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## ARTICLE

# Peanut Physiology and Tolerance to Abiotic Stresses

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## ABSTRACT

Peanut is a nutritious and highly-valued crop across the world. Achieving competitive yield and quality is challenged by biotic and abiotic stresses and the relatively high production requirements compared with other crops. To successfully address these challenges, it is important to understand peanut physiology and its essential requirements for growth and development. This article reviews the requirements for growth including soil characteristics, water, nutrients, and environmental conditions. The physiological effects of stresses during seed storage and germination and during plant growth, development, and reproduction are discussed. Phenotyping based on physiological responses are also discussed.

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## PEANUT GROWTH AND DEVELOPMENT

### Growth Requirements.

Peanut is a highly nutritious and high-valued crop worldwide; but achieving competitive yield and quality is often challenged by biotic and abiotic stresses as well as relatively high production requirements compared with other crops. To successfully address these challenges, it is important to understand peanut

physiology and its essential requirements for growth and development.

### Soil Requirements:

It is generally accepted that peanut grows and produces best on light-textured soils with a pH between 6.0 and 6.5 (USDA-ARS, 2005; Putnam *et al.*, 2014). Texture is an important soil physical property affecting the movement of water, nutrients, heat, and air with important effects on root development, crop growth and ultimately yield (Juma, 1993; Wu *et al.*, 2011a). Because peanut fruits develop in the ground, soil texture is even

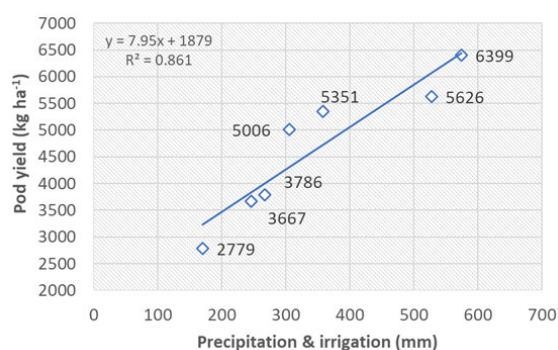
more critical for peanut compared with other crops (Adams *et al.*, 1993; Jackson *et al.*, 2011). Root dry matter accumulation and distribution were greater in sandy and loam soils than clayey soils; and the largest kernels along with increased pod number resulted from peanut grown in sandy or loam than clay soil (Jia *et al.*, 2013). However, enhanced crop establishment, more uniform stands, and improved seedling growth were observed on clayey soil and not sandy or silty soils (Zerbato *et al.*, 2017). Zhao *et al.* (2015) compared peanut growth and yield on three soil textures at pH between 5.9 and 6.1, i.e. sandy soil with particle distribution of 9% <0.001 mm and 65 % 1-0.05 mm; loam with particle distribution of 19% <0.001 and 23% 1-0.05 mm; and clay with particle distribution of 45% <0.001 and 9% 1-0.05 mm. They observed significant effects of soil texture on the dry matter accumulation of stems, leaves and pods; number of flowers per plant; and dynamic changes in peg number through the growing season. For example, dry matter accumulation of stems and leaves was greatest at 47 days after beginning flower on all soil types; but on sandy and loam soils, dry matter accumulation was approximately 15% over that on clay. Similarly, pod weight was 19% less on clay at 70 days from beginning flower, probably because pod number was consistently less during 27 to 57 days after beginning flower on clay. Finally, on clay soil the number of flowers was consistently lower than on sandy and loam soils (Zhao *et al.*, 2015). This and similar studies (Zheng *et al.*, 2012) clearly show that understanding the relationship between peanut physiology and soil texture is essential for increasing yield and providing insights on moving towards reduced tillage practices in peanut production. Indeed, reducing the tillage to lower production costs is a tempting option currently practiced by many peanut growers in the USA. In addition to the apparent economic advantage, reduced tillage positively impacts water runoff and infiltration, and soil physical properties (Rowland *et al.*, 2007). The main concerns with reduced tillage, however, are soil compaction, persistence of stubble from the previous crop, and inadequate soil bed-formation that could reverse the benefits of soil properties and decrease peanut yield (Jordan *et al.*, 2003). For example, Jackson *et al.* (2011) showed greater yield when planting on raised vs. flat beds, depending on whether the soil was coarse or fine textured. Ripping and bedding along with conventional till of fine-textured soils reduced compaction and digging losses, and increased yield. Others (Rowland *et al.*, 2007) were concerned with the inability of peanut gynophores to penetrate cover crop residue and produce pegs. They demonstrated that the combination of strip tillage and subsurface drip irrigation produced half the number of pods per plant compared with conventional tillage. Finally, sandy and coarse-textured soils may be preferred in peanut production.

Still, they have less water holding capacity, and the water deficit can easily develop in absence of sufficient rainfall or irrigation. Indeed, more research is needed to elucidate how soil physical properties affect peanut productivity to develop more sustainable production systems in the future.

### Water Requirements

To grow and produce profitable yields, peanut needs a reliable water supply throughout the growing season. Nevertheless, 60% of global production occurs in semi-arid tropics of Asia and Africa, where these conditions are hardly met (Mortley *et al.*, 2000). Even though considered resilient to water deficit, peanuts have relatively large water requirements, and yield and quality may be affected by erratic rainfall amounts and distribution (Singh *et al.*, 1999; Halilou *et al.*, 2015). Globally, only 16.2% of peanut acreage is irrigated, while the percentage of irrigated area is 49, 31, and 20% for cotton, wheat, and corn globally (Portmann *et al.*, 2010). In the USA, 35% of peanut acreage is irrigated, with differences among growing regions, i.e., in Texas 95% of peanut is irrigated. In comparison, the Virginia-Carolina (VC) region only has 15% irrigation availability (USDA/NASS, 2019).

In a semi-humid environment, data from the Peanut Variety and Quality Evaluation (PVQE) replicated trials in Virginia and North Carolina showed that peanuts produced 6399 kg ha<sup>-1</sup> pod yield under 574 mm rainfall and irrigation and yield decreased 8 kg ha<sup>-1</sup> for each mm water below 574 mm (Fig. 1). This dataset is based on 30 Virginia market type genotypes (yields are mean of the 30 genotypes) grown under seven year-location environments in 2009 and 2010 (Balota, 2010; Balota, 2011). Not just yield, but a good grade requires adequate amounts of water for maximum quality and economic value. For example, Balota and Phipps (2013) compared the yield and grade of nine Virginia and runner peanut cultivars grown under rainfed conditions at the Tidewater Agricultural Research and Extension Center (TAREC), Suffolk, VA, in 2009 and 2010. In 2009, rainfall in Jun, Jul, and Aug totaled 388 mm while in 2010 only 14 mm occurred during the same time frame. Under this condition, pod yield was reduced by 26 % and economic value by 33 %. The reduction of the economic value was related to the reduction of sound mature kernels (SMK), extra-large kernels (ELK) and total sound mature kernels (TSMK), and increases of damaged kernels (DK) in a dry versus a wet year in the absence of irrigation. Similar decreases of SMK and TSMK were observed on runner peanut in Georgia when water was withheld for 3 weeks (Dang *et al.*, 2013).



**Figure 1.** Dependence of peanut yield on the amount of water received from planting to maturity. Each data point represents an average of 30 Virginia market-type varieties tested in replicated trials of the Peanut Variety and Quality Evaluation (PVQE) test in Virginia and North Carolina at four locations in 2009 and three locations in 2010.

In Texas, in a semi-arid environment, Rowland *et al.* (2012a) showed similar water requirements for runner peanut, indicating that less than 550 mm of total rainfall and irrigation reduced yield and crop value significantly. In this study, the highest yields and values occurred when more than 600 mm of water was supplied to the crop; however, the authors also suggested that less than 600 mm can achieve similar economic value if irrigation is cut to 50 or 75% from the full norm at early growth stages, followed by full irrigation during late growth stages. This was called “primed acclimation” and was proposed as a new irrigation strategy in semi-arid regions conducive to acceptable peanut yields with less water (Vincent *et al.*, 2020). Primed acclimation is based on *translational stress memory*, i.e. changes in gene expression and function over repeated stress events, and *priming*, i.e. a stress event may improve the physiological function under subsequent stress cycles, two relatively new concepts in plant biology (Bruce *et al.*, 2007; Balmer *et al.*, 2015; Hu *et al.*, 2015; Racette *et al.*, 2020). Based on plant physiological adaptations to water limitation that allowed accelerated root and flower production, and improved root to shoot partitioning, water use, and photosynthetic characteristics, primed acclimation was shown to work in peanut and other crops (Rowland *et al.*, 2012a; Rivas *et al.*, 2013; Fleta-Soriano *et al.*, 2015; Racette *et al.*, 2019; Vincent *et al.*, 2019).

The temporal distribution of water is important in peanut production. Even though water is needed mainly during the flowering, pegging, and seed growth stages (Rowland *et al.*, 2012a), good stands also need a reliable continuous water supply. Depending on the growth stage and evaporative demand, peanut requires from 25 mm of water weekly in the early stages to 75 mm at seed filling stage, which is difficult to achieve in the absence of irrigation (Putnam *et al.*, 2014). For example, historical data in Virginia shows that 25 mm of rainfall per week is available during peanut early growth stages. However, 75 mm per week from the beginning seed to physiological maturity is rarely received. The weekly rainfall variation is also greater for later than for early peanut growth stages because of summer versus late spring rainfall patterns.

The demand for irrigation and timing can be based on simulations with daily monitored weather data using the Cropping System Model (CSM)-CROPGRO-Peanut. CSM-CROPGRO is a decision support system for agrotechnology transfer (DSSAT) and peanut is one of more than 40 crops that can be modeled using this system (Tsuiji *et al.*, 1994; Jones *et al.*, 2003; Hoogenboom *et al.*, 2023).

In the coming era of the “water crisis”, it is estimated that increased global food production, including peanuts, will continue to come from rainfed agriculture in developed and developing countries alike; resilience to water scarcity will have to come from more efficient water use by the new cultivars and innovative production systems that exploit plant adaptive physiological mechanisms to water deficit (Rosegrant *et al.*, 2002; FAO, 2012; Vincent *et al.*, 2019).

### Germination Requirements

Temperature affects peanut germination, growth, and development, with cardinal temperatures being different for each physiological stage. To germinate, peanut needs a base temperature ( $T_b$ ), i.e. minimum temperature triggering germination, of 13.3 °C; optimum temperature ( $T_o$ ), i.e. optimum temperature for maximum rate and percent of germination of 25.5 °C; and maximum temperature ( $T_m$ ), i.e. germination ceases at this temperature, of 43 °C (Cox and Martin, 1974; Caroca *et al.*, 2016; Grey *et al.*, 2016). Vegetative growth is best at average temperatures ranging from 25 to 30 °C. For reproductive growth, somewhat lower temperatures, in the range of 20 to 25 °C, are optimum; temperatures over 35 °C have a detrimental effect on pollen fertility and pollination and, consequently, yield (Ketring, 1984; Prasad *et al.*, 2003). However, temperature requirements and thresholds vary somewhat with genotype and environment. For example, in Chile, a study including four peanut genotypes showed that  $T_b$  for germination ranged from 11.3 to 12.5 °C;  $T_o$  from 30.5 to 33.4 °C, and  $T_m$  from 40.8 to 44.9 °C (Caroca *et al.*, 2016). In Florida, USA,  $T_b$  for the rates of emergence and development to  $V_2$  stage were 11.7 and 9.8 °C, respectively, with no significant difference among the six genotypes studied. The thermal time needed to reach 50% germination ranged from 77.2 to 155.2 °Cd, and to reach  $V_2$  stage, from 144.6 to 218.9 °Cd with significant effects of soil temperature and genotype (Prasad *et al.*, 2006). On a thermal gradient table, the germination pattern was non-linear, but the optimum range was similar to field conditions and varied from 22 to 30 °C (Grey *et al.*, 2011). However, these differences are likely related to the definition of germination among these researchers. Grey *et al.* (2016) found that the thermal time to reach max rate for germination and 80% germination, as indicators of seed vigor, were dependent upon genotype, i.e. Georgia Green had greater vigor than Florida-07 across experiments. Germination depended on the year in which seed was produced, at least compared among six years, 2006 to 2012. Seed size was important, and larger seeded cultivars had less seed vigor than smaller-seeded cultivars. In addition to genetic and pre-harvest conditions, post-harvest factors including seed age, i.e. the number of years seed was in storage, contribute to reduced germination and seed vigor, as well as subsequent plant growth. Among the post-harvest factors, seed moisture content, pest and

mechanical damage, and ambient storage temperature and relative humidity are the most important (Morton *et al.*, 2008; Isleib *et al.*, 2014).

## FACTORS AFFECTING SEED QUALITY, GERMINATION, AND EARLY GROWTH

Germination begins with water absorption, imbibition, and activation of enzymes needed to degrade seed compounds used for hypocotyl elongation, radicle extension, and cotyledonary leaf opening (Gonnety *et al.*, 2007; Wang *et al.*, 2018). This period is characterized by intense uptake of oxygen and production of carbon dioxide (Prasad *et al.*, 1969; Raymond *et al.*, 1985). Often, “natural anaerobiosis” can develop when the need for oxygen exceeds the supply even under adequate aeration, resulting in accumulation of ethanol, lactate, acid phosphatase enzymes, and cytokinin levels that reach maximum at 5 days after germination initiation (Leblova *et al.*, 1974; Swamy and Sandhyarani, 1986; Gonnety *et al.*, 2007).

On the first day of germination, the most notable change is water content increases up to 65% of the seed weight (Li *et al.*, 2014). Sugars and fatty acids in cotyledons provide the initial energy needed to begin synthesis of DNA, RNA, and new proteins and enzymes (Benítez *et al.*, 2013). Hydrolysis of storage proteins generates free amino acids such as methionine and proline with maximum production at approximately 8 days after imbibition (Isola and Franzoni, 2000). Enzyme and mitochondrial activity are also maximal at approximately 8 days after imbibition (Cherry, 1963) when storage lipids are converted into sugars, which are transported to the growing embryo (Castelfranco *et al.*, 1969). During germination, the cotyledons can lose 60% of their total dry weight and 70% of the proteins which are transferred as amino acids to the forming embryo (Ruiz *et al.*, 2013). Biotic and abiotic factors such as water, temperature, soil mineral and microbial composition, and post-harvest storage conditions can affect germination (Ruiz *et al.*, 2013).

Water availability plays a major role in germination, with larger seeded peanuts needing more water for imbibition than the smaller seeded cultivars (Pallas *et al.*, 1977). Depending on soil water availability, temperature can affect germination differently, for example, hot and dry soils may extend dormancy (Alpert, 2005; Brevedan *et al.*, 2013). Excessive soil moisture, on the other hand, decreases germination rate because of oxygen deprivation (Brevedan *et al.*, 2013).

Seeds drier than 1% may experience loss of viability from altered plasma membrane and electrolyte leakage (Retamal *et al.*, 1990; Walters and Engels, 1998). For overly dry seeds, desiccation signals the production of regulatory molecules inducing dormancy as a survival mechanism (Buitink, 2007). However, once germination begins, the ability of seed to survive desiccation through dormancy is lost and the radicle does not have desiccation tolerance (Hong and Ellis, 1992; Silva *et al.*, 2017).

Offspring of stress-exposed parents can become more tolerant to a particular stress through *transgenerational stress memory* (Iwasaki and Paszkowski, 2014). In this way, seeds of drought-stressed peanut parents belonging to *hypogaea* and *fastigiata* subspecies germinated better under water deficit than

seeds from non-stressed parents (Racette *et al.*, 2019). However, *stress memory* did not apply to peanut seeds previously grown in saline soils. Specifically, saline-grown seed resulted in germination decrease to 57% from 82%. A decrease in germination velocity from 70% to 33% was observed for saline-grown seed vs non-saline seed (Meena and Yadav, 2018).

Increased salinity of soils and irrigation water are becoming major concerns for global crop production (Meena *et al.*, 2016) with negative effects on seed germination, emergence, and early plant growth and survival (Demir and Mavi, 2008; Yuan *et al.*, 2010; Chakraborty *et al.*, 2019). Salt binds water molecules, reducing water availability to the plants, negatively affecting growth. While mechanisms of cellular and subcellular protection can be triggered by increased salt concentrations of soil water, i.e. accumulation of osmotic protectants, salinity applied to the parent plant has negative effects on peanut seed quality (Isola and Franzoni, 2000; Girija *et al.*, 2002; Lim *et al.*, 2012; Meena *et al.*, 2016).

The temperature of the soil at planting is a dominant factor for the onset and rate of seed germination. In standard tests, germination rate increases linearly with temperature from  $T_b$  to  $T_o$  and levels off or decreases after  $T_m$  is reached (Roberts, 1988). For example, in field trials, peanut emergence rate was 50 to 70% at 14 C and increased to 85% when temperature was 25 C, then leveled off or decreased as soil temperature increased to 32 C (Prasad *et al.*, 2006). The temperature effect is related to the enzymatic activity needed to produce carbohydrates from fatty acids *via*  $\beta$ -oxidation in the germinating seed (Bagley *et al.*, 1963; Ketring, 1979). It is also related to the regulation of genes encoding membrane and organelle protection under cold and dehydration from freeze (Luster, 1985; Tang *et al.*, 2011). Regions of the USA peanut belt like Virginia, Carolinas, Florida, Georgia, and Western Texas, and other global regions such as Pakistan, Northern India and Indonesia are prone to sub-optimal temperatures for peanut germination and emergence (Prasad *et al.*, 2006).

Mineral and microbial composition of seed and soil affect successful germination. Peanut germination is dependent upon calcium (Ca) and boron (B) content in the seed (Harris and Gilman, 1957; Adams and Hartzog, 1979; Guerke, 2005). Optimum germination of runner peanut, i.e. 95% germination, occurred when seed Ca concentration exceeded 600 mg kg<sup>-1</sup> (Howe *et al.*, 2012), but this can vary from a minimum of 450 mg kg<sup>-1</sup>, which has been recommended for runner and Virginia-type peanut (Spears, 2000; Spears, 2002), to over 700 mg kg<sup>-1</sup> (Guerke, 2005). Ca is diffused into the soil solution and then into the pods during pod and seed maturation (Beasley *et al.*, 1989). When seed B was less than 13 mg kg<sup>-1</sup>, B deficiency developed causing decay of the cotyledons and seed discoloration and malformation between the two cotyledons called “hollow heart” (Harris and Gilman, 1957; Netsangtip *et al.*, 1987). Because sandy soils are often deficient in Ca and B, the application of gypsum (CaSO<sub>4</sub>) and elemental B are essential in peanut production for quality seed. Current production guides in Virginia, Carolinas, and the SE peanut region recommend application of 300 kg Ca ha<sup>-1</sup> when soil Ca content is less than 670 kg ha<sup>-1</sup> for Virginia and 450 kg ha<sup>-1</sup> for runner types. Recommendations for B require application of 0.30 to 0.60 kg B ha<sup>-1</sup> when soil test indicates less than 0.2 kg

ha<sup>-1</sup> available B, even though relatively new research failed to identify a need for B under current production systems (Benton, 2016). There is increasing evidence that zinc (Zn) is becoming deficient in soils worldwide (Aboyeji *et al.*, 2019). Like Ca and B, Zn is essential for the seed development of many crops, including peanuts (Aboyeji *et al.*, 2019; Rahman *et al.*, 2019).

Specific soil pathogens and residual chemical compounds from previous crops can reduce germination. For example, peanut germination was reduced when sown after sorghum while sorghum roots decomposed (Sène *et al.*, 2000). To prevent infection and improve germination, seed is usually treated with commercial fungicides. Alternatively, naturally produced phytoalexins and polyphenolic antioxidants by germinating seed, or induced by seed microbial colonization with *Rhizopus oligoporus*, showed a positive effect on peanut germination (Bell, 1984; Cevallos-Casals and Cisnerose-Zevallos, 2010; Sobolev *et al.*, 2010; Wu *et al.*, 2011b; Ahuja *et al.*, 2012; Gan *et al.*, 2017).

Finally, post-harvest storage conditions can affect seed quality (Coffelt *et al.*, 1979). For example, excess rainfall close to harvest can induce sprouting. Sprouted seeds have low nutritional quality and are rejected by food processors; such seed cannot be stored for planting the following year (Vishwakarma *et al.*, 2016). Seed moisture, and storage temperature and humidity can alter germination of peanut (Steele, 1983). Usually, farmer-stock peanuts are dried to 8 to 10% seed moisture for short time storage, e.g. six months, with no significant effect on seed quality and fungal contamination (Smith *et al.*, 1989). In this way, seed can be stored up to one year at ambient temperature of 13 C and 55 to 70% relative humidity and maintain their germination and vigor potential (Butts *et al.*, 2017; Weaver *et al.*, 2021). Reducing seed moisture below 6% appears to allow for higher storage temperature and humidity without effecting seed vigor (HongYan *et al.*, 1997; Sastry *et al.*, 2007; Shinde *et al.*, 2012).

## PHYSIOLOGICAL GROWTH STAGES

As a day-neutral plant, peanut growth and development are not affected by day length; however, peanut needs approximately 2200 Cd growing degree-days (GDD) or approximately 90 to 150 days after planting (DAP) to mature. Boote (1982) developed growth stage descriptions for peanut based on vegetative (V) and reproductive (R) observable events. Except for VE and V0, which were based on the appearance of the cotyledonary leaves aboveground, V stages were numbered from V-1 to V-(N) based on the developed nodes on the main axis and unfolding of the tetrafoliolate leaflets from the first to N<sup>th</sup> tetrafoliolate. Eight R stages were identified, with R1 being beginning bloom, i.e. one open flower at any node on the plant; R2 beginning peg, i.e. one visible gynophore on the plant; R3

beginning pod, i.e. one peg swollen belowground; R4 full pod, i.e. one fully-expanded pod; R5 beginning seed, i.e. one seed with visible growth of cotyledon when cross-sectioned; R6 full seed, i.e. one pod with entire cavity filled by seed when fresh; R7 beginning maturity, i.e. one pod showing blotching of inner pericarp or testa; R8 harvest maturity, i.e. 75% of all developed pods have testa or pericarp coloration; and R9 over-mature pod, i.e. one undamaged pod showing orange-tan coloration of the testa or natural peg deterioration (Table 1; Fig. 2) (Boote, 1982). To reach each growth stage, specific thermal time or GDD is needed, and this is dependent upon the peanut type, cultivar, and environment. Runner type peanuts reach R8 in over 160 d after planting and spanish-type in approximately 140 to 145 d in West Texas; whereas in South Texas, spanish-type matured in only 110 to 135 d (Smith and Simpson, 1995; Lopez *et al.*, 2003; Burrow *et al.*, 2014b). The new runner 'Tamrun OL12' and spanish 'Schubert' peanuts developed in Texas reach R8 two weeks sooner than older cultivars (Burrow *et al.*, 2014a, b); the new Virginia type cultivars developed for the VC reach physiological maturity in approximately 1800 Cd in comparison with old cultivars at 2500 Cd (Caliskan *et al.*, 2008; Balota and Phipps, 2013; Jordan *et al.*, 2018). Developing early maturing cultivars has become an important goal for breeding programs in the USA, especially in drought-prone environments like Texas, Oklahoma and New Mexico because of limited ground water availability, and in SE and VC regions because late season disease pressure and excessive moisture may reduce yield of late maturing cultivars. In Virginia, runner and Virginia type cultivars required on average 400 Cd or 43 d from planting to reach stage R1<sub>50</sub>, i.e. 50 percent of the plant population has at least one open flower; and 200 to 300 Cd or 7 to 10 days from R1<sub>50</sub>, to R2, beginning peg (Balota and Phipps, 2013). This is within the ranges described for runners in Georgia and Florida (Prasad *et al.*, 2001; Rowland *et al.*, 2007). To reach R7, runner and Virginia cultivars grown in Virginia needed 954 Cd and 900 Cd, respectively, from R1. On average, both peanut types, 897 Cd was needed to reach R7 in a humid year and 956 Cd in a dry year (Balota and Phipps, 2013). Similarly, in Georgia, the duration of developmental phases and GDD requirements of 'Georgia Green' (Branch *et al.*, 1996) runner peanut were longer under water deficit (Suleiman *et al.*, 2013). Because peanut growth and development is dependent upon cultivar and environment, and direct measurements are time consuming and laborious, simulation models to predict peanut growth, development, and yield have been developed. CSM-CROPGRO-Peanut within DSSAT is one of them (Boote *et al.*, 1989; Suriharn *et al.*, 2008, 2011; Putto *et al.*, 2013). Others, i.e. APSIM (Keating *et al.*, 2003) and CropSyst (CROP System) (Stockle *et al.*, 1994), and Simple Simulation Model (SSM) (Noorhosseini *et al.*, 2018) have also been used for peanut and provided adequate levels of accuracy.



Figure 2. Peanut flower, pegs, and pods at different developmental stages: R1, R2 (2nd & 3rd), R3 (4th & 5th), and R5 (8th & 9th). R7 and R8 are the 10th & 11th pods in the image, assuming internal coloration.

Determining when harvest maturity (R8) is reached is essential for peanut producers. The most frequently used method is the Williams and Drexler (1981) method using “maturity profile boards” (Fig. 3). This method is based on the temporal change of pod mesocarp color as seeds fully develop from R6 to R7 to R8, i.e. mesocarp color changes from white, denoting immature pods, to yellow, orange, brown and black, with brown and black indicating fully mature pods. In this method, the proportion of these colors is determined in a sample of approximately 150-200 pods freshly collected from the field. To reveal the mesocarp, hull exocarp is removed by high pressure washing or sand blasting with glass beads under high pressure washing. Pods are then placed on profile board and grouped by color. Even though different profile boards exist for different peanut types, they all allow projection with sufficient confidence of the optimal harvest maturity based on the proportion of pods within each color group (Fig. 3).

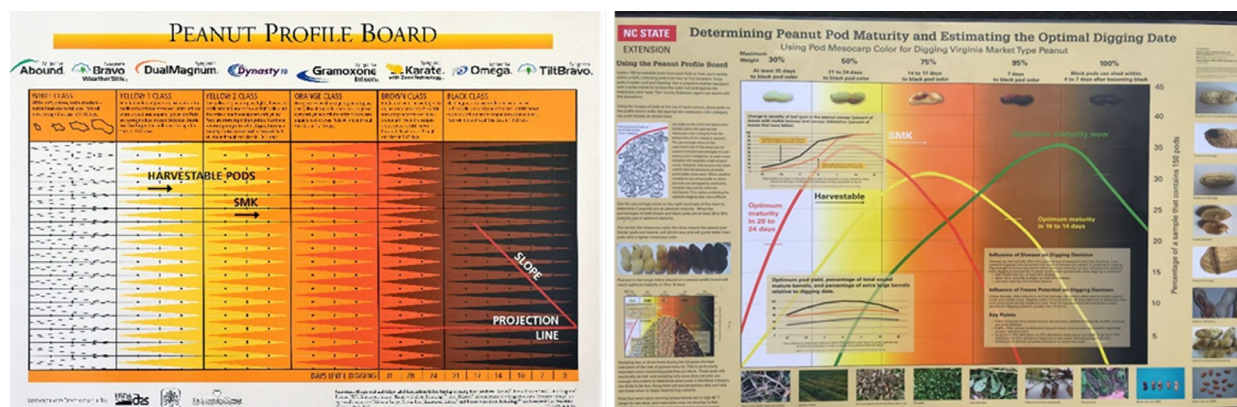
Table 1. Peanut growth stage description.

Stage Number	Stage name	Description
Vegetative Stages†		
VE	Emergence	Cotyledons near the soil surface with seedling showing some part of the plant visible.
V0		Cotyledons are flat and open at or below the soil surface.
V-1 V-(N)	First tetrafoliolate to the Nth tetrafoliolate	One to N developed nodes on the main axis; a node is counted when its tetrafoliolate is unfolded and its leaflets are flat.
Reproductive Stages†		
R1	Beginning bloom	One open flower at any node on the plant.
R2	Beginning peg	One elongated peg (gynophore).
R3	Beginning pod	One peg in the soil with turned swollen ovary at least twice the width of the peg.
R4	Full pod	One fully expanded pod, to dimensions characteristics of the cultivar.
R5	Beginning seed	One fully expanded pod in which seed cotyledon growth is visible when the fruit is cut in cross-section with a razor blade (Past the liquid endosperm phase).
R6	Full seed	One pod with cavity apparently filled by the seed when fresh.
R7	Beginning maturity	One pod showing visible natural coloration or blotching of inner pericarp or testa.
R8	Harvest maturity	Two-thirds to three-fourths of all developed pods have testa or pericarp coloration. Fraction is cultivar-dependent; lower for Virginia type.
R9	Over-mature pod	One undamaged pod showing orange-tan coloration of the testa and/or natural peg deterioration.
† For populations, V stages can be averaged. Reproductive stages should not be averaged. An R stage should remain unchanged until the date when 50% of the plants in the sample demonstrate the desired stage of the next R stage. The timing of a reproductive stage for a given plant is set by the first occurrence of the specific trait on the plant without regard to position on the plant. (Adapted from Boote, 1982).		

Table 2. Methods, equations, and reflectance indices used to estimate peanut maturity.

Method	Formula for calculation or estimation	Reference
Growing Degree Day (GDD)		
Emery's	$(AT_{max} + AT_{min}) - 13.3$	Emery et al., 1969
Mills'	$(AT_{max35} + 13.3 + ABS [AT_{min} - 13.3])/2 - 13.3 + \Delta T_{oc}$	Mills, 1964
Georgia 1	$((AT_{max35} + AT_{min})/2 - 13.3) + \text{Cumwater}$	Rowland et al., 2006
North Carolina 1	$(AT_{max35} + AT_{min13.3})/2 - 13.3$	
North Carolina and Virginia 2	$(AT_{max35} + AT_{min})/2 - 13.3$	
West Texas 1	$(AT_{max35} + AT_{min12.8})/2 - 12.8$	
West Texas 2	$(AT_{max35} + AT_{min})/2 - 12.8$	
West Texas 3	$(AT_{max35} + AT_{min})/2 - 7.2$	
	$(AT_{max} + AT_{min})/2 - 10$	
Bell-Wright	If $9 \leq AT_{avg} \leq 29$ , $GDD = AT_{avg} - 9$ If $29 < AT_{avg} \leq 39$ , $GDD = 20[1 - ((AT_{avg} - 29)/10)]$ If $AT_{avg} < 9$ ; $AT_{avg} > 39$ , $GDD = 0$	Bell & Wright, 1998
Air and soil temperature, and relative humidity	$((AT_{max} + AT_{min})/2 - 13.3) + ((ST_{max} + ST_{min})/2 - 18.3) + (90 - (RH_{max} + RH_{min})/2)$	Rowland et al., 2006
Air and soil temperature	$((AT_{max} + AT_{min})/2 - 13.3) + ((ST_{max} + ST_{min})/2 - 18.3)$	
Canopy spectral reflectance		
NDVI	$(\text{Red} - \text{Infrared}) / (\text{Red} + \text{Infrared})$	Carley et al., 2008
GNDVI	$(\text{Infrared} - \text{Green}) / (\text{Infrared} + \text{Green})$	Rowland et al., 2008
MCARI	$[(\text{Red edge} - \text{Red}) - (0.2 \times \text{Red Edge} - \text{Green})] \frac{\text{Red edge}}{\text{Red}}$	
SAVI	$(1 + 0.5) * \left[ \frac{\text{Infrared} - \text{Red}}{\text{Infrared} - \text{Red} + 0.52a} \right]$	Monsef et al., 2019
TDVI	$1.5 * \left[ \frac{(\text{Infrared} - \text{Red})}{\sqrt{\text{Infrared}^2 - \text{Red} + 0.5}} \right]$	
AT <sub>max</sub> , maximum daily air temperature; AT <sub>min</sub> , minimum daily air temperature; ΔT <sub>oc</sub> , ABS (AT <sub>max</sub> – 2.4); AT <sub>max35</sub> , maximum daily air temperature limited to 35 C; Cumwater, cumulative water from rainfall and irrigation from planting to harvest; AT <sub>min13.3</sub> , AT <sub>min12.8</sub> , minimum daily air temperature limited to low thresholds of 13.3 and 12.8 C; ST <sub>max</sub> and ST <sub>min</sub> , maximum and minimum daily soil temperature at 5 cm depth; RH <sub>max</sub> and RH <sub>min</sub> , maximum and minimum daily relative humidity; NDVI is normalized difference vegetative index; GNDVI is green normalized difference vegetation index; MCARI is modified chlorophyll absorption ratio index; SAVI is soil adjusted vegetation index; and TDVI is transformed difference vegetation index.		





**Figure 3.** Maturity profile boards for runner (left) and Virginia (right) market type peanut used to determine harvest maturity (R8) by the Williams and Drexler (1981) method. Drs. Marshall Lamb, USDA-ARS, and David Jordan, North Carolina State University, are kindly acknowledged for providing the photos for these charts.

Even though hull color is largely accepted by growers of the USA peanut belt, this method has been challenged as subjective, i.e. color assessment and grouping depend on the ability of the operator, and time consuming. Therefore, predictive models have also been developed, along with automated digital analysis of pod mesocarp color to improve the accuracy of the hull method (Colvin *et al.*, 2014; Bindlish *et al.*, 2017). Several methods were developed in the 60's and 70's; for some of these, descriptions are available in Sanders *et al.* (1982). Most models currently used are based on thermal time and cardinal temperatures ( $T_b$  and  $T_m$ ) necessary to achieve R8. Modern approaches using canopy spectral reflectance and peg strength are also underway to offer even more dependable solutions (Carley *et al.*, 2008; Rowland *et al.*, 2008; Sorensen *et al.*, 2015; Monsef *et al.*, 2019; Santos *et al.*, 2021; Santos *et al.*, 2022). Table 2 presents past as well as recently developed maturity predictive models.

## MORPHOLOGICAL CHARACTERISTICS

Morphological characteristics of crops are important determinants of yield. Because the harvestable peanut crop develops underground, reliable evaluations of crop progress during vegetative growth are difficult for peanut; during early growth stages, evaluations solely rely on the aboveground morphological traits and their association with plant physiology and yield. Even though time consuming and difficult to directly measure, traits such as biomass amount and color, plant height, lateral branching length and number, leaf area, and leaf area index (LAI), are associated with peanut environmental resilience and breeding for these traits has been shown to be superior to breeding for yield alone (Nigam *et al.*, 2005). Nonetheless, remote sensing tools that are now available can provide dynamic and accurate phenotyping of the morphological characteristics of a canopy and, depending on the application, with single plant and leaf detail (Jones and Vaughan, 2010; Tester and Langridge, 2010).

Plant architecture is an important morphological characteristic of crops. Plant height, leaf mass, LAI, i.e. leaf area distribution per unit land area, and leaf orientation relative to solar zenith angle are directly related to the light capture for photosynthesis, growth, and production of all crops including peanut (Radford, 1967; Mane *et al.*, 2017; Zurweller *et al.*, 2018a). Therefore, they are important determinants of yield.

For peanut, in addition to light harvest, plant architecture derived from the growth angle of the lateral shoots or so called “growth habit” is important because the peanut flowers are produced aboveground, but the fruits develop underground at the end of specialized fruiting organs called gynophores or pegs. The gynophores appear after pollination above ground and, after entering in the ground, their tips start to swell to produce the pods and then the seeds. Under drought, hot and dry soil may prevent gynophores from penetrating into the ground and forming pods (Fig. 4). In addition, high soil temperature can scorch the gynophore when the tip touches the soil, restricting seed development.



**Figure 4.** Elongated gynophores (pegs) on a lateral branch with prostrate growth. In this picture, “Titan” peanut has developed numerous pegs but their entry to the soil is delayed because of dry conditions.



Four distinct growth habits have been identified for domesticated peanut (Fig. 5 a, b, c, d) (Coffelt, 1974; Pittman, 1995). A prostrate growth habit is defined by lateral branches that spread on the soil surface while the main stem is easy to see but relatively short (Fig. 5a). A spreading growth habit is when lateral branches are only partially on the ground because their tips are curved upward; the main stem is easy to see, yet relatively short (Fig. 5b). A bunch growth habit is defined as semi-erect branches curved upwards, beginning at the base; the main stem is relatively taller than for the prostrate and spreading growth habits (Fig. 5c). Finally, erect growth habit peanuts have branches that grow straight up from the base and are generally 45° or less from the vertical; with relatively tall main stem (Fig. 5d). Growth habit differences among botanical types of cultivated peanut are apparent beginning at early growth stages (Fig. 6). For example, a study in Virginia in 2019 showed small differences among peanut types for the length of lateral branching, but differences were great for the main stem height (Sarkar, unpublished). In this study, Valencia and Spanish genotypes were taller than Virginia and runner types from 30 to 75 DAP; and at 75 DAP height, lateral branching, and LAI plateaued or started to decrease for all types, while biomass increased vigorously (Fig. 7).

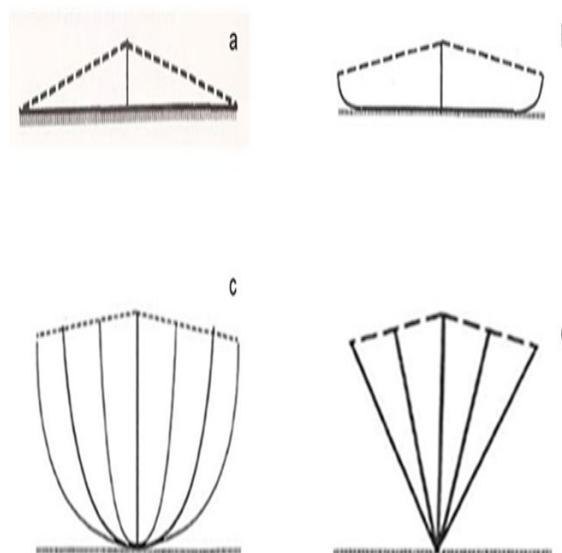


Figure 5. Main types of growth habit of cultivated peanut (from Pittman, 1995). Prostrate (a), spreading (b), bunch (c), and erect (d).

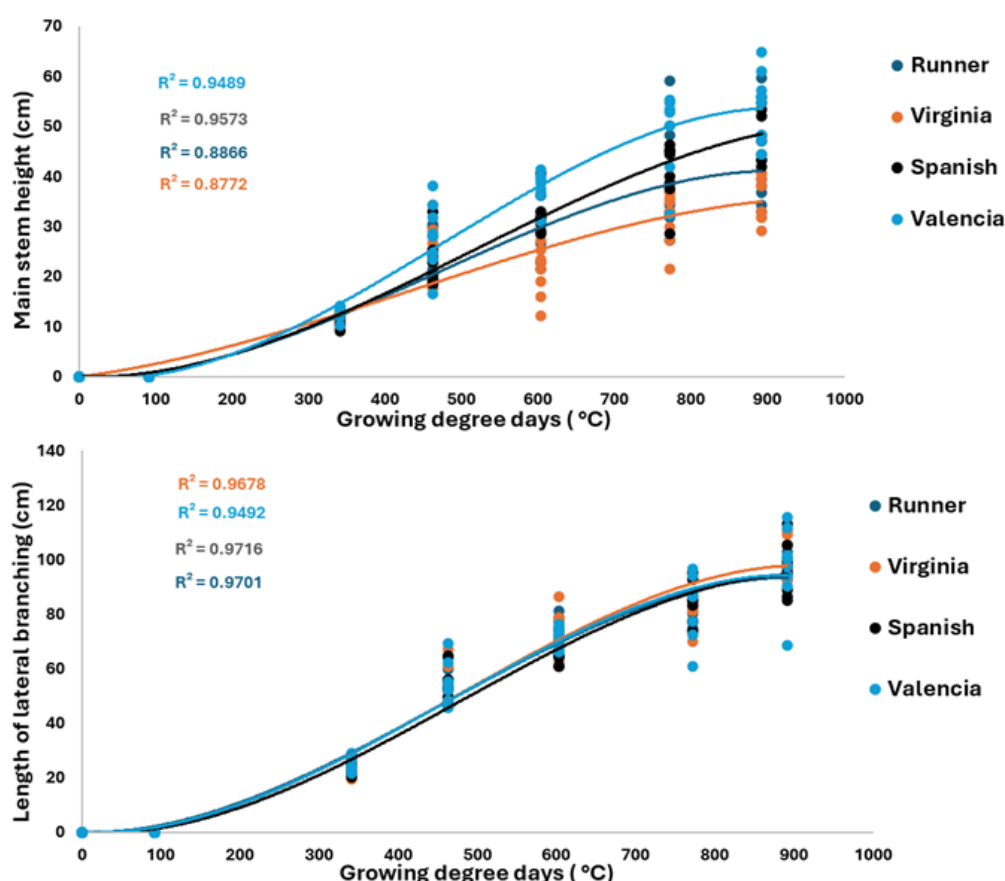


Figure 6. Early season differences for the main stem height and spread of lateral branching for the main types of peanuts grown at the Tidewater AREC in Suffolk, VA. Each type is an average of 2 genotypes and 3 replications (adapted from Sarkar, unpublished).

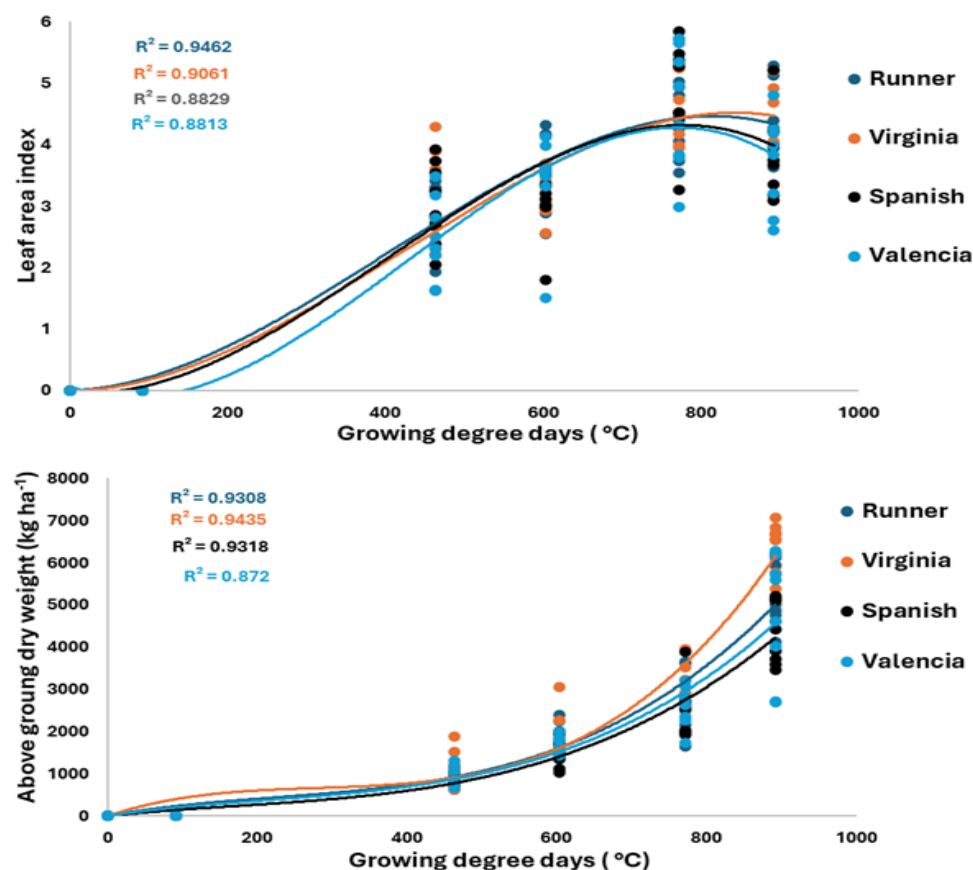
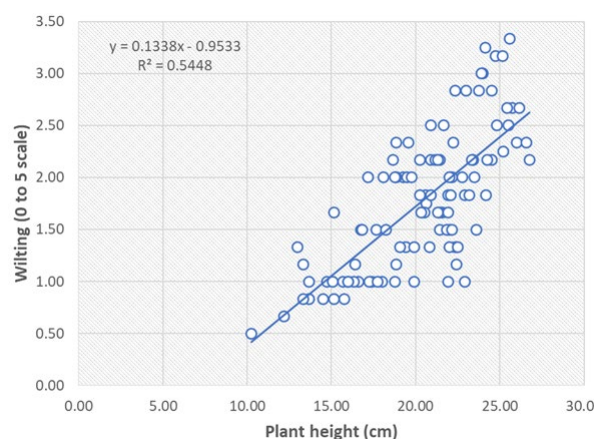


Figure 7. Development of the leaf area index and above ground biomass for the major peanut types up to 75 days after planting at the Tidewater AREC in Suffolk, VA (adapted from Sarkar, unpublished).

Since 1950, the USA peanut yield has increased approximately 46 kg ha<sup>-1</sup> yr<sup>-1</sup> (USDA-NASS, 2019). This increase is attributed to greater yield potential of newer cultivars with higher seed weight per seed, reproductive efficiency and disease resistance, and improved cultural practices (Coffelt *et al.*, 1989; Isleib *et al.*, 2001; Haro *et al.*, 2013). Nonetheless, in both North and South America, part of the yield increase has also been attributed to shifting the growth habit of the new cultivars from erect growth of the *fastigiata* types to prostrate growth of the *hypogaea* descendants (Haro *et al.*, 2013). This shift was associated with increased LAI, aboveground biomass accumulation, interception of photosynthetic active radiation, and harvest index (Haro *et al.*, 2017). The harvest index increase seems to have come from increased weight per seed and number, increased partitioning intensity to pods, and more efficient partitioning of thermal time towards greater seed-filling duration (Duncan *et al.*, 1978; Haro *et al.*, 2015).

Recognized as an important agronomic trait contributing to yield, peanut growth habit has been widely

studied to find the “ideotype” of peanut, i.e. peanut with optimum plant architecture that has comprehensive agronomic traits known to positively influence photosynthesis, growth, and yield. In addition, crop architecture has been considered as an important trait to breed for to improve mechanical cultivation, disease resistance and drought tolerance of peanut (Donald, 1968; Butzler *et al.*, 1998). Numerous studies identified that early biomass accumulation and LAI are important characteristics related to peanut tolerance to water deficit stress (Kiniry *et al.*, 2005; Nigam and Aruna, 2007; Arunyanark *et al.*, 2008; Zurweller *et al.*, 2018a; Zurweller *et al.*, 2018b). In these studies, water deficit stress reduced biomass and LAI more for drought susceptible than for drought tolerant cultivars; LAI was positively related to pod yield. The length of main axis and cotyledonary branches was reduced, and taller plants wilted faster than shorter peanuts under soil moisture deficit (Fig. 8) (Reddy *et al.*, 2003; Sarkar *et al.*, 2022). Drought also reduced plant density, light interception by plants, and dry matter accumulation (Pandey *et al.*, 1984; Bell *et al.*, 1993; Collino *et al.*, 2001).



**Figure 8.** The relationship between peanut height and wilting at the full pod stage (R4) in response to high temperature and soil drying in a sub humid environment. Each point represents an average of three replications for 104 genotypes of the Mini-core peanut collection. Wilting was visually scored on a scale from 0 to 5, i.e. 0 = no visual wilting; 2 = upper branches showing rolled leaves; 3 = upper and mid branches showing rolled leaves; 4 = upper and middle canopy becoming dry; and 5 = entire plant severely dry (Sarkar *et al.*, 2022).

In addition to crop water deficit stress, peanut canopy architecture can affect disease resistance. For example, upright and less dense canopies contributed to plant resistance to soil borne diseases by creating microclimates with reduced opportunities for plant contact with infested soil (Chappell *et al.*, 1995; Hollowell *et al.*, 2008). Upright canopies of Spanish market type peanut cultivars were more resistant than runner and Virginia types to *Sclerotinia* blight (Coffelt and Porter, 1982; Chappell, *et al.*, 1995; Goldman, *et al.*, 1995). Studies by Blad *et al.* (1978) compared soybean (*Glycine max* (L.) Merr.) cultivars with different canopy architectures. These authors found that dense and shorter canopies had the coolest, wettest microclimate and increased severity of white mold (caused by *Sclerotinia sclerotiorum* (Lib.) de Bary) than cultivars with open canopies and upright growth habits which were warmer, drier, and had a low incidence of white mold. Similarly, treatments supporting or maintaining dense foliar canopies such as irrigation resulted in the highest incidences of stem rot (caused by *Sclerotium rolfsii* Sacc.) in peanuts (Shew and Beute, 1984).

In other crops, e.g., corn (*Zea mays* L.), components of plant architecture such as plant height are directly related to yield and proposed as selection tools for increased yield (Freeman *et al.*, 2007; Yin *et al.*, 2011). Phenotyping for plant architecture by direct measurement of its components is tedious and logistically difficult to accomplish in large breeding populations. Fortunately, biomass, LAI, plant height, and lateral branching can be estimated with sufficient accuracy using remote sensing and imaging technologies; research of this type has recently started for peanut (Yang *et al.*, 2017; Sarkar *et al.*, 2020). Alternatively, the

development of molecular markers for marker assisted selection (MAS) may offer viable options to improve peanut architectural components contributing to improved yield, and resistance to biotic and abiotic stresses. Numerous recent studies in peanut are geared towards the development of high-density genetic maps to connect molecular markers to plant height, first lateral branching, and total branch numbers (Hake *et al.*, 2017; Kayam *et al.*, 2017; Li *et al.*, 2017; Lv *et al.*, 2018; Wang *et al.*, 2018; Li *et al.*, 2019).

Leaf color and specific leaf area are often associated with tolerance to water deficit stress in peanut via improved transpiration efficiency (TE) and water use efficiency (WUE), i.e. carbon assimilated, or biomass accumulated per unit of water used by or applied to the plants. For example, specific leaf area (SLA), i.e. leaf area divided by leaf weight, and leaf color or relative chlorophyll content determined non-destructively from light transmission through the leaf using a SPAD-502 color meter (Spectrum Technologies, Inc, Aurora, IL) showed good correlations with peanut yield and water use characteristics, i.e.  $^{13}\text{C}$  discrimination ( $\Delta^{13}\text{C}$ ), TE, and WUE, across numerous environments (Nageswara Rao and Wright, 1994; Bindu Mathava *et al.*, 2003; Rowland and Lamb, 2005; Upadhyaya, 2005; Sheshshayee *et al.*, 2006; Arunyanark *et al.*, 2008; Nigam and Aruna, 2008; Songsri *et al.*, 2008; Balota *et al.*, 2012a; Chen *et al.*, 2013; Singh *et al.*, 2014). However, in micro-plot experiments in India, under well-watered conditions, yield did not correlate well with TE (Vadez and Ratnakumar, 2016). In general, SPAD was positively, and SLA negatively related to yield (Janila *et al.*, 2015), but not always. In some studies, high rather than small SLA was associated with high yield (Balota *et al.*, 2012a; Suriharn *et al.*, 2011). Because significant diversity in response to water deficit was found in peanut genotypes and for simplicity of measurements, SLA and SPAD were further proposed and used as surrogate traits for breeding for high yield and efficient water use in cultivated peanut (John *et al.*, 2014; Vasanthi *et al.*, 2015). They were also proposed for evaluation of drought tolerance of wild species (Leal-Bertioli *et al.*, 2012), used with crop simulation models to design peanut “ideotypes” (Suriharn *et al.*, 2011), and were further studied to identify potential molecular mechanisms underlying these morphological characteristics (Dang *et al.*, 2013).

Root architecture is essential for the acquisition of water and nutrients, and its adaptation to specific environmental conditions is important for plant growth and development, especially under stressful conditions. For example, peanut genotypes with deeper roots produce relatively greater pod yields under water stress conditions than genotypes with more shallow roots (Rucker *et al.*, 1995; Songsri *et al.*, 2008; Jongrunklang *et al.*, 2011; Jongrunklang *et al.*, 2012). While shifting from erect to prostrate growth habit was clearly related to increased yield potential in peanut, little is known about how this shift affected root morphology; and how root morphology contributed to the current growth in yield (Coffelt *et al.*, 1989; Seaton *et al.*, 1992; Haro *et al.*, 2013). Zurweller *et al.* (2018a) showed that *fastigiata* genotypes had greater total root length than *hypogaea*, but similar root total surface area

distribution at 80 cm of soil depth. These authors concluded that more prolific root growth at depth may not necessarily result in an advantage for increased water acquisition and utilization, and higher yield of peanut. However, this conclusion may only reflect the years, location, and genotypes used in this work. Therefore, more research is needed to elucidate the role of root morphological characteristics for peanut yield and performance under environmental stress. Nonetheless, root analysis is more complicated when performed at field scale than with aboveground biomass, and current methods are imprecise, expensive and laborious. At the same time, relying on root analysis in controlled conditions is not an option for breeding programs because the physiological and morphological root adaptations are highly dependent on the environment in which plants grow (Cattivelli *et al.*, 2008; Sinclair, 2011). Identifying new methods for field scale root analysis under conditions where plants are grown seems to be an important benchmark for peanut in order to elucidate the importance of root morphology to yield and quality. New methods using remote sensing and non-invasive techniques such as ground penetrating radar (GPR) hold promise to address this aspect. Used with success to detect and measure coarse roots of trees nondestructively (Barton and Montagu, 2004; Cox *et al.*, 2005), GPR is now being tested for efficacy in detecting fine roots of agricultural crops (Liu *et al.*, 2018), including peanut. For example, the peanut breeding program in Lubbock, TX, is currently working with Dr. Hayes's group at Texas A&M University to evaluate the GPR efficacy to detect root traits (Burrow, personal communication).

## STRESS EFFECT ON PEANUT PHYSIOLOGY

### Water Deficit Stress

Water deficit stress is responsible for more crop loss than any other abiotic or biotic stress. In peanut, recent work is focusing on understanding physiological responses associated with plant dehydration (Borém *et al.*, 2012). Examination of these physiological responses is often done under the context of identifying specific plant traits governing possible tolerance to "drought" conditions. In general, water deficit tolerance refers to crop traits providing adaptations of dehydration avoidance or tolerance strategies to water limitation (Blum, 1988; Pallardy, 2007), while drought refers to the severity and timing of water deficit events occurring during crop development in a given environment. Avoidance is different from tolerance; avoidance can be accomplished by deeper rooting to sustain water uptake, while tolerance is more related to survival via osmotic adjustment. An intermediate strategy can be that of reducing transpiration (whether caused by stomatal response to VPD or naturally low hydraulic conductance) to maintain relatively high turgor and less stress, while forgoing some carbon gain from photosynthesis whereby some yield may be lost.

In the United States, peanut production is primarily in the southeast (GA, FL, AL, MS), southwest (TX, OK, NM), and the Virginia-Carolina (VC) region (VA, NC, SC). The

Ogallala aquifer is the primary source of irrigation for production of peanuts, cotton, corn, sorghum, and wheat in the southwestern U.S. This aquifer has been used heavily since the 1950s and, although irrigation efficiency has improved, the current rate of decline in the water table is 0.8 – 1.1 feet per year and it is estimated that the aquifer could be depleted within 30 to 40 years (Paxton, personal communication). Decline in some locales is already reducing the ability to irrigate when plant demand is the highest, during the midsummer months from flowering to mid-pod fill when air temperatures routinely exceed 40 °C. For the southeastern U.S. peanut producing region, there are also issues of water scarcity compounded with high growing season temperatures. This region is not inherently thought of as having water resource issues, but because rainfall is typically erratic during the growing season and groundwater supplies are increasingly being diverted to rapidly growing major urban areas, the issues related to water quantity are reaching critical proportions. Similarly, in the VC region, precipitation amount and distribution are erratic, and, unlike the other regions, irrigation is unavailable for over 90% of the peanut growing land. In addition to the obvious implications for yield, a significant concern is that water deficit stress promotes production of the highly carcinogenic aflatoxin mycotoxins (Butts *et al.*, 2023; Williams *et al.*, 2004), which can be minimized by irrigation.

Recent examples abound of abiotic stress affecting U.S. peanut production. Approximately one-third of Texas peanut acreage was not harvested in 2000 and again in 2011 due to drought and heat stress. In Georgia, drought and aflatoxin contamination of the crop resulted in an inability to market large quantities of peanuts in 2002 and 2019. In Virginia, severe drought in 2010 caused a 60% decline of the state average yield. The severe drought in 2006 and 2007 caused a 40% decline in southwest peanut production. On a global scale, the effects of these abiotic stresses on peanut crops are increasingly more severe and will continue to affect directly and indirectly through sparking of new diseases and pest insect cycles as the result of climate change (Prasad *et al.*, 2000; Ramsey, Tack & Balota, 2020; Paredes *et al.*, 2024; Porcuna-Ferrer *et al.*, 2024). Particularly in Africa and Asia, where irrigation water quantity and quality are limited, the effects of water stress are compounded by the effects of high temperature. In these regions, drought tolerant indigenous crops, including peanut, seem to lose their resilience in the face of climate change (Porcuna-Ferrer *et al.*, 2024).

Droughts and high temperatures reduce not just yield but also peanut seed size and quality, with negative effects on crop revenue (Balota, 2020; Ramsey, Tack & Balota, 2020). For example, Balota (2020) showed that a relatively moderate drought reduced sound mature kernel (SMK) content by 7.5% while severe drought depressed SMK by 25%. The SMK is an important grade factor with significant contribution to the revenue, i.e. the higher the SMK the higher the revenue. Similarly, Ramsey *et al.* (2020) predicted an approximately 11% revenue decline for Virginia-type peanut producers with 1 °C temperature increase due to both yield and seed size reduction. These authors examined the

varietal improvement as an adaptation strategy to heat and dryland conditions using data from a unique multi-state project, the Peanut Variety and Quality Evaluation (PVQE), collected on Virginia-type peanut accessions for over 35 years in the Virginia-Carolina peanut region of the USA. They concluded that breeding could offset moderate climate warming, but is unlikely to sustain revenue if warming exceeds 1 °C. With limited water resources to supply irrigation to peanut crops in the future, solutions must be found to support production and maintain economic sustainability. Recently, progress has been made toward identification of cultivated and diploid peanut accessions that exhibit phenotypic expression of traits associated with drought tolerance that can be used in breeding for resistance (Balota & Isleib, 2020; Bennett *et al.*, 2022; Kumar *et al.*, 2022; Kumar *et al.*, 2024; Massa *et al.*, 2024). Risk management tools have been, also, deployed along with management practices to reduce the effect of drought (Martins *et al.*, 2023; Nboyine *et al.*, 2023), but more research is needed to achieve sustaining yields and nutritional quality of peanuts under increasingly harsh conditions.

A decrease in gas exchange is one of the first physiological responses to drought in peanut, as evident by decreases in transpiration, stomatal conductance, and photosynthesis (Balota *et al.*, 2024; Mohandass *et al.*, 1989; Reddy *et al.*, 2003; Pilon *et al.*, 2018; Zhang *et al.*, 2022; Soba *et al.*, 2024). Ultimately, decreased growth and leaf area, as well as lower photosynthetic efficiency, leads to a decline in net canopy carbon assimilation, directly impacting yield (Reddy *et al.*, 2003; Soba *et al.*, 2024). Thus, of particular interest is the identification of the limiting factors and susceptibility of photosynthetic mechanisms to drought which reduce yield. These factors include stomatal and non-stomatal photosynthetic mechanisms that respond differently to abiotic stress depending on species and severity of the stress (Rucker *et al.*, 1995; Pilon *et al.*, 2018). Additionally, morphological factors such as root architecture, rooting depth, and plant acclimation capacity can contribute directly to plant water status and photosynthetic/source strength (Dang *et al.*, 2024; Puppala *et al.*, 2023; Rowland *et al.*, 2012a; Rowland *et al.*, 2012b). Pilon *et al.* (2018) addressed stomatal and non-stomatal limitations to carbon assimilation in peanut and showed that while declines in net CO<sub>2</sub> assimilation were driven by decreased stomatal conductance, the primary mechanisms contributing to low photosynthetic rates were non-stomatal (Soba *et al.*, 2024). These non-stomatal limitations included both disruption of electron transport rates through photosystem (PS) II, RuBP regeneration, rubisco carboxylation, and diffusional limitations in the chloroplast (Pilon *et al.*, 2018; Soba *et al.*, 2024). Presumably both the stomatal and non-stomatal mechanisms are affected by and even damaged by low leaf water potential status.

From a plant breeding perspective, research aimed at the discovery and modeling of targeted photosynthetic traits to improve yield and stress tolerance in peanut and other crops; these traits included early biomass accumulation and leaf area index (LAI), 'chlorophyll stability', and net

assimilation rate (A) (Balota *et al.*, 2024; Bennett *et al.*, 2022; Dang *et al.*, 2024; Zhang *et al.*, 2022; Rucker *et al.*, 1995; Fischer *et al.*, 1998; Kiniry *et al.*, 2005; Nigam and Aruna, 2007; Arunyanark *et al.*, 2008; Balota *et al.*, 2008; Songsri *et al.*, 2008). A comprehensive analysis of traits proposed to improve drought and heat resistance in peanut has been recently published by Puppala *et al.* (2023). Earlier research showed that LAI and early biomass accumulation had significant effects on peanut yield under stress conditions through improved light interception, radiation use efficiency, higher A, and extended photosynthetic duration (Collino *et al.*, 2001; Kiniry *et al.*, 2005; Arunyanark *et al.*, 2008). This research also emphasized that substantial genetic variation for these traits exists in peanut (Kiniry *et al.*, 2005; Nigam and Aruna, 2007; Arunyanark *et al.*, 2008). In particular, A seemed to be a key trait as its cumulative rate over the growing season is the main driver of biomass and yield. For example, experimental and theoretical analyses suggested that improvement of assimilation in C<sub>3</sub> plants is feasible and can be achieved through increasing photosynthetic rate per unit leaf area (Zhang *et al.*, 2022). Using carbon isotope composition and discrimination ( $\Delta^{13}\text{C}$ ) chemistry terms, Farquhar and colleagues (1989) developed the theory linking  $\Delta^{13}\text{C}$  to A, transpiration efficiency (TE, the ratio of A to transpiration rate), and water use efficiency (WUE, the ratio of biomass to water used to produce that biomass). Since then, numerous studies used  $\Delta^{13}\text{C}$  to estimate water use of C<sub>3</sub> plants, including peanut, but this analysis is expensive and low throughput for regular use in breeding (Nageswara Rao and Wright, 1994; Rowland and Lamb, 2005; Zhang *et al.*, 2022). Limited-transpiration (LT) rate at elevated vapor pressure deficit (VPD) and transpiration decrease (TD) early in the soil drying were also proposed as two physiological mechanisms by which soil water could be conserved and used by plants for a longer time in between rain events (Devi *et al.*, 2010).

A fundamental strategy that plants have evolved for regulating water use is altering hydraulic conductance, ultimately influencing transpiration flux. Alterations in transpiration flux can have significant impacts on crop yield because of its impact on CO<sub>2</sub> assimilation for photosynthesis (de Wit, 1958; Passioura, 1996; Blum, 2009). For warm-season C<sub>3</sub> plants like peanut, the general pattern of water use for non-stressed plants is a gradual increase in water use during morning hours peaking at mid-day and declining in the afternoon as leaf water potential decreases (Mohandass *et al.*, 1989). Declining leaf water potential has also been closely related to declines in stomatal conductance ultimately reducing water use (Brodrick and Holbrook, 2003).

Relative humidity (RH), dew, and rain vary greatly across the peanut producing regions of the U.S. For example, RH, the ratio of actual vapor pressure to saturation vapor pressure, depends greatly on temperature. In general, the western hot-semi-arid regions of the U.S. have lower vapor pressures than the hot-humid climate of the southeastern and eastern U.S. Vapor pressure deficit (VPD), i.e. the difference between the amount of actual moisture and how



much moisture air can hold, is a measure of how close air is to saturation. For a given environment, VPD is easily derived from RH and temperature, and has spatial and temporal variation through the crop growth cycle. When soil water is unlimited, because the sub-stomatal cavity of the leaf is saturated with water vapor, water diffuses through open stomata outside the leaf under high atmospheric VPD (less moisture in the air). This may result in leaf dehydration, faster soil water depletion, and on-set of water deficit stress.

Sinclair *et al.* (2017) and others (Turner *et al.*, 1985; Devi *et al.*, 2009; Shekoofa *et al.*, 2014, 2015a, b; Pradhan *et al.*, 2019) capitalized on the response of stomatal conductance to diurnal VPD variation and proposed that LT response to increased midday VPD could be a mechanism of dehydration avoidance. Through this mechanism, plants can conserve soil water at early growth stages for use later in the season to sustain seed filling. The predominant physiological mechanism most likely influencing the LT trait is stomatal regulation. Shekoofa *et al.* (2015a) documented the LT trait threshold occurring across peanut genotypes was not influenced by relative water content. This indicates that bulk leaf water status or active metabolic processes (abscisic acid transport) is not influencing the LT trait (McAdam and Brodribb, 2014; Sinclair *et al.*, 2017). The current evidence is that LT trait could be a result of particular genotypes having relatively lower hydraulic conductivity (passive metabolic process) (Sinclair *et al.*, 2008; Choudhary *et al.*, 2013; Choudhary *et al.*, 2014; Ocheltree *et al.*, 2014). The general concept is that low hydraulic conducting genotypes under higher VPD have insufficient water flux into leaves to match water loss via transpiration, thus reducing stomatal aperture (stomatal limitation) balancing the water flux in and out of the leaf (Sinclair *et al.*, 2017). Therefore, the presence of LT trait may be associated with resistance factors limiting leaf water transport between xylem and guard cells (Sinclair *et al.*, 2008).

When day/night temperature was maintained at 27/21 C in a growth chamber, Devi *et al.* (2009) reported the LT trait was present in 9 of the 17 peanut genotypes, i.e. 9 genotypes showed a break of linearity between transpiration and VPD when VPD was greater than 2.2 kPa. Other controlled chamber studies evaluating the impact of temperature on the genotypic LT response concluded that increasing temperature could cause a lack of expression of this trait (Shekoofa *et al.*, 2015a). When the chamber temperature was 31 C, three of the 6 genotypes expressed the LT trait, but at a temperature of 36 C the LT trait was diminished in all genotypes. The lack of response of this trait at warmer temperatures was also observed in a field study (Shekoofa *et al.*, 2015a). The impact of temperature on the expression of this trait seems to be more influential on peanut than *C<sub>4</sub>* determinate crops of sorghum and maize (Shekoofa *et al.*, 2013; Shekoofa *et al.*, 2015b). Transpiration decrease (TD) in response to soil drying expressed as the fraction transpirable soil water (FTSW) was also investigated as a peanut strategy to conserve soil water

at early stages for later use. Devi *et al.* (2009) studied 17 peanut genotypes and found large variation in the FTSW among the genotypes, i.e. FTSW ranged from 0.22 to 0.71. However, less variability of this trait has been reported for the U.S. commercial peanut cultivars (Devi *et al.*, 2011; Shekoofa *et al.*, 2013). Stomatal sensitivity to soil drying was observed in a field study when comparing genotypes of subspecies *fastigiata* and *hypogaea* (Zurweller *et al.*, 2022).

Crop production loss from water deficit stress primarily occurs because of reduction in photosynthesis from stomatal closure limiting CO<sub>2</sub> assimilation (de Witt, 1958; Pilon *et al.*, 2018; Tanner and Sinclair, 1983). Therefore, mechanisms that limit transpiration such as LT and TD must, to some extent, also reduce CO<sub>2</sub> assimilation and may result in counterproductive effects on yield. For peanut, LT and TD were documented with certainty under growth chamber conditions, but evidence of the traits' expression in the field is limited and their direct contribution to soil water conservation and yield advantage under drought is still to be determined.

Diurnal monitoring of air and canopy temperature allows measurement of canopy temperature depression (CTD), a surrogate for stomatal conductance and transpiration of plants in the field. This technique was used with success for decades in plant breeding for drought and heat tolerance (Ehrlir *et al.*, 1978; Blum *et al.*, 1982; Reynolds *et al.*, 1994; Amani *et al.*, 1996; Fischer *et al.*, 1998; Balota *et al.*, 2007). For field grown peanut in a sub humid environment, diurnal CTD variation was monitored with wireless infrared thermometers (Balota *et al.*, 2012a, b). As temperature and VPD increased, transpiration rate estimated from CTD increased from 8:00 to 10:00 EST, i.e., VPD went from 0 to 1.5 kPa during this time; CTD decreased at midday, i.e. from 11:00 to 14:00 when VPD went from 2 to 2.5 kPa; then CTD increased again in the afternoon until 15:00 when it started to decline, one hour after VPD began to decline (Fig. 9). A negative linear relationship between transpiration rate and VPD from 11:00 to 14:00 EST for field grown peanut was confirmed by directly measuring stomatal conductance on 8 peanut genotypes with a LI-6400 portable photosynthesis meter (LI-COR Biosciences Inc.) (Hawkins, 2014). This agrees with the classical model that stomata closes when the water content in the sub-stomatal cells declines from intensified water diffusion outside the leaf and reopens when the water content is replenished by hydraulic conductivity (Taiz *et al.*, 2014; Brodribb and McAdam, 2011). Unlike results noted in growth chamber tests, when LT and TD to soil drying were expressed in a handful of peanut lines when temperature was 32 C and even in fewer lines when temperature was 36 C (Shekoofa *et al.*, 2015a; Pradhan *et al.*, 2019), in tests in the field by Balota *et al.* (2012b) on 30 peanut genotypes, all genotypes partially closed stomata in response to midday VPD increase, regardless of temperature and soil moisture content (Fig. 10). However, by this mechanism of LT, yield variation among genotypes from 4992 to 6758 kg ha<sup>-1</sup> was not explained (Balota, 2010).

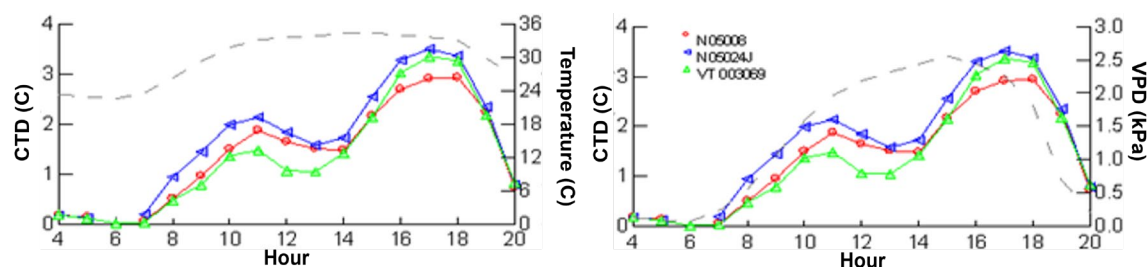


Figure 9. Diurnal variation of canopy temperature depression (CTD) as an estimate of transpiration and stomatal conductance response to increased temperature and vapor pressure deficit (VPD) in a sub-humid environment. CTD was calculated as air minus canopy temperature with high values denoting cool canopy due to increased transpiration. Air temperature and VPD are the dashed lines; the continuous lines with symbols represent CTD of three peanut breeding lines in the Peanut Variety and Quality Evaluation tests in 2009 (Balota *et al.*, 2012a, Balota *et al.*, 2012b). Data over 10 days of continuous temperature monitoring in mid-August are averaged.

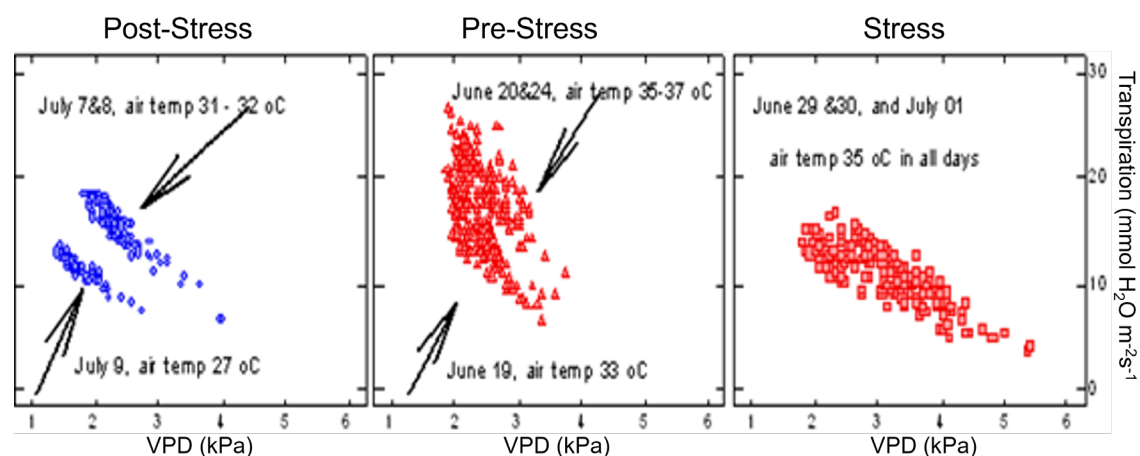


Figure 10. Response of transpiration to midday (11:00 to 14:00) VPD increase on days with different air temperatures and soil moisture content (Balota *et al.*, 2012a, Balota *et al.*, 2012b). Transpiration was measured with a LI-6400 portable photosynthesis meter (LI-COR Biosciences Inc.) 30 peanut genotypes grown in the field at Tidewater AREC, in Suffolk, VA. Each data point is an average of three replicates. Pre-stress represented a period with 10 d of no significant rain event at the beginning peg stage; stress period was after 20 consecutive days of no rain and peanut was at the beginning pod stage; post-stress was after 35.4 mm of combined rainfall and irrigation in 2009.

Similarly, there is little evidence that growth chamber selected peanut genotypes for LT response to increased VPD or TD with soil drying have yield advantage when grown in the field. For example, in growth chamber testing, Sinclair *et al.* (2018) found line N12006ol with decreased transpiration rate to soil drying in terms of FTSW, i.e. high FTSW, and speculated that TD may have caused higher yield of N12006ol in low-yield environments in the 2014 PVQE testing. Indeed, in 2014 PVQE trials, line N12006ol had an average yield of 5426 kg ha<sup>-1</sup> across five locations, like the popular cultivar Bailey, but its sister line, N12008olFCSmT, produced 15% more yield than Bailey and N12006ol when grown under the same environmental conditions (Balota *et al.*, 2015). N12008olFCSmT had significantly lower FTSW than N12006ol (Sinclair *et al.*,

2018) but was released as Bailey II in 2017 for its superior yield.

There is no evidence that LT and TD traits expressed early in the season can conserve water for use at later physiological growth stages of seed development under field conditions. In general, growth chamber studies not only provide conditions different than in the field and expressed phenotypes may be different in controlled conditions than in the field, but they disregard the soil-plant-atmosphere relationships, which are the driving force for crop production. For example, in the VC region, the soil is sandy and shallow, and drought stress can develop within 10 to 20 days of no rainfall. Also, at early growth stages, evaporation is more intense than later in the season when plants cover the ground. Under these conditions, field crops in Suffolk, VA, may become more drought stressed than crops in TX in

mid-July (Fig. 11). However, some phenotypes can withstand severe field dehydration. The peanut genotype that remains green and turgid plants in Fig. 11, while the entire field is water-stressed, is GP-NC WS 17 (Tallury *et al.*, 2014). This line is an exotic derived line from interspecific hybridization with *Arachis cardenasii* (Krapov. & W.C. Gregory) with drought and heat tolerance (Tallury *et al.*, 2014). This genotype was screened for LT in growth chambers by Shekoofa *et al.* (2015a) and did not show the LT trait. However, GP-NC WS 17 showed the greatest stomatal conductance recovery after water deficit stress, greater chlorophyll fluorescence estimated as the ratio of variable to maximum fluorescence ( $F_v/F_m$ ), and the least membrane injury, when compared with other genotypes in the field (Rosas-Anderson *et al.*, 2014; Singh *et al.*, 2014). Pilon *et al.* (2018) also documented that non-stomatal factors such as electron transport are important for maintaining relatively high levels of CO<sub>2</sub> assimilation under

drought. Similarly, under field conditions when drought was imposed by coverage with rainout shelters, Zhang *et al.*, (2022) showed that some peanut genotypes, i.e. PI 502120 and AU-NPL 17, maintained high photosynthetic and stomatal conductance rates, and produced high yields under drought. The authors called these genotypes “water spenders”, like cultivars of wheat (*Triticum aestivum* L.) and common bean (*Phaseolus vulgaris* L.) previously identified with similar responses to drought (Blum *et al.*, 2009; Sanz-Saez *et al.*, 2019). Other cultivars, however, developed an opposite strategy to cope with drought; they closed the stomata early during the onset of drought. These cultivars, i.e. Line-8 and AU16-28, called “water savers” showed lower stomatal conductance but similar yields with “water spenders” (Zhang *et al.*, 2022). The authors concluded that, indeed, water savers did not have a yield advantage over water spenders under field-imposed drought.



**Figure 11.** Left, a corn field in Suffolk VA, on July 17, 2010, after 20 days of no rainfall. At the right, an entire peanut field (the 2010 Peanut Variety and Quality Evaluation trials) at the same location after 2 months of rainfall absence on Sep 24, 2010. The green plot to the extreme left of the peanut picture is genotype GP-NC WS 17 (Tallury *et al.*, 2014) tested at line SPT 06-07.

Drought tolerance is a complex of morphological and physiological adaptive plant responses including escape, avoidance, and resistance (Blum, 1988). Considering that drought is usually accompanied by high temperatures, the complexity may become overwhelming and unrealistic to address with single traits identifiable through low-throughput techniques in controlled conditions. For agricultural production, adaptive responses must have a yield benefit under drought, while biotic resistance needs not to be forgotten; this makes drought tolerance even more complicated from a breeding perspective. The single trait selection approach has limited physiological applications in plant breeding and constitutes a major point of controversy among breeders and physiologists for decades. Hopefully, the next generation strategy of genomic breeding coupled with advances in phenomics, and machine learning will allow for increasingly more effective inclusion of physiology in breeding and accelerated development of peanut cultivars with improved drought tolerance. Because these strategies

have the power to combine a diversity of plant responsive traits, i.e. traits associated with yield, biotic and abiotic tolerance, the mechanisms mostly contributing to increased yield under various “drought” conditions will be more likely to be successfully identified and further used to develop drought tolerant peanut cultivars.

### Cold and Heat Effects on Peanut

Temperature influences peanut growth and development throughout the season. For optimal productivity, air temperatures for vegetative growth should be from 30 to 35 °C, whereas for reproductive development, the optimal range is from 22 to 30 °C (Wood, 1968; Cox, 1979; Williams and Boote, 1995).

Multiple physiological processes are affected by sub- or supra-optimal temperatures. Soil temperatures below 18 °C slow the germination rate and result in a high percentage of seedlings with thick hypocotyls and underdeveloped, curled root system (Kvien *et al.*, 2022). Conversely, a rise in soil

temperatures above 35 °C decreases the overall germination percentage and necrotic areas are likely to develop on hypocotyls and roots of seedlings due to disruption in cell membranes.

The balance between photosynthesis and respiration mediates cell growth and expansion in peanut leaves; thus, photosynthesis and respiration are essential physiological processes associated with tissue growth and development. The air temperature for optimal photosynthesis in peanut plants is around 30 °C, but photosynthesis occurs with variable rates over an extended temperature range (10 to 35 °C). Cold stress is more likely to occur over the first 30 DAP in spring-sown peanut fields, when temperatures are not consistently warm enough to sustain plant growth. Low temperatures can considerably impair early season growth. The lowest critical average temperature at which growth is interrupted, is near 12 °C (Cox and Martin, 1974). At temperatures below 20 °C, peanut seedlings produce fewer smaller leaves and shorter stems when compared to seedlings grown at 30 °C. Faster development of the first peanut true leaves contributes to overall plant growth at early season (Virk *et al.*, 2019). The reduced growth of leaves and stems caused by low temperatures is primarily associated with decreased photosynthetic rate. The underlying factors causing decreased photosynthetic rate under low temperatures include reduced quantum efficiency of PS II and poor performance of the PS II and PS I intersystem, which reduces the overall energy produced during the light-dependent reactions with further inhibition of photosynthetic performance (Virk *et al.*, 2019). Temperatures below 22 °C resulted in delayed flower appearance, decreased number of flowers, and impaired pollination (Zhang *et al.*, 2019a). Shifting planting to a later date can provide higher temperatures at the seedling stage. Moreover, temperatures lower than 10 °C or higher than 35 °C may promote irreversible damage to the photosynthetic system (Berry and Björkman, 1980).

High air temperatures generally accelerate the progress of reproductive growth stages in peanut. Plants initiate and complete flowering earlier and pods mature more rapidly under heat stress (Akbar *et al.*, 2017). In a study with 62 peanut genotypes, plants reached 75% flowering between 35 and 50 days under temperatures ranging from 28 to 30 °C. When the genotypes were exposed to temperatures from 33 to 39 °C, 75% flowering was achieved in 29 to 37 days (Akbar *et al.*, 2017). Pod maturity also occurred sooner under hot environments. Although early pod set and maturity may benefit planting and harvest logistics, overall yield is considerably decreased by warmer temperatures, partly because of shorter growth cycle and less resource capture (Prasad *et al.*, 2003).

The reproductive stages of peanut are more susceptible to the negative effects of high temperatures than the vegetative stages. Flower fertility is highly sensitive to temperatures above 35 °C, resulting in low fruit set (Prasad *et al.*, 2000). Flower bud temperature is typically similar to air temperature up to 30 °C. However, at air temperatures above 35 °C, the cooling effects are insufficient to prevent the flower buds' heat injury. Fruit-set may be reduced due to

impaired micro- and mega-sporogenesis, and reduced fertilization of flowers present on the plant (Prasad *et al.*, 2003). Reduced flower fertilization under high temperatures occurs due to poor pollen production and viability, and low pollen tube growth (Prasad *et al.*, 2003). Since self-pollination of peanut flowers occurs early morning and the flower opens only after fertilization, the most critical period for heat is the first hours of the day. Optimum temperatures for flower production are between 25 and 30 °C, whereas plants tolerate temperatures up to 34 °C for pod development. Pollen viability is above 90% at temperatures of approximately 32 °C, decreasing to 68% at 40 °C with a further decline to 0% at 44 °C (Prasad *et al.*, 2003).

High air temperatures also negatively impair the photosynthetic process in peanut leaves. Temperatures above 40 °C during flowering and pod development (74 DAP) decreased net photosynthesis and stomatal conductance by 35% on average for seven genotypes (Pilon *et al.*, unpublished). However, nighttime respiration was not impacted by midday high temperatures. The lower photosynthetic rate resulted in less pod dry weight only for two of the seven genotypes, suggesting that five peanut genotypes exhibited greater heat tolerance. These genotypes decreased photosynthesis during heat stress but subsequently increased their photosynthetic rates after the stress period, allocating a greater proportion of photoassimilates to pod development (Pilon *et al.*, unpublished).

Soil temperature is important in regulating pod initiation, pod growth rate, and mature seed mass. Soil temperatures near 20 °C in the fruiting zone improved pod initiation rate, resulting in a greater number of pods per plant; but 20 °C did not result in optimal pod growth rate, thus seed mass at maturity was low at this temperature (Golombek and Johansen, 1997). Temperatures between 30 and 32 °C are suitable for greater pod growth rate and mature seed mass (Golombek and Johansen, 1997). Yet, soil temperature increases to 35 °C may reduce peg and pod development by 33% (Ketring, 1984), and seed mass by 45%, resulting in lower overall pod yield (Akbar *et al.*, 2017).

Growth of vegetative tissues (leaves and stems) is generally accelerated by high temperatures up to 35 °C (Prasad *et al.*, 2003). In contrast, reproductive units (pegs and pods) require slightly lower temperatures (near 30 °C) for optimal growth. Under heat stress, crop growth rate (CGR) is high, suggesting great accumulation of photo-assimilates; however, pod growth rate (PGR) is generally low, thus indicating insufficient partitioning of accumulated photoassimilates (Craufurd *et al.*, 2003), which is caused by poor pod-set (Prasad *et al.*, 2003). The ultimate consequence of low pod-set and poor partitioning of photosynthates from the leaves to pods under heat stress results in significant reduction in pod yield, regardless of vigorous aboveground growth.

The partitioning factor (ratio of PGR to CGR) has been used as a criterion for heat tolerance selection in peanuts (Ntare *et al.*, 2001; Craufurd *et al.*, 2003). Other physiological assessments employed as screening techniques for temperature tolerance included cell membrane

thermostability, chlorophyll fluorescence, and flower to fruit-set ratio (Srinivasan *et al.*, 1996; Talwar *et al.*, 1999). Comprehensive knowledge of the physiological mechanisms underlying tolerance to cold and heat would contribute to identifying cultivars adapted to locations with predominant extreme temperatures.

## PHENOTYPING TOOLS FOR YIELD AND ENVIRONMENTAL STRESSES

### Phenotyping Is the Bottleneck for Crop Improvement

Phenotype corresponds to plant characteristics that can be quantitatively measured, and which depend on the interaction between genotype and environment ( $G \times E$ ). Plant physiologists and breeders have collected phenotypic data for decades to understand how plants respond to biotic and abiotic stressors, and how to breed for the most suitable phenotypes under specific environmental conditions. Historically, phenotypes of interest include but are not limited to plant height, biomass, LAI, photosynthesis, root angle, root length density, seed number, and hundred seed weight (Balota *et al.*, 2024; Kolhar and Jagtap, 2023; Sarkar *et al.*, 2020; Sarkar *et al.*, 2021). Currently, phenotypes can be taken using simple and more technologically complex methodologies that, although appropriate and accurate, are limited by the cost and time to collect the data. As breeding programs analyze hundreds of genotypes in multiple spatial and temporal conditions, deployment of high throughput methods is needed.

The development of DNA sequencing technologies has generated the opportunity to analyze plant genomes, providing scientists with tools to understand the genetic regulation of specific phenotypes in quick and affordable ways (Jiao and Schneeberger, 2017; Yang *et al.*, 2017). Development of recombinant inbred lines (RIL), near isogenic lines, and diversity panels of plant populations, makes it possible to map Quantitative Trait Loci (QTL) and thus code quantitative phenotypes needed to improve crop performance under different environments (Adachi *et al.*, 2011; Dhanaphal *et al.*, 2015; Oakley *et al.*, 2018; Kassie *et al.*, 2023). In peanut, QTLs have been identified for plant height, leaf length, yield components, and yield (Khedikar *et al.*, 2018; Lv *et al.*, 2018; Mondal *et al.*, 2019); seed composition traits such as oil content (Hu *et al.*, 2018; Liu *et al.*, 2024); seed dormancy (Wand *et al.*, 2022); mineral nutrient contents (Zhang *et al.*, 2019b); disease tolerance (for a review on this theme see Desmae *et al.*, 2018; Choudhary *et al.*, 2019; Liang *et al.*, 2021); and yield components related with drought tolerance (Faye *et al.*, 2015; Desmae *et al.*, 2018; Kumar *et al.*, 2024). However, to produce strong correlations between phenotypes and their genomic regions, thousands of genotypes have to be

phenotyped across environments, growth stages, and years; this is difficult to accomplish with traditional phenotyping methods. Thus, phenotyping has become the bottleneck for genomic discovery and the breeding efforts (Ninomiya, 2022).

In the past 30 years, improvements in digital image acquisition, automation, and robotics have made high-throughput phenotyping (HTP) possible (Furbank and Tester 2011; Fiorani and Schurr, 2013). HTP methods were initially developed for greenhouses and growth chamber applications using plants in early stages of growth; thus, they were unreliable for field screening and not valid for breeding (Araus *et al.*, 2014; Ninomiya, 2022). After 2010, field HTP platforms started to be developed (Araus and Cairns, 2014; Araus *et al.*, 2018a). Field HTP combines remote sensing via satellite and aerial sensing and uses terrestrial and unmanned aerial vehicle (UAV) platforms equipped with a variety of sensors to assess physiological phenotypes related with yield and stress adaptation (Araus and Cairns, 2014; York *et al.*, 2015).

### Field HTP: Platforms and Sensors

Remote sensing technologies are becoming increasingly more affordable to the end-users, breeders, and farmers. These technologies collect multiple plant characteristics in a relatively short time, repeatedly and consistently over the season with increased accuracy. Each of these technologies requires two main components. First, they require a vehicle or a platform to bring the sensors on site. Platforms are of different types, and they are complex and costly. The second part is the technology itself in the form of one or multiple sensors for data collection.

#### *Phenotyping platforms*

Several types of systems are currently available, with different levels of adaptability and upgradability, mobile or stationery, and with a drastic price range from hundreds to millions of dollars (Fig. 12) (Yuan *et al.*, 2023). Platforms can be immobile, using single or multiple cameras and other sensors mounted on single or multiple poles to take time-lapse images (Brocks *et al.*, 2016; Zhou *et al.*, 2017). Others are stationary field scanner systems on a movable gantry (Virlet *et al.*, 2017; Burnette *et al.*, 2018). The Field Phenotyping Facility at the University of Nebraska Lincoln is one acre in size, and includes sensors and cameras mounted on an automatic cable suspended carrier system (Spidercam) attached to four giant poles in each corner of the field (Kirchgessner *et al.*, 2017; Bai *et al.*, 2019). Significant limitations of the stationary platforms are the high maintenance cost and the limited number of experiments that can be accommodated, e.g. use of any chemicals as treatments may result in negative effects on the subsequent experiments.



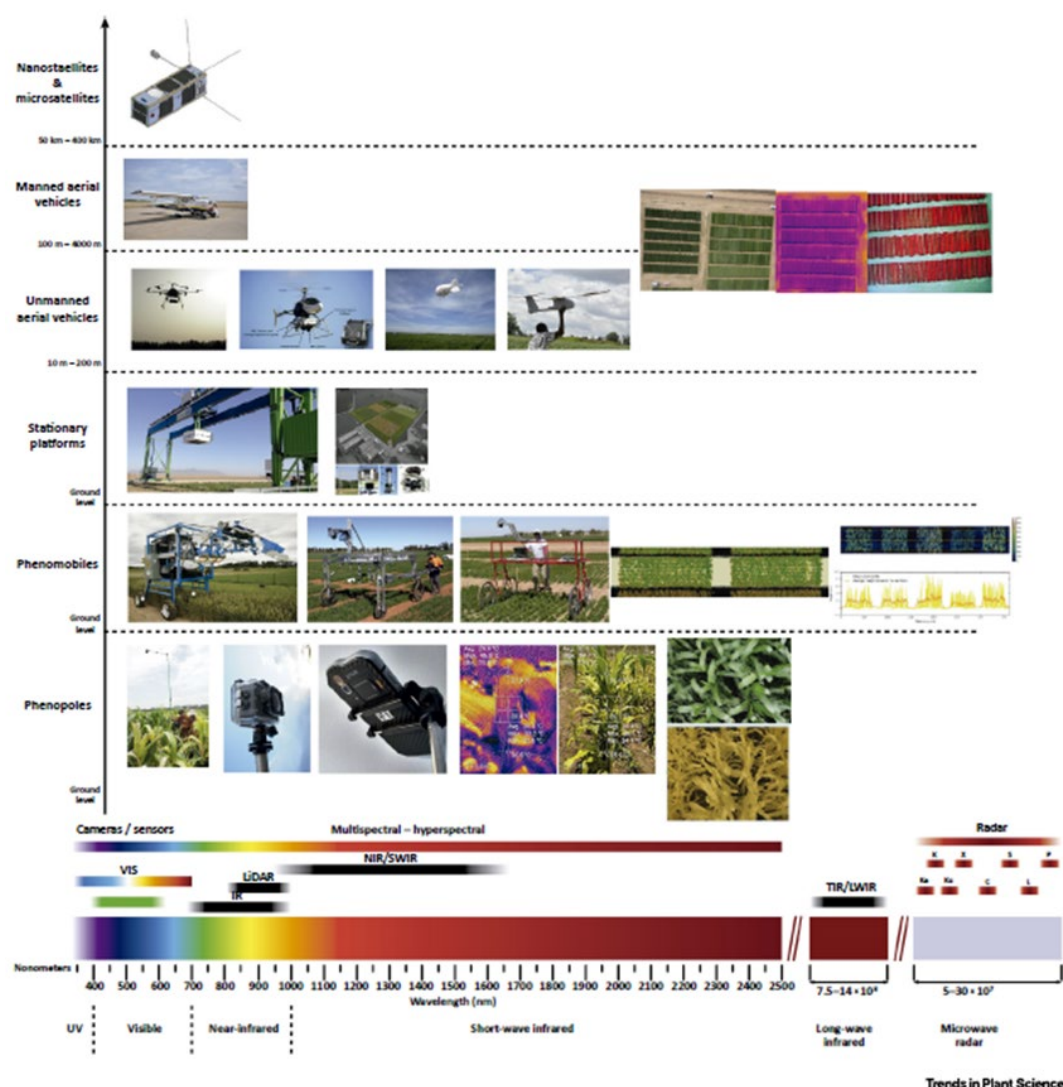


Figure 12. Different categories of potential and actual ground and aerial phenotyping platforms, along with the spectral ranges used for different remote-sensing tools. RGB cameras (VIS), multispectral and hyperspectral sensors and cameras, light detection and ranging (LiDAR) sensors, thermal sensors and cameras (TIR/LWIR), and the different categories of Radars. The ground stationary platforms correspond to the Maricopa Agricultural Center (USA) and the ETH field phenotyping platform (Switzerland). The images of the phenomobile correspond to (from left to right) a proximal remote sensing buggy, the phenomobile lite, and a phenocart. IR, infrared; LWIR, long-wave infrared; NIR, near-infrared; SWIR, short-wave infrared; TIR, thermal infrared; VIS, visible (Adapted from Araus *et al.*, 2018b).

Alternatives to the stationary platforms are mobile, manned or unmanned, platforms. Mobile remote sensing systems include phenomobiles, aircraft, and satellites. The phenomobiles are ground-based vehicles such as unmanned robots or manned diesel-powered tractors and pushcarts (Pittman *et al.*, 2015; Yuan *et al.*, 2018; Antonucci *et al.*, 2023). While phenomobiles allow freedom of use in multiple environments over stationary platforms, they are also limited by the geography of the land through which they can be driven. For example, their use can be limited for tall canopies, wide-spread ground cover crops, and uneven ground. For tractor-based platforms, a significant limitation

is the area where they can be safely and time-effectively moved to collect data.

Manned and unmanned aircraft bypass the terrain limitations of the terrestrial platforms. Aerial imaging allows faster and broader coverage of a field than ground-based vehicles. Manned aircraft are well-suited for large landscapes consisting of several hundred to thousands of acres, but their high cost, flight restrictions to certain zones, and the requirement and availability of pilots make their use limited. Drones or unmanned aircraft (UAVs) with either fixed wings or multi-rotors are better options for small farms and research areas. A disadvantage of UAVs, however, is that battery capacity limits the flight mission and payload.

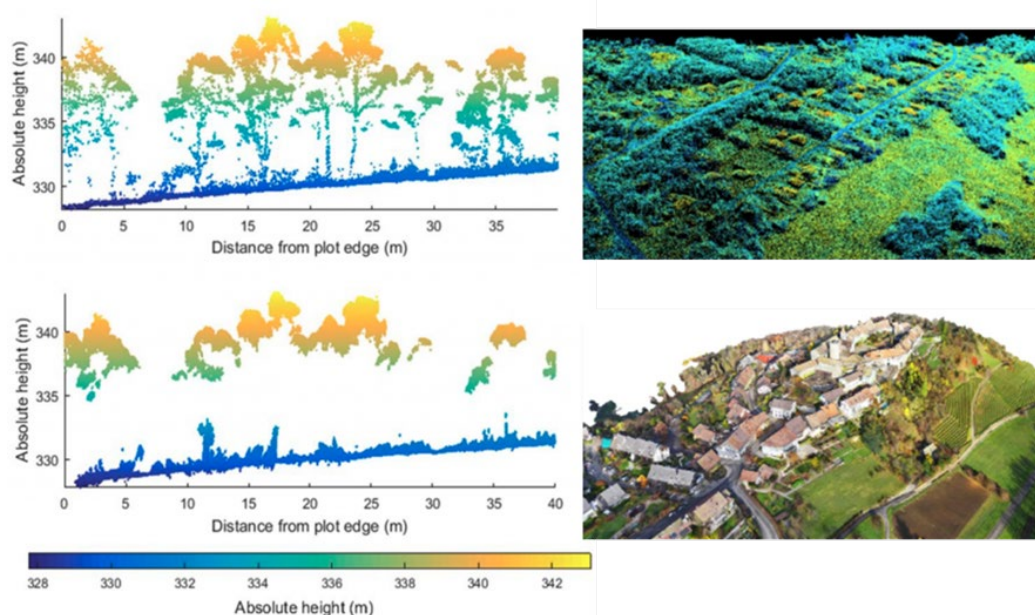
Satellite imagery collected from the Sentinels of the European Space Agency and Landsat from the US is used for phenotyping, mainly for large landscape areas. Satellite imagery is based on vegetation-derived reflectance at multiple wavelengths, from which numerous vegetative indices have been developed for different applications (Reed *et al.*, 1994; Labus *et al.*, 2002; Johnson *et al.*, 2003). The major disadvantage of satellites is their lower spatial resolution in comparison with aircraft. Image resolution is 30 m<sup>2</sup> or more for Landsat 8, 3 m<sup>2</sup> for PlanetScope, and 1 m<sup>2</sup> for SkySat, which eliminates small plot comparisons, and intra-plot and plant-level phenotyping. The passage of the satellite above the experiment area as well as the presence of clouds can also limit their use. A general disadvantage of all terrestrial and aerial HTP platforms is that they require expertise at multiple levels to use and maintain them.

#### *Sensors used in field phenotyping*

The sensors used in remote sensing are diverse. Laser and ultrasonic sensors are mainly used on ground-based vehicles to estimate plant height. These systems emit a laser

or an ultrasonic pulse at a recurrent frequency, which hit the ground or a plant, then reflect back to the sensor. The longest distance measured by the emitted pulse is the bare ground and the smaller is the plant. The subtraction of both distances gives the height of the plant. In this way plant height of maize, bermudagrass, wheat, and alfalfa (Fumiki and Omasa, 2009; Ehlert *et al.*, 2010; Selbeck *et al.*, 2010; Pittman *et al.*, 2015; Cazenave *et al.*, 2019a, b) was successfully estimated.

Light Detection and Ranging (LiDAR) technology has been used for several decades in meteorological applications. More recently, LiDAR is being used to phenotype crops, including peanut, by creating 3D images, either from terrestrial or aerial platforms (Yuan *et al.*, 2019; Sun *et al.*, 2017; Saeed *et al.*, 2023). LiDAR has been used to successfully estimate plant height and, in combination with ground-based platforms, estimate canopy architecture and its components, i.e. stem height, length of lateral branches, and canopy shape and density (Fig. 13).



**Figure 13.** Comparison between 3D reconstruction from LiDAR (top) vs photogrammetry RGB (bottom). The LiDAR can provide more details than RGB by penetrating denser canopy (left, Wallace *et al.*, 2016) while the RGB (bottom right) is allowing some high-resolution visual data in full color as compared to the colorized LiDAR version based on intensity of reflection (top right, USGS, 2018).

Photogrammetry uses high resolution cameras mounted on either terrestrial or aerial platforms to sense reflected light in the visible red, green, and blue (RGB) bands of the electromagnetic spectrum. In peanut, seedling vigor, main stem height, wilting, and yield under drought and late leaf spot disease [caused by the fungus *Northopassarola personata* (Berk and Curt)] were RGB-estimated with great accuracy (Balota and Oakes, 2016, 2017; Sarkar *et al.*, 2020; Sarkar *et al.*, 2021a; Sarkar *et al.*,

2021b; Kassim *et al.*, 2022; Sie *et al.*, 2022; Oteng-Frimpong *et al.*, 2023; Balota *et al.*, 2024; Chapu *et al.*, 2022; Chapu *et al.*, 2024).

Near infra-red and thermal multispectral sensors are used to assess crop color, temperature as result of transpiration, and biomass accumulation from reflectance in the near infra-red and other spectra. Reflectance-derived vegetation indices such as the Normalized Difference Vegetation Index (NDVI), Normalized Difference Red

Edge (NDRE), LAI, and canopy temperature in peanut (Balota and Oakes, 2017; Yuan *et al.*, 2018; Sarkar *et al.*, 2020) and other crops (Freeman *et al.*, 2007; Erdle *et al.*, 2011; Gnyp *et al.*, 2014; Pittman *et al.*, 2015; Cazenave *et al.*, 2019b) have been recently developed.

### Phenotyping complex physiological traits

Phenotyping complex physiological processes and hidden plant organs, e.g. roots and peanut pods, is challenging. For these, HTP and remote sensing can only be partially implemented. Therefore, phenotyping mainly relies on low throughput methods (LTP). However, recently Gimode *et al.* (2023) used Ground Penetrating Radar (GPR) to analyze the below-ground peanut pods non-destructively.

#### Gas exchange phenotyping

Photosynthesis is a complex process that includes different complex reactions that, for simplification, can be divided into light reactions driven by electrons passing the different photosystems, and CO<sub>2</sub> fixation. Measurement of CO<sub>2</sub> fixation parameters uses infrared gas analyzers (IRGA). Depending on the type of photosynthetic parameter, measurements can take between one min, i.e. midday CO<sub>2</sub> fixation (A), to 90 min, i.e. the maximum rate of Rubisco carboxylation (V<sub>max</sub>) and electron transport (J<sub>max</sub>), and A response to internal CO<sub>2</sub> (Ci) (A-Ci) curves (Farquhar *et al.*, 1980; Bernacchi *et al.*, 2003). Nonetheless, IRGA measurements only give periodic information that may not be representative of the whole plant performance over the growing season. Farquhar *et al.* (1989) used carbon isotope discrimination ( $\Delta^{13}\text{C}$ ), as it offers information on photosynthesis and WUE in a more integrated way over the life span of the plant.

#### WUE phenotyping through carbon isotope discrimination

In peanut, WUE has been demonstrated to be an important trait to select to improve drought stress tolerance (Vadez and Ratnakumar, 2016; Zhang *et al.*, 2022). Water use efficiency can be calculated as the amount of biomass fixed per amount of water used by the plant. The most accurate way to calculate the amount of water used by a plant is gravimetrically, i.e. weighing potted plants every day, re-watering to pre-calculated weights to achieve desired water levels and calculating the amount water lost through transpiration (Vadez and Ratnakumar, 2016; Zhang *et al.*, 2022). However, this method is time consuming, and few facilities can afford to perform such big scale, controlled experiments. Farquhar *et al.* (1989) reported a strong relationship between WUE calculated gravimetrically and  $\Delta^{13}\text{C}$ . This relationship has been demonstrated in several crop species such as common bean (Ehleringer *et al.*, 1991), soybean (Dhanapal *et al.*, 2015), wheat (Del Pozo *et al.*, 2016), and peanut (Wright *et al.*, 1993), allowing  $\Delta^{13}\text{C}$  to

be used as surrogate phenotyping for WUE. In peanut,  $\Delta^{13}\text{C}$  is highly inheritable (Hubick *et al.*, 1988), therefore allowing identification of the genomic regions responsible for changes in  $\Delta^{13}\text{C}$  and then WUE. However, the  $\Delta^{13}\text{C}$  method is expensive, i.e. mass spectroscopy analysis costs around \$8 per sample.; Due to the cost and complexity of the peanut genome,  $\Delta^{13}\text{C}$  method has not yet been connected successfully to QTLs in peanut breeding; it is more successfully used in soybean and wheat (Dhanapal *et al.*, 2015; Del Pozo *et al.*, 2016). In soybean and wheat, GWAS and QTL mapping have been performed and genomic regions codifying  $\Delta^{13}\text{C}$  are now available (Dhanapal *et al.*, 2015; Mora *et al.*, 2015). Despite its success,  $\Delta^{13}\text{C}$  is far from being considered an HTP technique because of the time required for biomass sampling and preparation, and the subsequent spectroscopy analysis. Near infrared (NIR) technology is based on the unique reflectance patterns that different leaf and seed chemical compounds produce when they are exposed to light with a known light spectrum. Ferrio *et al.* (2001) used NIR technology to accurately predict  $\Delta^{13}\text{C}$ , and thus WUE. These authors predicted  $\Delta^{13}\text{C}$  from NIR reflectance with an accuracy ranging from 82 to 86%.

#### Hyperspectral reflectance to predict photosynthetic parameters.

Hyperspectral sensors capture electromagnetic radiation reflected from vegetation in the visible (VIS, 400–700 nm), near-infrared (NIR, 700–1,300 nm), and short-wavelength infrared (SWIR, 1,400–3,000 nm) regions of the electromagnetic spectrum, which contain information about leaf physiological status including pigments, structural constituents of biomass, and water content (Curran, 1989; Penuelas and Filella, 1998). Variation of foliar reflectance at different wavelengths is specific to the variations in chemical and structural characteristics of the leaf and photosynthetic apparatus (Fig. 14a, b, c) (Serbin *et al.*, 2012). Hyperspectral reflectance spectroscopy as an HTP tool is becoming recognized as promising in agricultural research (Serbin *et al.*, 2012; Weber *et al.*, 2012; Araus and Cairns, 2014; Silva-Perez *et al.*, 2017; Yendrek *et al.*, 2017). Hyperspectral hand-held sensors such as the Field Spec Hi-Res-4, have been used to predict photosynthetic parameters including maximum rate of rubisco carboxylation V<sub>cmax</sub> (Fig. 14) and midday CO<sub>2</sub> assimilation of peanut plants (Buchaillot *et al.*, 2022). However, this technology is low throughput as individual plants need to be measured one by one. To reach high throughput phenotyping, researchers are currently using hyperspectral cameras mounted on drones to predict these parameters with similarly accurate results predicted with the hand-held equipment (Bagherian *et al.*, 2023). The combination of drone and hyperspectral technologies will allow breeding programs to phenotype plant photosynthetic parameters in a high throughput manner in the future.

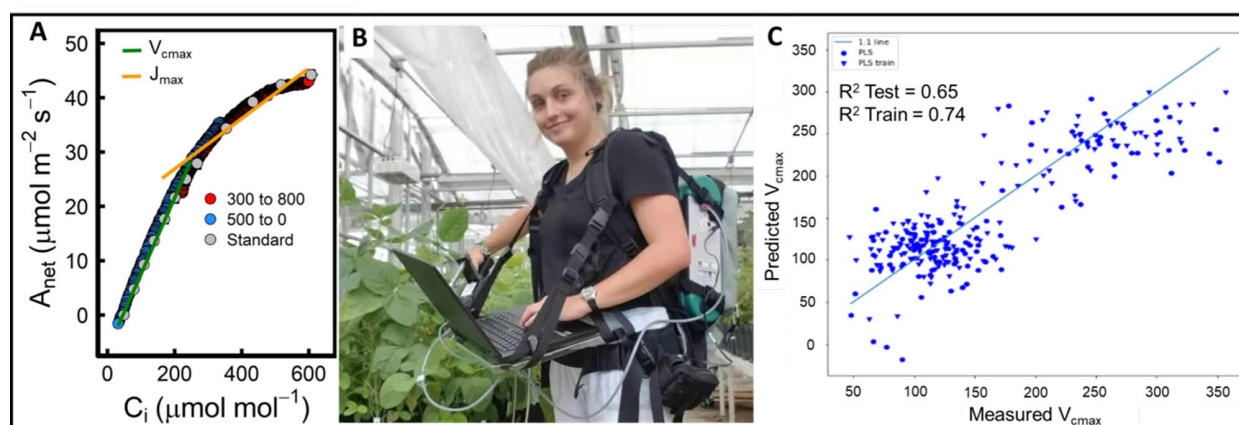


Figure 14. (A) Example of standard A-Ci curve (grey dots), Rapid A-Ci curve (blue and red dots), and data used to calculate  $V_{cmax}$  and  $J_{max}$ . Figure modified with permission from Stinziano *et al.* (2019). (B) Example of the FieldSpec HiRes4 (ASD technology) used to take hyperspectral data from the leaves. (C) Correlation test used to demonstrate the accuracy of the Partial-Least (PLSR) model and hyperspectral data to predict  $V_{cmax}$  for peanut and soybean (Buchaillot *et al.*, 2022).

#### Phenotyping roots - the hidden resource.

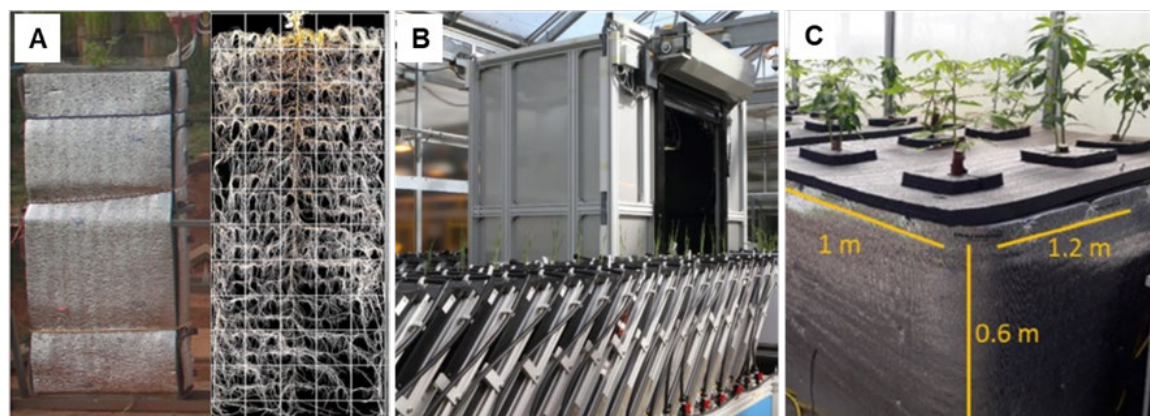
Roots provide water and nutrient uptake. Different root traits enable plants to respond, adapt and tolerate different environmental stresses. For example, peanut cultivars with drought tolerance showed greater root length at deeper depths than drought-sensitive cultivars (Thangthong *et al.*, 2017). As the root system is underground, historically, it has been difficult to phenotype (York *et al.*, 2015; Atkinson *et al.*, 2019). However, recently, technological improvements in image acquisition and data analysis have allowed great advancements in root and pod phenotyping, as mentioned earlier in this section (Gimode *et al.*, 2023). Regardless of various obstacles, e.g. soil type, heterogeneity and moisture, GPR technology can accurately detect below-ground plant parts significantly contributing to the understanding of plant response mechanisms to tolerate stress (Dobrev *et al.*, 2021; Gimode *et al.*, 2023).

Other non-destructive field measurements rely on rhizotrons and rhizo-boxes systems with different automation capabilities and, more recently, on X-ray computed tomography and GPR (Garbout *et al.*, 2012; Nagel *et al.*, 2012; Rogers *et al.*, 2016; Thangthong *et al.*, 2016; Liu *et al.*, 2018). For example, for peanut, Thangthong *et al.* (2016) developed a rhizotron that can be placed in the field to monitor root development in quadrants of  $10 \text{ cm}^2$  (Fig. 15a), from the beginning of the season until

harvest. Although this type of system is advanced and more representative of “normal” root development in the field, soil particles can interrupt the visibility of the roots causing missed data (Atkinson *et al.*, 2019). Soil and soilless systems (Fig. 15b, c) used in greenhouse applications are less informative as root phenotypes can be drastically different from the phenotypes in the field (Kuijken *et al.*, 2015).

In summary, research achievements in peanut physiology have been numerous in recent years. These achievements are predominant in the areas of crop requirements for sustainable production, plant growth and development, mechanisms of adaptation to biotic and abiotic factors, and, more recently, the development of high-throughput tools for phenotyping. Along with the achievements in genome sequencing and genetic mapping technologies, plant physiology discoveries and advancements in HTP technologies pave the way for the implementation of new strategies in peanut breeding, i.e. molecular breeding and genomic selection. These strategies appear more robust than traditional breeding for predicting valuable traits for increased yield and adaptation to environmental conditions; and allow pyramiding these traits more effectively in future peanut cultivars to meet production requirements for the specific geographical regions in which cultivars will be grown.





**Figure 15.** Examples of different root phenotyping platforms used in field and under controlled conditions. (A) Rhizotron used in field experiments to image root profile using RGB camera (Thangthong *et al.*, 2016). (B) Greenhouse based automated root phenotyping GROWSCREEN-Rhizo System (Nagel *et al.*, 2012). (C) Aeroponic system used to study cassava root development in the greenhouse (Gomez-Selvaraj *et al.*, 2019).

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