Chapter 2

SEED CHARACTERISTICS AND SEEDLING VIGOR

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INTRODUCTION

Why does seedling vigor matter? Without question, "high vigor" seedlings are universally desired by cotton producers. Vigorous early season growth and uniform stand establishment provide growers with peace of mind and indicate that the crop is off to a good start. This is particularly important for cotton because it is generally accepted that cotton exhibits poor seedling vigor relative to other major row crops (Pilon et al., 2016). Early work conducted by Wanjura et al. (1969) showed that seedlings which emerged rapidly (five days after planting in this instance) exhibited greater survival and higher relative yields than seedlings emerging eight or 12 days after planting. Furthermore, percent emergence at five days after planting had a pronounced impact on lint yield (Figure 1), indicating that early seedling vigor and stand establishment can be a major factor in realizing cotton's yield potential. Similarly, heat unit accumulation within a narrow window following planting has been positively associated with lint yield (Kerby et al., 1989). This implies that conditions conducive to vigorous early seedling growth can promote higher yields in some situations. To understand the mechanism by which seedling vigor might impact yield, it is important to view agriculture as a system designed to exploit solar energy through the process of photosynthesis (Gardner et al., 1985). Consequently, yield (Y) can be mathematically defined as the product of total absorbed photosynthetically active radiation (APAR) during a growing season, the efficiency with which the crop converts intercepted radiation into dry matter (RUE), and harvest index (HI) (Earl and Davis, 2003; Monteith, 1977, 1994; Stöckle and Kemanian, 2009), or $Y = APAR \times RUE \times HI$. Furthermore, it is well-established that crops typically do not attain maximum crop growth rate (CGR) until leaf area development is sufficient to intercept 95% of incoming solar radiation, a level of leaf area development known as critical leaf area index (LAI) (Gardner et al., 1985). Thus, poor early season vigor delays canopy development and results in lower APAR and inefficient utilization of available land area for a longer period of time when compared with a more vigorously growing canopy. While differences in seedling vigor do not always impact yield in cotton (Liu et al., 2015; Snider et al., 2016), it should be noted that there are other positive aspects associated with early season vigor. For example, vigorous early season growth lessens the potential damage that can be done by insect herbivory and plant pathogens, improves crop competitiveness with weedy plants, and might promote tolerance to drought at later stages in development (Elliot et al., 2008; Cook and El-Zik, 1992; Liu et al., 2015; Reddy and Boykin, 2010; Snider and Oosterhuis, 2015). Furthermore, the consequences of poor seedling vigor can be costly as growers are forced to replant to remedy stand establishment issues. Because cotton is not always planted under optimal conditions for seedling growth and development, the most ideal scenario would be for a grower to make planting decisions based on seedling vigor before the seed is ever planted. For this to be a possibility, researchers are required to identify which planting seed characteristics are most indicative of seedling vigor and to develop reliable, quantitative relationships between seed characteristics and seedling performance in the field. The current chapter provides a review of seed and seedling development, studies relating early seedling performance to seed characteristics, factors influencing seed composition and quality, and opportunities and challenges for future research.

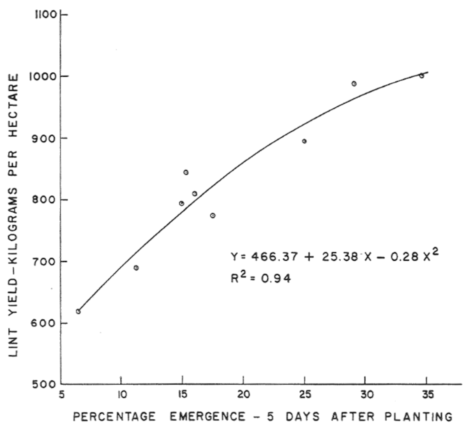

Figure 1. Relation between percentage emergence at 5 days after planting and lint yield for combinations of three seed qualities and three planting depths. [From Wanjura et al., 1969]

SEED AND SEEDLING DEVELOPMENT

Although other authors have provided extensive reviews of seed and seedling development in cotton (Hopper and McDaniel, 1999; Kloth and Turley, 2010; Oosterhuis and Jernstedt, 1999; Turley and Chapman, 2010), the authors feel that the impacts of genotype, management, and environment on seed characteristics and seedling vigor are best understood within the context of ontogeny. For the purposes of this review we will first consider the development of the seed from the initial fertilization event to boll maturity and then from seed germination to the development of photosynthetically self-sufficient, emerged cotyledons.

On the day of anthesis, the cotton flower opens after sunrise following a night of rapid cellular expansion for the floral bud (Beasley, 1975; Stewart, 1986). Subsequently, pollen is transferred to a receptive stigma and germinates; the pollen tube traverses the conducting tissue of the style and carries two sperm nuclei to the ovules; finally, double fertilization occurs (Beasley, 1975; Snider and Oosterhuis, 2011, 2012, 2015; Stewart, 1986). The timing of these events can vary substantially based on environmental factors such as temperature (Snider et al., 2011; Snider and Oosterhuis, 2011; Stewart, 1986), but it is generally accepted that fertilization occurs between 12 and 24 hours after pollination (Stewart, 1986). Beginning roughly on the day of anthesis and ending ~45 to 50 days past anthesis, fiber development occurs in the following phases: fiber cell initiation, elongation, thickening, and maturation (Haigler, 2010; Lee et al., 2007; Oosterhuis and Jernstedt, 1999). After fertilization, seed development occurs in the following phases: morphogenesis, maturation, and desiccation (Turley and Chapman, 2010; Snider and Oosterhuis, 2015). The maturation period is when the embryo is accumulating oil and protein reserves (Turley and Chapman, 2010; Snider and Oosterhuis, 2015) that serve as the primary compounds needed to fuel the earliest stages of seedling growth. While it seems out of place to discuss fiber development within the context of seed development, it is of particular importance that embryo maturation occurs at the same time as fiber thickening, resulting in intra-boll competition between fiber and seed for available photosynthate (Kloth and Turley, 2010).

Just as seed development from zygote formation to embryo desiccation has been extensively characterized, the key developmental events in the germination of the seed are also well-documented and predictable. For example the first stage of seed germination is imbibition, which results in the hydration of embryonic tissues (Cothren, 1999; Cristiansen and Rowland, 1986). The time required for the imbibition phase can vary greatly depending upon seed coat characteristics and environmental parameters such as the temperature at which germination occurs, but typically, cotton seeds are fully imbibed within the first 12 h after being placed in a moist environment (Wanjura and Minton, 1974; Cole and Christiansen, 1975; Christiansen and Rowland, 1986). Once embryonic tissues are hydrated, cellular repair and subsequent growth processes resume and are accompanied by an increase in oxygen uptake of the germinating cotton seed (Kuo et al., 1988; Turley and Chapman, 2010). The last stage of seed germination occurs when the radicle visibly protrudes beyond the seed coat. At this point, the radicle grows into deeper layers of the soil profile and the hypocotyl expands to eventually pull the cotyledons above the soil surface, where they will eventually become photosynthetically self-sufficient and begin to fuel additional vegetative growth (Snider and Oosterhuis, 2015). Post-germinative growth that occurs prior to photosynthetic self-sufficiency of the plant is largely driven by mobilized oil and protein reserves that were initially stored in the cotyledons of the quiescent embryo (Bradow and Bauer, 2010). For example, lipid mobilization and gluconeogenesis from lipid precursors provide carbohydrates that can be incorporated into the body of a developing seedling or utilized in respiration.

VARIATION IN SEED VIGOR IN COTTON

While it is not the primary focus of this review to discuss seed vigor, seed vigor can have a pronounced impact on seedling vigor and should at least be considered in this context. As noted elsewhere in this collection of reviews on seed and seedlings, Bourland (2013) defines high vigor seed lots as those that exhibit high germinability and emergence over a range of environmental conditions. Although a number of different tests are available to quantify seed vigor in cotton, seed vigor is commonly assessed by quantifying germination percent after a predefined incubation period at one or two temperatures. Examples include the cool germination test that quantifies percent germination at 18°C following a seven day incubation period and the cool-warm test (sum of germination at 18 and 30°C); these indicators of seed vigor more accurately reflect in-field performance than seed germination experiments conducted at optimal conditions alone (Bourland, in press; Pilon et al., 2016). For example, Bolek (2010) evaluated the germination response to temperature for 106 cotton cultivars across three different cotton species, and observed significant cultivar differences in seed germination percent under cool temperature conditions (18°C) for both *Gossypium hirsutum* and *G. barbadense*. Importantly, seed vigor assessments at 18°C were correlated with percent emergence in the field, and *G. barbadense* was more cold tolerant than most *G. hirsutum* cultivars. While seed vigor does not necessarily predict seedling vigor under field conditions, the ability of seeds to germinate rapidly under a wide range of conditions could potentially result in earlier emergence under less than optimum temperatures and promote more vigorous early seedling growth. At a minimum, having high emergence rates could potentially contribute to greater early season crop growth rates.

RELATIONSHIPS BETWEEN SEED CHARACTERISITICS & SEEDLING VIGOR

Seedling vigor can be defined in a number of different ways, but most measures of seedling vigor provide an indication of seedling size or growth rates (Bourland, 2013; Liu et al., 2015; Pilon et al., 2016). As noted elsewhere in this review, other measures of seedling vigor such as true leaf differentiation, development of lateral roots, and low incidence of disease may be better indicators of seedling vigor than plant size (Bourland, 2013), but our review will focus on shoot growth parameters since these are the most widely reported indicators of vigor. Chemical and physical characteristics of planting seed can strongly impact seedling vigor and are influenced by genotype, management, and environment (discussed later). Early studies indicated that seed size, density, and degree of seed filling could greatly impact seed and seedling performance, where large, high density seeds exhibited the greatest seed and seedling vigor (Bartee and Krieg, 1974; Ferguson and Turner, 1971; Leffler and Williams 1983; Krieg and Bartee, 1975). Recent work by Snider et al. (2014) characterized seedling vigor (whole-plant fresh weight at the 2-3 leaf stage of development) for 11 different cotton cultivars at 5 locations scattered across much of southern Georgia's cotton production area. When average seedling vigor across all locations for each cultivar was plotted versus seed characteristics such as seed mass, percent oil, and total oil content (mg seed^{-1}), seed mass and seed oil content most strongly and positively impacted seedling vigor (Figure 2). Subsequent work addressed the hypothesis that seed size and total seed oil + protein content (expressed as kcal per seed to account for different energy content in each type of macromolecule) would be strongly predictive of seedling vigor (dry weight per plant) (Snider et al., 2016). In the majority of production environments assessed, oil + protein kcal per seed provided slightly improved relationships over seed mass although the trends were very similar for both seed characteristics (Figures 3 and 4). This is likely because seed mass influences the quantity of reserves available to fuel metabolic processes; a large seed has a larger reserve available to fuel the earliest stages of growth. Another potentially important factor contributing to vigorous seedling growth in larger seeds is that large seeds have the ability to house larger cotyledons (Figure 5), and larger cotyledons should intercept more solar radiation, potentially leading to higher whole-cotyledon photosynthesis. Positive relationships between seed mass and seedling vigor have also been reported in Liu et al. (2015), and in their studies, they observed a strongly positive relationship between seedling dry weight during early growth (17 and 27 DAP) and cotyledon area.

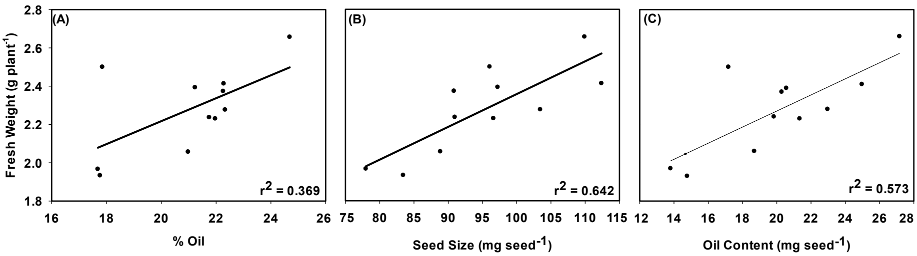

Figure 2. Linear regression of seedling fresh weight at the 2-3 leaf stage versus % oil (A), seed size (B), and total seed oil content (C) for 11 commercially-available cotton cultivars. Fresh weight data were averaged from 5 locations, 4 replicate plots, at each location, and 20 plants per plot (each data point represents the average weight of 400 seedlings). [From Snider et al., 2014]

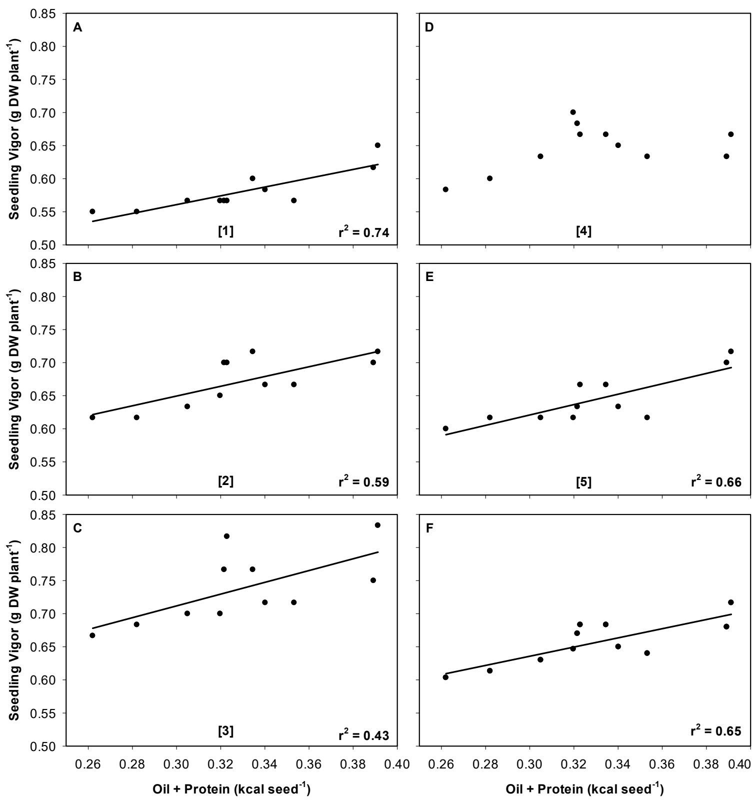

Figure 3. The relationship between planting seed oil + protein content (kcal seed-1) and seedling vigor (dry weight at the 2-3 leaf stage) for 11 different cultivars in each of five different growth environments (A-E; Bracketed numbers represent each growth environment noted in Table 1) or averaged for a given cultivar across all five environments during the 2012 growing season (F). [From Snider et al., 2016]

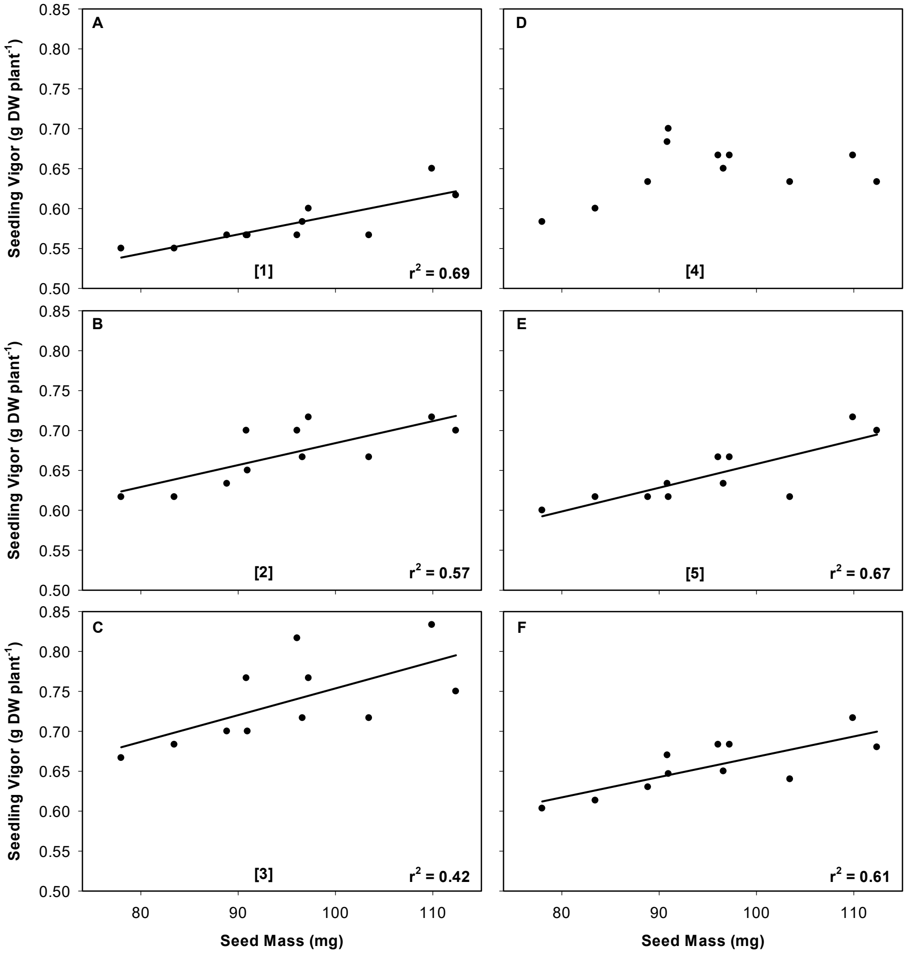

Figure 4. The relationship between planting seed individual seed mass and seedling vigor (seedling dry weight at the 2-3 leaf stage) for 11 different cultivars in each of five different growth environments (A-E; Bracketed numbers represent each growth environment noted in Table 1) or averaged for a given cultivar across all five environments during the 2012 growing season (F). [From Snider et al., 2016]

Figure 5. Visual differences in cotyledon area at approximately two weeks after planting for three cotton cultivars differing in seed mass and planted in Tifton, GA during the 2017 growing season. **1** = lightest seed (Upland, 72 mg seed^{-1}); **2** = intermediate weight seed (Upland, 94 mg seed^{-1}); **3** = heaviest seed (Pima, 138 mg seed^{-1}).

FACTORS AFFECTING SEED CHEMICAL AND PHYSICAL CHARACTERISTICS

As noted above, seedling vigor is influenced by seed mass and composition (oil and protein), so genotypic, cultural, or environmental impacts on these seed properties should have a pronounced impact on seedling vigor. In subsequent sections we provide a general overview of literature addressing the impact of genotype and production environment on seed characteristics.

Cultivar Influence on Seed Characteristics

Cotton breeding programs have dedicated a great deal of effort towards cultivar selection for high yield and fiber quality. Little attention has been given to seed composition and its relevance to vigorous seedling growth and stand establishment. Current commercial cotton cultivars vary in seed composition (USDA, 2015). Some seed characteristics are relatively dependent on genetics, which is the case for crude oil and fatty acid concentrations. For instance, according to research conducted from 1996 through 2013 using data from the Regional High Quality Trial of the National Cotton Variety Testing program, 20 to 57% of oil content variation in cottonseeds were due to genetic diversity, while environment contributed to 44 to 73% of protein content (Zeng et al., 2015). The influence of environment on seed composition is discussed in subsequent sections of this review chapter. A study by Dowd et al., (2010) suggested that approximately two-thirds of the variation in fatty acid composition in seeds is accounted for by genotype. Pettigrew and Dowd (2012) documented genetic variation in six cultivars for cottonseed composition traits such as for gossypol, oil, protein, carbohydrate, and fatty acid concentrations. A recent assessment of genotypic variation in seed oil and protein from 82 cotton germplasm lines and cultivars indicated that 21% of total variation in oil content is explained by genetics, while only 4% of the variation in protein is due to genetics (Campbell et al., 2016). Although the percentage of total variation in seed oil and protein accounted for by genotype is fairly low, genetic variation is present for these seed traits and can certainly be taken into consideration in cotton breeding programs for improved cottonseed composition. As noted above, seed mass strongly impacts seedling vigor by increasing the total oil (or oil + protein) content available to the growing seedling (Pettigrew and Dowd, 2012; Snider et al., 2014, 2016). Seed mass varies among modern cotton cultivars and breeding efforts over the past several decades have resulted in selection for cultivars with high lint percent and low seed index (g per hundred seed) (Campbell et al., 2011). Thus, seed mass has been strongly influenced by breeding efforts.

Environmental Influence on Seed Characteristics

While seed size and chemical composition can be drastically impacted by genotype, it is important to note that seed production environment and post-harvest storage environment can also influence seed composition. For example, Leffler et al. (1977) demonstrated that cotton seed amino acid profiles varied with sample date, and that total N content in cotton seed increased with later stages of boll development, concomitant with increases in seed protein content (King and Leffler, 1979; Leffler, 1986). Though this finding is intuitive, it illustrates that harvest timing should drastically impact variability in protein composition within a given seed lot. The aforementioned study also illustrated a positive relationship between N fertility and seed N content. A study by Egelkraut et al. (2004) further documented a linear increase in seed N concentration as N fertility levels increased, and defined a critical seed N concentration for attaining maximum relative yield. Because the N content of the cotton seed is largely reflective of seed protein content, other authors have illustrated increases in seed protein as N fertilizer rates increased (Main et al., 2013; Pettigrew and Dowd, 2014). Both the study by Main et al. (2013) and Pettigrew and Dowd (2014) reported a similar result; seed protein content increased in response to increasing N rates, whereas seed oil content declined at the highest N rates. These findings illustrates that N availability can substantially alter the oil and protein balance within the developing cotton seed. Another management factor that has an impact on seed composition is irrigation. For example, Pettigrew and Dowd (2011 and 2014) have found that irrigated cotton exhibits increased seed oil content and decreased seed protein content when compared with dryland cotton. The study conducted by Pettigrew and Dowd (2011) also illustrated a slight decline in the concentration of saturated fatty acids in response to irrigation, relative to dryland cotton. Varying planting dates or irrigation regimes alters cottonseed composition aforementioned study by Pettigrew and Dowd (2011), there was also a significant effect of planting date on seed oil content and a significant interaction between irrigation and planting date on both oil and protein content, depending upon year of the study. While it is likely that planting date effects were the result of the environment that seeds were exposed to during post-anthesis development, the authors do not identify the key environmental conditions contributing to planting date effects on seed composition. However, early work by Gipson and Joham (1969) illustrated that seed quality could be linked to temperature conditions during seed development. Specifically, they found that seed oil and protein content were lower in seeds that developed under low temperature conditions and that seed germination was positively correlated with growth temperature during seed development. Thus, the environment encountered during seed development can have a pronounced impact on seed composition and viability. Post-harvest seed storage environment can also have a pronounced effect on seed composition and quality. For example, Abdelmagid and Osman (1975) reported that seed oil content declined concomitantly with germination percentage when seeds were stored for a 16 month period. Over shorter storage durations (9 months) declines in seed germination percentage were primarily observed under high-temperature conditions and were associated with decreased seed protein content.

FUTURE DIRECTIONS

- Providing broadly-applicable, quantitative relationships between seed characteristics and seedling vigor has the potential to substantially aid in a producer's cultivar selection decisions. For example, in fields where high seedling vigor is essential, it would be important to know which seed lots have the greatest potential to develop an adequate stand under challenging production conditions. It is also highly likely that planting practices (seeding rate, depth) could be altered to account for seed characteristics. For example, a producer could potentially plant larger seed at deeper depths to access greater soil moisture (compared to small seeded cultivars), which is particularly important in dryland or water-limited production scenarios. However, the balance between protein and oil in the seed will influence the amount of chemical energy available to fuel seedling growth prior emergence. Thus, relatively novel methods that allow for non-destructive determination of seed oil and protein content in whole cotton seed (Horn et al., 2011) could prove useful in this endeavor.
- As noted above, cotton breeding efforts have increased yield by increasing lint percent, which has had the added effect of decreasing individual seed mass. Because smaller seeds typically produce less vigorous seedlings, this could potentially be problematic for producers if the trend toward decreased seed mass continues. It should be noted, however, that modern, commercially available cultivars have been shown to substantially differ in yield component characteristics (e.g. bolls per acre, lint mass per boll, seed number, seed mass), despite having similar per hectare lint yield (Bednarz et al., 2007). Lint yield is the product of seed number per hectare and lint weight per seed. Obviously, there must be an upper limit to the yield improvement that can be attained with increased lint percent while still producing viable seeds that will produce acceptable early season growth. It is the authors' opinion that yield improvement in cotton must eventually be brought about by manipulating other yield components (See Bourland, 2013 for a detailed overview of yield components) if early season risk is to be minimized while simultaneously maximizing economic productivity.

SUMMARY

Rapid and uniform stand establishment along with vigorous seedling growth are desirable characteristics of cotton. "High vigor" seedlings are generally less affected by early season insect herbivory and plant pathogens and are more competitive with weedy plant species, which lessens the potential for early season crop loss. In this review, we emphasize the importance of seed characteristics in determining seedling vigor. Specifically, high planting seed mass and total nutritive reserves (oil and protein) have a positive impact on early seedling vigor. Seed mass and nutrient composition can be influenced by genotype, but it is important to note that production and post-harvest storage environment can have a pronounced impact on these seed characteristics as well. Specifically, practices such as irrigation, fertility, and planting date have all been shown to influence seed oil and protein content as has growth temperature during seed maturation. Long periods of seed storage under high temperature have been closely associated with decreased oil, protein, and seed viability. Because seed quality can be impacted by a number of different factors, we suggest that seed mass and composition could be used as broadly applicable predictors of seedling vigor that integrate a number of variables. This could potentially allow growers to position high vigor seeds in locations where production conditions are challenging during the early season or alter planter settings to account for seed traits based on production needs. Continued breeding for high yielding cultivars has produced cotton genotypes with high lint percent but smaller seeds, which could negatively impact seedling vigor. Future research should be focused on opportunities to increase yield by manipulating yield components other than lint percent.

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