (version 4.0.4). This type of analysis allows for the testing of nonlinearities and interactions of water and temperature as independent variables. First and second order polynomials for both variables were tested as single effects and as interactions. The outline of a potential model is shown in Figure 4. The best model for every dependent variable was found by noting the smallest AIC value. If a nonlinear or interaction term appeared in the best model, the lower order components were included as well. The 18 replicates for each temperature-water treatment were averaged, then the model was ran again using this mean in addition to the raw data. The comparison was done to show the variation between the two types of models, which is indicative of experimental error and/or genetic variability. The differences in the $R^2$ values can be found in Table 3. To visualize the data, the best model for each dependent variable's raw data was plotted using contour plots (Figures 5-8). A smaller graph on top of the contour plot illustrates the dependent variable's relationship with soil water content, and the graph to the right of the plot shows the correlation to temperature.

$$\text{Dependent variable} \sim (\text{intercept}) + \underbrace{(a*T) + (b*W)}_{\text{Linear individual terms}} + \underbrace{(c*T^2) + (d*W^2)}_{\text{Nonlinear individual terms}} + \underset{\substack{\downarrow \\ \text{Linear interaction term}}}{(e*TW)} + \underbrace{(f*TW^2) + (g*T^2W) + (h*T^2W^2)}_{\text{Nonlinear interaction terms}}$$

Figure 4: Depicting all possible terms that were tested to reach a dependent variable's best model, with "T" standing for temperature, and "W" representing soil water content.

A driving goal for this thesis is the comparison of different dependent variables. However, because these variables utilize different scales and units, they cannot be compared directly. For the purpose of comparing the response variables, they must be set to a common scale. To do so, a grid of all possible combinations of the water and temperature treatments in this experiment was created, similar to Table 2. In Table 2, 25 potential pixels can be seen. This was then divided into 1,000,000 total pixels. This grid was treated as a simulated environmental space in which plant responses can operate, which allows for the direct comparison of the amount of environmental space that is necessary for each of the dependent variables. The best model for each dependent variable was applied to the grid, so every pixel formulated a value for how much of the dependent variable was found in that pixel. Response variables that only included one independent climate variable in their best model were added the other climate variable so they could be compared on the same scale; this only occurred in two out of 12 of the dependent variables. The value in each pixel was divided by the total value of all of the pixels (meaning the total amount of dependent variable) to get a proportion. These proportions were ordered largest to smallest, and the amount of pixels that it took to get to 90% of the total amount of dependent variable was recorded. This is effectively the 90th percentile for how much environmental space, defined by water and temperature, over which 90% of the given dependent variable operates. This is now the optimum environmental space for each response, which is a comparable measure between all dependent variables because they are percentages on the same scale. These percentages of space encompassing 90% of each dependent variable were all plotted in Figure 9.

Table 2: Grid of environmental space

| | **16°C** | **22°C** | **28°C** | **34°C** | **40°C** |
|---|---|---|---|---|---|
| **10%** | 16°C x 10% | 22°C x 10% | 28°C x 10% | 34°C x 10% | 40°C x 10% |
| **30%** | 16°C x 30% | 22°C x 30% | 28°C x 30% | 34°C x 30% | 40°C x 30% |
| **50%** | 16°C x 50% | 22°C x 50% | 28°C x 50% | 34°C x 50% | 40°C x 50% |
| **70%** | 16°C x 70% | 22°C x 70% | 28°C x 70% | 34°C x 70% | 40°C x 70% |
| **90%** | 16°C x 90% | 22°C x 90% | 28°C x 90% | 34°C x 90% | 40°C x 90% |

# 3. Results

## 3.1 Best Models and Plots

### 3.1.1 Effects of Individual Linear Variables

This study tested multiple climate variables over a broad range and measured a wide variety of response variables to address the controversy of ACC’s effects on plants. Examining treatments over a broad range of temperature and water orthogonally allowed the data to be analyzed using nonlinearities and interactions in the analysis. Table 3 displays all 12 of the dependent variables collected in this study, and their respective best models. Every dependent variable found linear temperature to be significant. For water, 10 out of 12 of the dependent variables found linear water to also be significant, save for root mass fraction and spikelet count. This provides supportive evidence that it is critical to include more than one climate factor in studies performed on plants to test ACC’s effects when the majority of responses found both water and temperature to be significant.

### 3.1.2 Linear Interactions

The interaction of linear water with linear temperature was significant in 10 out of 12 of the dependent variables. Only root mass fraction and spikelet count did not show a significant interaction between water and temperature. This further supports the hypothesis that studying the interaction among climate variables is critical to reach accurate results.

### 3.1.3 Nonlinearities

All 12 dependent variables showed a significant nonlinear interaction to temperature. In turn, only one dependent variable, spike count, showed a nonlinear response to the effects of soil water availability, as most responses to water were linear. The contrast between nonlinear responses to temperature and linear responses to water reveals the complexity of plant responses, but also could be a key argument that might explain the ongoing controversy of ACC’s effects on plant production. All 12 best models including at least one nonlinear variable demonstrates substantial confirmation that nonlinear factors are critical in effectively assessing ACC’s influence over plant productivity.

### 3.1.4 Nonlinear Interactions

All dependent variables, with the exception of root mass fraction and spikelet count, showed a significant interaction between nonlinear temperature and water availability. This indicates that the common bell-shaped response to temperature (see bell-shaped curved lines in the individual temperature graphs in Figures 5-8) varies depending on the soil moisture. Intriguingly, all dependent variables that related to grain production found the optimum temperature toward lower water availability (see individual water graphs in Figure 5), while the dependent variables relate to general biomass showed the optimum temperature toward high water availability (see individual water graphs in Figure 6). Production of spikes mainly occurred at the three intermediate temperature treatments, with only 4% of the plants in the two extreme temperatures producing spikes. Within the range of temperatures that spikes were produced, the largest spikes were observed where there was reduced water. The plot for spike mass fraction in Figure 7 also followed the trend of spikes towards medium temperatures and low water. The plot for leaf/tiller mass fraction is the inverses of this, shown to be most productive under medium temperatures and high soil water content. The prevalence of nonlinear interaction terms in this study reinforces both the hypotheses that multiple climate variables should be tested, and that nonlinearities are integral in clarifying ACC’s effect on plants. The contradiction between the optimum treatments for contrasting structures is further support for the importance of diverse dependent variable inclusion.

Table 3: Comparing dependent variables grown under different treatments of temperature in degrees Celsius (denoted by a “T” in the model) and soil water content in percent (“W”). All models, based on raw data or averages, proved significant with under a 0.001 level.

| **Dependent variable** | **Model** | **Adjusted $R^2$ with raw data** | **Adjusted $R^2$ with averages** | **Difference in $R^2$** |
|---|---|---|---|---|
| **Height change (HC, in mm)** | $HC \sim (652.36) + (-14.56*T) + (-5.48*W) + (0.12*T^2) + (0.61*TW) + (-0.012*T^2W)$ | 0.58 | 0.94 | 0.36 |
| **Total dry biomass (TB, in g)** | $TDB \sim (4.69) + (-0.22*T) + (-0.084*W) + (0.0031*T^2) + (0.0074*TW) + (-0.00014*T^2W)$ | 0.24 | 0.64 | 0.40 |
| **Tiller count (TC)** | $TC \sim (41.087) + (-2.53*T) + (-0.16*W) + (0.039*T^2) + (0.013*TW) + (-0.00021*T^2W)$ | 0.35 | 0.71 | 0.37 |
| **Leaf count (LC)** | $LC \sim (77.50) + (-4.49*T) + (-0.43*W) + (0.069*T^2) + (0.038*TW) + (-0.00065*T^2W)$ | 0.35 | 0.68 | 0.39 |
| **Longest leaf (LL, in mm)** | $LL \sim (-0.026) + (0.38*T) + (-1.92*W) + (-0.68*T^2) + (0.19*TW) + (-0.0033*T^2W)$ | 0.26 | 0.79 | 0.53 |
| **Longest spike (LS, in mm)** | $LS \sim (-0.032) + (0.29*T) + (1.11*W) + (-0.51*T^2) + (-0.10*TW) + (0.0018*T^2W)$ | 0.48 | 0.80 | 0.32 |
| **Spike count (SpC)** | $SpC \sim (-3.48) + (0.315*T) + (-0.095*W) + (-0.0056*T^2) + (0.0010*W^2) + (0.0081*TW) + (-0.000091*TW^2) + (0.00014*T^2W) + (0.0000016*T^2W^2)$ | 0.32 | 0.85 | 0.55 |
| **Spikelet count (StC)** | $StC \sim (-59.53) + (5.35*T) + (-0.097*T^2)$ | 0.35 | 0.77 | 0.38 |
| **Average spikelet size (ASS, in mm)** | $ASS \sim (-0.35) + (3.33*T) + (0.21*W) + (-0.060*T^2) + (-0.018*TW) + (0.00032*T^2W)$ | 0.37 | 0.72 | 0.35 |
| **Root mass fraction (RMF, in g $g^{-1}$ )** | $RMF \sim (0.41) + (-0.024*T) + (0.00059*T^2)$ | 0.47 | 0.90 | 0.43 |
| **Leaf/tiller mass fraction (LMF, in g $g^{-1}$ )** | $LMF \sim (2.12) + (-0.11*T) + (-0.011*W) + (0.0019*T^2) + (0.00099*TW) + (-0.000018*T^2W)$ | 0.37 | 0.86 | 0.49 |
| **Spike mass fraction (SMF, in g $g^{-1}$ )** | $SMF \sim (-1.56) + (0.14*T) + (0.011*W) + (-0.0025*T^2) + (-0.00098*TW) + (0.000018*T^2W)$ | 0.48 | 0.90 | 0.42 |

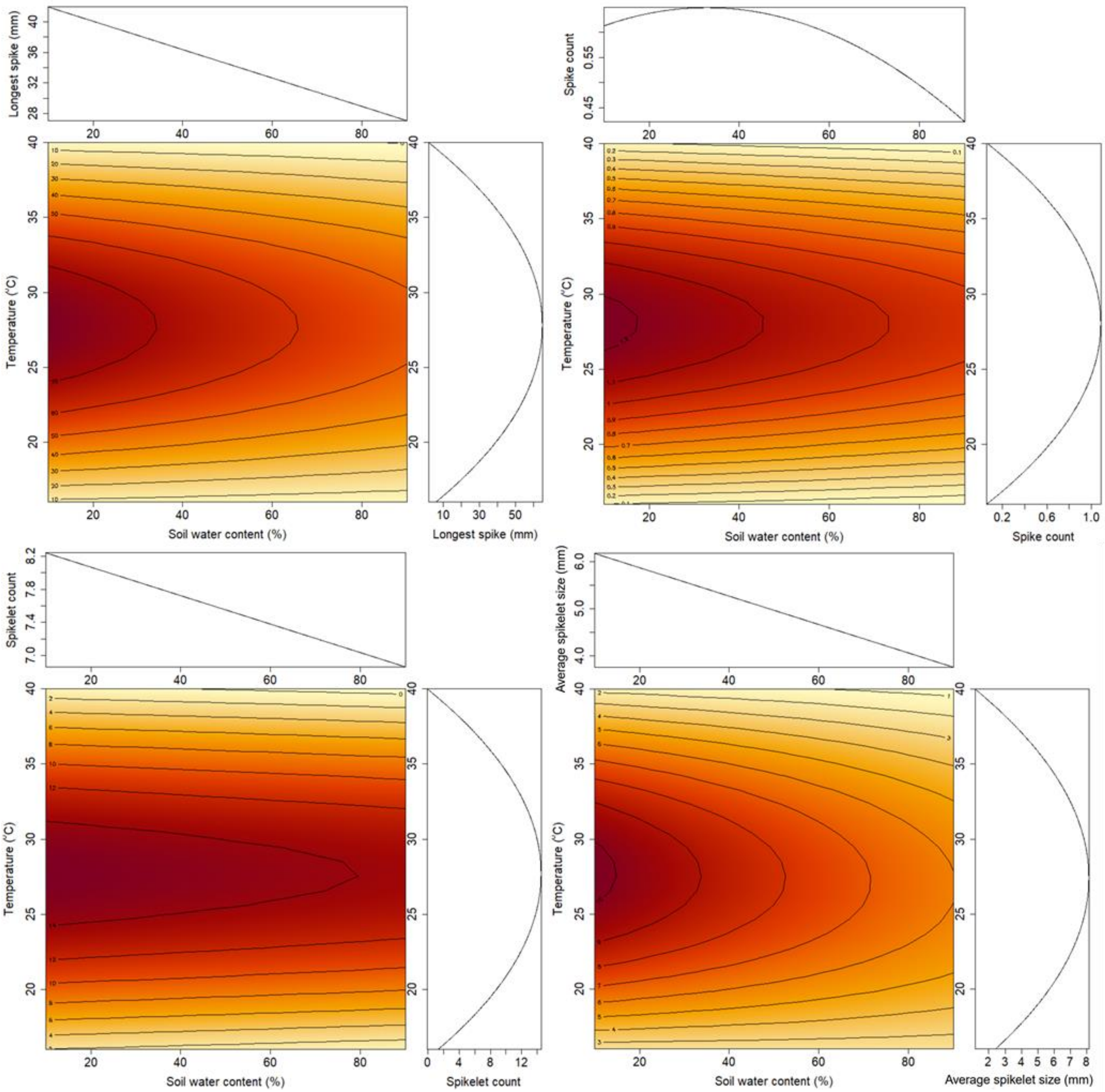

Figure 5: The effect of soil water content and temperature on (from left to right, top to bottom) longest spike length in mm, spike count, spikelet count, and average spikelet size in mm. On the top of each plot is the graph for the dependent variable's relationship with soil water content, and to the right is the relationship with water. The main plot shows the effect of soil water content and temperature together. The darker color signifies a higher value for the dependent variable under those conditions.

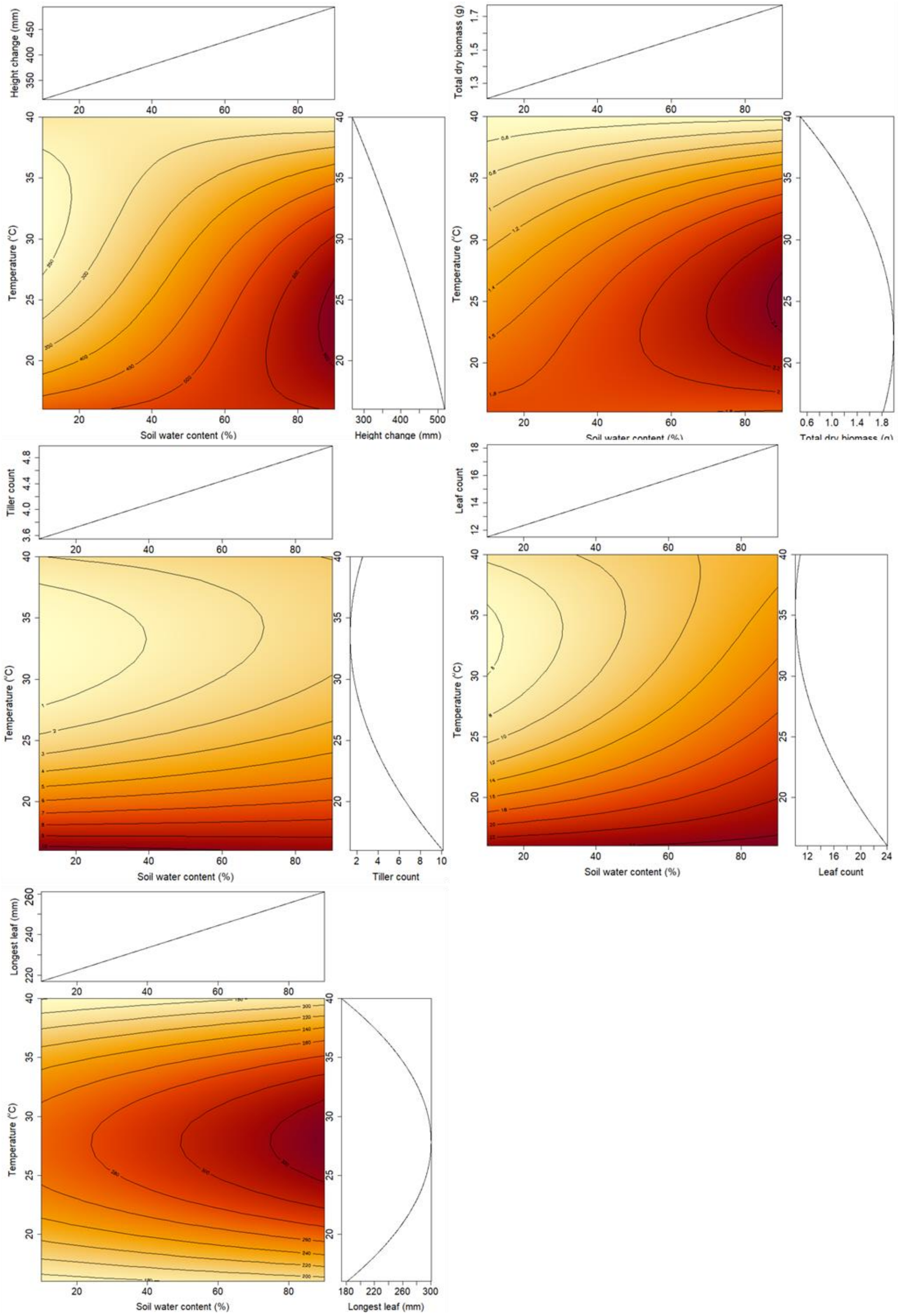

Figure 6: The effect of soil water content and temperature on (from left to right, top to bottom) height change in mm, total dry biomass in grams, tiller count, leaf count, and longest leaf in mm. On the top of each plot is the graph for the dependent variable's relationship with soil water content, and to the right is the relationship with water. The main plot shows the effect of soil water content and temperature together. The darker color signifies a higher value for the dependent variable under those conditions.

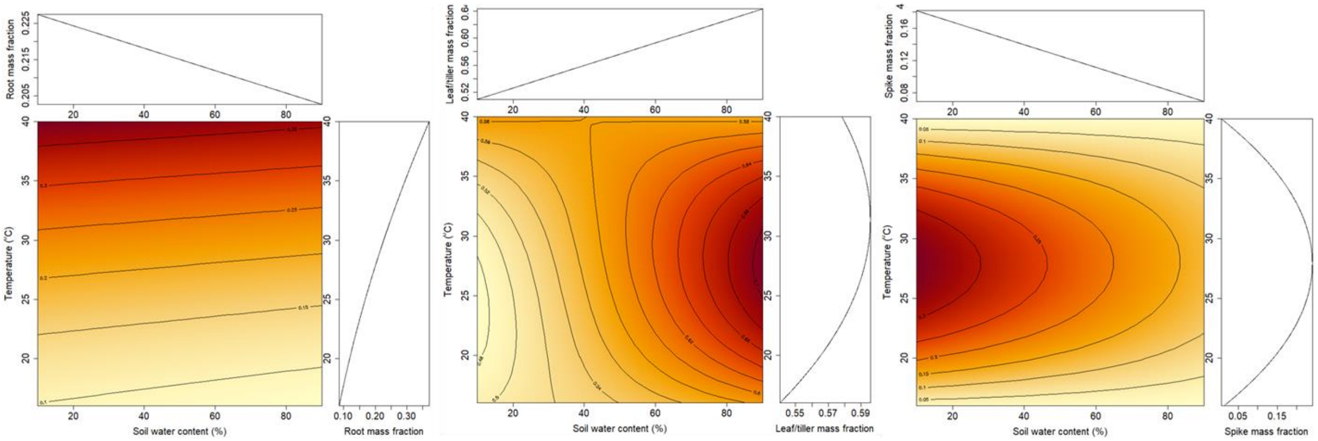

Figure 7: The effect of soil water content and temperature on (from left to right) root mass fraction, leaf/tiller mass fraction, and spike mass fraction. On the top of each plot is the graph for the dependent variable's relationship with soil water content, and to the right is the relationship with water. The main plot shows the effect of soil water content and temperature together. The darker color signifies a higher value for the dependent variable under those conditions.

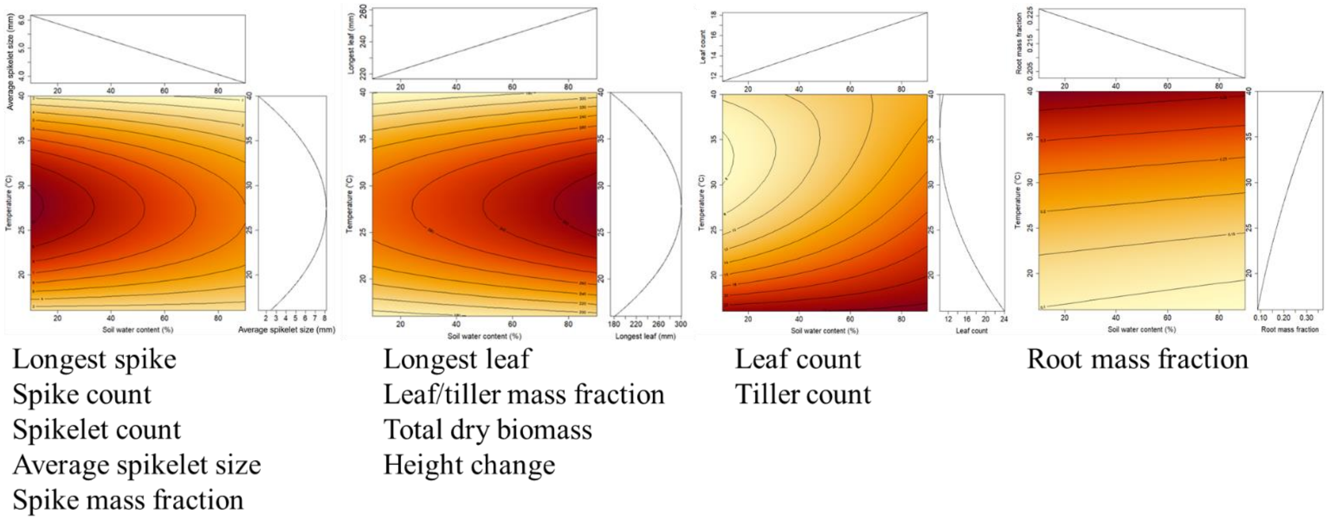

Figure 8: Summary of the four main patterns of response variables found in this experiment. Listed below each example plot are the variables that showed a similar trend. For example, the plot furthest to the left shows preference for low soil water content and medium temperatures, and all five of the variables listed below it also showed those conditions to be ideal.

## 3.2 Variability Among Response Variables

As shown in the section above regarding nonlinear interactions, optimum responses to temperature usually depended on the availability of water, which supports the hypothesis that measuring different phenotypic responses in plants can alter the perception of ACC’s pressure on plant productivity. Further, after standardizing the dependent variables over the broad range of the independent variables, the optimum environmental space (90% of the response variables’ value) was found to differ considerably. The cluster of variables related to grain production has their optimum conditions over a lower space than the response variables related to general biomass production (Figure 9). This comparison of a dozen variables enforces the importance of testing a broad range of temperature and water treatments to ensure accuracy when evaluating environmental space, and the usefulness of measuring and comparing many distinguished response variables.

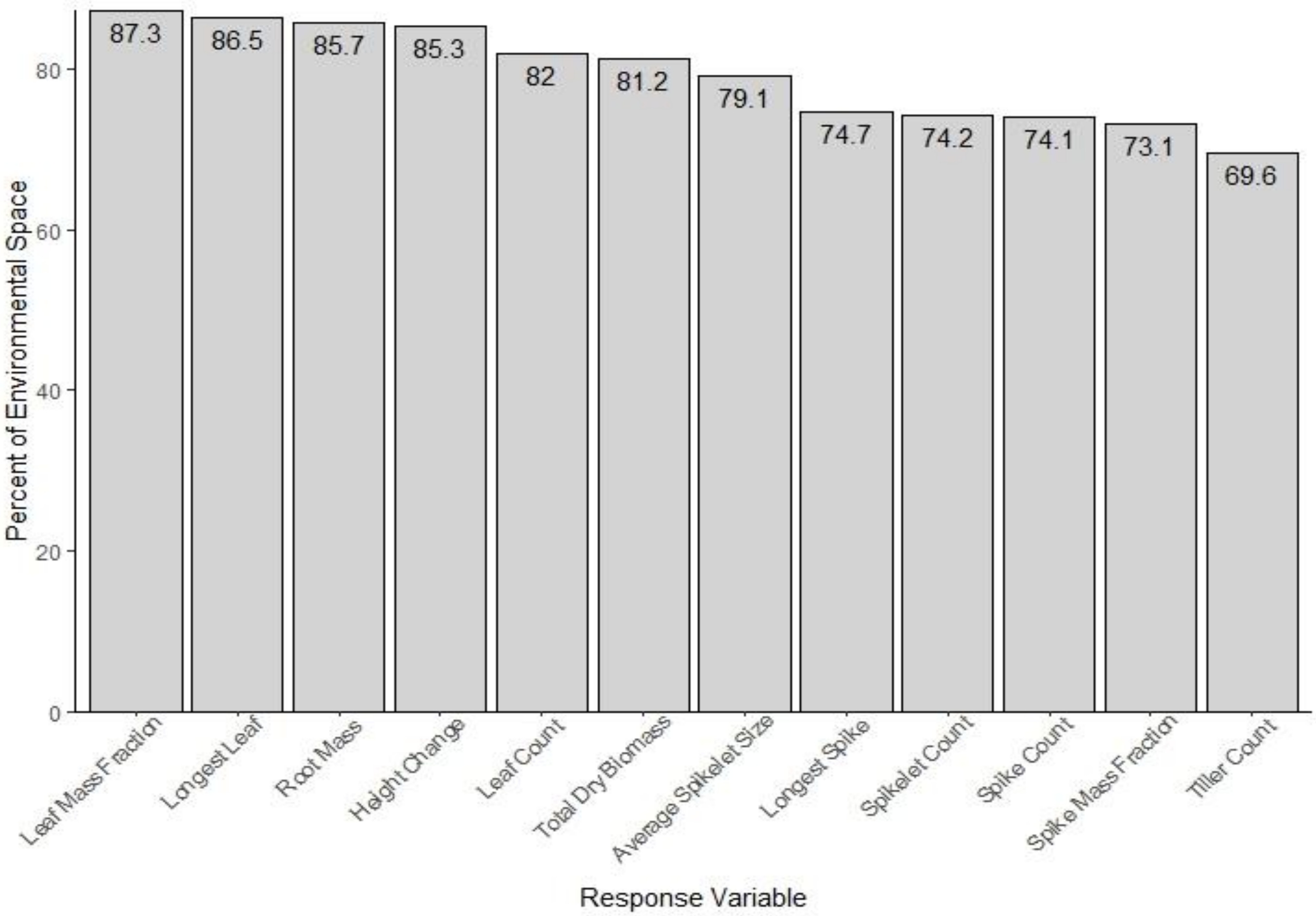

Figure 9: Comparing the percent of space each dependent variable requires to encompass 90% of its values.

# 4. Discussion

## 4.1 Insight into ACC Controversy on Plant Performance

The effects of anthropogenic climate change on plant performance has been controversial for many reasons. This thesis tested three reasons that might aid in resolving this controversy: (1) testing multiple climate variables as much of the climate is interconnected, (2) examining these climate factors nonlinearly, and (3) collecting a diverse set of response variables. The independent climate variables resulted in a variety of plant responses that were significant and nonsignificant individually, within interactions, linearly and nonlinearly, and even nonlinear interactions. This highlights the complexity of both biological and climate systems, which, as exemplified by this experiment, can be considerably underestimated by experiments that are simple in nature.

### 4.1.1 Explaining Interactions

Statistical interactions indicate that the variations in the dependent variables to one independent variable can be significantly larger or smaller under levels of a second independent variable. In this study, 10 out of 12 variables found a significant interaction between temperature and water. Interestingly, the subset of dependent variables related to grain production showed an increase in performance towards lower levels of water, while dependent variables unrelated to grain production found a positive trend to increases in temperature and water. These contrasting patterns can be easily explained through numerous physiological and evolutionary processes. For instance, one common mechanism for plants to deal with heat is evapotranspiration, which could then explain how a surplus or lack of water could lead to changes in plant performance (Chaouche et al. 2010; Valipour 2015). These results could potentially also indicate specific evolutionary strategies, in which unsuitable conditions such as heat and drought would select in favor of plants that optimize reproduction as opposed to climatic conditions that might favor increases in biomass (Lohani, Singh, and Bhalla 2019; Bykova, Chuine, and Morin 2019; Zinn, Tunc-Ozdemir, and Harper 2010; Senapati et al. 2019). For many annual plants such as wheat, a common mechanism for managing low water availability or similar environmental pressures is to accelerate the plants into the reproductive stage before the stress can catch up (Gupta, Rico-Medina, and Caño-Delgado 2020; Lauder, Moran, and Hart 2019). This is advantageous to avoid wasting potential resources on gaining biomass and instead ensuring reproduction.

### 4.1.2 Explaining Nonlinearities

In the case of this experiment, the occurrence of nonlinearities indicates the existence of an optimum condition for a given climate variable, where outside of the optimum range plant performance declines (Lobell et al. 2011; Peek et al. 2002; Zhu et al. 2019). The relationship between a given dependent variable and water was almost always found to be linear, while all dependent variables showed a nonlinear relationship with temperature. These results indicate that the plants in this experiment found an optimum range for temperature with decreasing performance in either direction outside of the optimum range, whereas changes in water were seen to simply increase or decrease productivity.

### 4.1.3 Explaining Variations Between Multiple Responses

Under different combinations of water and temperature, plants showed the prioritization of developing different parts of its structure. It was found that most dependent variables related to grain production showed the highest performance to medium temperatures and low water. On the other hand, general biomass measurements preferred mostly either medium temperatures and high water, or low temperatures and any water level. This indicates that energy allocation within the plant towards different body parts is optimized under specific climate conditions.

Another dependent variable with distinct responses to variations in climate was root mass fraction. Apparent in Figure 7, the wheat plant will devote more energy towards the root system under high temperatures and low water. Root mass fraction has typically been seen to be largest under conditions where the limiting factor is below ground, such as in the case of water availability (Poorter et al. 2012; Dai et al. 2019; Eziz et al. 2017). It was found in this experiment that root mass fraction did not even show a significant correlation to water, but it did with temperature. Soil moisture is more quickly evaporated in warmer conditions, meaning that as temperature increases, water will become increasingly limited belowground, spurring further root growth (Kelishadi et al. 2018; Lemon 1956). Although this experiment did not prove a significant interaction between water and root mass, the larger root growth seen under high temperatures does follow the patterns seen in previous studies (Delucia, Heckathorn, and Day 1992; Cairns et al. 1997; Y. Yang et al. 2009)

Above ground biomass allocation was measured in two dependent variables, spike and leaves/tillers, which showed distinctive responses as well. Both showed preference for medium temperatures but opposite inclinations for water availability (see Figure 7). Past studies have shown that low temperatures (<18°C) decrease above ground biomass due to cold temperatures limiting water uptake (Poorter et al. 2012; Waisel et al. 2002). This pattern holds true for the results of this experiment. Spike mass fraction, however, favored low water availability while leaf/tiller mass fraction thrived under high water content. This could be due to wheat remobilization, where a wheat plant forms a spike following the growth of multiple tillers and accompanying leaves, and energy from the non-grain associated organs are sent to the spike instead (Palta et al. 1994; Barbottin et al. 2005; Garnett and Graham 2005; Distelfeld, Avni, and Fischer 2014). The tradeoff between resources devoted to the spike as opposed to the leaf/tillers is clear in the patterns seen here: remobilization of energy to the spike instead of the leaves/tillers is most prominent under low water conditions. Bushier structures that have many leaves require more water, so there is less stress on them to remobilize if they are receiving all of the water that they demand (J. Yang et al. 2000; Zhang et al. 2015). Clearly, the results show that different combinations of climatic variables lead towards the prioritization of specific plant responses, which could potentially be rooted in evolutionary strategies to most efficiently acquire and allocate energy. These contrasting results in optimum growth conditions reinforces the importance of measuring responses in plants in all forms of their structures.

## 4.2 Food Production Implications

The results of this thesis give clues into the potential consequences of ACC as it relates to the capacity of plants to produce food. As seen in Figure 9, the dependent variables that represent food production are clustered at the lower end of the graph, signaling that they favor less variable temperature and soil water content to encompass 90% of the recorded values. This means that the structures that produce grain operate at a lower environmental space and are less apt to variability in temperature and water. This will be problematic as the range for optimum food production becomes narrower under ACC. It is known that plants are sensitive to their environmental conditions and in many cases, will be forced to adapt or relocate, but this is notably true for food production (Lenoir and Svenning 2015; Reilly and Schimmelpfennig 1999; Jump and Peñuelas 2005). The range that wheat finds optimal for grain production has been shown to be middle temperatures, which are already threatened by ACC (Z. Wu et al. 2011; Porter and Gawith 1999). Grain producing structures also showed affinity towards lower water availability, which is potentially optimistic for areas that face drought under ACC, though this finding is punctuated by its pairing with medium temperatures. Low water conditions are seen to be advantageous in this experiment only between 20-35°C. ACC is inflicting generally warmer temperatures on a wide range of regions, and warmer air is known to decrease soil moisture, but a region with low water and high temperatures would not be ideal for grain growth (Song et al. 2013; Forster et al. 2007). Additionally, areas that maintain medium temperature but experience higher precipitation as ACC continues will not achieve peak grain production. As ACC continues to alter temperature and water levels, wheat will become disadvantaged, but especially so in terms of food production.

A further concern with the diminished prospect of wheat production is the increased necessity for grain as the population increases (Jørgen E. Olesen and Bindi 2002; Curtis and Halford 2014; Hellin et al. 2014). The global population is increasing. It is predicted by 2050 the population will be around nine billion people, a little over a one billion increase from present day (Godfray et al. 2010). Similarly, crop yields have been improving over time, but are slowing (Jaggard, Qi, and Ober 2010). A large reduction in crop yields is due to extreme weather events, such as storms and other natural disasters, which are only expected to increase with ACC (Chakraborty and Newton 2011; Edame, Ekpenyong, and Fonta 2011). With more people on this planet, there will not be much additional land to expand agriculture into, so the gap between food production and population must be largely closed by genetic improvements, greater attention to resources, and reduction in food waste from farm to table (Godfray et al. 2010). This study found that the models who used the averaged response variables had an $R^2$ value that was at least one third higher than the $R^2$ in the models that used the raw data. The difference between the $R^2$ of these models is very likely related to experimental error or genetic/phenotypic variation among plants. Discerning between these two possibilities is not doable given the limited data, but given the environmental control of the machines used, it is unlikely that much of the difference is related to experimental error. If the majority of this variation is indeed related to genetic/phenotypic differences, this highlights the potential for improvements for grain production by directional selection alone (e.g., the preferential selection of more grain producing individuals).

## 4.3 Limitations and Future Directions

Not all of the plants in this experiment produced spikes, complicating the analysis of spike-related measures. This could potentially account for spikelet count not finding significance with water, and spike count have a nonlinear relationship with water. Spike count could also be skewed, as the only values that could be possible are zero to three. The outlying relationships these measures found with water could be a mathematical artifact of spike count's small values, and spikelet count's dependency on spike presence. In two of the treatments no spike was present, so variability was limited to the three intermediate treatments.  One solution for future studies could be to implement more treatments within the range viable for spike production.

The data collection of the responses in the plants was labor intensive and took multiple days to complete. To avoid any error that could be introduced to the dependent variables, all specimens were harvested in one day and frozen. This pauses the growth process and maintains consistency (Perry 1998; Mazur 1970). Ensuring that all of the plants were grown for the same number of days reduced possible limitation of this study.

The seeds used in this experiment were not genetically identical, so much of the variance in Table 3 between the adjusted $R^2$ with raw data versus the averages can be explained by genetic variation. This study could be improved by using inbreed seeds to reduce genetic variation and amplify the experimental results. Further improvements could be made by allowing the wheat to mature to full grain production under a longer growth period. This would also grant the ability to conduct nutrient analysis on the grain. Future studies should include $CO_2$ as an additional independent variable, as that is a large part of ACC that is expected to effect plants. Light is a strong determinant factor in biomass allocation, and because light was kept constant in this experiment, the patterns seen were based solely off of the temperature and water treatments (Mccarthy and Enquist 2007; Hermans et al. 2006; Eziz et al. 2017). To dive deeper into biomass allocation changes, light intensity in a future experiment could be varied by simulating the natural variation in light seen at different latitudes and seasons. This could be done by having lights with higher PAR on for 12 hours to simulate the tropics in certain chambers, while other chambers would have lower PAR lights that are on for more or less than 12 hours, depending on the seasons the experimenter aims to capture.

There is potential for future mapping applications of the environmental space calculated in this study. The overlap of dependent variables' 90% environmental space range could be calculated and mapped using future global projections for water and temperature under different climate scenarios. This will aid in determining specific countries that will be most affected, which will allow for the preparation of possible changes agriculturally, and the cascade those changes might have politically.

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