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## Field-scale evaluation of peanut genotype responses to drought: yield, quality, and the limits of physiological prediction

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**Abstract.** Understanding genotype-specific responses to drought is essential for improving crop resilience under variable climatic conditions. In this study, we evaluated 13 peanut (*Arachis hypogaea*) genotypes across two growing seasons (2023 and 2024) under irrigated and dryland field conditions. Irrigation increased pod yield across genotypes, with irrigated yields reaching up to 5.8 kg per plot compared to dryland maxima of 3.9 kg per plot, depending on genotype and year. The selected genotypes represent a range of drought tolerance ratings based on prior physiological characterizations. Our objective was to assess how water availability under natural weather conditions influences agronomic performance and seed quality. Across both years, genotype × environment interactions were strong, with yield responses varying substantially between seasons; dryland yield penalties were minimal in 2023 but pronounced in 2024. Commercial pod size distribution also shifted under irrigation, with Jumbo pod yield increasing by approximately 50–100% in high-performing genotypes such as AU18-35 and GA06G relative to dryland conditions. Results from this study indicate that expected physiological drought-response groupings did not consistently predict field-scale performance. Yield and commercial pod size were strongly influenced by environmental variability and stress timing, particularly early- versus late-season drought. These findings emphasize the importance of evaluating drought resilience under realistic field conditions to inform breeding and management strategies.

**Keywords:** commercial pod size, field evaluation, genotype-environment interaction, yield stability

### INTRODUCTION

Drought is a major constraint to peanut production, causing up to an 85% reduction in pod yield and impairing nutrient uptake, which limits biomass accumulation, seed filling, and pod quality. The extent of yield and quality loss depends heavily on the timing, duration, and severity of drought stress, with critical stages such as flowering, peg initiation, and seed development being particularly sensitive. While early-season drought followed by rewatering can sometimes enhance yield through synchronized flowering and pod set, sustained drought during reproductive stages often reduces yield by as much as 50% [Jongrunklang et al. 2013]. Drought stress also impairs peg penetration and pod expansion under low soil moisture, resulting in smaller, poorly filled pods and skewed size distributions [Okello et al. 2010]. Because drought can substantially reduce peanut yield and pod quality, irrigation is widely used in commercial peanut production to stabilize productivity and reduce economic risk, particularly in drought-prone environments [Lamb et al. 2020].

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Beyond total yield, pod size distribution (classified commercially into Jumbo, Medium, and U.S. No. 1 grades) plays a critical role in determining market value. Larger pods (Jumbos and Mediums) command higher prices and are favored in both domestic and export markets for direct consumption and processing. Drought conditions typically reduce the proportion of larger pods, thereby diminishing the overall economic value of a harvest even when some yield is retained. As such, evaluating genotype performance under drought must account for both yield and quality, particularly in terms of marketable size class distribution, to fully understand production risks and inform cultivar selection for water-limited environments.

In addition to reviewing the effect that duration and timing of climatic stress on yield and quality metrics, we also explore the practicality of using spectral or physiological traits as an indicator of potential yield penalty under stress. A multitude of recent reviews and small plot studies in peanut [Pilon et al. 2018, Zhang et al. 2022, Zhen et al. 2022] have highlighted significant differences in whole plant compensation mechanisms between genotypes under heat and drought stress. Differences in traits such as stomatal conductance, chlorophyll content, and carbon assimilation rate underlie variation in plant strategy, specifically resource acquisition, allocation, and reproductive output. These studies have shown that peanut response to stress is combated by employing varying stomatal control either limiting transpiration early in response to stress or keeping stomata open longer during mild and moderate stress to continue CO<sub>2</sub> uptake [Zhang et al. 2022]. These different strategies not only significantly impact carbon assimilation but influence daily and seasonal plant and soil water status. Other studies have found that other non-stomatal limitations linked to pigment contents were variable between genotypes and dependent on stress severity [Pilon et al. 2018]. Changes and variability in these characteristics lead to decline in plant performance due to declines in photosynthesis, actual quantum yield of PSII, and electron transport rate. By collecting additional physiological metrics in genotype × environment yield trials, we might further elucidate distinct tradeoffs between physiological characteristics. This complimentary information may substantially inform how we select for crop improvement strategies and how selection for agronomic traits influences crop fitness across ecosystem types and under changing environmental conditions.

## MATERIAL AND METHODS

### Field site and management

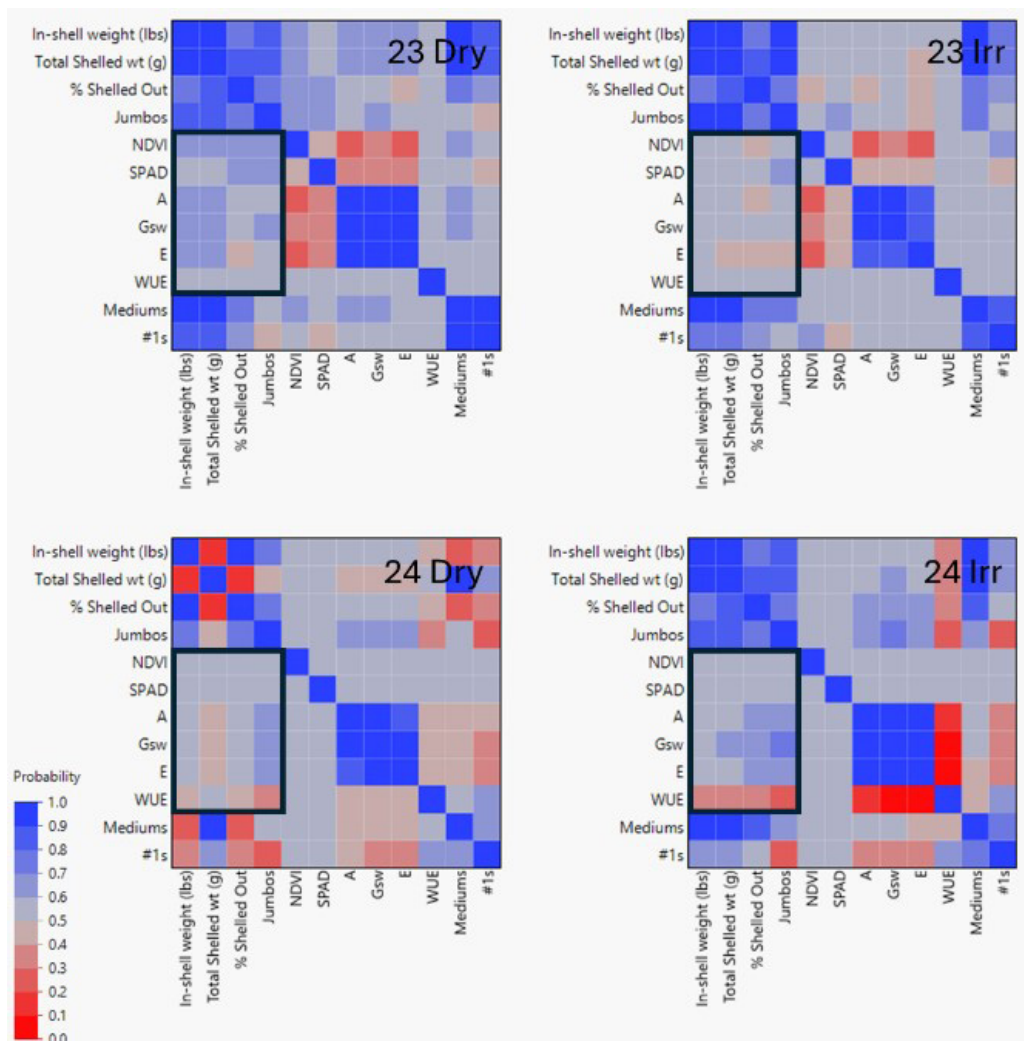
The study was conducted at the Hooks-Hanner Environmental Resource Center (HHERC farm, Greenville sandy loam; 31°43'52"N, 84°23'42"W) in Dawson GA, USA. Peanut genotypes (Supplementary table 1) were planted following a cotton–corn rotation all years. All genotypes were planted using a 91.44 cm row spacing after conventional tillage. Seeds were planted on 1 May 2023 and 23 May 2024 and the crop was managed for maximum yield with fertility, herbicides, fungicides, and insecticides being applied at recommended rates and timed as determined by field observation and manufacturer recommendation. While these applications varied year to year, soil pH was between 6.0–6.5 and macronutrient levels were kept within the guidelines reported by [Xie et al. 2020]. Each genotype was grown in side-by-side irrigation treatments. Dielectric water potential sensors (MPS2, Meter Environment, Pullman, Washington, USA) were placed at 25 cm and 50 cm depths and measurements were made every 15 minutes, uploaded to the cloud hourly and the data was observed daily. The irrigated plot was irrigated at –60 kPa, based on an average water potential measurements of both 25 cm and 50 cm depths. The dryland plot received no irrigation throughout the season and was dependent on rainfall events.

At harvest, all genotypes were considered to have similar maturity requirements, thus harvest time was determined by the hull scrape method [Williams and Drexler 1981] on GA06G. Peanuts were dug with a two-row inverter, field dried, and harvested using a field combine with bagging attachment in the field. Each sample of pods were dried to 10% of moisture for further evaluation of seed dormancy and germination, seed grading, and characteristics. Dried samples were shelled at the USDA-ARS National Peanut Research Laboratory following standard shelling protocols [Butts et al. 2016]. Peanut yield and grade were determined following official federal/state inspection guidelines [United States Department of Agriculture 1993].

## Physiology measurements

A variety of physiological and spectral traits (figure 1) were recorded simultaneously in both plots, twice a week, over a 5-week period from 26 Jul 2023 to 29 Aug 2023, and 21 Aug 2024 to 26 Sep 2024 from 11 a.m. – 1 p.m. when the plants were at 90 days after planting (growth stage R7, beginning maturity) [Boote 1982]. Spectral reflectance (NDVI) was measured using a GreenSeeker 505 hand-held optical sensor (N-Tech Industries, Ukiah, CA). Leaf chlorophyll concentration (SPAD) was measured spectrally with a handheld absorbance-based chlorophyll ‘SPAD’ meter (Minolta corporation, Ltd., Osaka, Japan). Mid-day leaf photosynthesis (A), stomatal conductance (gsw), and transpiration (E) were measured on the youngest fully expanded leaf on the apical meristem using the LI-6800 Portable photosynthesis system (LI-COR Biosciences, Lincoln, NE).

Figure 1. Correlation color plots representing highlighting observed pairwise relationships between yield and shelling characteristics compared to physiological measurements made during pod filling



Data is pooled between genotypes but separated by year and treatment. Bolded boxed area indicates hypothesized area of correlation expected between yield characteristics and physiological metrics.

## Statistics

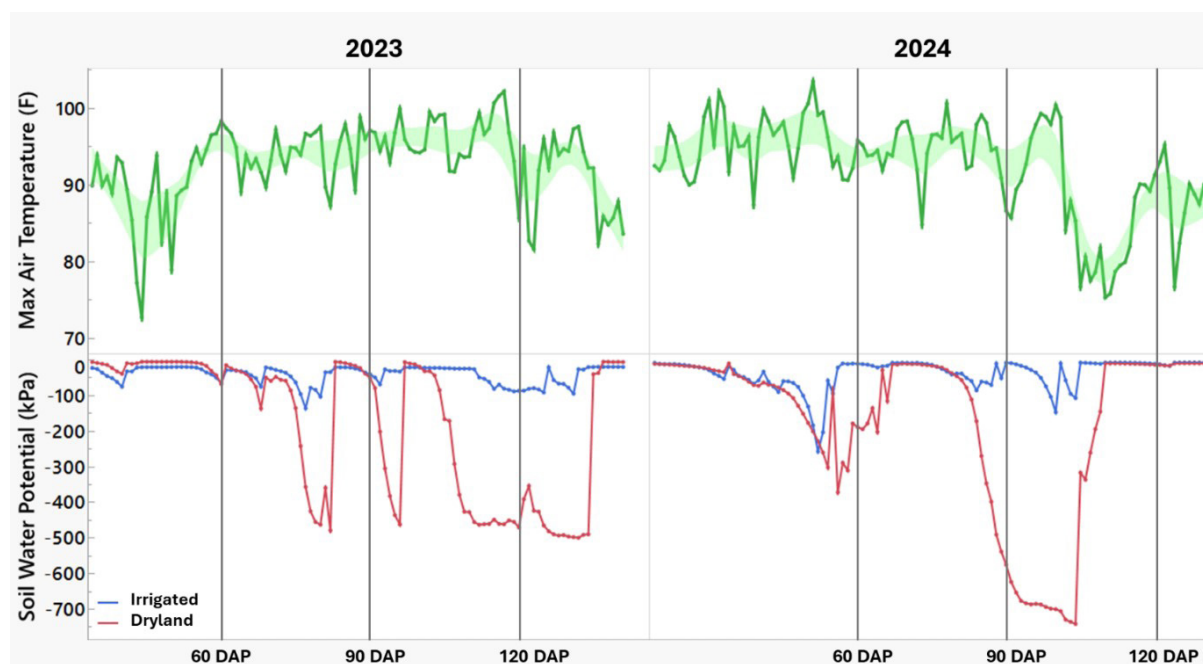
Trait values were tested for normality and equal variance using a Shapiro-Wilk test in R, and all values met those assumptions. ANOVAs were conducted for each measured variable across treatments and means were compared using both Tukey and Student T-tests. Bivariate trait relationships were analyzed with Pearson product–moment correlation using the Hmisc package in R. Figures were generated in both R and JMP (RStudio Team (2020) version 4.3.0; JMP, Version 17.2. SAS Institute Inc.).

## RESULTS

## Environment

In terms of environmental and soil moisture characteristics, we saw distinct differences between mean daily temperature and mean daily soil moisture between 2023 and 2024 (figure 2). The mean daily temperatures in 2023 were cooler in June, and warmer in August as compared to 2024. In terms of soil moisture, the dryland plot in 2023 experienced 3 significant dry down events, with the most prolonged event lasting 16 days, coupled with high temperatures. In 2024 the dryland plot also experienced a singular extreme dry down event lasting 10 days, however temperatures during this time were unseasonably cooler.

Figure 2. Average soil moisture (kilopascals) and maximum air temperature recorded at HHERC farm in irrigated and dryland plots during the 2023 and 2024 growing season



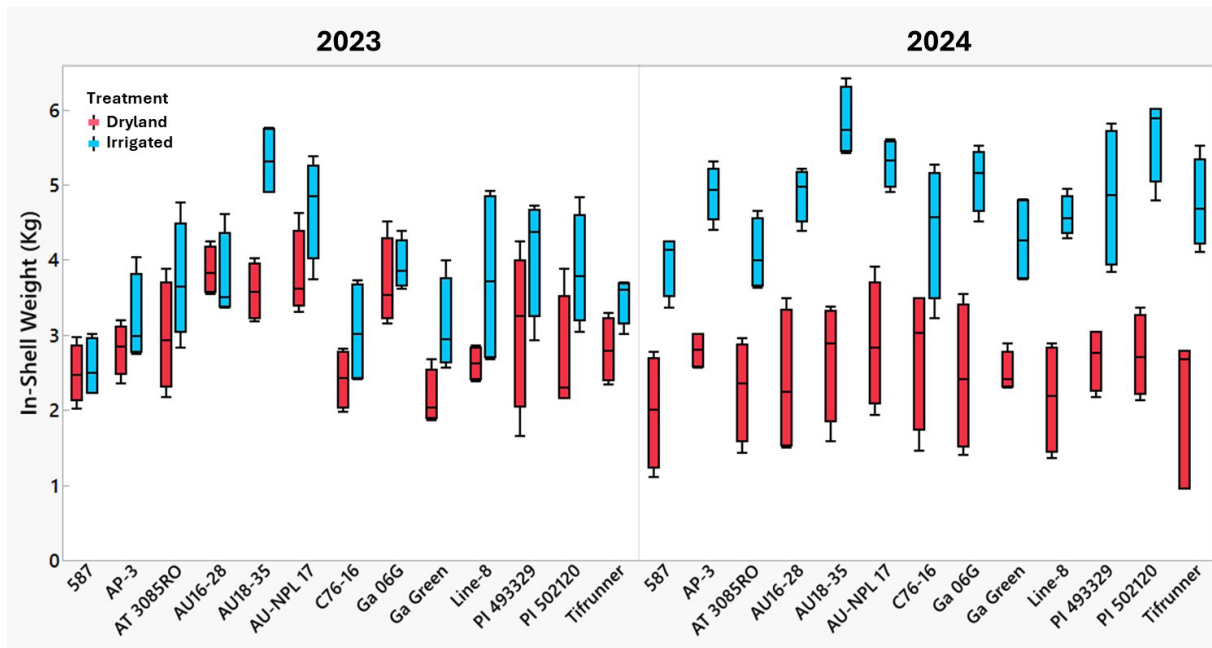
DAP – days after planting; red lines indicate dryland field soil water potential measurements whereas blue lines indicate irrigated field soil water potential measurements.

## Yield

Peanut pod yield varied significantly among genotypes and between irrigation treatments within each year (supplementary table 1, figure 3). In 2023, yield under dryland conditions ranged from 2.15 kg (GA GREEN) to 3.86 kg (AU16-28), while irrigated yield ranged from 2.56 kg (587) to 5.32 kg (AU18-35). Across genotypes, irrigation significantly increased pod yield compared to dryland conditions, with the magnitude of response varying by genotype. For example, AU18-35 and AU16-28 maintained high yields under both irrigation regimes, while genotypes such as 587 and GA GREEN showed lower productivity regardless of irrigation. In 2024, pod yields under dryland conditions again demonstrated genotype-specific responses, ranging from 1.97 kg (587 and LINE 8) to 2.87 kg (AUNPL17). Under irrigation, yield ranged from 3.96 kg (587) to 5.82 kg (AU18-35), confirming a consistent positive yield response to irrigation across years. Several genotypes, including AU18-35, PI 502120, and TIFRUNNER, were top performers under irrigation in both years, each exceeding 4.54 kg per plot in 2024. Statistical comparisons revealed that genotype rankings differed more under irrigated than dryland conditions, as reflected by the greater spread and significance groupings (Tukey HSD,  $p < 0.05$ ). Notably, AU18-35 and PI 502120 consistently ranked in the top statistical group under irrigation, suggesting superior yield potential and irrigation responsiveness. Conversely, 587 and GA GREEN consistently yielded less and were among the lower statistical groups across both years and treatments. Environmental conditions

in 2024 resulted in slightly higher dryland yields on average compared to 2023, likely due to improved rainfall distribution (not shown), though these differences between years were not directly tested due to year-specific environmental variation (figure 2). Overall, genotype by irrigation interactions were evident, underscoring the need to evaluate cultivar performance under variable moisture regimes to inform regionally optimized variety selection.

Figure 3. Peanut pod yield production for runner type cultivars (kilograms/plot)

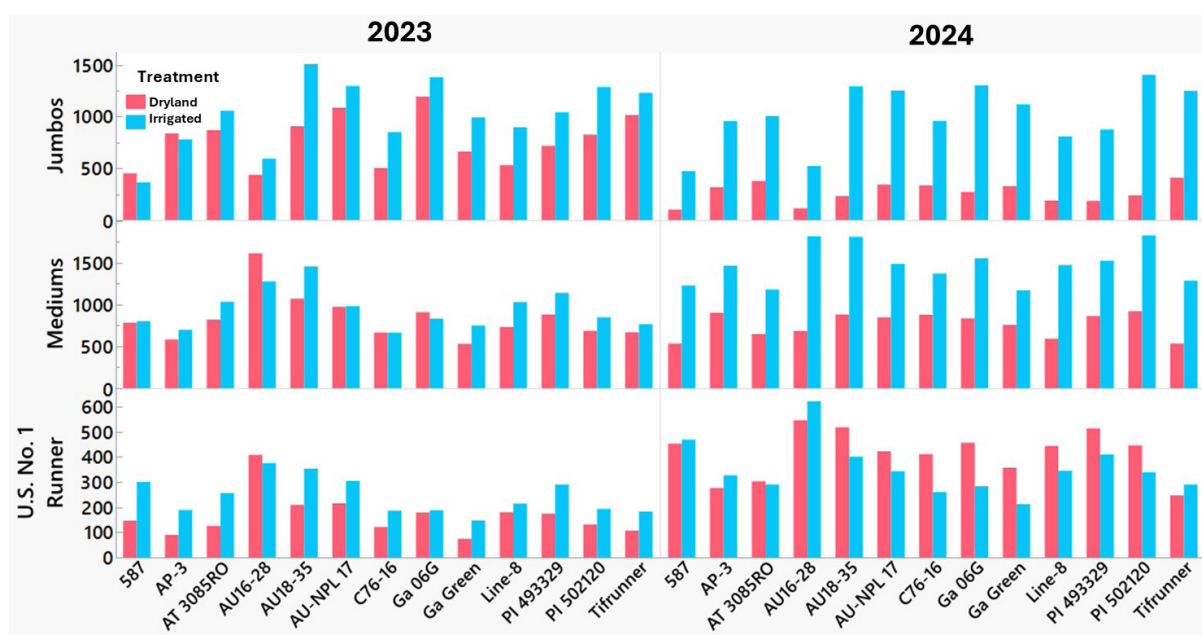


Red boxes denote dryland plot samples; blue boxes denote irrigated plot samples. For differences in mean values see supplementary table 1.

### Size distribution

Commercial pod size distribution differed significantly among genotypes and between irrigation treatments within each year (supplementary table 2, figure 4). Pod yield was classified into three market grades: Jumbos, Medium, and US No. 1. Across both years, irrigation generally increased the yield of all size classes, but the magnitude of response varied by genotype and grade. In 2023, irrigated treatments resulted in a marked increase in Jumbo pod yield for most genotypes. For example, AU18-35 produced the highest Jumbo yield under irrigation (1506.4 g), nearly doubling its dryland yield (907.0 g). Other top performers under irrigation included AT 3085RO (1057.0 g) and GA06G (1379.8 g), while AU16-28 and 587 consistently had lower Jumbo yields under both water regimes. Conversely, under dryland conditions, only a few genotypes such as GA06G, AUNPL17, and AT 3085RO exceeded 1000 g of Jumbos, suggesting superior performance under drought stress. Medium-grade pods followed a similar trend, with irrigated yields being substantially higher for most genotypes. In 2023, the highest Medium yield was observed in GA06G (1516.8 g) and PI 502120 (1306.3 g), while genotypes such as 587 and AP3 produced less than 350 g under irrigation. Notably, AU16-28 and AU18-35 also ranked among the top Medium yielders under irrigation in both years, demonstrating consistent size expansion in response to supplemental moisture. US No. 1 yield patterns showed more variability and smaller absolute differences across treatments. For instance, AU16-28 had the highest yield in 2024 under irrigation (545.8 g), whereas several genotypes including C7616, AP3, and AT 3085RO produced less than 300 g. In contrast, dryland treatments often resulted in low US No. 1 yields across all genotypes, with many producing <300 g. GA06G and TIFRUNNER were exceptions, consistently producing above-average US No. 1 yields in both years and treatments.

Figure 4. Peanut pod yield for runner type cultivars sorted by commercial size classification (grams/plot)



Red bars denote dryland plot samples, blue bars denote irrigated plot samples. For differences in mean values see supplementary table 2.

Among genotypes, AU18-35, GA06G, and PI 502120 exhibited strong and consistent performance across all size categories when irrigated, highlighting their responsiveness and potential for high-grade kernel production under managed water input. In contrast, genotypes such as 587 and GA GREEN yielded poorly in most size classes regardless of irrigation, underscoring their limited commercial value in variable environments. Year-to-year variation was evident, with overall higher size-class yields under irrigation in 2024 compared to 2023, particularly for Jumbos and Mediums. However, genotype by irrigation interactions remained prominent, emphasizing the need for cultivar-specific recommendations based on irrigation potential and targeted market grade.

### Physiology between genotypes

In association with this yield and quality assessment, a simultaneous/complimentary study focused measuring a suite of physiological mechanisms and responses that differentiated whole plant water use responses between genotypes. While presenting much of that data any analysis is outside the scope of this study, some physiological traits were analyzed in conjunction with yield and quality data to determine if there was a functional metric that might correlate with yield. Standard gas exchange metrics were measured with the Li6800 including photosynthetic rate ( $A$ ), stomatal conductance ( $g_{sw}$ ) and water use efficiency (WUE). For all genotypes, we saw a very distinct negative linear relationship between  $A$  and  $g_{sw}$  both between irrigation regimes and years. In 2023  $R^2$  values ranged from 0.45 to 0.79, whereas in 2024 (where mid-day temperatures were significantly higher),  $R^2$  values ranged from 0.78 to 1.0. In both irrigated and dryland plots, as well as across both years we did not find a significant or distinct response between genotypes and their response to declining soil moisture or temperature. Within treatment and between treatment, the rates of compensation as well as conductance and assimilation values varied greatly. We began to see slight separation in WUE between the genotypes at a soil water potential of  $-500$ , which was an observed inflection point in which some genotypes (Tifrunner, AP3, AU18-35) had extremely low WUE, as compared to genotypes whose WUE was almost five times greater (PI 493, Ga06G, Line 8). Spectral metrics including NDVI and SPAD were also measured. For these metrics of plant greenness we would expect to see that NDVI decreases with reduced soil moisture while SPAD slightly increases. However, for all genotypes we again found no sig-

nificant linear trends between or within treatments, and across years. While visually you could justify that the observed values meet standard biological assumptions, differences between genotypes were insignificant.

### Physiology in relation to yield/quality

To see if some of these measured physiological or spectral metrics may indicate a relationship to total yield or shelling characteristics, we ran a multivariate correlation matrix split between irrigation regimes, and year (figure 1). In all 4 cases, we found that there was no significant correlation between our variables (as highlighted in the black rectangles). The only marginal significance we saw was in 2024 between Jumbos and gsw, and WUE ( $p < 0.02$ ,  $p < 0.03$  respectively) in the irrigated plots. Both traits showed a significant and positive linear relationship with the largest of the seed sizes.

## DISCUSSION

### Physiological strategy and field expression

This study evaluated peanut genotype performance under irrigated and dryland conditions at the whole-farm scale, with a particular focus on yield quantity and commercial size class distribution. The genotypes used in this trial were previously characterized in controlled, single-plant studies at Auburn University [Zhang et al. 2022, Zhen et al. 2022], where distinct physiological strategies were observed. Specifically, PI 502120 and AUNPL17 were classified as anisohydric, exhibiting high transpiration and dynamic water potential responses, while AU16-28 and Line 8 displayed more conservative, isohydric behavior. In theory, these divergent water-use strategies should drive predictable differences in drought tolerance, carbon allocation, and yield under field conditions [Martínez-Vilalta et al. 2017].

However, our field-scale observations did not reflect this expected physiological stratification. Gas exchange and spectral trait data were highly variable within genotypes, across irrigation treatments, and between years. As a result, the hypothesized link between intrinsic water-use strategy and yield performance was not consistently confirmed in practice. For example, although PI 502120 exhibited strong performance under irrigation, it did not consistently outperform under dryland conditions, despite its anisohydric classification. Likewise, isohydric genotypes such as AU16-28 did not exhibit the level of yield penalty under water-limited conditions that might be expected from early stomatal closure and reduced carbon gain.

This lack of concordance may be explained by the complexity of the soil–plant–atmosphere continuum at field scale, where root-soil dynamics, evaporative demand, and plant–plant interactions add layers of variability absent in single-plant experiments. Additionally, annual weather variation – especially in the timing and intensity of rainfall – likely contributed to differential expression of physiological traits. Our findings align with recent literature emphasizing that plant water use strategies may be context-dependent and plastic, rather than fixed [Martínez-Vilalta et al. 2017]. This challenges the notion of a consistent genotype “fingerprint” and underscores the need for integrated field-based assessments across environments. The absence of clear physiological stratification at field scale also suggests that additional structural indicators, including canopy development, biomass allocation, and reproductive architecture may be necessary to better explain how water use strategies utility influence yield formation and pod size distribution under variable environmental conditions [Sreelatha 2019].

### Yield, size distribution, and drought priming

Despite the physiological variability observed, genotype-specific differences in yield and commercial pod size class were evident and influenced strongly by irrigation regime and year. In both 2023 and 2024, genotypes such as AU18-35, GA06G, and PI 502120 consistently produced higher

yields of Jumbo and Medium pods under irrigation, suggesting strong responsiveness to supplemental moisture. However, year effects were substantial. In 2023, dryland yields were comparable to irrigated yields across many genotypes, while in 2024, the yield penalty in dryland plots was much more pronounced.

These differences could be possibly attributed to a form of drought priming de Camargo Santos et al. 2024, Ru et al. 2025. In 2023, soil moisture was limited early in the season, potentially inducing mild, non-lethal stress that activated drought acclimation mechanisms such as osmotic adjustment or root proliferation. These responses are known to enhance WUE and reproductive resilience in peanut [Rowland et al. 2012, Zurweller et al. 2018]. In contrast, in 2024, early- and mid-season soil moisture remained high, but a late-season drought event occurred during pod filling – a critical period when stress can severely impact yield. This scenario likely caught many genotypes unprepared, particularly in dryland plots, leading to sharper yield declines and greater separation from irrigated performance.

Commercial pod size class distribution further illustrated the interaction between genotype and seasonal stress dynamics. While AU18-35 and GA06G maintained high proportions of Jumbos and Mediums under both treatments in 2023, their performance under dryland conditions declined in 2024. Conversely, genotypes like C7616 and GA GREEN showed consistently lower size-class yields across treatments and years, reflecting limited plasticity or adaptation.

Together, these results suggest that yield and quality metrics in peanut are shaped not only by genotype and water regime, but also by the timing and intensity of stress exposure. Drought priming and stress memory effects, especially when they occur during early vegetative stages, may play a critical role in shaping yield outcomes and buffering against reproductive failure. These insights have important implications for cultivar selection and irrigation timing in water limited environments. Rather than classifying genotypes strictly by isohydric or anisohydric behavior, emphasis should be placed on identifying genotypes with flexible and resilient responses to variable moisture regimes.

## CONCLUSIONS

This study demonstrates the complexity of translating genotype-specific physiological strategies into consistent agronomic outcomes under field-scale conditions. While controlled environment and single-plant studies have successfully characterized intergenotype differences in drought response strategies such as isohydric versus anisohydric behavior, these distinctions were not clearly expressed at the whole-farm scale. Yield and commercial pod size distributions were shaped not only by genotype and irrigation treatment, but also by seasonal weather variability, soil conditions, and the inherent complexity of the soil–plant–atmosphere continuum.

It is worth emphasizing that small-plot and individual-plant studies remain critical for uncovering fundamental physiological traits and informing breeding and phenotyping frameworks. However, as our findings suggest, these insights do not always scale predictably to larger, operational environments where interacting stressors, plant-plant dynamics, and environmental heterogeneity may mask or modify physiological expression. In particular, irrigation increased peak pod yield from approximately 3.9 kg per plot under dryland conditions to 5.8 kg per plot under favorable moisture conditions, depending on genotype and year, highlighting the magnitude of management effects relative to genotype classification.

In particular, the concept of drought priming emerged as a potential explanation for year-to-year variation in performance. Early-season water deficits in 2023 may have conferred a degree of stress acclimation that buffered yield losses, while the absence of such priming in 2024 left crops more vulnerable to late-season drought. These observations underscore the importance of timing and sequence in stress exposure factors that are often absent from controlled trials but critical in real-world settings.

Ultimately, while it remains important to understand plant survival and tolerance traits, this study highlights the need for a more nuanced approach to genotype evaluation one that accounts for environmental variability and the emergent properties of complex production systems. Future breeding and management strategies should emphasize not only trait potential, but also trait plasticity and resilience under variable field conditions.

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