Genotypic Differences in Current Peanut (*Arachis hypogaea* L.) Cultivars in Phenology and Stability of These Traits under Different Irrigation Scheduling Methods

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ABSTRACT

Understanding differences among peanut (*Arachis hypogaea* L.) cultivars in growth and phenology and the interactions with environment (G X E interactions) for these traits allows predictions for yield potential or performance in variable environments. Despite the importance of this information, very little quantitative data exists on the differences in aboveground growth, canopy architecture, and reproductive phenology for currently grown peanut cultivars. This study quantified differences in these traits among eight peanut cultivars and explored whether irrigation scheduling method (a factor of environment) affected the development in these traits through the season in 2004 and 2005. As expected, year to year variability in environmental conditions (most likely timing of rainfall events during the growing season) significantly affected growth habit across cultivars. However, the irrigation scheduling method, despite differences in total water applied among methods during the season, had no effect on any of the measured traits. This result is likely due to the fact that all methods were adequately supplying crop water demand. Genetic variability in all of the measured growth and phonological traits was strong despite the expectation that cultivars were genetically similar. Further, the lack of significant interactions between year and cultivar for most of the plant growth and reproductive characteristics also indicated a strong genetic component to these traits. One overall trend noted was that late-maturing cultivars had, on average, higher maximum values of LAI, stem mass, and leaf mass measured in the late growth period. Differences in isotopic composition were also strong among cultivars; the cultivars Georgia-02C and Tifrunner had significantly higher isotopic levels (and thus water-use efficiency) than Georgia-01R, Georgia Green, and AP3 across years. Aside from the obvious relationships between pod number and weight, the strongest predictors of reproductive output were late-season traits including leaf weight and LAI. This study successfully documented variability among peanut cultivars in many important traits linked to overall production.

Key Words: irrigation, peanut growth, dry matter partitioning, water-use efficiency.

While all eyes in crop production research are typically focused on assessing, manipulating, and propagating variability in yield among crop cultivars, all too often very little is known about cultivar differences in growth habit, phenology, and ontogeny that are causal agents of that yield variability. This is certainly the case among today's cultivated peanut (*Arachis hypogaea* L.) genotypes where almost no information is available regarding cultivar differences in aboveground growth habit, leaf size, flowering potential, tissue nutrient contents, harvest index, nor on the differences in development of these traits through the season. On the surface it may appear that this information has relatively little value to either scientist or producer. However, in the ever-narrowing gap between economic viability and bankrupted ruin in the U.S. farm environment, these traits can have very significant implications on final peanut production and can increase the chance of economic success. Cultivar choice can be a ''make or break'' decision for a producer and having information about a cultivar's growth habit can be a critical component of this decision. In today's southeastern U.S. peanut production environment, there are roughly 8–10 cultivars that are available for a producer to choose from. Up front, this means that information regarding variability among cultivars in growth habit and reproduction could help a grower choose cultivars that will yield optimally under particular field conditions. Beyond these producer benefits, science can also reap the rewards of further information about cultivar variation because it represents essential input into both breeder programs and crop model development.

The existence of peanut cultivar variability in growth and development is questionable because of

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the increasingly narrow gene pool foundation of current peanut germplasm as a result of industry and grower preferences. The cultivars used in the southeastern U.S. peanut production are almost solely runner market types because of the preference of the processing industry towards their shelling, size, and flavor characteristics. In addition, there is an absolute necessity for the sole use of *Tomato spotted wilt virus* resistant runner peanut genotypes, often derived from similar parental germplasm, because of the devastating economic effects of this plant virus. Both of these conditions have significantly narrowed the genetic background and variability among peanut cultivars making them genetically quite similar in many ways (Kottapalli *et al.*, 2007). Therefore, any variation among current cultivars is essential to document and quantify.

Of course environmental growth conditions can have an impressive influence on the expression of inherent genetic differences in peanut cultivars. One such influence is the application of supplemental irrigation during the growing season. Nearly 50% of U.S. peanut production is under irrigation and this percentage is expected to expand as the global climate becomes warmer and droughts become more frequent and severe in many of these production regions (Lamb *et al.*, 2004). Surprisingly, within the southeast U.S., irrigation is vital to production of economically sustainable yields despite the widely presumed image of the area as receiving adequate rainfall. Although irrigation can increase yields by as much as 50% (Lamb *et al.*, 1997; Lamb *et al.*, 2004), skyrocketing fuel prices ($30.00 U.S. per hectare – Nathan Smith pers. comm.) necessitate that irrigation application be as efficient as possible or it will quickly lose its cost effectiveness.

Currently there are three established and utilized irrigation scheduling methods for peanut: 1) Irrigator Pro (IP), 2) the EASY Pan (Evaporation-based Accumulator for Sprinkler-enhanced Yield - EZ), and 3) the University of Georgia's Extension check book method (UGA-EXT). Irrigator Pro is based on monitoring soil temperatures and incrementing water application with crop growth stage (Lamb *et al.*, 1993; Davidson *et al.*, 1998). The EASY Pan method uses a galvanized washtub and float with different sized mesh screening over the top of the tub to simulate evaporation losses affected by different levels of crop cover (Thomas *et al.*, 2004). The University of Georgia's Extension checkbook method is an incrementally increasing model linked to crop stage and has now been updated by J.P. Beasley (unpublished data). To date, no studies have actually compared the efficacy of these methods on peanut production. Variation among peanut cultivars as to how they respond to irrigation scheduling methods is most likely due to: 1) differences in growth habits; 2) variation in the time period required for fruit maturation; and 3) genetic differences in water use strategies and water-use efficiency (Rowland and Lamb, 2005). Irrigation scheduling method could have critical effects on the plasticity of these traits that translate into long-lasting effects on final crop yield.

The current study was aimed at documenting and quantifying any variability among several currently grown peanut cultivars in traits that could have significant impact on physiological functioning of the crop and thus influence yield. Secondly, the differential effects on peanut development of the three most commonly used irrigation scheduling methods (IP, EZ, and UGA-EXT) were tested. The following specific objectives were addressed: 1) is there any variation in morphology, ontogeny, and reproduction among currently grown peanut genotypes? and 2) what is the effect of irrigation scheduling method on these traits, especially on carbon isotope discrimination as a representation of seasonal water-use efficiency?

Materials and Methods

Field Preparation and Management

The experiment was carried out at the University of Georgia's C.M. Stripling Irrigation Research Park in Camilla, GA during the 2004 and 2005 growing seasons. Soil was classified as a Lucy loamy sand (loamy, kaolonitic, thermic, Arenic, Kandiudults). Soil samples were collected in the previous fall seasons and commercial lime was added according to extension service recommendations to modify soil pH by planting. Also during the previous fall seasons, the field was chiseled and cultivated prior to planting a rye cover crop (*Secale cereale* L. cv Wrens' Abruzzi). This cover crop was then terminated approximately 60 days prior to planting in both years using glyphosate (Roundup®, Monsanto Co., St. Louis, MO, USA). Just prior to planting peanut, the field was strip tilled using a KMC (Kelley Manufacturing Co., Tifton, GA) strip till unit with double coulters.

Peanut was planted on 11 May 2004 and 24 May 2005. Peanut rows were planted in a twin row design with an intra-row plant distance of 18 cm and seed spacing within each twin approximately 5 cm using a Monosem planter. Seed were treated with *Rhizobium* inoculant prior to planting and phorate insecticide was applied in the row during planting for early season thrips control. Separate peanut genotypes

were planted in plots consisting of two twin rows spaced 91 cm apart and 16.8 m in length. Plots were arranged in a randomized split plot with irrigation scheduling methods as main plot factors and cultivars as subplot factors Eight peanut genotypes were tested in both 2004 and 2005: AP-3 (Gorbet, 2007), Carver (Gorbet, 2006), Tifrunner (Holbrook and Culbreath, 2007), C-99R (Gorbet and Shokes, 2002), Georgia-01R (Branch, 2002), Georgia-02C (Branch, 2003), Georgia-03L (Branch, 2004), and Georgia Green (Branch, 1996). These cultivars differed in relative maturity level: AP-3 (142–147 days after planting – DAP), Carver (135–140 DAP), Tifrunner (149–154 DAP), C-99R (149–154 DAP), Georgia-01R (149–154 DAP), Georgia-02C (149–154 DAP), Georgia-03L (135–140 DAP), and Georgia Green (135–140 DAP).Peanut genotypes were subjected to three different irrigation scheduling methods currently utilized in peanut production in the southeastern USA: 1) Irrigator Pro (IP); 2) the UGA EASY Pan (EZ); and 3) the UGA extension check book method (UGA-EXT). When each method called for water application, irrigation was applied through a lateral move irrigation system with drop down nozzles. The crop was maintained using recommended applications of herbicides and fungicides during the year. The crop was harvested on 17 September and 8 October in 2004 and 30 September and 24 October in 2005 based on the maturity level of the developing pods (Williams and Drexler, 1981).

Plant Collection and Analysis

Leaf Area Index (LAI) measurements and plant collections were conducted on the following dates in 2004: 15 June, 12 July, and 17 August; and in 2005: 23 June, 1 August, and 6 September. LAI measurements were taken using an LAI-2000 meter (LI-COR Biosciences, Lincoln, NE, USA) across a single row in each plot, using one above canopy measurement and four below canopy measurements spaced in line with the row and every 23 cm away from that point for a total area coverage of 91 cm. Within each genotype X irrigation scheduling method plot, one second nodal position leaf was collected on the main apex stem. Just after excision, chlorophyll content was measured using the Minolta SPAD (Soil-Plant Analyses Development Unit, Minolta Corp., Ramsey, N.J., U.S.A.) chlorophyll meter directly after removal from the plant. The SPAD chlorophyll meter measures absorbance by plant tissues of wavelengths in the visible spectrum and serves as a measure of the relative internal concentration of chlorophylls a and b. One SPAD chlorophyll reading was taken on each of the four leaflets, avoiding the midrib, and then averaged for one chlorophyll reading per plant to correct for possible non-homogeneous distribution of chlorophyll throughout the leaf (Monje and Bugbee, 1992). After collection of the second nodal leaf, the entire plant was dug up leaving the upper root system intact. Tetrafoliate leaves and whole plants were then placed on ice and refrigerated at 4 C until further analysis. A second intact plant was collected and analyzed for: percent N, P, K, Mg, Ca, S, and ppm of B, Zn, Mn, Fe, and Cu (Waters Laboratory, Camilla, GA).

In the laboratory, whole plants were examined and measured for: total number of live flowers, total number of pegs, total number of pods, and internode length on the apex stem. The plants were then divided into leaves, internodes, and pods. Sampled second nodal leaves were hydrated in distilled water for at least three hours prior to leaf area measurement in order to bring them all to a standardized turgor level (Nageswara Rao *et al.*, 2001). Leaflets were removed from each petiole and the leaf area of the four leaflets was measured with an LI-3000A leaf area meter (LI-COR Inc., Lincoln, NE, U.S.A.) and summed to give total leaf area. Whole plant biomass components and second nodal leaves were oven dried at 60 C for 72 hours and weighed. Leaves were then fine ground using a Braun ® (model KSM2) coffee grinder and analyzed for carbon isotope composition ($\delta^{13}C$), $\delta^{15}N$, %C, and %N. Specific leaf area (SLA) was calculated as the ratio of leaf area to leaf dry weight. Harvest index on whole plants was calculated as the ratio of pod weight to the sum of pod, internode, and leaf weights.

Isotope Analysis

In both years leaf samples from each peanut genotype and irrigation scheduling method were collected for analysis of the following traits: $\delta^{13}C$, $\delta^{15}N$, percent carbon (%C), percent nitrogen (%N) and C/N ratio from four replications in 2004 and three in 2005. One second nodal apex leaf was collected from each plot. Sampling was completed in a single day and within the morning hours (800–1200 EDT). In both years, peanut leaf tissue was collected approximately 90 days after planting. This phenological period is associated with the highest ribulose bisphosphate carboxylase (rubisco) levels and concomitantly the highest photosynthetic levels of the season thereby ensuring isotopic differences among genotypes would be most evident (Nageswara Rao and Wright, 1994; Nageswara Rao *et al.*, 1995). Tissue collection was standardized to the second nodal apex position on leaves that had relatively no insect or disease damage. The tetrafoliate second nodal leaf was excised, placed on ice, and refrigerated at 4 C until further analysis.

Isotopic composition of the leaf samples was analyzed at the Colorado Plateau Stable Isotope Laboratory, Department of Biological Sciences, Northern Arizona University. Samples of the ground leaves (2 mg, +/− 0.2 mg) were weighed, sealed in capsules and, along with standards, loaded into the elemental analyzer autosampler (a ''Zero Blank'' autosampler from Costech Analytical Technologies in Valencia, CA). Samples and standards were combusted in the elemental analyzer (Carlo Erba NC2500 elemental analyzer coupled with a Thermoquest Finnigan Delta plus isotope ratio mass spectrometer). Lab standards, which were calibrated against internationally distributed isotope standards, were analyzed at regular intervals throughout the sample runs. The resulting N_2 and CO_2 gases (along with isotopic reference gases for N_2 and CO_2) were admitted to the mass spectrometer via Finnigan's Conflo II interface. Data were collected and processed by Finnigan's Isodat software. Sample results are based on one analysis per sample ($\delta^{13}C$, $\delta^{15}N$, %N and %C were all determined with the same analysis). Isotope results are reported in delta notation vs. Air (for nitrogen) and vs. PDB (for carbon) in permil. Stable carbon isotope composition was expressed as $\delta^{13}C$ where $\delta^{13}C$ (‰) = [(R sample/R standard)-1] $\times$ 1000, and where R is the $^{13}C/^{12}C$ ratio. Composition of $^{13}C/^{12}C$ ($\delta^{13}C$) rather than discrimination of ^{13}C (Δ) is reported due to the possible differences in atmospheric components linked to natural or man-made C emissions between seasons.

Data Analysis

Statistical analyses were performed using JMP SAS (SAS 1997). Factorial analysis of variance (ANOVA) was used to determine the effect of year, period within the season (early, mid, and late), cultivar, irrigation scheduling method, and all possible two-way interactions on growth, tissue nutrient, and reproductive traits. Factorial ANOVA was also used to determine the effect of year, cultivar, irrigation scheduling method, and all two-way interactions on isotope, C, and N composition of leaf tissue collected at the optimal physiological time period. Differences among multiple levels of a given factor were determined using a Tukey's HSD multiple comparisons test. Pearson product-moment correlations were used to determine the relationship between late season pod number and pod weight with growth, nutrient, and reproductive characteristics. For those traits showing significant correlation with either late season pod number of pod weight, a stepwise regression analysis with forward selection was performed individually to determine the predictive value of those correlated traits.

Results

Environmental Conditions

Total irrigation applied in each irrigation scheduling method differed among methods with the greatest water amounts applied for the UGA Extension method in both 2004 and 2005 respectively (216 mm, 240 mm), followed by the Irrigator Pro method (184 mm, 160 mm), and least for the EZ Pan method (114 mm, 124 mm) (Table 1). Differences in *total* rainfall during the growing season between years were minimal (604 mm in 2004 and 615 mm in 2005). However, seasonal patterns of rainfall for the growing seasons of 2004 and 2005 did differ (Figure 1; Georgia Weather Net; http://www.georgiaweather.net/). Most notably, the rainfall received during the critical periods of peak flowering and fruit set/maturation (June–August) was 315 and 541 mm in 2004 and 2005, respectively. Maximum ambient temperatures were similar in 2004 and 2005 across the growing season and predominantly hovered between 30 and 35 C with lower maximums both early (1 May–15 May) and late in the season (1 October - harvest) (Figure 2; Georgia Weather Net; http://www.georgiaweather.net/). Minimum temperatures were also similar for both years with the predominant range between 17 and 23 C.

Growth, Nutrient, and Reproductive Traits

ANOVA results for growth, tissue nutrient, and reproductive traits showed significant differences in most traits between 2004 and 2005 and period within the growing season during these years. (Table 2). Significant year differences illustrate possible annual differences in climatic patterns (likely rainfall during fruit initiation and maturation), while period differences indicate the obligate changes in phenology as the crop develops. Less predictable were the significant differences among peanut cultivars in all of the measured traits, indicating the presence of inherent genetic differences in growth, nutrient, and reproductive characteristics despite the often assumed lack of variability among cultivated peanut germplasm. The lack of significant interactions between year and cultivar for most of the plant growth (except LAI) and reproductive (except number of pods) traits indicated that the environment may have had minimal impact on changing these inherently genetic traits. Irrigation scheduling method showed a lack of effect across the board among all measured traits, including no significant interactions between irrigation scheduling method and cultivar (Table 2).

Patterns in growth trait means across the season in 2004 and 2005 indicate some differences in

Table 1. Water application amounts (in mm) and dates for each irrigation scheduling method in 2004 and 2005: EZ = EZ Pan; UGA Extension = UGA-EXT growth stage model; IP = Irrigator Pro. In 2004 and 2005, plots were planted 11 May and 24 May, respectively.

		Irrigation Scheduler		
Event No.	Date	EZ	UGA-EXT	IP
1	11 May 2004	12.7	12.7	12.7
2	24 May 2004	19.05	19.05	19.05
3	25 May 2004	19.05	19.05	19.05
4	7 July 2004	0	25.4	0
5	14 July 2004	0	0	31.75
6	20 July 2004	0	0	25.4
7	24 July 2004	25.4	25.4	25.4
8	26 July 2004	12.7	12.7	0
9	4 August 2004	0	25.4	25.4
10	9 August 2004	25.4	25.4	25.4
11	18 August 2004	0	25.4	0
12	30 August 2004	0	25.4	0
TOTAL		**114.3**	**215.9**	**184.15**
TOTAL + RAINFALL		**718.3**	**819.9**	**788.15**
1	25 May 2005	16.26	16.26	16.26
2	26 May 2005	12.7	12.7	12.7
3	27 June 2005	25.4	0	0
4	19 July 2005	0	20.32	0
5	22 July 2005	25.4	0	0
6	26 July 2005	0	0	25.4
7	12 August 2005	0	25.4	0
8	15 August 2005	0	0	25.4
9	17 August 2005	0	25.4	0
10	22 August 2005	0	0	25.4
11	24 August 2005	0	0	15.24
12	25 August 2005	0	25.4	0
13	6 September 2005	0	25.4	0
14	9 September 2005	0	25.4	0
15	14 September 2005	25.4	25.4	0
16	16 September 2005	19.05	0	0
17	19 September 2005	0	25.4	25.4
18	23 September 2005	0	0	14.22
19	12 October 2005	0	12.7	0
TOTAL		**124.21**	**239.78**	**160.02**
TOTAL + RAINFALL		**739.21**	**854.78**	**775.02**

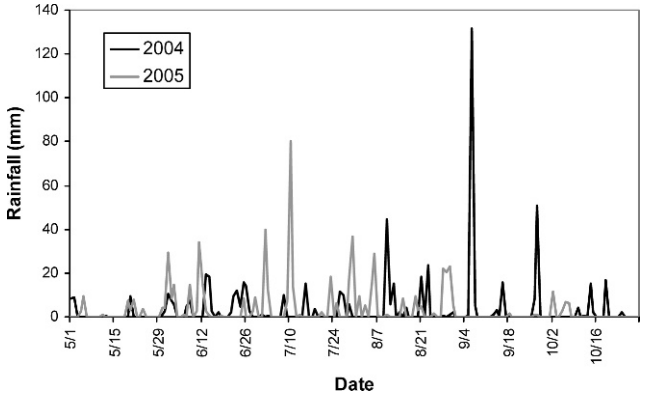

Fig. 1. Annual rainfall totals for 2004 and 2005 at the University of Georgia Stripling Irrigation Research Park, Camilla, GA.

growth and reproduction between mid- and late-maturing cultivars. The late-maturing cultivars (C99R, GA01R, GA02C, Tifrunner) on average had higher maximum values of LAI, stem mass, and leaf mass measured in the late growth period, with the Georgia-01R cultivar having the highest values overall (Figure 3). The larger LAI of late-maturing cultivars was due in part to the larger late season production of stems and leaves over mid-maturing cultivars. The overall pattern across cultivars showed a customary linear increasing pattern for LAI, stem mass, and leaf mass as the season progressed and as plant size increased. Contrastingly, internode length peaked in mid-season and declined into late season, likely indicating a shift in allocation patterns from stems to leaves and reproductive structures. Trade-offs between allocation patterns to different tissue types revealed interesting variability in growth strategies among cultivars. For example, the cultivar Georgia-01R had a large biomass allotment to stems and leaves, but maintained short internode lengths, thereby maintaining a mid-level LAI. In contrast, the cultivar Carver had high LAI values probably attributed to its large internode lengths; while the relatively small LAI values for Georgia-03L were linked to its short internode lengths (Figure 3).

Tissue nutrient levels showed minimal variability among cultivars with higher differences occurring among periods during the growing season (Table 3). SPAD chlorophyll content showed an increasing accumulation as the season progressed. Late-maturing cultivars appeared to accumulate chlorophyll somewhat faster than mid-maturing genotypes and variation in SPAD chlorophyll was maximal at mid-season indicating a difference among cultivars in their ability to accumulate chlorophyll during the early and peak reproductive periods. The patterns in SPAD levels did not reflect leaf nitrogen as would be expected. Across all cultivars, mean N was highest in the early season and lowest during the late season (Table 3).

Reproductive characters showed variability among cultivars that was likely genetically based because patterns of variation were similar across years (data not shown) and irrigation scheduling method had no significant effect within years. Flower and peg production peaked in mid season for most cultivars except for AP-3 (mid-maturing) and Georgia-01R (late-maturing) which showed maximum peg number per plant at the late season period, while number of pods per plant showed a positive linear pattern and pod mass an exponentially increasing pattern across cultivars as the

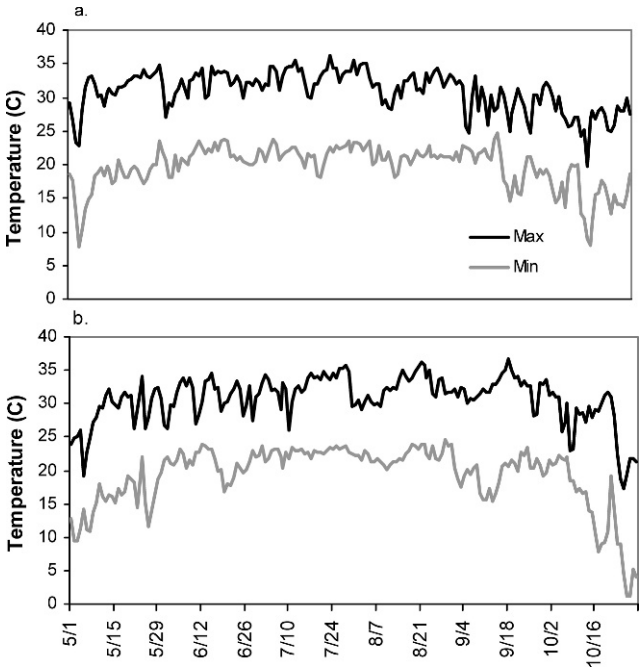

Fig. 2. Maximum and minimum temperatures in 2004 and 2005 at the University of Georgia Stripling Irrigation Research Park, Camilla, GA: a) 2004, b) 2005.

season progressed (Figure 4). Similarly, Georgia-01R had a high number of flowers and a higher number of pegs and pods per plant than all of the other cultivars except Georgia-03L for pegs and Georgia Green, Georgia-03L, and Carver for pods. Pod weight showed slightly different patterns of variability among cultivars: Georgia-03L had the heaviest pods, while the high peg and pod producer, Georgia-01R had only medium weight pods significantly lighter than Georgia-03L but significantly heavier than Tifrunner only (Figure 4). Patterns of conversion from flowers to pegs and eventually pods can be ascertained by examining the relative numbers of each consecutive tissue type. High ''efficiency'' of conversion of flowers into pegs and pegs into pods could be seen in the cultivar Carver which had low numerical flower production but mid numbers of pegs and pods in the late season. Alternatively, low ''efficiency'' of tissue conversion could be seen in the cultivar AP-3 which had the highest numerical flower counts per plant at mid-season among mid-maturing cultivars but the lowest numerical pod count per plot in the late season indicating that many of its flowers were never converted to pegs and pods. Overall high numbers of flowers, pegs, and pods throughout the season were evident in the cultivars Georgia-01R and Georgia-03L cultivars, with overall low counts of these tissues evident in Tifrunner (Figure 4).

Differences among cultivars in the efficiency of tissue assimilation and conversion to yield were illustrated in the variability in harvest index at the end of the season (Figure 5). The cultivar Georgia-03L had the highest harvest index value of any of the cultivars except Georgia Green. Interestingly, it appears that the low harvest indices seen in Tifrunner and Georgia-01R resulted from two different partitioning strategies: Tifunner had overall low leaf and stem mass coupled with low pod mass while Georgia-01R had overall high leaf and stem mass coupled with high pod mass. The resulting ratios produced the same relative low harvest index. In contrast, the high harvest index of Georgia-03L was a consequence of modest leaf and stem production coupled with high pod mass in relation to the other cultivars.

Isotopes

Isotope analysis measured at the time period when physiological assimilation is maximal showed a strong year effect similar to that experienced by the growth, reproductive, and tissue traits (Table 4). Also similar to these other traits, isotope composition was not affected by irrigation scheduling method. However, year did have a significant interaction with irrigation scheduling method for all the traits except $\delta^{15}N$. For $\delta^{13}C$, this interaction was likely significant because the isotopic composition in the EZ treatment responded differently among years; EZ plants were more water-use efficient in 2004 but showed the lowest efficiency among the scheduling treatments in 2005 (Figure 6). For %C, %N, and C/N ratio the significant interaction between year and irrigation scheduling method was driven by different directional responses between years in the IP treatment (data not shown). Among cultivars, Georgia-02C and Tifrunner had significantly higher $\delta^{13}C$ (and thus water-use efficiency) than Georgia-01R, GA Green, and AP-3 across years; AP-3 had the lowest levels of leaf $\delta^{13}C$ than any of the cultivars except Georgia-01R and Georgia Green (Figure 7).

Correlation and Regression Analyses

The correlation between pod number and pod weight in the late season was examined for all the growth, reproductive, and nutrient analyses in all three seasonal periods (early, mid, and late) across years and cultivars to determine the possible causal and predictive strength of these measured traits. Across all these traits, late-season pod number was significantly correlated only with mid-season LAI, peg number per plant, and pod number per plant, and late-season pod weight per plant, leaf weight per plant, and stem weight per plant (Table 5). Likewise, late-season pod weight per plant was correlated with mid-season LAI, peg number, pod number, pod weight, and SPAD, and late-season LAI, pod number, harvest index, and

Table 2. ANOVA for the growth traits of 8 peanut genotypes that were grown in both 2004 and 2005 at the Stripling Irrigation Research Park; F-values and P-values given. Factors include year (2004, 2005), period during the growth season (early, mid, and late), peanut cultivar, and irrigation scheduling method (EZ, UGA-EXT, and IP). Statistically significant effects are listed in bold **type.**

	Traits									
	LAI		Stem Wt.		Leaf Wt.		SLA		Internode Length	
Factors	*F value*	*P value*	*F value*	*P value*	*F value*	*P value*	*F value*	*P value*	*F value*	*P value*
Plant growth										
Year, df=1	**37.5**	**0.0001**	**22.9**	**0.0001**	**30.5**	**0.0001**	2.4	0.1184	2.5	0.1130
Period, df=2	**1729.1**	**0.0001**	**459.6**	**0.0001**	**325.5**	**0.0001**	**35.0**	**0.0001**	**414.6**	**0.0001**
Cultivar, df=7	**17.5**	**0.0001**	**4.4**	**0.0001**	**7.3**	**0.0001**	**2.0**	**0.0489**	**7.4**	**0.0001**
Irrigation, df=2	1.6	0.2004	0.1	0.9281	1.0	0.3773	0.3	0.7199	0.2	0.8401
Year*Period, df=2	**12.5**	**0.0001**	**4.0**	**0.0183**	**6.9**	**0.0011**	**6.6**	**0.0016**	**28.8**	**0.0001**
Year*Cultivar, df=7	**3.8**	**0.0005**	1.0	0.4184	0.8	0.6218	1.1	0.3427	0.9	0.5097
Year*Irr, df=2	0.0	0.9877	0.8	0.4345	1.5	0.2303	0.6	0.5251	**4.9**	**0.0078**
Period*Cult, df=14	**7.0**	**0.0001**	**3.0**	**0.0002**	**3.6**	**0.0001**	**1.8**	**0.0384**	**5.0**	**0.0001**
Period*Irr, df=4	**2.6**	**0.0348**	0.5	0.7321	1.2	0.3262	1.1	0.3575	0.2	0.9191
Cult*Irr, df=14	0.5	0.9482	0.6	0.8775	0.6	0.8494	0.6	0.8853	0.8	0.7154

	Leaf P		Leaf Ca		Leaf K		Leaf N		SPAD[1]	
	F value	*P value*	*F value*	*P value*	*F value*	*P value*	*F value*	*P value*	*F value*	*P value*
Canopy nutrients										
Year, df=1	**9.3**	**0.0025**	**13.1**	**0.0003**	**5.7**	**0.0173**	**306.0**	**0.0001**	**232.6**	**0.0001**
Period, df=2	**92.3**	**0.0001**	**211.2**	**0.0001**	**232.0**	**0.0001**	**569.2**	**0.0001**	**77.7**	**0.0001**
Cultivar, df=7	**3.0**	**0.0042**	**4.6**	**0.0001**	**4.2**	**0.0002**	**15.8**	**0.0001**	**16.4**	**0.0001**
Irrigation, df=2	0.9	0.3894	1.1	0.3319	0.0	0.9948	1.7	0.1768	1.6	0.1943
Year*Period, df=2	**11.6**	**0.0001**	**4.0**	**0.0185**	**17.1**	**0.0001**	**101.0**	**0.0001**	**90.0**	**0.0001**
Year*Cultivar, df=7	**2.4**	**0.0188**	**2.1**	**0.0451**	**4.0**	**0.0003**	**3.7**	**0.0007**	0.7	0.6370
Year*Irr, df=2	0.7	0.5014	0.5	0.6162	0.2	0.7815	2.7	0.0704	2.4	0.0961
Period*Cult, df=14	**2.4**	**0.0031**	**4.0**	**0.0001**	**2.5**	**0.0020**	**2.5**	**0.0023**	1.4	0.2059
Period*Irr, df=4	0.7	0.5911	0.5	0.7451	1.3	0.2715	0.6	0.6922	0.3	0.07333
Cult*Irr, df=14	0.9	0.5318	0.8	0.6718	0.6	0.8672	1.4	0.1697	0.1	0.9999

	No. Flowers		No. Pegs		No. Pods		Pod Wt.		Harvest Index	
	F value	*P value*	*F value*	*P value*	*F value*	*P value*	*F value*	*P value*	*F value*	*P value*
Reproduction										
Year, df=1	**18.8**	**0.0001**	0.1	0.7250	0.2	0.6578	1.2	0.2701	**26.5**	**0.0001**
Period, df=2	**35.1**	**0.0001**	**296.3**	**0.0001**	**374.1**	**0.0001**	**643.8**	**0.0001**	**2096.7**	**0.0001**
Cultivar, df=7	**3.4**	**0.0017**	**6.8**	**0.0001**	**12.6**	**0.0001**	**9.4**	**0.0001**	**30.2**	**0.0001**
Irrigation, df=2	0.1	0.8937	0.3	0.7491	0.1	0.8989	1.2	0.3055	0.1	0.8636
Year*Period, df=2	**40.0**	**0.0001**	0.5	0.6233	1.2	0.3081	2.9	0.0589	**6.8**	**0.0013**
Year*Cultivar, df=7	0.8	0.5558	0.1	0.9955	**3.0**	**0.0041**	1.6	0.1279	1.7	0.1196
Year*Irr, df=2	1.3	0.2627	**3.2**	**0.0435**	0.5	0.6166	0.1	0.9088	1.3	0.2624
Period*Cult, df=14	**2.0**	**0.0167**	**4.1**	**0.0001**	**6.2**	**0.0001**	**5.5**	**0.0001**	**9.8**	**0.0001**
Period*Irr, df=4	1.3	0.2843	1.6	0.1700	2.2	0.0648	**2.5**	**0.0432**	1.6	0.1676
Cult*Irr, df=14	0.6	0.8811	0.7	0.7627	0.7	0.8134	0.8	0.6153	0.6	0.8486

[1]df for Period = 1, Year*Period =1, Period*Cult = 7, Period*Irr = 2; samples were collected only during early and mid periods.

tissue Ca. When the respective significant traits were added into stepwise regression models for late-season pod number and for late-season pod weight separately, there were even fewer traits that were predictive of reproductive output . For late-season pod number, the following traits were significant in the model and resulted in a cumulative R^2 value of 0.86: late-season pod weight and leaf weight, and mid-season peg number and pod number (Table 6). Similarly, the following traits were significantly predictive of late-season pod weight with a cumulative R^2 value of 0.92 for the model: late-season pod number and LAI, and mid-season peg number.

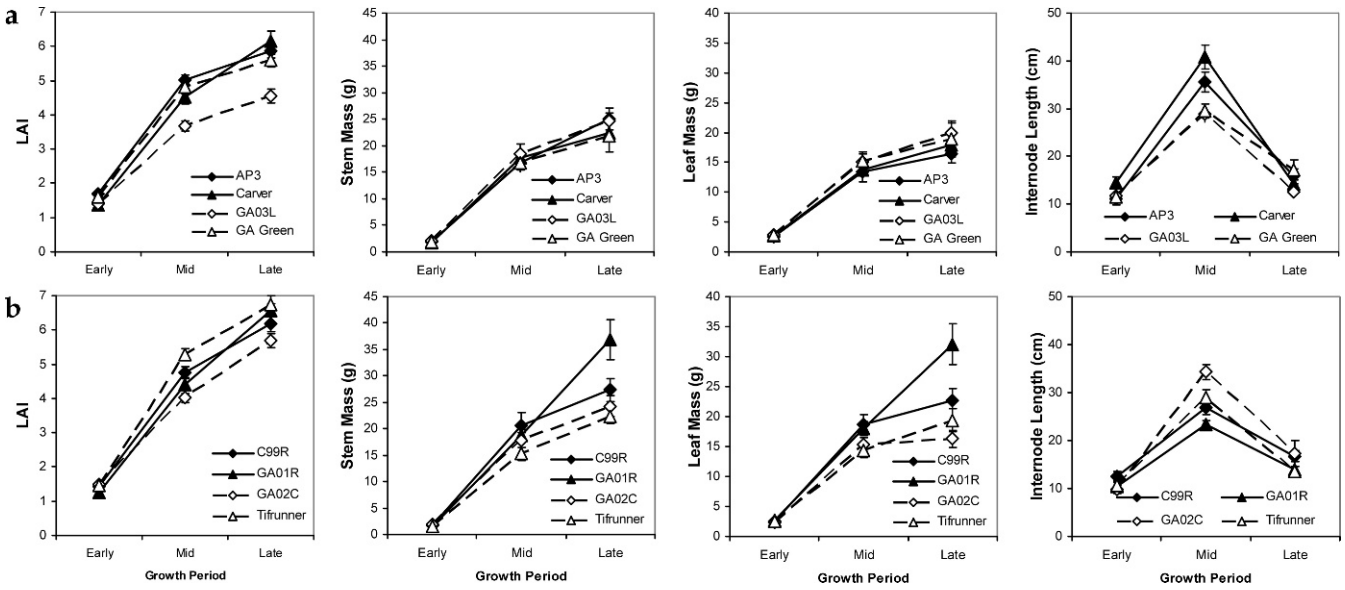

Fig. 3. Mean values and standard errors of biomass characteristics throughout the growing season for mid- (a) and late- (b) maturing peanut cultivars. Average values calculated across years and irrigation scheduling methods. Periods refer to developmental stages in the growing season.

Discussion

There is true value in studies that examine growth and developmental differences among crop cultivars because they describe genetic variability that can either be utilized in breeding programs or crop models (Bell *et al.*, 1991b; Bell *et al.*, 1993a; Craufurd *et al.*, 2002; Baterng *et al.*, 2003; Kiniry *et al.*, 2005). For breeding programs, a description of the differences among cultivars is essential for exploiting available genetic variability during the development of new germplasm. For crop modelers, knowledge of how cultivars can differ in their growth and reproductive responses can be essential

Table 3. Mean trait values for peanut cultivars calculated across years and irrigation scheduling methods. Periods refer to developmental stages in the growing season.

	Trait								
Cultivar	SPAD			SLA			Leaf N		
period:	*early*	*mid*	*late*	*early*	*mid*	*late*	*early*	*mid*	*late*
AP-3	36 b	38 d	39 a	192 ab	181 ab	159 a	5.1 a	4.4 ab	3.4 bc
Carver	38 ab	40 bcd	36 a	183 ab	167 b	174 a	4.6 a	4.1 b	3.4 bc
Georgia-03L	39 ab	44 a	42 a	192 a	181 ab	159 a	5.0 a	4.6 ab	3.8 a
Georgia Green	38 ab	42 ab	40 a	189 ab	189 a	147 a	4.7 a	4.4 ab	3.5 abc
C-99R	42 a	44 ab	42 a	172 b	171 ab	154 a	4.9 a	4.7 a	3.8 a
Georgia-01R	39 ab	42 abc	42 a	174 ab	179 ab	166 a	4.7 a	4.5 ab	3.7 ab
Georgia-02C	38 ab	43 ab	40 a	192 a	185 ab	149 a	4.7 a	4.6 ab	3.7 ab
Tifrunner	36 b	39 cd	42 a	181 ab	171 ab	127 a	4.6 a	4.2 ab	3.3 c

	Trait								
Cultivar	Leaf P			Leaf K			Leaf Ca		
period:	*early*	*mid*	*late*	*early*	*mid*	*late*	*early*	*mid*	*late*
AP-3	0.71 a	0.30 abc	0.23 ab	4.1 a	2.1 a	1.8 a	1.9 a	1.9 ab	2.3 bc
Carver	0.44 ab	0.26 c	0.21 b	3.4 ab	2.0 a	1.7 a	1.4 ab	1.9 ab	2.4 b
Georgia-03L	0.44 ab	0.31 abc	0.24 ab	2.9 b	2.0 a	1.5 a	1.3 ab	1.9 ab	2.7 a
Georgia Green	0.41 b	0.29 bc	0.24 ab	2.9 b	1.9 a	1.6 a	1.3 b	2.0 a	2.4 bc
C-99R	0.55 ab	0.32 ab	0.23 ab	3.3 ab	1.9 a	1.5 a	1.6 ab	1.9 ab	2.2 bc
Georgia-01R	0.45 ab	0.34 a	0.26 a	2.9 b	2.2 a	1.7 a	1.3 b	1.8 ab	2.1 c
Georgia-02C	0.50 ab	0.33 ab	0.23 ab	3.2 ab	2.1 a	1.7 a	1.3 b	1.7 b	2.2 bc
Tifrunner	0.40 b	0.29 abc	0.21 b	2.8 b	2.0 a	1.6 a	1.3 ab	2.0 a	2.2 bc

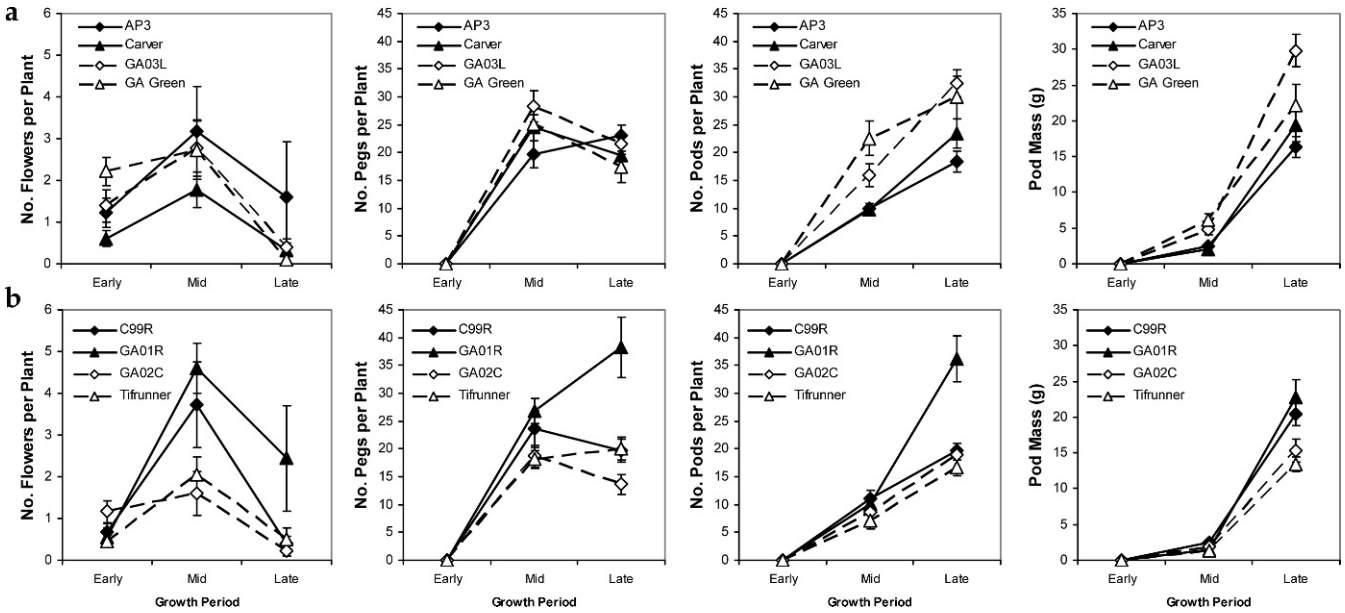

Fig. 4. Mean values and standard errors of reproductive characteristics throughout the growing season for mid- (a) and late- (b) maturing peanut cultivars. Average values calculated across years and irrigation scheduling methods. Periods refer to developmental stages in the growing season.

to the success of the model's predictive ability. For example, the crop model PNUTGRO requires over 40 cultivar-specific inputs for successful simulation of growth and yield in peanut (Hammer *et al.*, 1995). Previous work has shown that there is variability in growth and reproduction in peanut but comparisons have typically been made among widely different peanut species and botanical types (Bell *et al.*, 1991a,b; Bell *et al.*, 1993a,b; Bell *et al.*, 1994; Craufurd *et al.*, 2002; Banterng *et al.*, 2003). But the existence of variability among current peanut cultivars whose genetic pedigrees have become increasingly similar due to the type of traits that have been favored for several years is questionable at best. However, this study has documented and quantified several important growth and reproductive characteristics that differ among currently cultivated peanut genotypes. It also appears that there are differences among cultivars in resource allocation strategies for canopy development that can translate into effects on pod production.

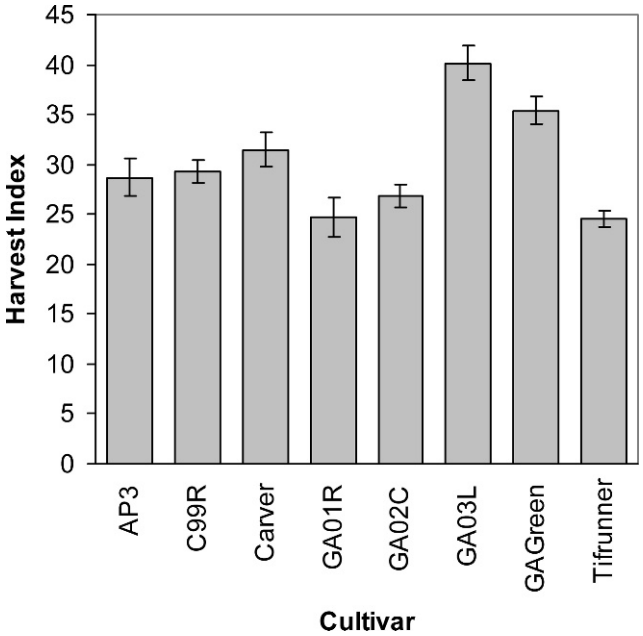

Fig. 5. Mean values and standard errors of harvest index measured during the late season period for 8 peanut cultivars across 2004 and 2005 and irrigation scheduling methods.

Despite expectations of a kind of genetic dilution to phenotype variability among cultivars, genotype differences were quite strong for growth traits. Previously documented cultivar differences in leaf weight and harvest index do exist, but again these were in widely diverse botanical types (Bell *et al.*, 1993a; Craufurd *et al.*, 2002; Banterng *et al.*, 2003), making the current study's documentation of growth variability among closely related cultivars unique. Although year had a significant effect on these traits indicating an effect of climate on peanut physiology, there were largely no interactions between year and genotype indicating that the changes caused by climate were relatively low in magnitude and did not alter the overall genetic pattern of development for each cultivar. A lack of an effect of irrigation scheduling method or interaction between irrigation scheduling method and cultivar for growth traits also illustrated the fairly strong genetic control over aboveground biomass development among the cultivars in this study.

Overall, the pattern and magnitude of LAI measurements across the season in this study were

Table 4. ANOVA for the leaf carbon and isotope composition of 8 peanut genotypes that were grown in both 2004 and 2005 at the Stripling Irrigation Research Park; F-values and P-values given. Factors include year (2004, 2005), peanut cultivar, and irrigation scheduling method (EZ, UGA-EXT, and IP). Statistically significant effects are listed in bold **type.**

Factors	Traits									
	$\delta^{13}C$		$\delta^{15}N$		% C		%N		C/N	
Plant growth	*F value*	*P value*	*F value*	*P value*	*F value*	*P value*	*F value*	*P value*	*F value*	*P value*
Year; df = 1	**19.0**	**0.0001**	**19.7**	**0.0001**	**54.4**	**0.0001**	**7.6**	**0.0066**	**12.2**	**0.0007**
Cultivar; df = 7	**10.1**	**0.0001**	1.3	0.2805	**4.5**	**0.0002**	**3.0**	**0.0056**	**2.6**	**0.0161**
Irrigation; df = 2	0.3	0.7363	0.5	0.6252	1.5	0.2250	1.2	0.2984	0.5	0.6061
Year*Cultivar; df = 7	1.0	0.4150	0.6	0.7866	1.7	0.1093	0.2	0.9720	0.3	0.9648
Year*Irr; df = 2	**9.0**	**0.0002**	0.5	0.5828	**6.0**	**0.0033**	**7.7**	**0.0007**	**4.8**	**0.0098**
Cultivar*Irr; df = 14	0.5	0.9361	0.2	0.9989	0.4	0.9577	0.6	0.8891	0.5	0.9075
Year*Cult*Irr; df = 14	0.9	0.5863	0.3	0.9885	1.5	0.1111	0.5	0.9259	0.5	0.9451

typical for other peanut cultivars (Banterng *et al.*, 2003; Kiniry *et al.*, 2005), but some studies have documented a more parabolic pattern for LAI development (Kar and Kumar, 2007) as well. Patterns of growth in the current study indicated that late-maturing cultivars had higher late-season growth than mid-maturing cultivars. Trade-offs in allocation patterns among LAI, stem, and leaf growth indicated cultivars had different strategies for canopy development. For example, although the late-maturing cultivar Georgia-01R had high partitioning to leaves and stems, its short internode lengths maintained a mid-level LAI. Two mid-maturing cultivars alternated between large internode lengths and thus high LAI (Carver) and short internode lengths and low LAI (Georgia-03L). Variability in partitioning strategies was also illustrated by similar harvest indices that were arrived at by coupling low below- and aboveground biomass in Tifrunner, while Georgia-01R coupled high below- and aboveground biomass. Biomass partitioning especially between leaves and stems or between vegetative and reproductive traits can vary among cultivars in other legumes such as cowpea (*Vigna unguiculata* (L.) Walp.) and chickpea (*Cicer arietinum* L.), and some diversely related peanut cultivars (Bell *et al.*, 1993b; Bell *et al.*, 1994; Krishnamurthy *et al.*, 1999; Banterng *et al.*, 2003; San José *et al.*, 2004).

Unlike growth traits, the separation among cultivars in reproductive traits was not related to maturity class. On average, mid- and late-maturing cultivars had similar flower, peg, and pod production. With elevated canopy growth but equal reproductive rates, late-maturing cultivars were expected to have lower harvest indices than mid-maturing genotypes. This was certainly the case, especially for the later maturing cultivars Georgia-01R, Georgia-02C, and Tifrunner which had the lowest harvest indices among all eight cultivars. This pattern of lowered harvest indices in late-maturing cultivars indicates a somewhat lower efficiency of yield return for the amount of energy invested in aboveground canopy structures. These results concur with differences in harvest index that have previously been found between peanut cultivars of different maturity classes with late maturing cultivars having low relative harvest indices (Bell *et al.*, 1991b; Bennett *et al.*, 1993). This is true across all grain/seed producing food crops, legumes, or cereals.

Aside from the contribution of genetics, harvest index can be significantly affected by various environmental factors that affect peanut growth and reproduction including: temperature (Vara Prasad *et al.*, 2000); heat stress (Vara Prasad *et al.*, 1999); irradiance and photoperiod (Bagnall and King, 1991a,b); ozone stress (Booker *et al.*, 2007; Burkey *et al.* 2007); and even planting pattern (Lanier *et al.*, 2004) Of course one of the greatest influences on harvest index can be irrigation amount and timing (Reddy *et al.*, 2003). That is why perhaps the most surprising result from this study was the lack of impact of irrigation scheduling method on peanut growth and reproduction. Even though there was over a 100 mm difference in the total water applied in both years between the top and bottom irrigation scheduling methods, the crop performed well under all systems and was not significantly affected. This is likely due to the fact that all three irrigation scheduling methods in both years provided more than enough water to meet maximal cultivar yield potential. Based on sap flow water-use measurements in southeastern peanut, seasonal water-use can be approximately 710–735 mm (unpublished data). For both 2004 and 2005, water receipt (from both irrigation and precipitation combined) topped these levels indicating that irrigation application could have been reduced while still meeting crop demand.

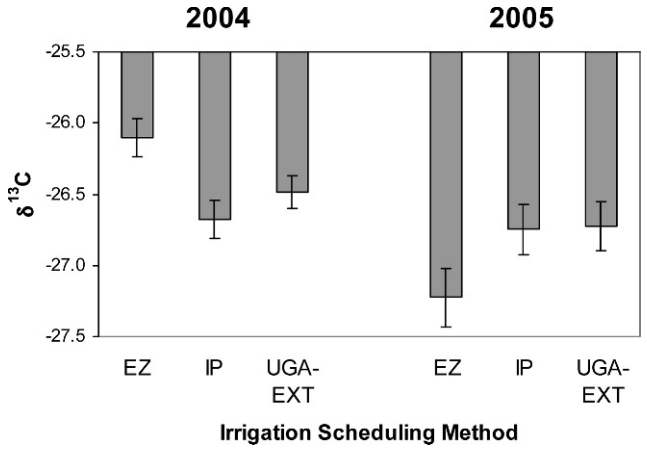

Fig. 6. Mean values and standard errors of leaf $\delta^{13}C$ for 2004 and 2005 in different irrigation scheduling methods (EZ, UGA-EXT, and IP) across 8 peanut cultivars.

Although the irrigation environment did not affect growth and reproduction to an appreciable degree, yearly variation did. Looking at the climatic data, the most likely factor was the timing and amount of rainfall, with 2005 having the highest rainfall total during the period of flowering and fruit maturation. However, the crop did not utilize this higher water availability in reproduction (as evidenced by the lack of significance for year in peg number and pod number and weight). The effect of this difference in water application between years was in the growth characteristics; namely stem and leaf weight (Table 2) which were actually *lower* across cultivars in 2005 (data not shown). Additional water "availability" coupled with lower leaf and stem production might indicate some degree of water over-saturation in the soil. Tissue nitrogen was also lower in 2005 than in 2004 (data not shown) which indicate deleterious effects on nitrogen fixation under hypoxic soil conditions. Either way, water availability appeared to be more than adequate for the crop in both years.

Harvest index measured in these eight cultivars showed relatively low values across years in comparison to 14 studies examining harvest index in peanut reviewed by Kiniry *et al.* (2005). The low harvest indices in the current study are even more surprising given all treatments were irrigated because harvest index is predicted to be as high as 0.58 under *efficient* irrigation (Kiniry *et al.*, 2005). This result also provides evidence that all three irrigation scheduling methods used in this test were likely applying too much water to the crop, thereby increasing canopy growth without a concomitant increase in yield and thus leading to low harvest indices. Based on these results, it appears that irrigation scheduling methods for southeastern U.S. peanut have a lot of room to

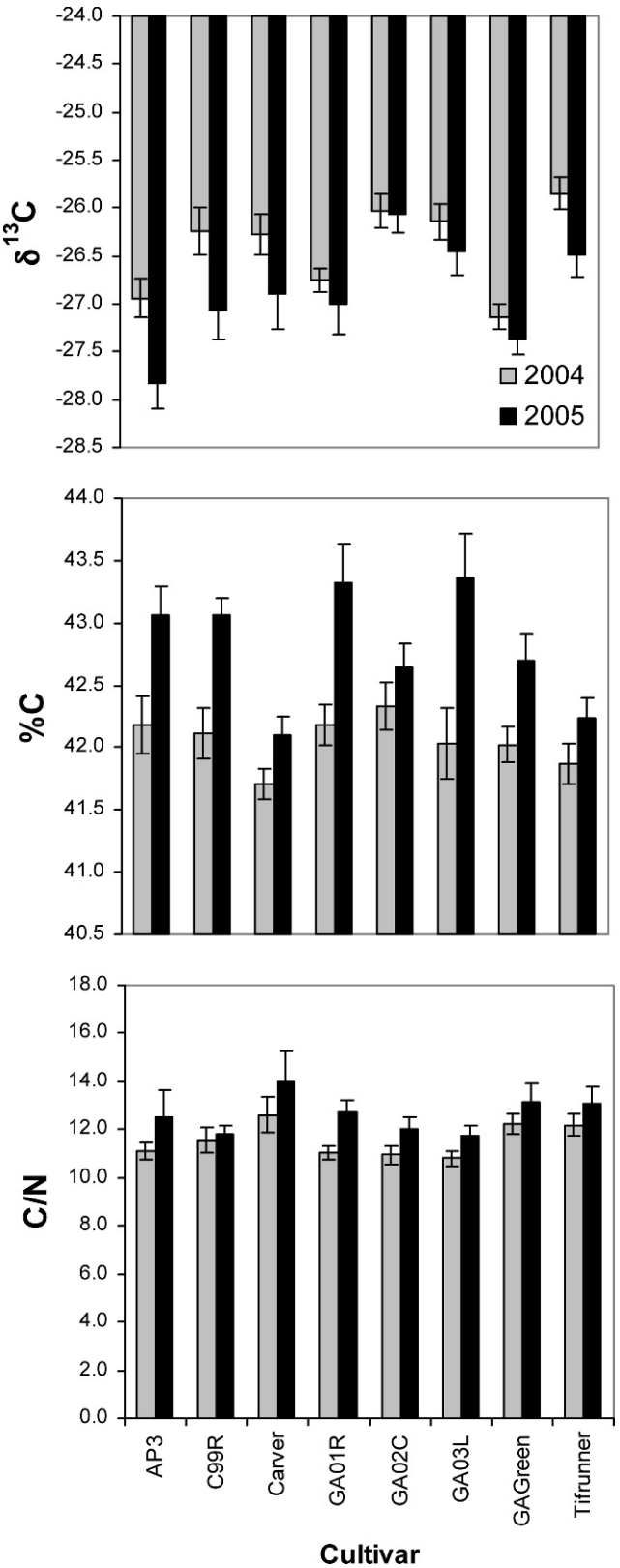

Fig. 7. Mean values and standard errors of leaf isotope, carbon, and nitrogen levels among peanut cultivars for 2004 and 2005.

Table 5. Significant Pearson correlations between late-season pod number and pod weight with growth, reproductive, and tissue nutrient traits.

Trait	Late-season pod number		Late-season pod weight	
	correlation	p-value	correlation	p-value
Mid-season LAI	−0.53	0.0348	−0.66	0.0055
Mid-season peg #	0.77	0.0005	0.75	0.0007
Mid-season pod #	0.58	0.0178	0.62	0.0103
Mid-season pod wt.	ns[1]	ns	0.57	0.0222
Mid-season SPAD	ns	ns	0.61	0.0125
Late-season LAI	ns	ns	−0.64	0.0070
Late-season pod #	-	-	0.85	0.0001
Late-season pod wt.	0.85	0.0001	-	-
Late-season HI	ns	ns	0.65	0.0064
Late-season leaf wt.	0.60	0.0139	ns	ns
Late-season stem wt.	0.54	0.0299	ns	ns
Late-season tissue Ca	ns	ns	0.62	0.0110

[1]non-significant.

Table 6. Stepwise regression with forward selection for those traits found to be correlated with late-season pod number and pod weight.

Predicted Trait Factors in model	Cumulative R^2	Cp[1]
Late-season pod number		
Late-season pod wt.	0.71	7.22
Late-season leaf wt.	0.78	4.67
Mid-season peg #	0.83	3.33
Mid-season pod #	0.86	3.75
Late-season pod weight		
Late-season pod #	0.71	37.80
Late-season LAI	0.86	14.24
Mid-season peg #	0.92	6.32

[1]Mallow's Cp criterion for total squared error.

lower total water application during the season and increase efficiency of crop water use.

Variation among cultivars in $\delta^{13}C$ showed there is room to develop peanut germplasm with increased seasonal water-use efficiency as well. The larger canopies of late-maturing cultivars necessarily spell a larger area for transpirational water loss. For this reason, it might be expected that water-use would be higher in late- than mid-maturing cultivars and thus lead to decreased water-use efficiency. However, patterns of $\delta^{13}C$ did not reflect lower seasonal water-use efficiency for late-maturing cultivars. In fact two of the cultivars exhibiting the highest seasonal water-use efficiencies (Georgia-02C and Tifrunner) were late-maturing cultivars. Seasonal water-use efficiency appears to be under tight genetic control in U.S. peanut cultivars because irrigation scheduling method had no effect on $\delta^{13}C$ composition. Isotopes are often affected by irrigation regime, but the current results agree with previous results that found very little effect of irrigation on the isotope composition of southeastern cultivars (Rowland and Lamb, 2005). The only slight indication of irrigation scheduling changing the pattern of peanut water-use was the differing $\delta^{13}C$ levels in the EZ method between years. In 2004, the EZ treatment showed much higher water-use efficiency in the crop while in 2005, this trend was opposite. Therefore, irrigation scheduling appears to have the *potential* to affect crop water-use efficiency but is highly dependent on prevailing climatic conditions.

The existence of varying partitioning strategies among cultivars in this study necessitates the assumption that reproduction might be predicted from patterns in certain growth traits throughout the season. Although an early study indicated that peanut yield was determined more by genetic pedigree than growth habit (Norden and Lipscomb, 1974) more recent studies show a strong link between growth and reproduction for other legumes (Krishnamurthy *et al.*, 1999) and other peanut culitvars (Bennett *et al.*, 1993; Banterng *et al.*, 2003). In the current study, traits relating to canopy development (and thus assimilation capacity) as well as mid-season reproductive potential appeared to be causally linked to final reproductive output in the late season. LAI and leaf weight had some correlative relationships with the yield-determining traits of pod number and pod weight. As expected, pod number and weight were highly correlated with one another; a result that has recently been supported in different peanut cultivars (Haro *et al.*, 2007). This relationship between pod number and weight indicates there is no real trade-off between pod number and pod size likely due to the indeterminate nature of peanut. Aside from the relationships between pod number and weight, the strongest predictors of reproductive output were late-season traits including leaf weight and LAI. However, the correlation pattern was different for these two canopy traits; there was a negative relationship between LAI and pod weight, but for leaf weight, there was a positive relationship with pod number. This disparity may reflect an allocation trade-off where the more energy put into an overall larger canopy (LAI) had no real pay-off in production, while increased leaf production alone does have benefits because assimilation potential would be expected to increase. Mid-season traits that were important predictors of pod production were peg and pod numbers. These relationships really illustrate that the reproductive potential of the crop is determined at that mid-season point. Therefore, although the overall

growth habit of peanut is indeterminate, any energy allocated to reproductive structures by the crop later in the season goes to waste because the plant cannot adequately mature these fruits.

This study documented no large differences among cultivars in nutrient accumulation or allocation of a magnitude that would have biological relevance. This result has importance to the application of the nutrient predictor model that uses the nutrient levels of leaf tissue in the late-season to predict optimum peanut harvest maturity (Rowland *et al.*, 2008). Because genotype appears to have little effect on nutrient levels in leaf tissue across the season, application of this maturity model across different peanut genotypes is likely to give reasonable predictions of peanut maturity. The overall parabolic pattern of tissue nutrient levels confirms what Rowland *et al.* (2008) found for the cultivar Georgia Green. A decline in vegetative nitrogen late in the season found in these eight peanut cultivars shows a possible remobilization of nitrogen from vegetative parts to developing fruits which consequently drops nutrient levels in the late season as the crop matures (Bell *et al.*, 1994).

While yield is the basis on which genotypes are compared and evaluated in peanut breeding trials, much less information is known about differences in growth and developmental traits because many of these characteristics are largely ignored (Banterng *et al.*, 2003). By selecting for yield alone and not examining other traits that are causally related to yield may be a less successful strategy in breeding programs because these traits can be important predictors of yield (Wallace *et al.*, 1993). Information on the physiological basis to yield variation among cultivars can be used to explain the mechanisms behind such variation and even determine alternate management strategies in the field that can optimize a particular genotype's performance (Baterng *et al.*, 2003). Therefore, knowing the causes behind yield variability can ultimately aid in maximizing it.

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