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ECOPHYSIOLOGICAL ANALYSIS OF YIELD DETERMINATION IN SOYBEAN OF DIFFERENT RELATIVE MATURITIES

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ECOPHYSIOLOGICAL ANALYSIS OF YIELD DETERMINATION IN SOYBEAN OF DIFFERENT RELATIVE MATURITIES

THESIS

A thesis submitted in partial fulfillment of the requirement for the degree of Master of Science in the College of Agriculture, Food and Environment at the University of Kentucky

by

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2018

ABSTRACT OF THESIS

ECOPHYSIOLOGICAL ANALYSIS OF YIELD DETERMINATION IN SOYBEAN OF DIFFERENT RELATIVE MATURITIES

Soybean yield differences are a combination of the genotype, environmental conditions, and management practices. Understanding how these factors interact through the analysis of the components involved in yield determination, provides a way to increase potential and actual yields in Kentucky.

Two irrigated experiments were conducted to quantify differences in the mechanisms of yield determination across soybean maturity groups (MG) 2 to 5 (Chapter 1), and to quantify management options (seeding rate and choice of MG cultivar) that increase yield potential of double crop soybean systems (Chapter 2).

Results showed that cultivars used different physiological strategies to achieve high yields, but these were not always consistent across the environments studied. High yields were often associated to a higher efficiency partitioning biomass to seeds that lead to a higher seed number in some cultivars, as well as associated to low seed growth rates (Chapter 1). The choice of MG cultivar had a greater impact on double-crop soybean yields than increasing seeding rates from 40 to 54 seed m^{-2}. The higher seeding rate increased yields by 5% without an interaction with cultivar. Optimal MG choices for double-crop soybean in KY were dependent on the environment.

KEYWORDS: Soybean, yield, maturity group (MG), physiological traits

Maria Morrogh Bernard
September 17th, 2018

ECOPHYSIOLOGICAL ANALYSIS OF YIELD DETERMINATION IN SOYBEAN OF DIFFERENT RELATIVE MATURITIES

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INTRODUCTION

Soybean yields in the United States have increased by 51.7 kg ha^{-1} yr^{-1} on average from 2000 to 2018 (Figure 1). In Kentucky, soybean yields have increased by 47.3 kg ha^{-1} yr^{-1} during the same period (Figure 2) (USDA-NASS, 2017). Identifying strategies that can maintain and/or increase soybean productivity while maximizing the use of resources is critical for sustainable development of grain production regions. Quantifying the yield potential under environmental conditions in Kentucky, and its response to the range of management conditions for this region, is the first step for identifying sustainable management options that will maximize productivity.

Soybean cultivars are divided into maturity groups (MGs) depending on their response to photoperiod and temperature (Cober et al., 2001; Summerfield et al., 1998). There are 13 soybean MGs ranging from 000 to 10. In the United States, MGs from 0 to 6 are recommended across the range of latitudes in the country (Mourtzinis and Conley, 2017). In western and southern Kentucky, MG 4 to 5 cultivars are planted from mid-May to early-June, while in eastern and northern Kentucky, relative MGs from 3.5 to 4.5 are planted from late-April to early-June (Vernard et al., 2018).

Soybean yield can be divided in to different components and processes to analyze differences in the mechanisms of yield determination. Traditionally, soybean yield is defined as the product between seed number on an area basis and the individual seed weight or mass. Each of these components can be further analyzed as a function of other crop physiological traits. Seed number can be modeled as a function of the daily canopy

photosynthesis, the partition of assimilates to seed, and the minimum amount of assimilates required per grain (Egli and Yu, 1991). The weight of individual seeds can be described as the product of the duration of the seed filling period and the rate of growth per seed (Egli, 1998).

We conducted two irrigated experiments in Kentucky to quantify soybean yield and physiological traits related to yield component determination. In Chapter 1, sixteen soybean cultivars from MG 2 to 5 were grow in three different environments (location x planting date combinations). In Chapter 2, six soybean cultivars from MG 2 to 4 with two seeding rates (SR) were grow in a double-crop soybean system in two locations. All the experiments were irrigated and managed to bring yields close to the potential. The specific goals of Chapter 1 were to analyze the relationships among physiological traits and genotypes to i) identify traits that are associated with higher and/or lower yields in each environment, and ii) understand mechanisms that lead to similar yields among cultivars. In chapter 2, our goal was to quantify yield responses to MG and SR in a double-crop soybean system to identify management recommendations that can maximize yield potential under environmental conditions in Kentucky.

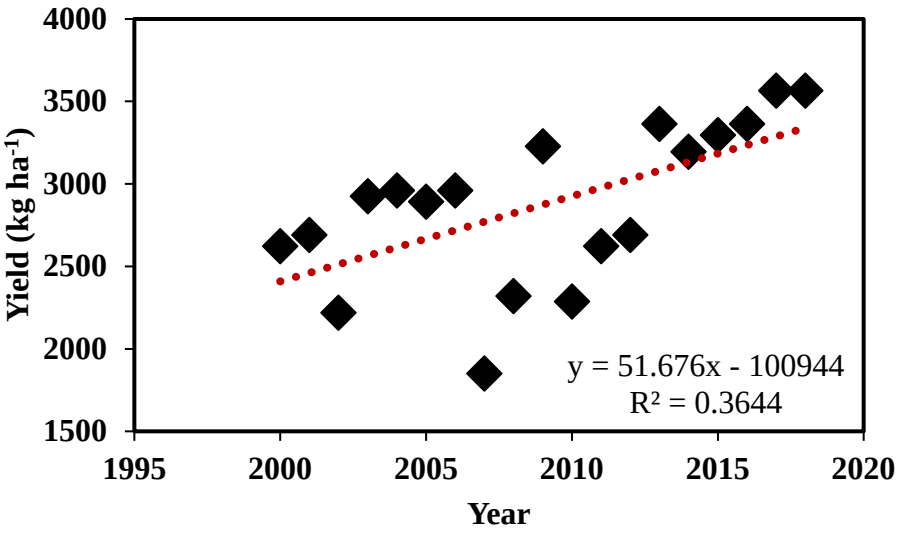

Figure 1. Average soybean yields in the United States from 2000 to 2018. Source: USDA-NASS, 2018

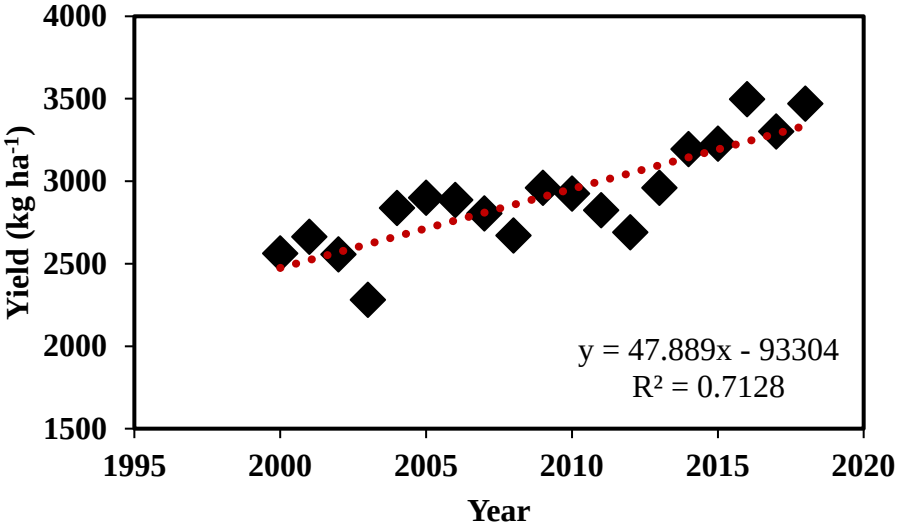

Figure 2. Average soybean yields in the state of Kentucky from 2000 to 2018. Source: USDA-NASS, 2018

Chapter 1: Physiological differences in yield determination across soybean maturity groups

ABSTRACT

Soybean maturity groups (MG) adapted to a region provide a range in the duration of the crop cycle that not always translates into higher yields. Sixteen cultivars from MG 2 to 5 were tested in three irrigated environments in Kentucky during 2017 to analyze differences in their mechanisms of yield determination. We analyzed differences in seed number as a function of crop growth rate (CGR) during seed set period, the partitioning coefficient to reproductive organs (PC), the individual seed growth rate (ISGR), and individual seed weight (ISW) as the product between ISGR and the effective filling period (EFP). The crop cycle duration increased from 71 to 123 days with MG 2 to 5 cultivars. However, highest yields were achieved by MG 2 to 4 cultivars in environment 1 (Lexington, planted in May), MG 4 in environment 2 (Princeton, planted in May), and MG 3 and 4 in environment 3 (Lexington, planted in June). Bi-plot figures based on a principal component analysis were constructed to study the relationship between physiological traits related to yield component determination that explained 80 to 90% of the data variability. Our results, indicated that yield differences across all environments were primarily explained by seed number (r= 0.89), and MG cultivars with the highest seed numbers were associated with a high PC in environments 1, and 2, (r= 0.97 and 0.71), with low ISGR in environment 1 and 3 (r= -0.63 and -0.60), and with low CGR in environment 1 (r=-0.70). Individual seed weight (ISW) explained yield differences to lesser extent (r= 0.51) across environments. A longer duration of EFP was the trait that better explained ISW across environments (r=

0.40). Individual seed growth rate was not related to ISW, but was negatively correlated to the EFP (r=-0.91) across environments. The bi-plot analysis showed that cultivars used different strategies for yield component determination that were not always stable across environments.

INTRODUCTION

Yield potential across soybean maturities

Crop productivity is determined in large part by the environment in which crops are grown and the timing and duration of developmental phases. In soybean [*Glycine max L. (Merr.)*], the duration of developmental phases can be largely influenced by the cultivar maturity group (MG). Soybean cultivars are classified in different MGs ranging from 000 to 10 based on the length of their growth cycle due to different sensitivity to photoperiod and temperature (Cober et al., 2001; Summerfield et al., 1998). Early MG cultivars are usually best adapted to high latitudes, whereas later MGs are often recommended for lower latitudes (Mourtzinis and Conley, 2017). However, a range of MG cultivars can be usually grown within the same region, providing flexibility on the length of the crop cycle. For instance, cultivars from MG 3 to 5 in Kentucky have growth cycle durations ranging from 111 to 135 days (Egli, 1994), and MG 3 to 6 cultivars in the Mid-South have a growth cycle that ranges from 95 to 128 days (Salmeron and Purcell, 2016).

Full-season soybean cultivars within a region have a longer growth duration often produce higher yields compared to earlier maturities (Board et al., 2003; Chen and Wiatrak, 2010). In contrast, short-season maturities can have a reduced yields due to a shorter growing season and/or insufficient aboveground canopy cover before time of reproductive stages

(Board and Harville, 1992; Santachiara et al., 2017a). However, yield results from MG trials do not always follow this trend and relatively short-season cultivars can provide higher or similar yields compared to later maturities (Egli, 1993, 2010; Salmerón et al., 2016; Santachiara et al., 2017a). For instance, MG 3 to 5 cultivars had similar yields with planting dates from March to May in the Mid-South (Salmeron et al., 2017). A two year experiment in Arkansas also showed similar yields across three soybean isolines of MG 4 to 6 (Mastrodomenico and Purcell, 2012). Understanding the mechanisms that lead to similar or different yield levels across MGs can be useful to identify genetic and management strategies that increase productivity and resource use efficiency.

In the upper Mid-South and Mid-West regions of the United States, most of the soybean is grown under rainfed conditions. For instance, at KY only 5% of soybean production is irrigation (USDA-NASS, 2018). At KY, soybean from MG 2 to 4 and early MG 5 can be planted (Vernard et al., 2018), and provide similar yields depending on the year and location (Egli, 1993). In agricultural areas like the upper Mid-South where soybean is usually non-irrigated, yields are a combined result of the environment, the crop cycle duration, the genetic yield potential, but also the availability of water. Under conditions of no biotic (pest and diseases) and abiotic (water, nutrient) stress, yields are close to what is known as yield potential (Lobell et al., 2009). Yield potential reflects the maximum productivity level for a given environment, genotype, and management options (planting date and seeding rate). An irrigated soybean crop with adequate soil fertilization and pest control will have yields close to the environmental and genetic potential. Under these conditions, differences in weather and duration of developmental phases could explain

large part of the soybean yield variability, allowing to better quantify differences in the mechanisms of yield determination across soybean maturities.

Yield physiological model

Yield physiological frameworks can be applied to understand the mechanisms of yield determination across environments and genotypes (Egli and Yu, 1991; Rotundo et al., 2012; Santachiara et al., 2017a; Vega et al., 2001). A simple model defines yield as the product of seed number per area and individual seed weight (ISW). From these two components, seed number often explains a greater fraction of the yield variability (Board et al., 2003; Calvino and Sadras, 1999). A model developed by Charles-Edwards et al. (1986) describes the number of grains per unit area as a function of the daily canopy net photosynthesis, the partitioning of daily canopy photosynthesis to reproductive organs, and an inverse function of the minimum amount of assimilate that a potential seed needs to grow. This approach has been widely tested and applied under field conditions (Ball et al., 2000b; Egli and Yu, 1991), where the daily canopy net photosynthesis was approximated by crop growth rate (CGR) during seed set, and the individual seed growth rate (ISGR) during seed-fill was used as a proxy for the minimum assimilate supply per seed. Modified versions of this approach were used by Vega et al. (2001), Rotundo et al. (2012) and Santachiara et al. (2017a).

From the components in the above-mentioned model, CGR measured during the flowering and set setting phase has received the most attention, and the strong relationship between this trait and seed number is well known (Egli and Yu, 1991). Less attention has been given to quantifying differences in ISGR (Egli, 1975), and even less for the partitioning

coefficient to reproductive organs (PC) (Ball et al., 2000b; Egli et al., 1985). In addition, few studies have tested a range of soybean MG cultivars across environments. A combined study in the United States (Iowa) and Argentina (Zavalla, Santa Fe) indicated diversity in the physiological strategies used by different soybean cultivars (MG 2 and 3 in the United States, MG 4 and 5 in Argentina) to reach high yields (Rotundo et al., 2012). This study showed that cultivars with the highest seed number in Argentina had a high seed set efficiency and PC, and intermediate CGR. In the United States, cultivar with the highest seed number had maximum values for the three physiological traits mentioned before (Rotundo et al., 2012). In another study conducted in Argentina under rainfed conditions, cultivars within MG 3 and 5 yielded similarly but through a different physiological mechanism (Santachiara et al., 2017a). While MG 3 cultivars had a longer duration of the seed set phase (R1-R5), MG 5 cultivars intercepted more solar radiation due to more biomass produced during the vegetative phase (Santachiara et al., 2017a).

The other important component of yield is the ISW. Individual seed weight is a function of the rate and duration of the seed dry weight accumulation (Egli, 1975). The ISGR is estimated from the slope of the linear phase of the seed growth curve (sigmodal), (Egli, 1975). The duration of the seed dry weight accumulation can be estimated from the effective filling period (EFP), calculated as the division between ISW and ISGR (Egli, 2004). Longer EFP increase ISW. A positive correlation was found between the EFP and ISW across a wide range of cultivars (14 genotypes in 1981 and 59 genotypes in 1982) grown in Lexington, KY (r=0.6-0.71) (Egli et al., 1984). The length of seed-fill duration is affected by environmental (Egli, 2004; Meckel et al., 1984) and genetic conditions (Egli, 2004; Egli et al., 1984). The duration of the EFP in MG 00, 1, 3 and 5 cultivars ranged

from 24 to 37 days in Lexington, KY, with the MG 5 cultivars having the longest EFP (Egli, 1993). Temperature during seed fill can influence the duration of the EFP. Egli and Wardlaw (1980) found a relatively small effect on the duration of the seed fill phase (measured from R5.5 to R7) with a range of day/night temperatures from 24/19 to 30/25 °C, and a reduction of the seed fill phase by 3 days at 33/28 °C (day/night). Environmental conditions during seed fill also influence the ISGR; in particular, low temperatures can reduce the rate of seed growth. Increasing temperature from 18/13 to 27/22 ºC (day/night) from approximately the beginning of seed growth until physiological maturity increased ISGR by 30% (Egli et al., 1981).

Objectives and hypotheses

A limited number of studies that have evaluated the mechanisms of yield determination in soybean across cultivars of different maturity and under no water limitation in the United States upper Mid-South. In this region, most of the soybean is grown under rainfed conditions but the crop is still subject to significant water limitations depending on the year and location. This understanding is critical to design genotype x environment x management strategies that can target a high yield potential while having an efficient use of resources (e.g. water, nutrients, and solar radiation). We quantified the yield potential of soybean cultivars from MG 2 to 5 under irrigated conditions and three environments in Kentucky. In addition, we quantified physiological traits related to yield and yield component determination and analyzed the relationship between physiological traits and genotypes with principal components and bi-plot analysis (GGEbiplot, version 8.0; Yan (2001). The specific goals of this study were to i) identify traits associated with higher

and/or lower yields in each environment, and ii) understand mechanisms that might lead to similar yield potential in cultivars of different maturity. We hypothesized, that soybean cultivars will have different physiological strategies to determine yield components that will be partially associated to soybean maturity and the duration and timing of developmental stages.

MATERIAL AND METHODS

Field experiments

Field experiments were conducted in three different environments in Kentucky that were a combination of planting date and location (Table 1.1). The experimental design was a split plot design with four replications. The main factor was soybean MG that included MG 2, 3, 4 and 5 cultivars. Four cultivars were nested within each MG, for a total of 16 commercial cultivars (Table 1.2). Plots consisted of six rows, 6 m long with a 38 cm row spacing. The seeding rate was 37 seed m^{-2}. Soils were classified as Bluegrass-Maury silt loam at environments 1 and 3 (Lexington) and as Crider silt loam at environment 2 (Princeton) (Table 1.1). Experiments were irrigated with a drip-tape system when the cumulative deficit in net crop evapotranspiration demand reached 30 mm. Daily net evapotranspiration demand was estimated with a daily balance of crop evapotranspiration, precipitation and irrigation (Allen et al., 2006). Weeds were controlled with tillage before planting and chemical control was applied during the growing season when necessary. Other pests were controlled during the growing season when required.

Measurements and Methodology

Ten plants per plot were marked to weekly monitor the occurrence of developmental stages according to the Ferh and Caviness scale (1977). Date of emergence (VE), beginning bloom (R1), beginning pod (R3), beginning seed (R5), full seed (R6), beginning maturity (R7) and full maturity (R8) were recorded. The duration (days) between VE-R1, R1-R5 and R5-R7 were used as an approximation of the vegetative ($Days_{VE-R1}$), seed set ($Days_{R1-R5}$) and seed fill ($Days_{R5-R7}$) phases, respectively. Node number in the main stem was measured in six plants per plot at harvest maturity (R8). Final grain yield was measured by harvesting a length of 2.44 m from each of the four central rows (total area of 3.72 m^2) and expressed at 13 % moisture. One hundred seeds were weighed to determine ISW and seed number per area. The CGR during the $Days_{R1-R5}$ was determined by sampling one linear meter of aboveground biomass from one of the four central rows at R1, R3 and R5. Biomass samples were dried at 65ºC and weighted. Crop growth rate (g biomass m^{-2} day^{-1}) was estimated as the slope of the linear regression between the dry matter and time (Egli and Yu, 1991). Cultivars were sampled by MG when most or all cultivars within a MG had reached a developmental stage. The biomass of a cultivar at R1 ($Biom_{R1}$) and R5 ($Biom_{R5}$) was calculated from the relationship between biomass and time, and the actual date of occurrence of the R1 and R5 developmental stages.

Individual seed growth rate (ISGR) was calculated from three aboveground biomass samplings during the linear phase of rapid seed growth. The first sample was taken close to the R6 stage, and three plants per plot were sampled at each sampling date on 5-10 day intervals. Pods, seeds and vegetative tissue (leaves and stem) from the three plants were dried and weighed separately. The weight of individual developing seeds was determined

by weigh 100 seeds, and ISGR (mg $seed^{-1}$ day^{-1}) was calculated as the slope of the linear regression between the ISW and time. The effective filling period (EFP) was obtained from the division of ISW at harvest by the ISGR. Harvest index (HI) of developing plants during the $Days_{R5\text{-}R7}$ period was obtained from the division between the total seed weight and total plant biomass on each sampling date after R6. The dry matter allocation coefficient (DMAC) from plant biomass to seeds was calculated as the slope of the relationship between HI and time.

Physiological framework for yield determination

One of the most common frameworks used to describe crop yield is the product between seed number per unit area and ISW (Equation 1).

$$Yield\ (g\ m^{-2}) = Seed\ number\ (seeds\ m^{-2}) * ISW\ (g\ seed^{-1}) \quad (1)$$

The first component of Equation 1, seed number, is determined during the critical period of flowering and pod set, estimated to occur from approximately R1 to R5 (Egli and Yu, 1991; Jiang and Egli, 1995). Charles-Edwards et al. (1986), proposed the model in Equation 2 to determine the number of potential grain sites per unit area (N_g), as a function of the daily canopy net photosynthesis (∇_F), the partitioning of daily canopy photosynthesis to reproductive organs (γ) and an inverse function of the minimum amount of assimilate that a potential seed needs to grow (A_g^{-1}) (Equation 2).

$$N_g = \nabla_F * \gamma * A_g^{-1} \quad (2)$$

The number of seeds on an area basis can be estimated from the model above (Equation 2) by indirectly approximating its components as shown in Equation 3 (Egli and Yu, 1991). The daily canopy photosynthesis was replaced by the CGR (g biomass m^{-2} day^{-1}) from R1 to R5. The minimum amount of assimilates required per seed was approximated from the ISGR during $Days_{R5\text{-}R7.}$ Finally, the partitioning coefficient to reproductive organs (PC, g biomass g $seed^{-1}$) was calculated from Equation 3 as the product between seed m^{-2} and ISGR, divided by CGR. The sink activity (SA, g seed m^{-2} day^{-1}) is the actual capacity of the plant to carry reproductive growth (Egli, 1993) and was estimated according to Equation 4.

$$Seed\ m^{-2} = CGR * PC * ISGR^{-1} \qquad (3)$$

$$Sink\ activity = seed\ m^{-2} * ISGR^{-1} \qquad (4)$$

Some limitations of Equation 3 are that ISGR is further affected by environmental conditions during pod set and seed filling. Despite this limitation, this approximation has been used previously (Egli and Yu, 1991). In this study, ISGR during seed fill is used as an approximation of the minimum assimilate required per seed, in absence of a better measurement.

Individual seed weight (ISW, mg $seed^{-1}$) is the other component of equation 1 and can be defined as the product between ISGR (mg $seed^{-1}$ day^{-1}) and the duration of the EFP (days), (Equation 5). These two variables were obtained from field measurements.

$$Individual\ seed\ mass = ISGR\ * EFP \qquad (5)$$

The EFP was estimated from the fraction between individual seed mass (g seed^{-1}) and ISGR (g seed^{-1} day^{-1}). By merging Equation 3 and 5, yield can be re-written as in equation 6. Harvest index can be described as the product between the dry matter allocation to seeds during seed fill (DMAC, g seed g biomass^{-1} day^{-1}) and the EFP (Equation 7).

$$Yield\ = CGR * PC * EFP \qquad (6)$$

$$Harvets\ index = DMAC * EFP \qquad (7)$$

Data Analysis

A general linear mixed model with the MIXED procedure (SAS 9.4, SAS institute Inc. Cary, NC, USA) was used to analyze all data, except for rate variables that were expressed on a time basis (CGR, ISGR, DMAC). Environment, MG, cultivar nested within MG, and their interactions were considered as fixed factors in the model, while block (nested within environment) and its interaction with other factors were considered as random factors. A significant interaction between environment and the fixed factors in the model (MG and cultivars within MG) was found, thus, the analysis of variance was conducted by environment. At environment 2 (Princeton, May), ISGR data was only available for MG 2 to 4 cultivars. In consequence, the analysis of variance of EFP, SA and PC does not include MG 5 cultivars at environment 2.The percentage of variance explained by each factor was

estimated as the sum of squares of each factor divided by the total sum of squares in the model. The Fisher's least significant difference (LSD) was used to separate means when $p<0.05$.

An analysis of covariance (ANCOVA) was conducted by environment using the MIXED procedure (SAS 9.4, SAS institute Inc. Cary, NC, USA) to test MG and cultivar within MG treatment effects on rate variables (CGR, ISGR and DMAC). Aboveground biomass, ISW, and HI were modeled with MG and cultivar within MG as fixed effects, and time as an independent variable. The interaction of time with aboveground biomass, ISW, and HI was used to test fixed treatment effects on CGR, ISGR, and DMAC, respectively. When the interaction of time with MG and cultivar within MG was significant ($p<0.05$) mean differences by treatment were tested using CONTRAST statements.

The relationship between physiological traits was analyzed with the CORR PEARSON procedure (SAS 9.4, SAS institute Inc. Cary, NC, USA) using data averaged by cultivar and environment (Table 1.8). The variables involved in seed number (Equation 3 and 4) and ISW determination (Equation 5 and $Days_{R5\text{-}R7}$) that were significantly related to each yield component ($P<0.10$) were further analyzed with a cultivar-by-trait principal component analysis using the GGE bi-plot software (version 8.0) developed by Yan et al. (2000). In addition, from the total of 15 physiological traits studied, those that showed a significant correlation with yield ($p<0.10$) were used to construct a cultivar-by-trait bi-plot across the three environments. The goal was to visualize the relationship between multiple physiological traits (testers) as well as identify the ranking of the entry (cultivars) in relation to a particular tester (Yan, 2001).

RESULTS

Environmental conditions

Solar radiation from R1 to R5 ($SolarRad_{R1-R5}$) ranged from 18.8 to 21.0 MJ m^{-2} day^{-1} across environments, while the solar radiation from R5 to R7 ($SolarRad_{R5-R7}$) ranged from 15.5 to 20.3 MJ m^{-2} day^{-1} (Table 1.3). At environment 1 (Lexington, May), the $SolarRad_{R1-R5}$ was similar across MG (20.4-20.9 MJ m^{-2} day^{-1}), while the $SolarRad_{R5-R7}$ was higher for MG 2 cultivars (20.3 MJ m^{-2} day^{-1}) and lower for MG 5 cultivars (18 MJ m^{-2} day^{-1}) (Table 1.3). At environment 2 (Princeton, May), differences in $SolarRad_{R1-R5}$ across soybean MG cultivars were relatively small (19.9 – 21.1 MJ m^{-2} day^{-1}). During the $Days_{R5-R7}$ phase, the $SolarRad_{R5-R7}$ was highest in MG 2 (19.8 MJ m^{-2} day^{-1}) and lowest in MG 5 cultivars (18.3 MJ m^{-2} day^{-1}). At environment 3 (Lexington, June), the $SolarRad_{R1-R5}$ showed a tendency to be higher in MG 2 cultivars (20.8 MJ m^{-2} day^{-1}) and decline with later maturities up to 18.8 MJ m^{-2} day^{-1} in MG 5 cultivars (Table 1.3).

The average temperature from R1 to R5 ($Temp_{R1-R5}$) was higher across environments (21.5 - 25.7 ºC) compared to the average temperature from R5 to R7 ($Temp_{R5-R7}$) (19.7 to 24.2 ºC) (Table 1.3). Overall, MG 5 cultivars had the lowest $Temp_{R1-R5}$ and $Temp_{R5-R7}$ in all three environments. At environment 1 (Lexington, May), MG 3 and 4 cultivars had on average higher $Temp_{R1-R5}$ (25.6 ºC) than MG 2 and 5 cultivars (24.2 – 24.6 ºC). In environment 2 (Princeton, May), MG 2, 3 and 4 had a similar $Temp_{R1-R5}$ (25.7 - 25.9ºC), while $Temp_{R5-R7}$ was higher in MG 2 cultivars (24.19 ºC) compared to MG 3 to 5 cultivars (21.2 – 22.4 ºC). At environment 3 (Lexington, June), MG 3 and 4 had the highest $Temp_{R1-}$

$_{R5}$ (23.3 -23.9ºC), while MG 2 and 3 cultivars had the highest $Temp_{R5-R7}$ (21.4 ºC) (Table 1.3).

Final yield and yield components

There was a significant effect of MG on yield and most of the yield components studied in all the environments (Table 1.4). Cultivars within MG also had a significant effect on some variables depending on the environment but to a lesser extent. Therefore, results averaged by MG and environment are presented in Tables 1.5 and 1.6, and means by cultivar within MG and environment are shown for some variables in Table 1.7.

There was a significant effect of MG on yield in all the environments that explained 29 to 42 % of the sum of squares in the model (Table 1.4). Yield differences across cultivars within MG where only significant ($p<0.05$) in one out of the three environments studied (Lexington, PD: June), where it explained 29% of the total sum of squares in the model, vs. 42% explained by MG (Table 1.4). Yields averaged by environment and MG ranged from 3692 to 5758 kg ha^{-1}. Yields in environment 3 planted in June were 989 and 343 kg ha^{-1} lower on average compared to environments 1 and 2, respectively (planted in May) (Table 1.5).

Yields were highest for MG 2 to 4 cultivars at environment 1 (Lexington, May), MG 4 at environment 2 (Princeton, May), and MG 3 and 4 cultivars at environment 3 (Lexington, June) (Table 1.5). Overall, MG 5 cultivars had the lowest yields across all environments compared to the highest yielding MG treatments (19 to 23% lower) (Table 1.5). Yield differences within cultivars of a same MG were only significant in environment 3 (Lexington, June), and largely due to high yield variability in MG 5 cultivars (2963 to 4660

kg ha^{-1} range from the lowest to highest yielding cultivar) (data not shown). Although the cultivar within MG effect was only significant at environment 3 (Lexington, June), it is worth noting that in all environments, the earliest MG 5 cultivar (rMG 5.0; P50T64R) of determinant growth habit had yields 28% higher on average compared to the other MG 5 cultivars (P52T50R, P54T94R and P55T81R), and similar to yields of MG 3 and 4 cultivars (data not shown).

Seed number on an area basis (seeds m^{-2}) was dependent on the MG choice in all environments and had a significant effect of cultivar within MG at environment 1 (Lexington, May) and 3 (Lexington, May) (Table 1.4). Across all environments, MG explained 20 to 34 % of the total sum of squares of the model, and cultivars within MG explained 32 to 34 % at environment 1 (Lexington, May) and 3 (Lexington, June) (Table 1.4). Seed number averaged by environment and soybean MG cultivar ranged from 1960 to 2894 seed m^{-2} at environment 1 (Lexington, May), from 1959 to 2673 seed m^{-2} in environment 2 (Princeton, May), and from 1670 to 2512 seed m^{-2} at environment 3 (Lexington, June). At environment 1 (Lexington, May) and 3 (Lexington, June), cultivars of MG 2 to 4 had the greatest seed number, 15-26% greater than MG 5 cultivars (Table 1.5). At environment 2 (Princeton, May), MG 4 cultivars had the greatest seed number, and it was reduced by 18% in other MG choices (Table 1.5).

Differences in final ISW (mg $seed^{-1}$) in mature seed were mainly explained by cultivars within MG (46 - 52 % of the total sum of square in the model), and to a lesser extent by MG (20 - 28%) (Table 1.4). Individual seed weight ranged from 141 to 178 mg $seed^{-1}$ at environment 1 (Lexington, May), 140 to 169 mg $seed^{-1}$ at environment 2 (Princeton, May), and 130 to 174 mg $seed^{-1}$ at environment 3 (Lexington, June) (Table 1.7). Individual seed

weight did not show a clear trend associated to the cultivar maturity, but was more associated to genetic differences instead. For instance, cultivar P38T42R had the highest ISW on average in all environments (Table 1.7). Within each MG, there were cultivars that consistently ranked at both the top and bottom of the ranking for ISW across all the three environments (Table 1.7). However, MG 3 cultivars ranked more frequently at the top (3 MG cultivars were within the top 5).

Duration of developmental phases

Both soybean MG and cultivar had a significant ($P<0.05$) effect on the duration of all developmental phases ($Days_{VE-R1}$, $Days_{R1-R5}$ and $Days_{R5-R7}$) at environment 1 (Lexington, May) and 3 (Lexington, June) (Table 1.4). However, at environment 2 (Princeton, May) the $Days_{R1-R5}$ was not affected by MG or cultivar within MG, and $Days_{R5-R7}$ was only affected by MG (Table 1.4). Overall, the MG effect explained a much larger fraction of the variability in duration of developmental phases compared with cultivar within MG. Across all environments, MG explained 75-88, 43-54, and 36-61% of the total sum of squares in the prediction of $Days_{VE-R1}$, $Days_{R1-R5}$ and $Days_{R5-R7}$ phases, respectively (Table 1.4). Cultivars within MG explained 11-22%, 17-25% and 21-29% of the total sum of square of the model for the duration of the $Days_{VE-R1}$, $Days_{R1-R5}$ and $Days_{R5-R7}$ phase, respectively (Table 1.4). The $Days_{VE-R1}$ increased within longer-season maturities in all environments, being 20 to 28 days longer for cultivars within MG 5 than MG 2 (Table 1.5). The duration of $Days_{R1-R5}$ was longest for MG 3 and 4 at environment 1 (Lexington, May), MG 3 to 5 at environment 2 (Princeton, May) and MG 5 at environment 3 (Lexington, June) (Table 1.5). Differences in the duration of $Days_{R1-R5}$ across cultivars within a MG were only 4 to 5 days

on average (Table 1.5). The $Days_{R5-R7}$ were longest for MG 3 to 5 (environment 1, Lexington, May), MG 3 and 4 (environment 2, Princeton, May) and MG 3 to 5 cultivars (environment 3, Lexington, June) (Table 1.5). The duration of this phase ($Days_{R5-R7}$) had a relatively low variation across cultivars within a MG (1 to 9 days across all environments) (Table 1.5).

The ratio between the duration of reproductive phases (days from R1 to R7) and the vegetative (days from VE to R1) ($Ratio_{R/V}$) had a significant MG and cultivar within MG effect in all environments (Table 1.4). Differences in $Ratio_{R/V}$ were mostly explained by soybean MG, with 63-80% of the total sum of square explained in the model (Table 1.4). The $Ratio_{V/G}$ ranged from 0.99 to 1.57, 1.08 to 1.85 and 1.19 to 1.66 at environments 1 (Lexington, May), 2 (Princeton, May) and 3 (Lexington, June), respectively (Table 1.5). The $Ratio_{V/G}$ was highest in the short-season MGs and decreased with later maturities in all environments. In consequence, cultivars of later MGs had a longer total growing season, but due to a much longer duration of the $Days_{VE-R1}$ compared to reproductive growth.

Biomass production

There was a significant effect of soybean MG on $Biom_{R1}$ in all the environments, which explained most of the variation with 65 to 88% of the total sum of square in the model (Table 1.4). Cultivar within MG had a significant effect on $Biom_{R1}$ only at environment 1 (Lexington, May) and 3 (Princeton, May), where it explained a smaller amount of variation (6-13%) (Table 1.4). In all the environments, $Biom_{R1}$ was lowest in MG 2 cultivars (174-219 g biomass m^{-2}) and increased with soybean maturity group to 473 to 654 g biomass m^{-}

^{2} in MG 5 cultivars, with the exception of MG 3 cultivars at environment 3 (Lexington, June) that had similar $Biom_{R1}$ to MG 2 cultivars (Table 1.5).

In all the environments, $Biom_{R5}$ was dependent on the soybean MG that explained 33 to 61 % of total sum of squares in the model (Table 1.4). The effect of cultivar within MG on $Biom_{R5}$ was only significant at environment 1 and explained 16 % of the total variation (Table 1.4). At environment 1 (Lexington, May) and 2 (Princeton, May), MG 2 cultivars had the lowest $Biom_{R5}$ (581-599 g biomass m^{-2}), followed by MG 3 and 4 (775-872 g biomass m^{-2}) and by MG 5 cultivars (1057-1087 g biomass m^{-2}). At environment 3 (Lexington, June), $Biom_{R5}$ was similar across MG 2 to 4 (480-613 g biomass m^{-2}), and was highest for MG 5 cultivars (8001 g biomass m^{-2}) (Table 1.5).

Growth and Partitioning

Variables that represent a rate of growth or change in partitioning over time were calculated as the slope of total aboveground biomass, ISW, or harvest index over time (for CGR, ISGR, and DMAC, respectively). The effect of MG and cultivar within MG on these variables was tested by analyzing the time x MG and time x cultivar (MG) interactions in the analysis of covariance (ANCOVA) with time as an independent variable and MG and cultivar (MG) as fixed effects (Table 1.4).

Crop growth rate was affected by MG at environment 1 (Lexington, May) and 2 (Princeton, May), but not at environment 3 planted in June (Table 1.4). Cultivars within MGs did not have a significant effect on CGR in any of the environments. On average, environments 1 (Lexington, May) and 2 (Princeton, May), had larger CGR values (23 and 25 g biomass m^{-2} day^{-1}, respectively), compared to environment 3 (Lexington, June; 18 g biomass m^{-2} day^{-}

^{1}) (Table 1.6). At environment 1 (Lexington, May), MG 5 had the largest CGR (28.5 g biomass m^{-2} day^{-1}), followed by MG 3 and 4 (22.5 g biomass m^{-2} day-1), and MG 2 cultivars with the lowest CGR (18.1 gm^{-2} day^{-1}). At environment 2 (Princeton, May), MG 3 and 5 cultivars had the largest CGR (29.3 and 27 g biomass m^{-2} day-1, respectively), followed by MG 2 and 4 (22 g biomass m^{-2} day-1). At environment 3 (Lexington, June), CGR was similar across MG cultivars (Table 1.6).

Individual seed growth rate (ISGR) was dependent on the MG cultivar in all environments, but not on the cultivar within MG (Table 1.4). At environment 1 (Lexington, May), MG 5 cultivars showed the largest ISGR (5.74 mg $seed^{-1}$ day^{-1}), and it was reduced by 36 to 45 % in MG 2 to 4 cultivars (Table 1.6). At environment 3 (Lexington, June), MG 5 and 4 cultivars had the largest ISGR (5.23 and 5.30 mg $seed^{-1}$ day^{-1} respectively), and it was reduced by 37 to 42 % in MG 2 and 3 cultivars (Table 1.6). A different pattern was observed at environment 2 (Princeton, May), were short season MG 2 and 3 showed the largest ISGR (5.0 g $seed^{-1}$ day^{-1}), and it was reduced by 31% in MG 4 cultivars (Table 1.6).

The rate of dry matter allocation to seeds (DMAC) (g seed g $biomass^{-1}$ day^{-1}) was only affected by the MG cultivar at environment 3 (Lexington, June), and by the cultivar within MG at environment 1 (Lexington, May) and 3 (Lexington, June) (Table 1.4). On average, DMAC was highest at environment 3 (Lexington, May; 0.05 g seed g $biomass^{-1}$ day^{-1}), followed by environment 1 (Lexington, May; 0.03 g seed g $biomass^{-1}$ day^{-1}) and environment 2 (Princeton, May; 0.02 g seed g $biomass^{-1}$ day^{-1}) (Table 1.7). At environment 1, the DMAC was similar across most cultivars (0.019-0.039 g seed g $biomass^{-1}$ day^{-1}), and only cultivars P41T33R and P50T64R had a higher DMAC (0.055 g seed g $biomass^{-1}$ day^{-1}) (Table 1.7). At environment 2, the DMAC was similar across MGs and cultivars (0.018

g seed g biomass^{-1} day^{-1}) (Table 1.6). At environment 3, the DMAC was highest in MG 2 and 3 cultivars (0.062 g seed g biomass^{-1} day^{-1}), and lower for MG 4 and 5 cultivars (0.030 g seed g biomass^{-1} day^{-1}) (Table 1.6). Differences across cultivars within MG in environment 3 were mostly due to a high DMAC in cultivar P32T16R (0.123 g seed g biomass^{-1} day^{-1}) and low DMAC in cultivar P55T81R (0.015 g seed g biomass^{-1} day^{-1}) (Table 1.7).

The PC was dependent on the MG and cultivar within MG in all environments ($p<0.001$-0.05) (Table 1.4). Cultivars within MG explained most of the variation in PC across environments with 34 to 77% of the total sum of square in the model, while MG explained 19 to 37 % (Table 1.4). The PC ranged from 0.36 to 0.67 g biomass g seed^{-1} at environment 1 (Lexington, May), from 0.31 to 0.57 g biomass g seed^{-1} at environment 2 (Princeton, May) and from 0.34 to 1.08 g biomass g seed^{-1} at environment 3 (Lexington, June) (Table 1.7). At environment 1 (Lexington, May), MG 2 cultivars had the highest PC value. In this environment, cultivars AG29X8, AG21X8, P50T46R and P22t24X had the highest PC values (>0.60 g seed g biomass^{-1}) (Table 1.7). Cultivars P35T58R, P47T36R and P55T81R had the lowest PC value at environment 1 (<0.40 g seed g biomass^{-1}) (Table 1.7). At environment 2 (Princeton, May), MG 2 and 4 had the highest PC values (Table 1.6). Cultivars P45T11R, P22T24X and AG29X8 had the highest values of PC (>0.5 g seed g biomass^{-1}) (Table 1.7). At environment 3 (Lexington, June), cultivar P50T64R had the highest PC value (1.08 g seed g biomass^{-1}), and cultivars P22T24R, P32T16R and P54T94R had the lowest PC values (<0.4 g seed g biomass^{-1}) (Table 1.7). Overall, the PC values atn environment 3, planted in June, were higher than in the other two environments.

Maturity group and cultivar within MG had a significant ($p<0.05$) effect on SA at environment 1 (Lexington, May) and at environment 3 (Lexington, June), but not at environment 2 (Princeton, May). At environment 1 and 3, cultivars within MG explained 39 to 44% of the variation in SA, while MG cultivar explained 33 to 45% (Table 1.4). The SA ranged from 8.9 to 14.2 g seed m^{-2} day^{-1} at environment 1 (Lexington, May), from 8.4 to 12.2 g seed m^{-2} day^{-1} at environment 2 (Princeton, May) and from 6.3 to 13.8 g seed m^{-2} day^{-1} at environment 3 (Lexington, June) (Table 1.7). At environment 1 (Lexington, May), MG 5 cultivars had the highest SA (13.04 g seed m^{-2} day^{-1}), and it was reduced by 19 to 26% in MG 2 to 4 cultivars, respectively (Table 1.6). At environment 3 (Lexington, June), MG 4 cultivars had the highest SA (12.34 g seed m^{-2} day^{-1}), followed by MG 5 (23% lower) and by MG 2 and 3 cultivars (46% lower) (Table 1.6).

The duration of the effective filling period (EFP) was dependent on the MG cultivar in all three environments, explaining 61 to 66 % of the total sum of squares in the model (Table 1.4). Additionally, cultivars within MG had a significant effect on the EFP in all environments, explaining 30 to 36% of the sum of squares in the model (Table 1.4). The EFP across environments ranged from 27 to 42 days (Table 1.6). At environment 1 (Lexington, May), MG 3 and 4 cultivars had the longest duration EFP (40.5 days), and it was reduced by 2 and 14 days in MG 2 and 5 cultivars, respectively (Table 1.6). At environment 2 (Princeton, May), the duration of the EFP was longest for MG 4 cultivars (42 days) and was reduced by 12 and 10 days for MG 2 and 3 cultivars, respectively. Finally, at environment 3 (Lexington, June), the duration of the EFP was longest for MG 3 cultivars (42 days), and was reduced by 3, 12 and 14 days for MG 2, 4, and 5 cultivars, respectively (Table 1.6).

Relationship between physiological traits

From the total of 15 physiological traits studied, 7 showed a significant correlation with yield ($p<0.10$) across the three environments and were selected to construct a cultivar-by-trait bi-plot. This analysis included yield, seed number, ISW, duration of developmental stages ($Days_{VE-R1}$, $Days_{R1-R5}$, $Days_{R5-R7}$), $Biom_{R1}$, and the $Ratio_{V/R}$ (Figure 1.1, a and b). Across all environments, the variables plotted explained 82% of the variation based on the sum of principal component 1 (53.8%) and 2 (28.3%) (Figure 1.1, a and b). In the cultivar-by-trait bi-plot figure, the relationships among physiological variables (traits) is represented by the angle between vectors (solid lines) (Figure 1.1, a). The correlation between two traits can be estimated as the cosine of the angle formed between them, and can range from -1 (negatively correlated) to 1 (positively correlated). Thus, an angle <90º indicates a positive correlation, and an angle >90º indicates a negative correlation. Traits are more highly correlated with angles close to 0º (positive) or 180º (negative), and an angle close to 90º means that two traits are independent according to the percentage of data variability explained by principal component 1 and 2 in the model. In Figure 1.1a, the solid lines starting from the center of the bi-plot represent the vectors for each trait. The yield vector showed an acute angle with the vector of seed number, ISW, duration of the $Days_{R1-R5}$, $Days_{R5-R7}$, and the $Ratio_{V/R}$. The correlation analysis also supported that yield was positively correlated with seed number ($r= 0.89$, $p<0.0001$), ISW ($r= 0.51$, $p<0.0001$), $Days_{R5-R7}$ ($r= 0.33$, $p<0.0001$), and the $Ratio_{V/R}$ ($r= 0.24$, $p=0.0008$) (Table 1.8). The $Biom_{R1}$ and $Days_{VE-R1}$ showed a negative (obtuse angle) relationship with yield, with an $r=-0.19$ ($p=0.007$) and -0.14 ($p=0.054$) respectively (Table 1.8). Seed number was the trait

more highly related to yield and was negatively (angle >90°) associated with $Days_{VE-R1}$ and $Biom_{R1}$. Individual seed weight was associated most strongly with the duration of $Days_{R5-R7}$ phase, since the angle formed between the two traits was <90° (Figure 1.1, a).

The cultivar ranking for a specific trait can be also deducted from the cultivar-by-trait bi-plot figure. Figure 1.1b exemplifies the ranking of cultivars for the yield trait across the three environments. The intersections of the lines passing through each cultivar and crossing the yield vector perpendicularly determine the ranking of cultivars, with cultivars at the top of the yield ranking crossing higher in the direction of the vector (Figure 1.1b). For example, across all environments, late MG 3 cultivars (rMG 3.8) where at the top of the yield ranking, followed by early MG 3 cultivars (rMG 3.2 and 3.5), MG 4 cultivars, and MG 5 cultivar P50T64R (rMG 5.0) of indeterminate growth habit (Figure 1.1b). Next in the yield ranking were MG 2 cultivars, followed by the rest of MG 5 cultivars (excluding P50T64R) in the last place (Figure 1.1b).

The ranking of cultivars for other traits in Figure 1.1a can be obtained by the ranking of the perpendicular lines passing through each cultivar and crossing perpendicularly to a given trait vector. For example, MG 3 and 4 placed similarly at the top of the ranking for seed number, followed by MG 2. The MG 5 cultivars were grouped at the end the ranking for seed number, with exception of the rMG 5.0 cultivar (P50T64R) that placed close to MG 4 cultivars. Applying the same analysis for the ranking of cultivars for ISW trait, we can deduce from Figure 1.1a, that cultivars P38T61BR and P38T42R had the largest seed, followed by other MG 3 and 4, MG 2 cultivars, and finally MG 5 cultivars (except for cultivar P50T64R that placed next to MG 4). Cultivars within MG 5 (except for P50T64R) were grouped on the opposite direction from the yield vector, representing the lowest yield

across environments (Figure 1.1a). The low yield in MG 5 cultivars was coincident with a long $Days_{VE-R1}$ phase, high $Biom_{R1}$, and low $Ratio_{V/R}$ (Figure 1.1a). Overall, MG 5 cultivars had the lowest seed number, and ISW lower than MG 3 and 4 cultivars, but similar to cultivars within MG 2 (Figure 1.1, a).

In the analysis of physiological traits by environment, yield was significantly related to seed number in all environments ($r= 0.82-0.88$, $p<0.0001$) (Table 1.8). The ISW was also significant and positively related to yield in all the environments, but to a lesser extent ($r =0.60$, 0.26, and 0.50 in environment 1, 2, and 3, respectively) (Table 1.8). Significant physiological traits related to seed number from Equation 3 and 4, and physiological traits related to ISW (Equation 5) plus the duration $Days_{R5-R7}$ were included in the bi-pot analysis by environment to further study of the mechanisms that determine seed number and ISW (Figure 1.2,1.3 and 1.4).

Based on principal component 1 (58.8%) and 2 (29.9%), the variables plotted in the bi-plot model for the analysis of seed number determination (Figure 1.2, a) explained 88.7% of the total data variation at environment 1 (Lexington, May). On one hand, seed number was positively correlated with PC ($r= 0.57$, $p<0.0001$) and SA ($r= 0.23$, $p=0.084$). On the other hand, seed number showed a negative relation with ISGR ($r= -0.50$, $p< 0.0001$) and CGR ($r= -0.43$, $p= 0.0005$) (Table 1.8). Cultivars AG29X8 and AG21X8 produced the highest number of seeds per area, followed by the other two MG 2 cultivars (P22T24X and P28T08R), P45T11R, P50T64R, the MG 3 cultivars, the rest of MG 4 cultivars (P41T33R, P49T97R and P47T36R), and P54T49R. Cultivars P52T50R and P55T81R had the lowest number of seeds per area in this environment. Different mechanisms can be identified that contributed to a higher seed number for some genotypes in this environment. In one hand,

cultivars AG29X8 and AG21X8 had a high PC, a low CGR, and a relatively low ISGR. On the other hand, cultivars P45T11R, P35T58R and P47T36R had a relatively low PC, but benefited from low ISGR values. In contrast, cultivars P50T64R and P54T94R had high ISGR values but high PC values.

The variables plotted in the bi-plot for the analysis of ISW determination (Figure 1.2b) explained 82.7% of the total data variability at environment 1 (Lexington, May). Individual seed weight was positively correlated with the EFP (r= 0.43, p=0.0004), $Days_{R5\text{-}R7}$ (r= 0.12, ns), and negatively correlated with ISGR (r= -0.12, ns) (Table 1.8). In addition, the duration of the EFP and the ISGR were highly negatively correlated with an angle between vectors close to 180º (r= -0.93; p<0.0001). Relative MG 3.8 (P38T61BR and P38T42R) were the first in the ISW ranking, followed by P41T33R, P312T16R, P50T64R, P28T08R, P47T36R, P49T94R, P54T94R, P55T81R, AG29X8, P45T11R, P22T24X and P35T58R. Finally, the smallest seeds were produced by P52T50R and AG21X8. Cultivars with the heaviest seeds (rMG 3.8) had the longest duration of $Days_{R5\text{-}R7}$ and a relatively long EFP. Cultivars P32T16R, P41T33R, and P28T08R had a relatively high ISW thanks to a high EFP and relatively long $Days_{R5\text{-}R7}$. Cultivar P50T64R was the only cultivar with a relatively high ISW that was a result of a high ISGR combined with high $Days_{R5\text{-}R7}$. In the rest of MG 5 cultivars, small seeds were associated with a high ISGR but short EFP. In contrary, in the rest of MG 2, 3, and 4 cultivars, small seeds were due to low ISGR despite relatively high EFP, as well as due to low $Days_{R5\text{-}R7}$.

At environment 2 (Princeton, May), cultivars within MG 5 were excluded from the analysis since EFP, PC, SA and ISGR data were not available (Figure 1.3a and b). The bi-plot model with traits related to seed number determination explained 79.6% of the total variation

based on principal component 1 and 2 (Figure 1.3a). Seed number was positively correlated with SA (r= 0.54, p<0.0001) and PC (r= 0.49, p=0.004), and negative correlated with ISGR (r= -0.57, p<0.0001) (Table 1.8). Cultivar P45T11R produced the greatest number of seeds per area, followed by the other MG 4 cultivars, AG29X8, P22T24X and P35T58R. The other MG 2 (rMG 2.2 and 2.8) and MG 3 (rMG 3.2 and 3.8) cultivars were located on the opposite side of the seed number vector, meaning a lower seed production; P32T16R produced the lowest number of seed in this environment. Two main mechanism can be identified that explained seed number variation, a low ISGR and/or a high assimilate partitioning to seeds during the $Days_{R1\text{-}R5}$ period (PC).Cultivars within MG 2 and 3 (except for AG29X8, and P35T58R) had a fast ISGR, contributing to less seeds m^{-2}. In contrast, MG 4 cultivars and AG29X8 had low ISGR, which contributed to a greater seed number per area. Cultivar P45T11R and AG29X8 had the highest PC value, which contributed to their high seed number. The lowest seed number was found in cultivars P38T42R and P32T16R, associated to a fast ISGR and low PC value (Figure 3, a). In the analysis of traits related to ISW, the bi-plot model explained 90% of the variability in environment 2 (Princeton, May) (Figure 1.3b). The ISW was positively correlated with the EFP (r= 0.46, p=0.001), the $Days_{R5\text{-}R7}$ (r= 0.17, ns), and negatively correlated with ISGR (r= -0.02, ns) (Table 1.8). Except for cultivar P35T58R, MG 3 cultivars produced the largest seeds, followed by cultivars P47T36R, P49T97R and P41T33R. Third in the ranking of ISW were MG 2 cultivars, P41T33R and P45T11R. The smallest seeds were produced by P35T58R. Cultivars P38T42R and P32T61R, that produced the largest seeds, presented and intermediate ISGR and relative short duration of the EFP, cultivars P38T61BR that it is third in the ranking of ISW had relative low ISGR while the duration of the EFP was

relative long. Overall, the lowest cultivars presented an intermediate ISGR as well as duration of the EFP (Figure 1.3, b).

Based on principal component 1 (68.3%) and 2 (18%), the variables plotted in the bi-plot model for the analysis of seed number determination (Figure 1.4,a) explained 83.6% of the total data variation at environment 3 (Lexington, June). Sink activity ($r= 0.56$, $p<0.0001$) and PC ($r= 0.53$, $p<0.0001$) were positive and significantly correlated with seed number. (Table 1.8). However, the CGR ($r= -0.42$, $p=0.0005$) was negative and significantly related with seed number (Table 1.8). Sink activity and PC showed a positive and close relation between each other in this environment, since the angle between traits (SA and PC) is very small. Based on this, the variation in seed number was explained in the same way by the SA and the PC. In addition, CGR was almost independent from seed number and negative related with SA and PC, according to the variation explained by the model. The seed number ranking was highest for P35T58R; followed by cultivars P50T64R, P41T33R, P47T36R, P28T08R and AG21X8R, that produced a similar number of seeds. Relative MG 3.8, P45T11R and P55T81R, produced similar seed number too, and were positioned in the third place of the seed number ranking, followed by P49T94R and P52T50R. The lowest seed number in this environment was produced by P54T94R. This last cultivar had the largest CGR, while the highest seeding number cultivar (P35T58R) had the smallest CGR. The second highest seeding number cultivar (P50T64R) as well as P41T33R presented the highest SA and PC, while P35T58R (highest seed number) was third in the ranking of SA and PC (Figure 1.4, a). Based on the principal component 1 (57.6%) and 2 (32%), the variables plotted in the bi-plot model analysis for ISW determination (Figure 1.4b) explained 59.6% of the total data variation at environment 3 (Lexington, June).

Individual seed weight was positively correlated with the duration of the EFP (r= 0.26, p=0.04) and $Days_{R5-R7}$ (r= 0.24, p=0.05) (Table 1.8). Individual seed growth rate was positive but not significant related with ISW, however the correlation coefficient was very small (r= 0.07, ns) (Table 1.8), since the angle formed between traits is close to 90º. Once again, the rMG 3.8 had the heaviest seeds, followed first by P32T16R, and second by MG 4 cultivars, P35T58R and three MG 5 cultivars (P50T64R, P55T81R and P52T50R). Maturity group 2 cultivars and P54T94R had the small seeds; however, P54T94R and AG21X8 were the smallest seeds. The largest seed cultivars (rMG 3.8), were third in the ranking of the duration of EFP and seed-fill period and had an intermediate ISGR. One of the cultivars that produce the lightest seed (AG21X8) had intermediate duration of EFP and $Days_{R5-R7}$ period as well as ISGR, however the other cultivar (P54T94R) that produce small seed had the highest ISGR and shortest EFP (Figure 1.4, b).

DISCUSSION

Average yield obtained at environment 1 (5347 kg ha^{-1}), environment 2 (4701 kg ha^{-1}) and environment 3 (4358 kg ha^{-1}) reflect yields in the high range for the state of KY (average state yield in 2017 was 3564 kg ha^{-1}) (USDA-NASS, 2017). Average yields from Lexington, June 21 planting date (environment 3) were 24% (1387 kg ha^{-1}), 18% (1031 kg ha^{-1}), 11% (574 kg ha^{-1}) and 21 % (964 kg ha^{-1}) lower for MG 2, 3 , 4 and 5 cultivars, compared to yields from a May 16 planting at the same location (environment 1). These results are consistent with previous works, where yield declined by 16 to 36% with MG 2 to 4 cultivars in Kentucky (Egli and Bruening, 2000) and by 7 to 18% with MG 3 to 6 cultivars in several locations across the US Mid-South (Salmeron et al., 2014). Moreover,

in Lexington, KY under irrigation, reduction in yield of 36% were found when planting date was delayed from May 19th to July 7th , and reduction of 18% and 29% were found when planting date was delayed from May 5th to June 8th and from June 8th to July 12th, respectively (Egli, 1975).

A range of MG choices provided similar yields in all environments. For example; MG 2 to 4 had similar yield at environment 1 (Lexington, May), MG 2, 3 and 5 had similar yields at environment 2 (Princeton, May), and MG 3 and 4 had similar yields at environment 3 (Lexington, June) (Table 1.5). Egli and Bruening (2000), found that cultivars of MG 2 to 4 yielded similar within a planting date and year in Kentucky. In addition, in Santa Fe, Argentina, similar yields were found between MG 3 and 5 cultivars (Santachiara et al., 2017a). Similar yields across MGs are common in the literature, but there is often insufficient understanding of the physiological bases for these yield differences. The results from this study provide a good opportunity to test our objectives of (i) identifying traits that are associated with higher and/or lower yields in each environment and (ii) understand mechanism that lead to similar yields by different cultivars. Our hypothesis was that cultivars within a MG will share similar mechanisms due to similar timing and duration of developmental stages.

Soybean MG explained 29 to 42 % of the total yield variability across environments, while the effect of soybean cultivars was only significant at environment 3 (Lexington, June) explaining a 29% of the yield variability (Table 1.4). Traditionally, yield is defined as the product between seed number and ISW (Equation 1). Our data suggested that soybean MG explained 20 to 34.2% of the total seed number variation across environments, and soybean cultivars explained 33.7 and 32.3% of the total variability of seed number at Lexington

planted in May (environment 1) and June (environment 3), respectively (Table 1.4). The variability in ISW was mainly explained by soybean MG by 45.6 to 51.9%, while soybean cultivars only explained 23.3 and 28.4 % of the ISW variability at Lexington planted May (environment 1) and June (environment 3), respectively (Table 1.4). Variables related to the developmental stages ($Days_{VE-R1}$, $Days_{R1-R5}$, $Days_{R5-R7}$ and EFP) and biomass production ($Biom_{R1}$ and $Biom_{R5}$) were mainly explained by the soybean MG effect, while the PC was mainly explained by the soybean cultivars effect (Table 1.4).

In our experiment, the main physiological trait that explained yield differences across cultivars was seed number (r= 0.82 to 0.88, Table 1.8). However, we also found a positive relationship between ISW and yield (r= 0.23-0.59) (Table 1.8). The better relationship of yield with seed number vs. ISW is well known (de Felipe et al., 2016; Kahlon et al., 2011; Rotundo et al., 2012), and is due to seed number being determined earlier in the growing season. In the following sections, we will analyze the different mechanism in determination of yield components across cultivars and MGs.

Duration of developmental phases

The duration of the $Days_{VE-R1}$ phase increased with later MGs in all environments, but this was not associated with higher yields. For example, MG 5 cultivars had the longest duration of $Days_{VE-R1}$ on average (54 days) but also the lowest yields (4220 kg ha^{-1}). Hence, longer $Days_{VE-R1}$ or growth cycle is not always related with high yield (Santachiara et al., 2017b).

The period of $Days_{R1-R5}$ is critical for seed number determination in soybean. The duration of $Days_{R1-R5}$ ranged from 8 to 16 days across environments and delaying planting date from

May to June at Lexington shortened this phase by 1 to 7 days (Table 1.5). We found a negative correlation between the $Days_{R1-R5}$ duration and seed number at environment 1 and 2, however, a negative correlation ($r= -0.61$, $p<0.0001$) was found at environment 3. At environment 3, MG 4 cultivars had the shortest $Days_{R1-R5}$ duration and the highest yield (Table 1.5). No relationship between seed-set phase and seed number was found by Rotundo et al. (2012) across a wide range of cultivars in the United States (61 cultivars) and Argentina (25 cultivars). Egli and Bruening (2000), found a positive relationship ($R^2= 0.56$) between seed number and the duration of the seed-set phase for a range of MGs (1 to 4) in Kentucky. Based on our data, the $Days_{R1-R5}$ might not be a good estimate of the real seed-set period across different soybean maturities, in particular because we had different cultivars of different growth habit (determinate and indeterminate).

Differences in the duration of the $Days_{R5-R7}$ phase were mainly associated to the choice of soybean MG (Table 1.4). According to Egli (2004), the seed-fill duration is influenced by environmental condition and the genotype. In our study, the increase in $Days_{R5-R7}$ with later maturities was relatively small (5 days on average). A delay in plating date from May to June at Lexington reduced $Days_{R5-R7}$ by 3 days on average (Table 1.5). High temperature usually shorten the developmental phases. Maturity group 2 cultivars, at environment 1 and 2 had the shortest duration of $Days_{R5-R7}$ and the highest $Temp_{R5-R7}$ (Table 1.3 and 1.5). However, when planting date was delay from May to June a different pattern was observed, since MG 2 cultivars also presented the shortest $Days_{R5-R7}$ but a relative high $Temp_{R5-R7.}$ These results might be related with the time of the year in which this phase took place, since the length of days are getting shorter and this accelerate developmental rate towards reproductive stages and will shorten this phase. In addition, with temperatures higher than

30/25ºC, the seed fill period was reduced due to a faster leaf senesce (Egli and Wardlaw, 1980)

There was an overall positive relationship between duration of the $Days_{R5\text{-}R7}$ and yield. However, no positive relation between yield and seed fill duration was found in a planting date and soybean MG (4 to 8) study, when combining all the MGs together (Chen and Wiatrak, 2010), but a positive relation between yield and seed-fill was found by Kantolic et al. (2007).

Physiological traits influencing seed number determination

Seed number has been closely associated with the crop growth rate during the period of seed set (Egli and Bruening, 2000; Egli and Yu, 1991; Kantolic et al., 2013; Rotundo et al., 2012). However, in our study CGR was negatively correlated with seed number at environment 1 (Lexington, May) and 3 (Lexington, June) (r= -0.43 and r= -0.42, respectively), and we found no significant relationship in environment 2 (Table 1.8). The negative or lack of relationship between seed number and CGR in our study could be due to relatively small differences in CGR values (17.4 to 29.3 g biomass m^{-2} day^{-1}) generated from different environments and cultivars, compared to CGR values generated from plant population and/or shade treatments in other studies that included lower minimum CGR values (4 – 11 g biomass m^{-2} day^{-1}) (Egli and Bruening, 2000; Egli and Yu, 1991; Kantolic et al., 2013). Overall, MG 5 cultivars had the highest CGR across environment in our study (29.5% higher on average compared with the short season MG 2 cultivar). One exception was MG 3 cultivars at environment 2 that had similar CGR to MG 5 (Table 1.6). However, MG 5 cultivars also had the lowest seed number in two out of three environments (except

environment 2, Princeton, May). In contrast, MG 2 cultivars had a lower CGR compared to MG 3 and 4 at environment 1 (Lexington, May) (19% lower), but produced a similar seed number (Table 1.6). Surprisingly, our results indicate that CGR was not a good indicator of differences in potential seed number across cultivars of different maturity. It is likely that there were factors associated with a high CGR that had a negative effect on seed number, such as high biomass production or delay in the occurrence of the developmental stages.

Genetic differences in seed size can influence seed number determination by a compensatory mechanism between seed number and a genetically determined ISGR (Egli and Yu, 1991). The SA (g seed m^{-2} day^{-1}) is the product of seed number and the ISGR, and therefore takes into account genetic differences seed size in the determination of seed number. The relationship between CGR and SA was still negative at environment 3 (Lexington, June) (r= -0.30), but it was positive at environment 1 (Lexington, May) and 2 (Princeton, May) (r= 0.27-0.4). It is important to notice that SA was not estimated for MG 5 cultivars at environment 2 (Princeton, May).

The modified model from Charles-Edwards et al. (1986) by Egli and Yu (1991) provided a framework to study processes influencing seed number determination with two additional traits: the partitioning to reproductive organs (PC) and the minimum assimilate supply required per seed (approximated in our study as ISGR). Our results showed, the PC was the physiological trait that better explained differences in seed number across cultivars in all the environments (r= 0.57, 0.49 and 0.53) (Table 1.8). In addition, nine of the eleven combinations of soybean MG x environment (excludes MG 5 cultivars in environment 2, Princeton, May), also showed highly significant correlations between seed number and PC

(r= 0.52 - 0.97). Higher PC values mean that plants are more efficient producing seeds per unit of vegetative biomass produced during the $Days_{R1-R5}$ period. The PC values found in our study ranged from 0.34 to 1.08 g seed g $biomass^{-1}$ across environments and cultivars (Table 1.7). These results are within the range of PC values reported in the literature (0.13 to 1.1 g seed g $biomass^{-1}$) (Egli and Yu, 1991; Rotundo et al., 2012; Santachiara et al., 2017a).

Despite the significant influence of PC in seed number determination that we found in this study, there are limited studies where PC was quantified across a range of cultivars (Rotundo et al., 2012; Santachiara et al., 2017a). In addition, different methodologies in quantifying PC across studies may limit its interpretation. For example Egli and Yu (1991) estimated PC similarly to our study, whereas Rotundo et al. (2012) and Santachiara et al. (2017a) calculated PC as the ratio between reproductive biomass at R5 (pod plus developing seeds) and total biomass accumulation between R1 and R5.

Overall, PC values by cultivars were not consistent across environments only P45T11R presented very consistent values of PC across environments (Table 1.7). The standard deviation of the mean PC by cultivar and across environments ranged from 0.07 to 0.20 g seed g $biomass^{-1}$. Previous studies found that PC was relatively stable across environments (Egli et al., 1985; Rotundo et al., 2012), growth habits, and genotypes (Egli et al., 1985; Vega et al., 2001). This is contrasting with data from our study that did not show a consistent cultivar ranking for PC values, with the exception of cultivar P45T11R (Table 1.7). Egli and Yu (1991) found a negative relationship between PC and CGR (R^2= 0.42) in a combined study of shade (Kentucky, United States) and seeding rate (China) treatments. In addition, Rotundo et al. (2012) found a negative relationship between PC and CGR using

a cultivar by trait bi-plot model analysis of cultivars of MG x traits in the United States. Our study is consistent with these results, with a negative (R^2=0.47) relationship between PC and CGR across environments and cultivars. The negative correlation between PC and CGR can be due to an inverse relationship between these two variables in Equation 3 and the fact that PC is not directly measured but estimated from Equation 3.

We quantified the ISGR during the linear phase of rapid seed growth as an approximation of the minimum amount of assimilates required per seed to avoid abortion in Equation 2 (Charles-Edwards et al., 1986). Individual seed growth rate is mainly regulated by the seed genetic potential (Egli et al., 1981), and is relatively insensitive to environmental factors (Egli and Wardlaw, 1980; Meckel et al., 1984) that affect the assimilate supply to the seed. In this study, ISGR was dependent on the soybean MGs, but not the cultivar within MG (Table 1.4). Differences in ISGR (3.8 to 6.5 mg $seed^{-1}$ day^{-1}) due to MG effect were also found by Egli (1993) but one cultivars within MG (00,1,3 and 5) was tested in this study. Egli (1975), found that the ISGR of 4 cultivars of contrasting seed growth rate (3.4-8.3 mg $seed^{-1}$ day^{-1}) were relatively stable across planting dates under irrigation in Lexington, KY. In our study, ISGR values by cultivars were inconsistent across environments. For instance, when planting date was delayed at Lexington (environment 1 (May) vs. 3 (June)), ISGR of MG 2, 3 and 5 cultivars changed by -13, - 8, +25%, and -8.3 % in MG 2, 3, 4, and 5 cultivars, respectively (Table 1.6). In environment 2 (Princeton, May) that is located southern than environment 1 (Lexington, May) and it was planted a week later, MG 2 and 3 had a higher ISGR while MG 4 slower compared with environment 1. Based on these results, it is likely that the differences found in ISGR are due to genetic component, but also have a significant environmental effect in our study. High ISGR will be associated

with high temperatures. For instant, at environment 2 (Princeton, May) MG 2 and 3 had the fastest ISGR and $Temp_{R5\text{-}R7}$. However, this same trend was not observed at environment 1 (Lexington, May), where MG 5 cultivars had the highest ISGR but lowest $Temp_{R5\text{-}R7,}$ this result might be related to the timing of the year in which $Days_{R5\text{-}R7}$ took place for these cultivars. Similar pattern was found with MG 4 and 5 cultivars at environment 3 (Lexington, June) (Table 1.3 and 1.6). A negative relation between seed number and ISGR was found at environment 1 (Lexington, May) and 2 (Princeton, May), (Table 1.8, Figure 1.2a and 1.3a). These results are consistent with others works were seed number decreased with increments in ISGR (Ball et al., 2000b; Egli and Yu, 1991).

Physiological traits influencing individual seed weight determination

In our data, seed number followed a similar pattern as yield in environments 1 (highest seed number in MG 2 to 4 cultivars) and 2 (highest seed number in MG 4 cultivars), but not at environment 3 planted in June (highest seed number in MG 2 to 4 cultivars, but MG 4 cultivars had the highest yields). Therefore, achieving a high seed number did not always translate to higher yields, due to a reduction in ISW.

The highest yielding MGs had the largest or relative large ISW; hence, ISW has a partial effect on yield. In the literature some works suggested not variation in yield due to seed weight (Rotundo et al., 2012). Individual seed weight it is associated to a genetic component (Egli, 1998), based on this we found that soybean cultivars explained a higher percentage (46-52%) of the ISW variability across environments compared with MGs, that only had a significant effect at environments 1 (Lexington, May) and 3 (Lexington, June),(Table 1.4). According with Equation 4, ISW is directly related with the ISGR and

the duration of the EFP, increments in the duration of the EFP or higher ISGR might produce bigger seeds. In the current works, no significant relation was found between ISGR and ISW across cultivars by environment. However, the duration of EFP was significant and positive correlated with ISW in all environments, but not the duration of the $_{DaysR5\text{-}R7}$ phase (Table 1.8). The correlation coefficient between ISW and the duration of the EFP periods were r= 0.43, 0.46 and 0.25 for environment 1 (Lexington, May), 2 (Princeton, may) and 3 (Lexington, June), respectively (Table 1.8). Based on this, EFP was found to be the physiological trait that better explained ISW variations across environments. Overall MG 3 cultivars produced the largest seeds in all three environments, and the duration of the EFP was the longest at environment 1 (Lexington, May) and 3 (Lexington, June) while at environment 2 (Princeton, May) was second longest duration (Table 1.5 and 1.6). Maturity group 5 produced the smallest seed at Lexington (environment 1 and 3), and had the shortest EFP. The duration of the EFP can be shorted under different environmental condition such as water stress, the seed growth rate was not affected and the seed size was reduced due to shorter EFP (Meckel et al., 1984). A temperatures study, suggested that both component of Equation 4 (seed growth rate and EFP) were relative insensitive to temperatures ranging from 24/19 to 30/25 ºC during the seed fill period (Egli and Wardlaw, 1980). The relationship between the duration of the EFP and the $Temp_{R5\text{-}R7}$ was similar to the relationship between ISGR and $Temp_{R5\text{-}R7}$ (Table 1.3 and 1.6). Surprisingly, in environment 1 and 3 the lowest $Temp_{R5\text{-}R7}$ was associated to the shortest duration of EFP, MG 5 cultivars. These results are likely related to the ISGR values (Table 1.6). However, without taking into account MG 5 cultivar in environments 1 and 2, increments in $Temp_{R5\text{-}R7}$ were related to shorter duration of EFP. For instance, MG 2 has the shortest duration of

EFP at environment 1 (Lexington, May) and 2 (Princeton, may) and the highest $Temp_{R5\text{-}R7}$ (Table 1.3 and 1.6).

CONCLUSION

The crop cycle duration across the three environments increased from 71 days in MG 2 cultivars to 123 days in MG 5 cultivars. However, highest yields were achieved by MG 2 to 4 cultivars at environment 1 (Lexington, planted in May), MG 4 at environment 2 (Princeton, planted in May), and MG 3 and 4 at environment 3 (Lexington, planted in June). Our data indicated that yield differences were mainly explained by seed number (r= 0.82-0.88) across environments, and to a smaller extend by ISW (r= 0.59-0.50) in two out of three environments. Differences in seed number were primarily explained by a higher efficiency partitioning biomass to seeds (estimated from the PC) in all environments (r=0.49-0.54), whereas CGR and ISGR had a negative effect on seed number in 2 out of 3 environments (r=-0.43 to -0.57). The final individual seed weight was mainly explained by the duration of the EFP in all environments (r=0.26-0.46). In addition, ISGR was negative correlated with ISW in 2 out of 3 environments (r=-0.49 to -0.57)

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Chapter 1: Tables and Figures

Table 1.1. Location, latitude and longitude, planting date, and soil type for Environments 1 to 3.

Environment	Location	Latitude and Longitude	Planting date	Soil type
1	Lexington, KY	38º 2’ 53’’ N - 84º 30’ 6’’ W	May 16th, 2017	UBlmB †
2	Princeton, KY	37º 6’ 33’ N - 87º 52’ 55’’ W	May 23rd, 2017	CrB2*
3	Lexington, KY	38º 2’ 53’ N - 84º 30’ 6’’ W	June 21st ,2017	UBlmB †

† UBlmB: Bluegrass-Maury silt loam and *CrB2: Crider silt loam.

Table 1.2. Soybean maturity group (MG), cultivar name, and growth habit (determinacy) of the commercial cultivars planted in environments 1 to 3.

Maturity Group	Cultivar names	Growth habit
2	AG21X8, P22T24X, P28T08R, AG29X8	Indeterminate
3	P32T16R,P35T58R,P38T61BR,P38T42R	Indeterminate
4	P41T33R, P45T11R, P47T36R, P49T97R	Indeterminate
5	P50T64R†,P52T50R,P54T94R,P55T81R	Indeterminate and determinate

† Indeterminate growth habit

Table 1.3. Average daily incident solar radiation from R1 to R5 ($SolarRad_{R1-R5}$) and R5 to R7 ($SolarRad_{R5-R7}$) and average daily temperature from R1 to R5 ($Temp_{R1-R5}$) and R5 to R7, ($TempR5_{-R7}$) by environment and soybean maturity group cultivars.

Maturity group	$SolarRad_{R1-R5}$	$SolarRad_{R5-R7}$	$Temp_{R1-R5}$	$Temp_{R5-R7}$
	MJ m^{-2} day^{-1}	MJ m^{-2} day^{-1}	ºC	ºC
Environment 1, Lexington, May				
2	20.5	20.3	24.6	24.2
3	20.4	19.5	25.6	22.4
4	20.9	19.1	25.6	21.6
5	20.5	18.0	24.2	21.2
Environment 2, Princeton, May				
2	20.7	19.8	25.7	24.2
3	20.8	19.4	25.9	22.5
4	21.1	18.7	25.9	22.2
5	19.9	18.3	24.4	22.2
Environment 3, Lexington, June				
2	20.8	18.5	23.0	21.4
3	20.2	18.3	23.3	21.4
4	19.7	17.2	23.9	20.8
5	18.8	15.5	21.5	19.7

Table 1.4. Probability and % of sum of squares in the model of the effect of maturity group (MG) and cultivars within MG from the analysis of variance (ANOVA) by environment for yield, seed number, individual seed weight (ISW), the duration of the time from emergence to beginning flowering ($Days_{VE-R1}$), the time from beginning flowering to beginning seed ($Days_{R1-R5}$), the time from beginning seed to physiological maturity ($Days_{R5-R7}$), the ratio between reproductive and vegetative phases ($Ratio_{V/G}$), aboveground biomass at beginning flowering ($Biom_{R1}$) and at beginning seed (BiomR5), partitioning coefficient to seed (PC), sink activity (SA), and duration of the effective filling period (EFP). Probability of the interaction of time with MG and cultivars within MG from the analysis of covariance (ANCOVA) by environment for crop growth rate (CGR), individual seed growth rate (ISGR), and dry matter allocation coefficient (DMAC).

	Environment 1†		**Environment 2**		**Environment 3**	
	Sources of variation					
Response variable	**MG**	**Cultivar (MG)**	**MG**	**Cultivar (MG)**	**MG**	**Cultivar (MG)**
	---------- P-value (% sum of squares) ----------					
Yield	** (29.2)	NS‡	** (32.2)	NS	*** (41.5)	*** (29.2)
Seed number	** (20.0)	** (33.7)	** (24.0)	NS	** (34.2)	*** (32.3)
ISW	**(23.3)	*** (46.3)	NS	*** (45.6)	*** (28.4)	*** (51.9)
$Days_{VE-R1}$	*** (87.6)	*** (10.9)	*** (75.2)	*** (22.1)	*** (83.5)	*** (13.7)
$Days_{R1-R5}$	*** (53.9)	* (16.6)	NS	NS	*** (43.1)	** (24.7)
$Days_{R5-R7}$	** (36.4)	*** (29.4)	** (60.7)	NS	*** (42.5)	* (21.6)
$Ratio_{R/V}$	*** (79.9)	*** (12.4)	*** (65.7)	*** (25.8)	*** (63.2)	* (15.5)
$Biom_{R1}$	*** (88.3)	*** (6.0)	*** (73.8)	NS	*** (65.3)	* (12.6)
$Biom_{R5}$	*** (61.0)	** (15.7)	*** (54.6)	NS	* (33.2)	NS
PC	*** (37.3)	*** (44.0)	** (26.0)	* (33.7)	*** (18.5)	*** (77.0)
SA	*** (32.7)	*** (39.0)	NS	NS	*** (44.8)	*** (43.7)
EFP	*** (65.4)	*** (29.8)	*** (60.7)	*** (30.8)	*** (61.6)	*** (35.9)
CGR	***	NS	*	NS	NS	NS
ISGR	**	NS	**	NS	*	NS
DMAC	NS	*	NS	NS	**	***
Degrees of freedom	3	12	2¥, 3	9¥, 12	3	12

† Environment 1: Lexington, planted in May; Environment 2: Princeton, planted in May: Environment 3: Lexington, planted in June.

¥ Only data from MG 2 to 4 were available for SGR, DMAC, PC, SA and EFP in Environment 2

‡ NS: Not significant (P≥0.05), * P≤ 0.05, ** P≤0.01 and *** P≤0.001

Table 1.5. Mean values by environment and soybean maturity group (MG) cultivar for yield (kg ha^{-1}), seed number (seeds m^{-2}), individual seed weight (ISW, mg $seed^{-1}$), the time from emergence to beginning flowering ($Days_{VE-R1}$), the time from beginning flowering to beginning seed ($Days_{R1-R5}$), the time from beginning seed to physiological maturity ($Days_{R5-R7}$), the ratio between reproductive and vegetative phases ($Ratio_{V/G}$), aboveground biomass at beginning flowering ($Biom_{R1}$) and at beginning seed ($Biom_{R5}$). Values followed by different letters within an environment represent significant differences between MG means ($p<0.05$).

	Yield	**Seed Number**	**ISW**	**$Days_{VE-R1}$**	**$Days_{R1-R5}$**	**$Days_{R5-R7}$**	**$Ratio_{V/R}$**	**$Biom_{R1}$**	**$Biom_{R5}$**
	kg ha^{-1}	seed m^{-2}	mg $seed^{-1}$	days	days	days		g biomass m^{-2}	g biomass m^{-2}
Environment 1†									
MG 2	5599 a	2618 a	162.1 b	34 d	11 c	41 b	1.51 a	218 d	599 c
MG 3	5758 a	2570 a	169.9 a	40 c	16 a	47 a	1.57 a	279 c	872 b
MG 4	5373 a	2611 a	156.3 bc	46 b	16 a	46 a	1.35 b	396 b	853 b
MG 5	4659 b	2280 b	153.3 c	62 a	14 b	47 a	0.99 c	654 a	1087 a
Environment 2									
MG 2	4344 b	2173 b	152.1	28 d	8 b	35 c	1.55 b	174 d	581 c
MG 3	4694 b	2241 b	160.4	30 c	14 a	42 ab	1.85 a	248 c	827 b
MG 4	5460 a	2597 a	159.1	37 b	11 ab	44 a	1.52 b	351 b	775 b
MG 5	4307 b	2107 b	154.9	50 a	12 ab	39 b	1.08 c	558 a	1057 a
Environment 3									
MG 2	4212 b	2217 a	144.4 c	29 b	10 b	38 b	1.66 a	219 c	480 b
MG 3	4727 a	2245 a	159.9 a	34 c	10 b	44 a	1.60 a	253 c	509 b
MG 4	4799 a	2368 a	153.6 b	38 b	9 b	44 a	1.40 b	305 b	613.b
MG 5	3695 c	1878 b	147.9 c	49 a	13 a	44 a	1.19 c	473 a	801 a

† Environment 1: Lexington, planted in May; Environment 2: Princeton, planted in May: Environment 3: Lexington, planted in June.

Table 1.6. Mean values by environment and soybean maturity group (MG) cultivar for crop growth rate during R1 to R5 (CGR, g biomass m^{-2} day^{-1}), individual seed growth rate (ISGR, mg $seed^{-1}day^{-1}$), dry matter allocation coefficient (DMAC), partitioning coefficient to seed(PC, g seed g $biomass^{-1}$), sink activity (SA, g seed $m^{-2}day^{-1}$) and effective filling period (EFP, days). Different letters represent significant ($p<0.05$) differences between MGs means within each environment.

	CGR	**ISGR**	**DMAC**	**PC**	**SA**	**EFP**
	g biomass m^{-2} day^{-1}	mg $seed^{-1}$ day^{-1}	g seed g $biomass^{-1}$ day^{-1}	g seed g $biomass^{-1}$	g seed m^{-2} day^{-1}	days
Environment 1†						
MG 2	18.1 c	4.21 b	0.031	0.61 a	10.98 b	39 b
MG 3	23.0 b	4.17 b	0.026	0.46 b	10.63 b	41 a
MG 4	22.0 b	3.95 b	0.031	0.47 b	10.36 b	40 ab
MG 5	28.5 a	5.74 a	0.031	0.48 b	13.04 a	27 c
Environment 2						
MG 2	22.3 b	5.03 a	0.023	0.50 a	10.9	30 b
MG 3	29.3 a	5.05 a	0.017	0.38 b	11.2	32 b
MG 4	21.8 b	3.85 b	0.015	0.46 a	9.98	42 a
MG 5	26.9 ab					
Environment 3						
MG 2	17.4	3.74 b	0.056 ab	0.48 c	8.32 c	39 b
MG 3	17.4	3.87 b	0.067 a	0.52 c	8.72 c	42 a
MG 4	17.7	5.23 a	0.036 b	0.71 a	12.34 a	30 c
MG 5	19.5	5.30 a	0.034 b	0.58 b	10.04 b	28 d

† Environment 1: Lexington, planted in May; Environment 2: Princeton, planted in May: Environment 3: Lexington, planted in June.

Table 1.7. Mean values by environment and soybean cultivar and minimum significant difference ($p<0.05$) for individual seed weight (ISW, mg seed^{-1}), partitioning coefficient (PC, g seed g biomass^{-1}), sink activity (SA, g seed m^{-2}day^{-1}), and dry matter allocation coefficient (DMAC, g seed g biomass^{-1} day^{-1}).

		Environment 1†				Environment 2				Environment 3			
MG	**Cultivars**	**ISW**	**PC**	**SA**	**DMAC**	**ISW**	**PC**	**SA**	**DMAC**	**ISW**	**PC**	**SA**	**DMAC**
		mg seed^{-1}	g seed g biomass^{-1}	g seed m^{-2} day^{-1}	g seed g biomass^{-1} day^{-1}	mg seed^{-1}	g seed g biomass^{-1}	g seed m^{-2} day^{-1}	g seed g biomass^{-1} day^{-1}	mg seed^{-1}	g seed g biomass^{-1}	g seed m^{-2} day^{-1}	g seed g biomass^{-1} day^{-1}
2	AG21X8	152.7	0.61	10.0	0.039	150.4	0.45	11.4	0.021	130.2	0.55	9.9	0.078
2	AG29X8	159.1	0.67	10.4	0.027	147.0	0.54	11.4	0.024	144.4	0.44	7.2	0.035
2	P22T24X	161.2	0.60	12.3	0.028	158.2	0.55	9.8	0.025	148.0	0.35	6.7	0.071
2	P28T08R	175.4	0.56	11.2	0.030	152.6	0.45	11.1	0.023	154.8	0.59	9.5	0.041
3	P32T16R	176.5	0.51	11.4	0.031	164.1	0.37	11.1	0.018	155.6	0.34	6.3	0.123
3	P35T58R	153.8	0.39	9.1	0.027	140.1	0.40	12.2	0.026	146.7	0.68	9.5	0.043
3	P38T42R	177.3	0.47	11.1	0.021	170.9	0.31	10.7	0.011	173.8	0.59	10.2	0.059
3	P38T61BR	172.2	0.48	11.0	0.025	166.6	0.35	10.7	0.014	163.4	0.45	8.9	0.043
4	P41T33R	169.2	0.52	9.1	0.053	160.3	0.37	8.4	0.015	156.4	0.93	13.8	0.046
4	P45T11R	144.7	0.56	13.1	0.030	147.9	0.57	11.0	0.021	148.4	0.59	11.7	0.033
4	P47T36R	156.8	0.37	8.9	0.023	164.1	0.46	10.7	0.015	152.4	0.73	12.1	0.034
4	P49T97R	154.4	0.45	10.3	0.019	164.0	0.45	9.9	0.010	157.0	0.60	11.8	0.033
5	P50T64R	162.5	0.61	13.2	0.056	169.3				153.6	1.08	13.7	0.055
5	P52T50R	140.9	0.39	11.4	0.026	150.0				150.9	0.43	9.1	0.022
5	P54T94R	147.8	0.54	14.2	0.023	144.5				134.4	0.35	9.3	0.040
5	P55T81R	161.9	0.36	13.2	0.021	156.0				152.6	0.46	8.0	0.015
Mindif($p<0.05$)‡		11.8	0.07	1.6	0.023	14.7				7.9	0.07	1.8	0.052

† Environment 1: Lexington, planted in May; Environment 2: Princeton, planted in May: Environment 3: Lexington, planted in June.

‡ Minimum significant differences calculated with LSD for ISW,PC and PC, and with CONTRAST statement for DMAC

Table 1.8. Pearson correlation values and probability (P-values) by environment of the relation of yield, seed number and individual seed weight (ISW) by environments with 15 physiological traits studied.

	Environment 1†			Environment 2†¥			Environment 3		
Variable	**Yield** kg ha^{-1}	**Seed number** seed m^{-2}	**ISW** mg seed^{-1}	**Yield** kg ha^{-1}	**Seed number** seed m^{-2}	**ISW** mg seed^{-1}	**Yield** kg ha^{-1}	**Seed number** seed m^{-2}	**ISW** mg seed^{-1}
	correlation coefficient (r)								
	p-value								
Yield kg ha^{-1}	1.00	0.82 ***	0.59 ***	1.00	0.87 ***	0.23 ns	1.00	0.88 ***	0.50 ***
Seed number seed m^{-2}	0.82 ***	1.00	0.03 ns	0.87 ***	1.00	-0.27 ns	0.88 ***	1.00	0.05 ns
ISW mg seed^{-1}	0.59 ***	0.03 ns	1.00	0.23 ns	-0.27 ns	1.00	0.50 ***	0.05 ns	1.00
Days$_{VE-R1}$ days	-0.57 ***	-0.45 ***	-0.40 **	0.56 ***	0.47 **	0.15 ns	-0.43 **	-0.50 ***	-0.04 ns
Days$_{R1-R5}$ days	-0.01 ns	0.02 ns	-0.03 ns	0.17 ns	0.16 ns	0.08 ns	-0.57 ***	-0.61 ***	-0.10 ns
Days$_{R5-R7}$ days	0.01 ns	-0.09 ns	0.12 ns	0.45 **	0.34 *	0.21 ns	0.25 *	0.15 ns	0.24 ns
Ratio$_{R/V}$	0.60 ***	0.43 **	0.48 ***	-0.15 ns	-0.14 ns	0.03 ns	0.38 **	0.44 **	0.04 ns
Biom$_{R1}$ g biomass m^{-2}	-0.51 ***	-0.40 **	-0.37 **	0.46 **	0.23 ns	0.45 **	-0.41 **	-0.48 ***	0.00 ns
Biom$_{R5}$ g biomass m^{-2}	-0.38 **	-0.38 **	-0.17 ns	0.30 *	0.11 ns	0.37 **	-0.32 *	-0.29 *	-0.16 ns
PC g seed g biomass^{-1}	0.54 ***	0.57 ***	0.13 ns	0.35 *	0.49 **	-0.32 *	0.55 ***	0.53 ***	0.18 ns

Continuation of Table 1.8

Variable	Environment 1†			Environment 2†¥			Environment 3		
	Yield kg ha^{-1}	**Seed number** seed m^{-2}	**ISW** mg seed^{-1}	**Yield** kg ha^{-1}	**Seed number** seed m^{-2}	**ISW** mg seed^{-1}	**Yield** kg ha^{-1}	**Seed number** seed m^{-2}	**ISW** mg seed^{-1}
	correlation coefficient (r)								
	p-value								
SA	0.18	0.22	-0.02	0.36	0.54	-0.35	0.56	0.56	0.13
g seed m^{-2} day^{-1}	ns	Φ	ns	*	***	*	***	***	ns
EFP	0.57	0.43	0.43	0.60	0.36	0.46	0.14	0.04	0.26
days	***	**	**	***	*	**	ns	ns	*
CGR	-0.43	-0.43	-0.19	-0.08	-0.09	0.05	-0.47	-0.42	-0.27
g biomass m^{-2} day^{-1}	**	***	ns	ns	ns	ns	***	0.00	0.03
ISGR	-0.43	-0.49	-0.12	-0.59	-0.57	-0.02	-0.01	-0.07	0.07
g seed^{-1} day^{-1}	**	***	ns	***	***	ns	ns	ns	ns
DMAC	0.10	0.03	0.12	-0.38	-0.07	-0.58	0.11	0.15	-0.01
g seed g biomass^{-1} day^{-1}	ns	ns	ns	**	ns	***	ns	ns	ns

† Environment 1: Lexington, planted in May; Environment 2: Princeton, planted in May: Environment 3: Lexington, planted in June.
¥ Only data from MG 2 to 4 were available for SGR, DMAC, PC, SA and EFP in Environment 2
‡ ns: Not significant (P≥0.10), Φ p<0.10, * P≤ 0.05, ** P≤0.01 and *** P≤0.001

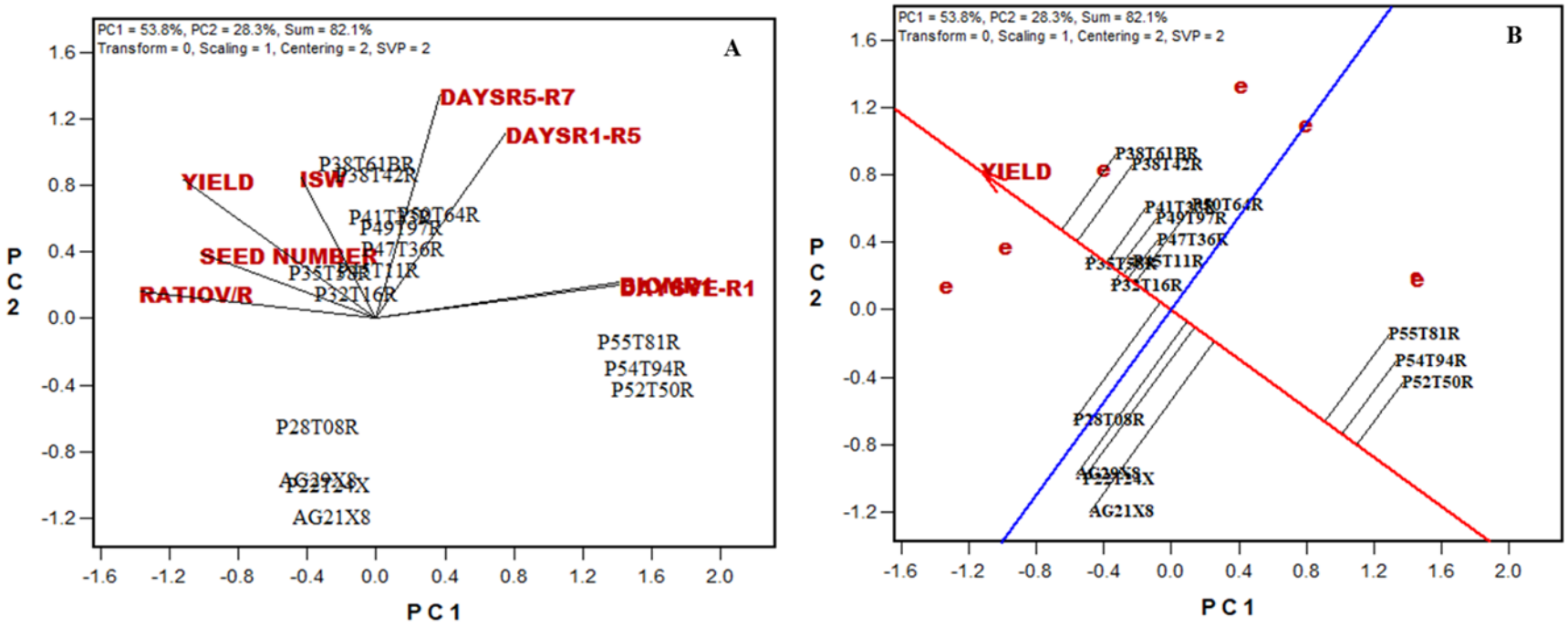

Figure 1.1 (A) Cultivar by trait bi-plot figure of the principal component (PC) 1 and 2 of the scaled principal component analysis of yield, seed number (Seed number), individual seed weight (ISW), biomass at beginning flowering ($Biom_{R1}$), ratio of the duration of reproductive/vegetative phases ($Ratio_{V/R}$), $Days_{VE-R1}$: vegetative phase duration, $Days_{R1-R5}$: seed-set phase duration and $Days_{R5-R7}$: seed-fill phase duration across all cultivars and the three environments. The PC 1 and 2 in the model explained 82% of the total data variability. The solid lines from the center represent the vector for each physiological trait. (B) Example of the yield raking in the bi-plot. The red arrow represents the direction of the yield ranking. The black solid lines represent the interception of each cultivar with the yield vector and provide a yield ranking from highest yield in cultivar P38T61BR to lowest yield in cultivar P52T50R. The 'e' represents the position of the rest of traits different from yield in the bi-plot.

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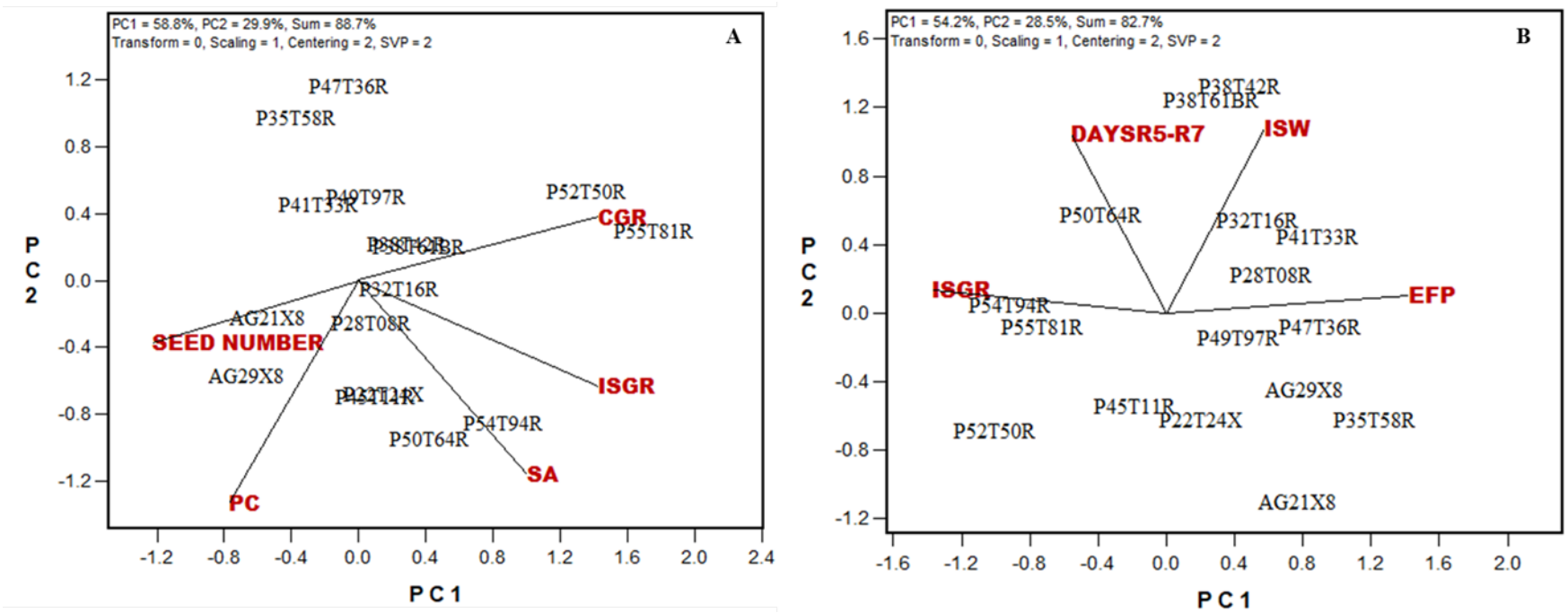

Figure 1.2. Cultivar by trait bi-plot model across soybean MGs based on principal component one (PC1) and two (PC2) in Environment 1 (Lexington, planted in May). (A) Model with seed number (Seed number) and physiological traits significantly related to seed number (Equation 3 and 4: CGR: crop growth rate, PC: partitioning coefficient, ISGR: individual seed growth rate and SA: sink activity). (B) Model for individual seed weight (ISW) and physiological traits significantly related to individual seed weight (Equation 5: effective filling period (EFP), Individual seed growth rate (ISGR), and seed-fill duration phase ($Days_{R5\text{-}R7}$).

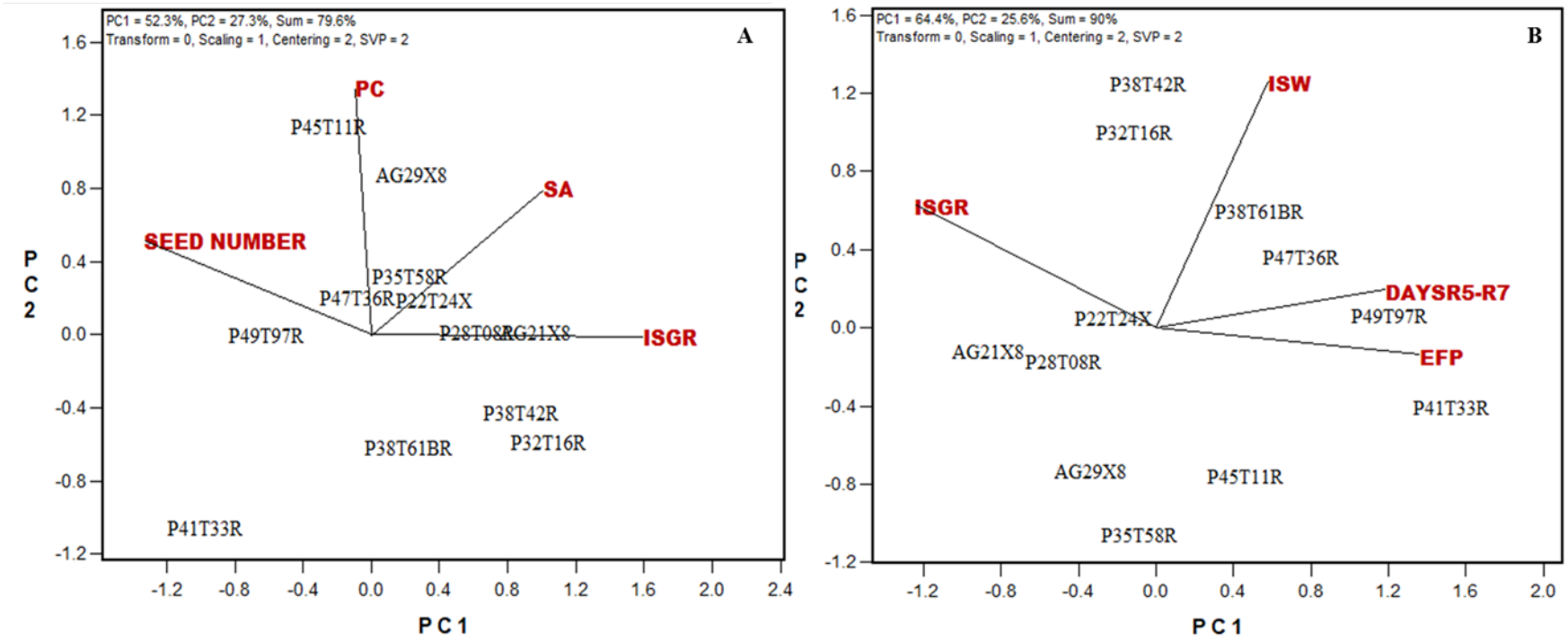

Figure 1.3 Cultivar by trait bi-plot model across soybean MGs based on principal component one (PC1) and two (PC2) in Environment 2 (Princeton, planted in May, MG 5 cultivars were excluded from the analysis). (A) Model with seed number (seed number) and physiological traits significantly related to seed number (Equation 3 and 4: PC: partitioning coefficient, ISGR: individual seed growth rate and SA: sink activity). (B) Model for individual seed weight (ISW) and physiological traits significantly related to individual seed weight (Equation 5: effective filling period (EFP), Individual seed growth rate (ISGR), and the seed fill phase duration ($Days_{R5\text{-}R7}$).

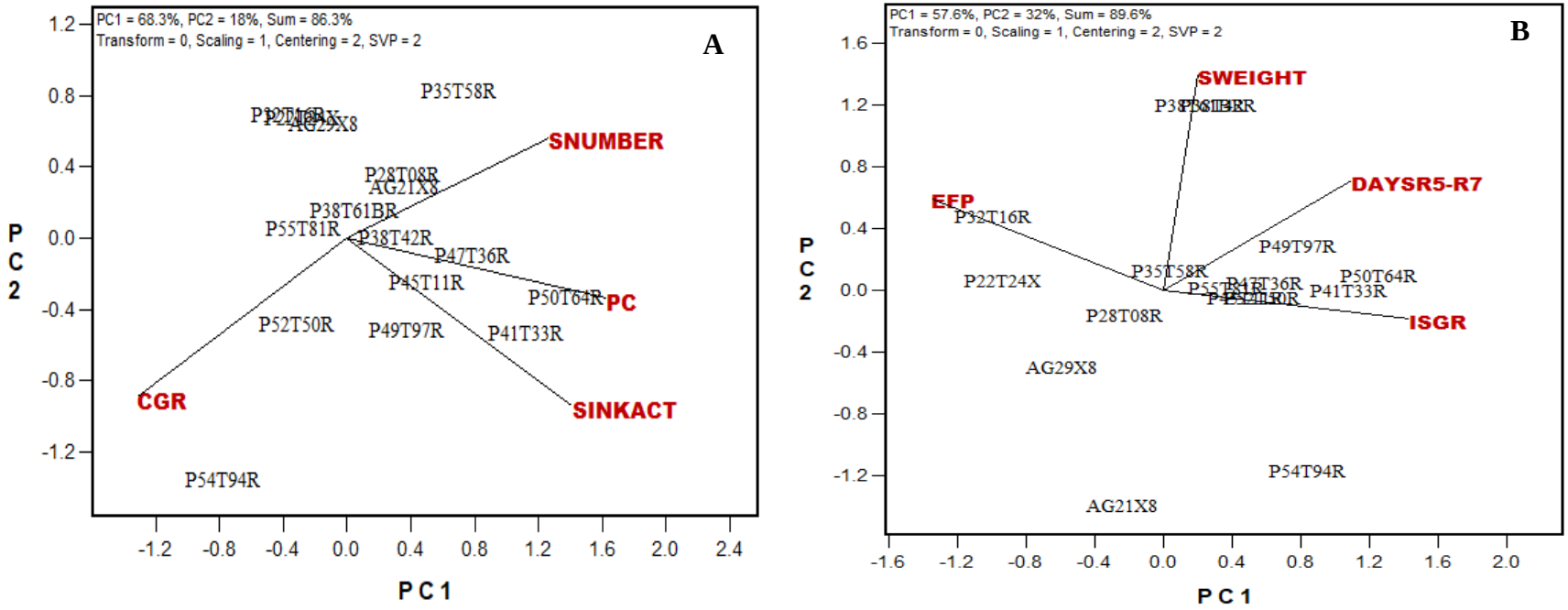

Figure 1.4. Cultivar by trait bi-plot model across soybean MGs based on principal component one (PC1) and two (PC2) in Environment 2 (Lexington, planted in June). (A) Model with seed number (seed number) and physiological traits significantly related to seed number (Equation 3 and 4: CGR: crop growth rate, PC: partitioning coefficient, and SA: sink activity). (B) Model for individual seed weight (ISW) and physiological traits significantly related to individual seed weight (Equation 5: effective filling period (EFP), Individual seed growth rate (ISGR), and days from the seed fill duration ($Days_{R5\text{-}R7}$).

Chapter 2: Management recommendations to maximize yield potential in double crop soybean

ABSTRACT

There is a yield penalty in double-crop soybean planted after a winter cereal due to a delay in planting date. Increasing plant population and/or using short-season maturity group (MG) cultivars could partially reduce this yield penalty. Full season MG are usually recommended for late planting date. We hypothesized that short-season MG cultivars at high seeding rates (SR) will reach reproductive stages under more optimal environmental conditions and increase yield relative to full-season cultivars. Field experiments were conducted in 2016 in Lexington (Lex-16) and in 2017 in Princeton (Pri-2017), KY with six cultivars ranging from MG 2 to 4 under two levels of SR (40 and 54 seed m^{-2}). Results showed that yields increased by 5% from high (54 seed m^{-2}) to normal (40 seed m^{-2}) SR, without an interaction with genotype. Reproductive stages started 6 to 11 days earlier in MG 2 cultivars compared with MG 4 cultivars and benefitted from better environmental conditions during reproductive stages. However, the fraction of light interception at the beginning of flowering was reduced in MG 2 compared to later maturities. Overall, yield of MG 2 cultivars were similar to those of MG 4 cultivars in 3 out of 4 cases. Other benefits associated to advancing harvest dates in double-crop soybean might offset the relatively low yield penalties observed with short-season MG cultivars.

INTRODUCTION

Soybean (*Glycine max (L.) Merr*.) is an important crop in Kentucky. The total area planted with soybean has increased by 60% from about 500.000 ha in 2000 to 800,000 ha in 2017 (USDA-NASS, 2017). During the same period, the average state yield in KY has increased from 2.6 to 3.6 t ha^{-1}. From the total soybean acreage in KY, about 36 % is double-cropped after a cereal (estimated from the average wheat planted area in KY) (USDA-NASS, 2017). The double-crop soybean area between 2000 to 2008 was 16 and 12 % of the total soybean area in Arkansas and Missouri, respectively (USDA-NASS, 2017). Therefore, double-crop soybean is a common and important practice in Kentucky.

A double-crop soybean system can have several benefits when compared with a full-soybean system. Planting soybean after a winter cereal allows harvesting two crop in one season, increasing the productivity of the environment (Egli, 2011). Some benefits of a double-crop system are: (i) more efficient capture and use of precipitation and photosynthetically active radiation (Caviglia et al., 2004), (ii) increase net returns (Kyei-Boahen and Zhang, 2006), (iii) nitrogen incorporation (biological nitrogen fixation), (iv) improve weed control, and (v) reduce erosion since the soil is covered all year.

Limited yield potential in double-crop soybean

Double-crop soybean is sown after harvest of a winter cereal. As a result, soybean sowing may be delayed to June or July compared to a full-season soybean sown in April or May. This delay in sowing date has a large impact on the crop yield potential (Bruns, 2011;

Calvino et al., 2003; Egli and Bruening, 2000; Egli and Cornelius, 2009; Hu and Wiatrak, 2012; Salmeron et al., 2014).

Yield reductions of 10 to 40% have been reported by Kyei-Boahen and Zhang (2006), when delaying planting date from mid-April to early June. A combined analysis of different planting dates, determined that yield starts declining after May 30th, June 7th and May 27th in the United States Midwest (0.7 % day^{-1}), Upper south (1.1 % day^{-1}) and deep south (1.2 % day^{-1}), respectively (Egli and Cornelius, 2009). Another irrigated, planting date and soybean MGs (3, 4, 5 and 6) study in the United States Mid-south concluded that delay planting date from mid-May to late June decreased yield by 0.09 to 1.69% per day of delay and overall cultivars within MG 4 maximized yield (Salmerón et al., 2016). Yield reduction of 7, 12, 18 and 11% have been also found by Salmeron et al. (2014), for soybean MG 3, 4, 5 and 6 respectively in the Mid-south due to delay in planting dates (April to July). Bruns (2011) also suggested reduction in yield (40%) across row types (single and twin) due to delay in planting date (mid-April, mid-May and early June) in South Carolina, United States.

Late planting dates in double-crop soybean modify the environmental conditions (photoperiod, temperature, solar radiation intensity) during the crop growing cycle. Thus, yield of double-crop soybean can be reduced compared to a full-season due to a combination of factors: reduction in the length of the growing season (Board and Settimi, 1986; Chen and Wiatrak, 2010), reduced vegetative growth and insufficient light interception (Egli et al., 1987), less favorable environmental conditions during late reproductive stages (Calvino et al., 2003), and/or reduced plant height and node number, that results in reduced pod number (Bruns, 2011; Pedersen and Lauer, 2004).

A delay in planting date from May to June in Kentucky decreased yield by 13 to 36% due to fewer seeds (Egli and Bruening, 2000). Environmental conditions during the period of flowering and pod set are critical for seed number and yield determination in soybean. Assimilate availability during this critical period is known to influence pod and seed number (Egli and Yu, 1991; Jiang and Egli, 1995). Yield reduction due to fewer seeds number and smaller seeds were observed in Kentucky when planting date was delayed from mid-May to early July as a result of a reduction in the length of the vegetative period, less biomass produced by R5, and a reduced solar radiation interception during the flowering and pod setting period (Egli et al., 1987). A simulation study with no water stress (irrigation) and planting dates from May 1st to June 30th , also concluded that the primary reason of lower yields with late planting dates was a lower insolation during the seed-set as well as low temperatures during seed-fill (Egli and Bruening, 1992).

Pods and seeds per area are usually the main components that explain yield variations (Egli, 2005). Long photoperiod after flowering increases node number, pods and seed per plants (Kantolic et al., 2013; Kantolic and Slafer, 2001; Nico et al., 2016; Nico et al., 2015), this is due to the more daily solar radiation per day under longer photoperiods, but also due to a direct effect of photoperiod uncoupled from assimilate supply according to Nico et al. (2015). According to Kantolic et al. (2013), more seeds under long photoperiods are also due to a longer duration of the flowering (R1) to seed set (R5) period. Some studies show that long photoperiods can extended the duration of the post flowering phases (Kantolic et al., 2007; Kantolic et al., 2013), and increase the cumulative intercepted radiation, the number of pods per node, and yield (Kantolic and Slafer, 2005).

Long-season MG (Egli, 1993; Egli and Bruening, 2000; Egli et al., 1985) and early planting dates (Bastidas et al., 2008) lead to longer vegetative periods and a larger total node number compared with short-season MG and late planting dates.(Egli, 2013). Some authors suggested that a larger number of nodes is required to produce high yield (Bastidas et al., 2008; Board and Tan, 1995). Increasing plant population (26 to 78 plants m^{-2}) under irrigation reduced the number of nodes per plant, but increased the nodes per area by approximately 60% (Egli, 2013).

Management practices to increase yield potential in double-crop soybean

The selection of MG cultivars varies according to the region. In Western, and Southern Kentucky it is common to grow early MG 4 to 5 cultivars, wheare.in Northern and Eastern Kentucky the relative MG 3.5 to 4.5 are recommended (Vernard et al., 2018). In addition to the maturity group selection, it is important to select the right planting date (determined by the winter cereal maturity) and seeding rate (SR) to maximize yield. The combination of these management decisions will determine the environmental conditions in which the crop will grow and define yield.

High solar radiation intensity and long photoperiods during flowering and seed-set are critical for seed number determination and achieving high yield (Kantolic et al., 2013; Nico et al., 2015). In addition, low temperatures during seed-fill can reduce seed growth rate (Calvino et al., 2003). Short-season MG have a shorter duration of the vegetative period compared to full season cultivars (Egli, 1993; Egli and Bruening, 2000; Egli et al., 1985); however the duration of the seed-fill period can be similar (Egli, 1993). The use of short-

season MGs when planting date is delayed could advance the start of the reproductive stages to increase solar radiation and avoid low temperatures during the seed-fill period, increasing yield potential relative to full-season cultivars. Short-season MG will have relatively short vegetative phase and might not produce enough biomass and leaf area to intercept maximum solar radiation by the start of reproductive stages (Ball et al., 2000a; Board and Harville, 1992). Plant population studies (Ball et al., 2000a, b; Lee et al., 2008; Purcell et al., 2002) have found yield gains due to a faster canopy closure (Ball et al., 2000b) and more total intercepted radiation (Purcell et al., 2002).

In the United Sates Mid-South long-season MG have been usually recommended for late planting dates since they can avoid summer drought during seed-set and for high precipitation and medium temperatures by the end of the growing season (Purcell et al., 2003). For example, MG 5 and 6 cultivars were recommended for late planting in Arkansas. A regional study conducted in the United States Mid-South with MG 3 to 6 cultivars, found that MG 4 and 5 cultivars were maximized yield in April-May planting dates while late MG 3 and 4 were recommended were recommended for planting dates in June early July (Salmeron et al., 2014). Under no water limitations, short-season MG in KY could benefit from better environmental conditions during the reproductive stages. In addition, short-season MGs will require less water than long season MGs under irrigation (Edwards and Purcell, 2005).

For growing areas in KY that rely little on irrigation and that might have enough soil water holding capacity to sustain the short growing season of a double-crop soybean, understanding what management factors that target higher yield potential is essential. We hypothesize that under no water limitation early MG cultivars at high seeding rate will

reach reproductive stages under better environmental conditions and increase yield compare to full-season maturities. Our goal is to quantify yield, environmental conditions during reproductive stages, and yield physiological traits across MG 2 and 4 and two seeding rates (high 54 seed m^{-2} and normal: 40 seed m^{-2}) to identify management option that increase the potential of double-crop soybean

MATERIALS AND METHODS

Field experiments

Field experiments under irrigation were planted after a winter cereal on July 12th, 2016 and June 26th, 2017 in Lexington (Lex-2016) and Princeton (Pri-2017), KY respectively (Table 2.1). The experimental design was a split plot with four replications. Seeding rate (normal and high, 40 and 54 seed m^{-2}) was the main factor, and six commercial cultivars of MG 2 to 4 were randomized (Table 2.2). Different cultivars were planted in each environment; however, the range of relative MG was consistent across both location (Table 2.2). Plots consisted in six rows wide with a length of 6 m and a distance between rows of 38 cm. A drip-tape system was used to irrigate the experiments when the cumulative net crop evapotranspiration demand reached 30 mm. Daily evapotranspiration deficit values were estimated with a daily balance of crop evapotranspiration, precipitation and irrigation (Allen et al., 2006). Pests were controlled with chemical application during the growing season when required.

Measurements and methodology

Ten plants per plot were marked to monitor the occurrence of developmental stages according to the Ferh and Caviness scale (1977). Date of emergence (VE), beginning bloom (R1), beginning pod (R3), beginning seed (R5), full seed (R6), physiological maturity (R7) and harvest maturity (R8) were recorded. The duration (days) between VE-R1, R1-R5 and R5-R7 were used as an approximation of the vegetative ($Days_{VE-R1}$), seed-set ($Days_{R1-R5}$) and seed-fill ($Days_{R5-R7}$) period, respectively. Node number in the main stem was measured in six plants per plot at harvest maturity (R8). A length of 6.70 m from one of the four central rows (total area of 2.55 m^2) was harvested and threshed with a stationary combine for yield determination. One hundred seeds were weighted to determinate individual seed weight (ISW) and seed number per area.

Crop growth rate (CGR) was determined from three aboveground biomass samples of one linear meter from one of the four central rows. In Lex-2016, the first sample was at R3, the second sample between R3 and R5 and the last sample was at R5. In Pri-2017, the first sample was after R1, the second sample was at R3 and the last sample was at R5. Biomass samples were dried at >65ºC,weighted, and CGR (g biomass m^{-2} day^{-1}) was estimated as the slope of the linear regression of aboveground biomass over time (Egli and Yu, 1991). Forty pods were marked with acrylic paint when seeds were 3-4 mm in diameter in one of the four central rows at the beginning of the seed filling period to determine individual seed weight (Egli, 1975). Three samples of 10 pods each were sampled every 7-10 days and individual seed growth rate (ISGR) was calculated as the slope of the lineal regression between ISW and time. The effective filling period (EFP) was obtained from the division

between ISW at harvest and ISGR. Harvest index (HI) was estimated from three plants at harvest as the ratio between the seed weight and the total weight of the plants sampled. Dates of the developmental stages and digital images were taken with a camera (Nikon, COOLPIX S6900) mounted in a pole to estimate the fraction of light interception at R1 (FLI-R1) and R5 (FLI-R5) from the fraction of canopy cover following the approach by (Purcell, 2000). Maximum and minimum temperature as well as the altitude and latitude of each environment were used to calculate the daily solar radiation (MJ m^{-2} day^{-1}) based on a modification of the Hargreaves and Samani equation (Ball et al., 2004; Purcell, 2000). The photosynthetic active radiation (PAR, MJ m^{-2}) was estimated as one half of daily solar radiation (Monteith, 1972) and the crop daily intercepted solar radiation (iPAR, MJ m^{-2} day^{-1}) was calculated as the product between the daily photosynthetic active radiation (PAR, MJ m^{-2}) and daily FLI (Purcell et al., 2002).

Yield components

Yield was analyzed as the product between seed number per unit area and ISW (Equation 1).

$$Yield\ \ (g\ m^{-2}) = seed\ number\ (seeds\ m^{-2}) * \ ISW\ (g\ seed^{-1}) \qquad (1)$$

The number of seeds per area is determined approximately from R1 to R5. Charles-Edwards et al. (1986) proposed equation 2 where the potential grain sites per unit area (N_g) is a function of the daily canopy net photosynthesis (∇_F), the partitioning of daily canopy

photosynthesis to reproductive organs (γ), and an inverse function of the minimum amount of assimilate that a potential seed needs to growth (A_g^{-1}) (Equation 2).

$$N_g = \nabla_F * \gamma * A_g^{-1} \qquad (2)$$

Equation 2, was modified by Egli and Zhen-wen (1991) as shown in Equation 3. The N_g, was estimated as the final seed m^{-2} since it was assumed that the potential grain sites of soybean is always bigger than the final seed per area. The daily canopy photosynthesis was replaced by CGR from R1 to R5 and the minimum amount of assimilate require by a seed to growth was approximated as the ISGR (mg $seed^{-1}$ day^{-1}). The partitioning coefficient to reproductive organs (PC, g seed g $biomass^{-1}$), was estimated from Equation 3 as the product between seed m^{-2} and ISGR, divided by CGR.

$$Seed\ m^{-2} = CGR\ (g\ biomass\ m^{-2} day^{-1}) * PC(g\ seed\ g\ biomass^{-1}) * ISGR^{-1}(g\ seed^{-1} day^{-1}) \qquad (3)$$

The radiation use efficiency (RUE) was estimated as the slope of the linear relationship between the three aboveground biomass samples for CGR estimation and the cumulative solar radiation. Furthermore, CGR can be also expressed as the product between the daily intercepted solar radiation, (iPAR (MJ m^{-2} day^{-1}) and the radiation use efficiency, RUE (g biomass MJ^{-1}) (Egli, 1993) (Equation 4).

$$CGR = iPAR_{R1-R5}\,(MJ\,m^{-2}day^{-1}) * RUE\,(g\,biomass\,MJ^{-1}) \qquad (4)$$

Based on equation 3 and 4, the seed number per unit area can be re-write as equation 5. Sink activity (SA) is the maximum capacity of the plant to carry reproductive growth (Egli, 1993) and was estimated according to equation 6.

$$Seed\,m^{-2} = iPAR_{R1-R5} * RUE * ISGR^{-1} * PC \qquad (5)$$

$$Sink\ activity\,(g\,seed\,m^{-2}day^{-1}) = seed\,m^{-2} * ISGR \qquad (6)$$

Individual seed weight (mg seed^{-1}) is the other component of equation 1 and can be define as the product between the ISGR (g seed^{-1} day^{-1}) and (EFP, days) (Equation 7).

$$Individual\ seed\ weight = ISGR * EFP \qquad (7)$$

Finally, by merging Equations 5 and 7, yield can be expressed as shown in equation 8 and 9.

$$Yield = (iPAR_{R1-R5} * RUE * ISGR^{-1} * PC) * (ISGR^{-1} * EFP) \qquad (8)$$

$$Yield = CGR * PC * EFP \qquad (9)$$

Data Analysis

A general linear mixed model with the MIXED procedure (SAS 9.4, SAS institute Inc. Cary, NC, USA) was used to analyze all the data, except for rate variables that were expressed on an over-time basis (CGR and, ISGR) and cumulative solar radiation (RUE). Environment, seeding rate (SR), soybean maturity group (MG), cultivars (nested with MG and environment) and their interactions were considered fixed factors in the model. Block nested with environment and their interaction with the fixed factors were considered random factors. The percentage of variance explained by each factor was estimated as the sum of squares of each factor divided by the total sum of squares in the model. The Fisher's least significant difference (LSD) was used to separate means when $p<0.05$.

An analysis of covariance (ANCOVA) was conducted using the MIXED procedure (SAS 9.4, SAS institute Inc. Cary, NC, USA) to test the environment, SR, MG, cultivars and their interactions effects on rate variables (CGR, ISGR and RUE). Aboveground biomass and ISW were modeled with environment, SR, MG, cultivars and their interactions as fixed effects, and time or cumulative solar radiation as an independent variable depending on the rate variable. The interaction of time with aboveground biomass and ISW, and the interaction of cumulative solar radiation with aboveground biomass was used to test fixed treatment effects on CGR, ISGR, and RUE, respectively. Only the significant covariant factor were presented in the ANCOVA, to increase the power of the analysis (pooling). CONTRAST statements, was used to presented mean difference of the significant ($p<0.05$) covariant factors.

The relationship between physiological traits was analyzed with the CORR PEARSON procedure (SAS 9.4, SAS institute Inc. Cary, NC, USA) using data averaged by cultivar

and environments (Table 2.11). The variables significantly ($p<0.05$) with seed number and the variables related to ISW determination (Equation 5 and 6 and $Days_{R5-R7}$) were further analyzed with a cultivar-by-trait principal component analysis using the GGE bi-plot software (version 8.0) developed by Yan et al. (2000). The goal was to visualize the relationship between multiple physiological traits (tester) as well as identify the ranking of the entry (cultivars) in relation to a determinate tester (Yan, 2001).

RESULTS

Environmental conditions

The daily incident solar radiation averaged from R1 to R5 ($SolarRad_{R1-R5}$) decreased with late soybean maturity, but differences were small (0.94 and 0.14 MJ m^{-2} day^{-1} at Lex-2016 and at Pri-2017, respectively) (Table 2.3). A similar pattern was found for the daily solar radiation averaged from R5 to R7 ($SolarRad_{R5-R7}$), that decreased with late soybean maturities by 1.12 MJ m^{-2} day^{-1} in Lex-2016, and by 1.41 MJ m^{-2} day^{-1} at Pri-2017 (Table 2.3). The daily temperature averaged from R1 to R5 ($Temp_{R1-R5}$) was similar across MGs at Lex-2016 (23.5°C), whereas at Pri-2017, $Temp_{R1-R5}$ was 1 °C higher on average in MG 2 cultivars (Table 2.3). The daily temperature averaged from R5 to R7 ($Temp_{R5-R7}$) decreased with late soybean maturity from 19.7 to 17.8 °C in Lex-2016, but only from 21.8 to 21.5°C at Pri-2016 (Table 2.3).

Yield and yield components

A significant ($p<0.05$) effect of the environment x cultivar x MG interaction was found on yield, seed number and ISW (Table 2.4). The environment x MG interaction explained most of the yield variability, with 20% of the total sum of squares of the model, followed by the environment x cultivar x MG interaction (12%). Yield averaged by environment and cultivar ranged from 4005 to 5320 kg ha^{-1}. At Lex-2016, the two MG 3 cultivars (AG3533 and P93Y92) had the highest yields (5128 kg ha^{-1}), followed by the early MG 4 cultivar AG4336 (11% yield reduction). The two MG 2 cultivars (AG2733 and P28T33R) and the late MG cultivar AG4730 had the lowest yields (15% lower than MG 3 cultivars) at Lex-2016 (Table 2.4). At Pri-2017, the MG 4 cultivars (P41T33R and T47T36R,) and the late MG 2 cultivar AG29X8 had the highest yields (4901 g ha^{-1}), followed by MG 3 cultivars (12 % lower), and the late MG 2 cultivar P28T08R (18% lower). Seeding rate explained only 2.7% of the sum of square for the yield model and increasing SR from 40 seed m^{-2} to 54 seed m^{-2} increased yield by 5% (Table 2. 4).

Seed number variation was mainly explained by the environment x MG interaction (18%), followed by the environment (14 %), the environment x cultivar x MG interaction (13%) and the SR effect (2%). Average values of seed number across environments and cultivars ranged from 2080 to 3038 seed m^{-2} (Table 2.4). At Lex-2016, P28T33R reached first in seed number (3830 seed m^{-2}), but fourth in yield (4403 kg ha^{-1}). Cultivar P93Y92 reached highest in yield (5320 kg ha^{-1}), but third in seed number (2657 seed m^{-2}). The lowest yielding cultivar, AG4730 also reached the lowest seed number (2420 seed m^{-2}). At Pri-2017, the highest yield cultivars (AG29X8, P41T33R and P47T36R) also reached the

highest seed number (Table 2.4). Increasing SR to 54 seed m^{-2} increased seed number on average by 4%, with no interaction with environment and MG cultivar (Table 2.4).

The ISW had a significant effect of environment, MG, environment x MG interaction and environment x cultivar x MG interaction that explained 14%, 12%, 26% and 25% of the sum of square of the model, respectively (Table 2.4). However, the ISW was not affected by the SR treatments. Individual seed weight ranged from 177 to 150 mg $seed^{-1}$ across environments and cultivars. At Lex-2016, the highest yield cultivar P93Y92 had the heaviest seed (177 mg $seed^{-1}$), followed first by AG4336 (-7%), second by AG3533, AG4730 and AG2733 (-13%), and lastly by P28T33R (-28%; 128 mg $seed^{-1}$). At Pri-2017, MG 2 cultivars, P38T61R and P41T33R had the largest seeds (128 mg $seed^{-1}$), followed by P47T36R (-5%) and AG3533 (-8%) (Table 2.4).

Harvest index was dependent on the environment x Cultivar x MG interaction and was not affected by the SR treatments (Table 2.4). The HI ranged from 0.62 to 0.67 across environments and cultivars (Table 2.4). At Lex-2016, cultivars of MG 2 to 3 and early MG 4 (AG4336) had similar HI (0.63), and it that was slightly lower in the late MG 4 cultivar (AG4730, 0.61). At Pri-2017, AG29X8 and AG3533 had the highest HI (0.67), followed first by P28T08R, P38T61R and P41T33R (0.65), and last by the late MG 4 cultivar (P47T36R) with the lowest HI (0.62) (Table 2.4).

The number of nodes on the main stem had a significant effect of the environment x MG interaction but was not affected by the SR treatment. At Lex-2016, the node number increased with later MG, from 13.3 nodes in the early MG 2 cultivar to 16.5 nodes in the late MG 4 cultivar. At Pri-2017, the differences in node number across cultivars were small (<0.8 nodes) (Table 2.4).

Growth and Partitioning

Table 2.5, 2.6 and 2.7 summarize treatment effects on rate variables (CGR, RUE and ISGR) after non-significant factors were removed from the analysis of covariance (ANCOVA) model.

The CGR measured from R1-R3 to R5 was dependent on the environment, SR and MG cultivar (Table 2.5). At Lex-2016, CGR was more than two folds higher than at Pri-2017 (Table 2.5). Maturity group 3 cultivars (had the highest CGR (27.8 g biomass m^{-2} day^{-1}), followed by MG 4 cultivars (19% lower than MG 3), and by MG 2 cultivars (28% lower than MG 3) (Table 2.5). The high SR treatment increased CGR by 20% in MG 4 cultivars but not in MG 2 and 3 cultivars (Table 2.5).

After removing non-significant factors from the analysis of covariance model, RUE was dependent on the environment, MG and was not affected by SR (Table 2.6). Radiation use efficiency at Lex-2016 was 57% higher than at Pri-2017 (Table 2.6). Maturity group 3 cultivars had the highest RUE on average (1.41 g MJ^{-1}), similar to that of MG 4 cultivars (1.26 g MJ^{-1}), but higher than MG 2 cultivars (1.09 g MJ^{-1}) (Table 2.6).

Individual seed growth rate measured during $Days_{R5\text{-}R7}$ was affected by SR and cultivar depending on the environment (Table 2.7).The high SR treatment reduced ISGR by 8 % at Pri-2017, but did not affect ISGR at Lex-2016 (Table 2.7).The ISGR ranged from 2.8 to 4.0 mg $seed^{-1}$ day^{-1} at Lex-2016, and from 4.4 to 5.0 mg $seed^{-1}$ day^{-1} at Pri-2017. At Lex-2016, cultivar AG2733 had the highest ISGR (4.02 g $seed^{-1}$ day^{-1}), followed by MG 3 cultivars (-8%). Cultivars AG3533 and AG29X8 had the highest ISGR at Pri-2017 (4.98 mg seed day), followed by P28T08R (-0.6%). In both environments, the late MG 4 cultivars

had the smallest ISGR, which was 22-8% smaller than the than the highest ISGR within each location (Table 2.7).

A significant effect of SR x cultivar x environment x MG interaction was found on PC and SA. Thus, means by environment, SR, and cultivar are of PC and SA are presented in Table 2.8. Environment explained most the variation in PC (75% of sum of squares in the model), followed by cultivar within MG (9%) and the environment x MG interaction (7%) (Table 2.8). Average PC values ranged from 0.20 to 1.42 g seed g biomass^{-1} across environments, cultivars and SR treatments.

At Lex-02016, SR did not affect the PC in any cultivar (Table 2.8). However, AG2733 and the late MG 4 (AG4730) the high SR reduced the PC by 11 and 17 % respectively. The other MGs all had a higher PC value under high SR compared with the normal SR (Table 2.8). The PC at Lex-2016 decreased on average from 0.34 to 0.22 with soybean relative maturity under both SR treatments, although differences were not always significant (Table 2.8). At Pri-2017, MG 2 cultivars had the highest PC, but similar to those of cultivar T47T36R under the normal SR (Table 2.8). The high SR reduced the PC of cultivar P38T61R and MG 4 cultivars (P41T33R and P47T36R) by 54 % and 27 % respectively (Table 2.8).

Environment follow by the environment x MG interaction and the SR x cultivar x environment x MG interaction were the factors that explained most of the variation in SA (Table 2.8). Sink activity ranged from 6.6 to 12.4 g seed m^{-2} day^{-1} across environments and SR levels. At Lex-2016, the high SR increased the SA by 37-51% in two of the cultivars (P28T33R and AG43336) (Table 2.8). At Pri-2017, the high SR reduced SA by 28% in cultivar P38T61R (Table 2.8). At Lex-2016, the SA by cultivar and SR ranged from 8.6 to

11.6 g seed m^{-2} day^{-1} in MG 2 and 3 cultivars; whereas MG 4 cultivars had much lower SA values (<7 g seed m^{-2} day^{-1}) in 3 out of 4 cases (Table 2.8). aT Pri-2017, the SA ranged from 9.3 to 12.9 g seed m^{-2} day^{-1} and was highest or not significantly different than the highest SA value in all cultivars and SR combinations in MG 4 cultivars, and in 2 out of 4 cases in MG 2 and 3 cultivars (Table 2.8).

Fraction of light interception and daily intercepted solar radiation

The FLI_{R1} was significantly affected by environment, SR, the environment x SR interaction, MG, the cultivar x environment x MG interaction and the SR x cultivar x environment x MG interaction. Maturity group explained most of the variation in FLI_{R1} (52% of the sum of squares) (Table 2.9). Values of FLI_{R1} ranged from 0.33 to 0.82 across environments, SR, and cultivars treatments (Table 2.9). At Lex-2016, the high SR did not increase FLI_{R1} in any of the cultivars (Table 2.9). However, the FLI_{R1} was 1.3 to 16% higher on average under the high SR (except for cultivar P93Y92) at Lex-2016 (Table 2.9). The FLI_{R1} increased with later maturities, ranging from 0.6 in MG 2 cultivars to 0.87 in MG 4 cultivars (Table 2.9). At Pri-2017, the high SR increased the FLI_{R1} by 64 and 45 % in two out of the six cultivars (AG29X8 and AG3533) (Table 2.9). The other cultivars had a greater FLI_{R1} on average under the high SR, with the exception of cultivar P28T08R (-14%). (Table 2.9). Similarly, to Lex-2016, the FLI_{R1} at Pri-2017 increased with later maturities, from 0.42 in MG 2 to 0.72 in MG 4 cultivars (Table 2.9).

The FLI_{R5} had significant treatment effects (Table 2.9). However, by R5, all the cultivars planted had reached a FLI_{R5} higher than 0.94 (Table 2.9).

Developmental stages

The vegetative phase estimated from emergence to beginning flowering ($Days_{VE-R1}$) was dependent on the environment, the environment x MG interaction, and the MG effect (Table 2.10). Soybean MG explained most of the variation on the duration of the $Days_{VE-R1}$ phase with a total sum of square of 70.3% (Table 2.10). At Lex-2016, the $Days_{VE-R1}$ in MG 4 cultivars was 29 days, and $Days_{VE-R1}$ was shorter in MG 3 (25 days) and 2 cultivars (23 days) (Figure 2.1, a). A similar pattern was observed at Pri-2017, where cultivars within MG 4 and 3 had a duration of $Days_{VE-R1}$ phase of 28 and 26 days respectively with no significant differences between each other. Cultivars within MG 2 had the shortest duration (20 days) of $Days_{VE-R1}$ period in this environment too (Figure 2.1, b). In average, both environments had a similar duration of $Days_{VE-R1}$ phase, 25 days (Figure 2.1).

The time from R1 to R5 ($Days_{R1-R5}$), was only affected by the environment that explained a 64.5% of the total sum of square in the model (Table 2.10). The duration of $Days_{R1-R5}$ averaged 22 days (Figure 2.1, a) and 30 days (Figure 2.1, b) at Lex-2016) and Pri-2017, respectively.

The duration from R5 and R7 ($Days_{R5-R7}$), had a significant effect of environment, MG and the environment MG interaction that explained 13.1 %, 32.1 % and 9.4 % of the total sum of square of the model respectively (Table 2.10). At Lex-2016, the duration $Days_{R1-R5}$ was longest for cultivars within MG 3 (40 days) and 4 (42 days) and was reduced by 4 days in cultivars within MG 2 compared with MG 4 cultivars (Figure 2.1, a). At Pri-2017, the $Days_{R1-R5}$, was the longest for MG 4 cultivars (42 days), and was reduced in 9 days in MG 3 and 8 days in MG 2 (Figure 2.1, b).

The EFP was estimated with Equation 6. A significant effect of all the factors studied was observed except for SR; however, environment and soybean MG explained most of the variation in the duration of the EFP, with 41.9 and 21.8 % of the total sum of square of the model (Table 2.10). At Lex-2016, cultivars P28T33R and AG4336 showed significant differences in the duration of EFP when growing under different SR, both cultivars had a longer duration of the EFP under low SR (42 and 59 days) compared with high SR (36 and 41 days) (Data not shown). The other cultivars grew in this environment did not presented significant differences in the duration of the EFP between high and low SR (Data not shown). Cultivars within MG 4 had the longest duration of EFP at Lex-2016 and was reduce by 9 and 15 days for cultivars within MG 3 and MG 2, respectively (Figure 2.1, a). At Pri-2017, significant differences in the duration of the EFP between SR were found for cultivars P38T61R and MG4 cultivars (data not shown). Opposite from what we observed at Lex-2016, the duration of the EFP of these cultivars was longer under high SR compared with normal SR (data not shown). Cultivars within MG 4 (36 days) had the longest duration of EFP, follow by cultivars within MG 3 (33 days) and 2 (34 days), that did not show significant differences between each other (Figure 2.1, b).

Relationship between yield and intercepted solar radiation

The analysis of variance of $CumiPAR_{VE\_R7}$ showed that the environment and MG were the factors that better explained variability in this variable, with 36.5% of the total sum of square in the model (data not shown). The SR treatment had no effect on $CumiPAR_{VE\_R7}$. The high SR only increased $CumiPAR_{VE\_R7}$ on average by 1.76 to 17.3 MJ m^{-2} at Lex-2016, and by 17 to 91 MJ m^{-2} at Pri-2017. In both environments, MG 4 cultivars had the

highest $CumiPAR_{VE\_R7}$ and it decreased with earlier maturities (data not shown). The relationship between yield and the $CumiPAR_{VE\_R7}$ was studied in Figure 2.2a. Yields were normalized to relative yield by dividing yields within each environment by the yield of the highest yielding cultivar. An increase in yield with increments in $CumiPAR_{VE\_R7}$ was found at Pri-2017 (R^2 = 0.39) but not at Lexington (Figure 2.2a). Higher yields were associated to more $CumiPAR_{VE\_R7}$ in MG 2 and 3 in both environments. However, more $CumiPAR_{VE\_R7}$ in MG 4 cultivars did not translate to higher yields at Lex-2016 (Figure 2.2 a).

An increase in yield with increments in FLI_{R1} was found at Pri-2017 (R^2 = 0.26), but not at Lex-16 (Figure 2 2b). Increments in yield were associated with more FLI_{R1} in MG 2 (FLI_{R1}=0.56, relative yield =0.78) and 3 (FLI_{R1}=070, relative yield =0.91) cultivars at Lex-2016. However, MG 4 cultivar at Lex-2016 had higher FLI_{R1} that did not translate into higher yields (FLI_{R1}=0.80, relative yield =0.79), that were similar to MG 2 cultivars with a much lower FLI_{R1} (Figure 2.2b). At Pri-2017, MG 2 and 3 cultivars on average had similar yield (relative yield = 0.84) however MG 2 cultivar had a lower FLI_{R1} (0.41) compared to MG 3 cultivars (0.64) (Figure 2.2b).

Analysis of yield component determination

At Lex-2016, yield was correlated with seed number (r= 0, 68, p<0.001) and ISW (r= 0,45, p=0.013), while at Pri-2017 yield was only significant correlated with seed number (r=0.94, p<0.001) (Table 2.11). Based on this, bi-plot figures based on principal components (PC) 1 and 2 were constructed for each environment for seed number and ISW (Figure 2.3 and 2.4). Traits from Equation 7 and the $Days_{R5\text{-}R7}$ were used to construct the bi-plot figures

for the analysis of ISW determination (Figure 2.3 and 2.4, b). Significant traits from Equation 5 and 6, plus any significant ($p<0.05$) developmental variables were used to construct the bi-plot figure for the analysis of seed number determination (Figure 2.3 and 2.4, a). The correlation between two traits can be estimated as the cosine of the angle formed between vectors (black lines) and can range from -1 (negatively correlated) to 1 (positively correlated). Thus, an angle <90º indicates a positive correlation, and an angle >90º indicates a negative correlation. Traits are more highly correlated with angles close to 0º (positive) or 180º (negative), and an angle close to 90º means that two traits are independent according to the percentage of data variability explained by principal component 1 and 2 in the model. The cultivars ranking is defined by the position of each cultivar in relation to each trait.

The bi-plot figures constructed with principal component 1 and 2 explained 91 to 98% of the variability across traits and genotypes and provided a good visual representation of the data to analyze physiological traits related to seed number and ISW (Figure 2.3 a and b, Figure 2.4 a and b). At Lex-2016, seed number was positively (angle <90°C) correlated with PC (r= 0.83) and SA (r= 0.78), and it was negatively (angle>90°) correlated with the duration of $Days_{VE\text{-}R1}$ (r= -0.33) (Table 2.11, Figure 2.3a). The highest number of seeds in cultivar P28T33R was associated to a high PC, SA, and was also coincident with a low duration of the $Days_{VE\text{-}R1}$ phase. In contrast, low seed number in MG 4 cultivars was coincident with long durations of the vegetative period. Individual seed weight was positively correlated with the duration of the EFP (r= 0.43), the duration of $Days_{R5\text{-}R7}$ (r= 0.23) and the ISGR (r= 0.22; non-significant) (Table 2.11, Figure 2.3b). The heaviest seed was produced by P93Y92 mainly due to a high ISGR. Cultivar AG4333, AG2733 and

AG3533 had similar ISW but though different mechanisms (Figure 2.3b). For instance, AG4730 had a long EFP and $Days_{R5\text{-}R7}$ but a low ISGR. In contrast, cultivars AG2733 and AG3533 had shorter duration of EFP and $Days_{R5\text{-}R7}$ but a higher ISGR. Cultivar P28T33R had a low ISW due to a shorter duration of EFP and $Days_{R5\text{-}R7}$ and a relatively low ISGR (Figure 2.3b).

At Pri-2017, seed number was positively correlated with SA ($r= 0.82$, $p<0.0001$), the $Days_{VE\text{-}R1}$ ($r= 0.33$, $p=0.02$) and $iPAR_{R1\text{-}R5}$ ($r= 0.32$, $p=0.03$), and negatively correlated with ISGR ($r= -0.32$, $p=0.03$) (Table 2.11, Figure 2.4). The highest seed number in cultivar P47T36R was associated with a high SA and relative high $Days_{VE\text{-}R1}$ and $iPAR_{R1\text{-}R5}$. In addition, there was a negative relationship of seed number with the ISGR, indicated by the obtuse angle between the vectors of these two traits (Figure 2.4b). The lowest seed number in cultivar P28T08R was coincident with the fastest ISGR and lowest SA. The other cultivars in this environment produced an intermediate number of seed per area (Figure 2.4a). Individual seed weight was positively correlated with the duration of EFP ($r= 0.40$, $p=0.005$) at Pri-2017 (Table 2.11). The ISGR and $Days_{VE\text{-}R1}$ were positive and negative related with ISW. The heaviest seeds were produced by AG29X8, due to a high EFP and ISGR, however the longest duration of the EFP was achieved by P41T33R (Figure 2.4b). The lowest ISW produced by AG3533 was due to a short EFP duration and an intermediate ISGR. The other cultivar that produced light seed was P47T36R, but in this case due to a low ISGR.

DISCUSSION

We hypothesized that under no water limitation, short-season MG cultivars at high SR will reach reproductive stages under better environmental conditions and increase yield compare to full-season maturities. In both environments, the start of reproductive stages (R1) occurred earlier in the season for MG 2 cultivars compared to MG 3 (2-9 days earlier) and MG 4 cultivars (6-11 days earlier). No differences were found in the duration of $Days_{R1\text{-}R5}$ between soybean MGs at both environments. However, the duration of $Days_{R5\text{-}R7}$ was shorter for MG 2, by 2 and 4 days compared with MG 3 and 4 cultivars at Lex-2016. At Pri-2017, the duration of $Days_{R5\text{-}R7}$ was similar for MG 2 and 3 cultivars, but 9 days shorten compared with MG 4 cultivars. The increase in average daily solar radiation with earlier maturities was small during flowering and seed set ($SolarRad_{R1\text{-}R5}$ = 0.1-0.7 MJ m^{-2} day^{-1}) but was greater during the seed fill phase ($SolarRad_{R5\text{-}R7}$ = 1.0-1.41 MJ M^{-2} day^{-1}). In contrast, the fraction of canopy cover and light interception by the start of flowering measured from FLI_{R1} was higher on average with later MGs, due to the longer duration of $Days_{VE\text{-}R1}$ (Figure 2.1a and Figure 2.2b) and more biomass produced by this stage compared to earlier maturities.

Low temperatures during the seed fill phase can reduce ISGR and decrease final seed size. The temperature during this phase estimated from $Temp_{R5\text{-}R7}$ decreased with later maturities, from 19 to 17 °C at Lex-2016, but only from 21.5 to 21.8 °C at Pri-2017. Low temperatures during seed-fill can also reduce developmental rate and increase the duration of this phase. Thus, low temperatures during seed-fill could partially explain why $Days_{R5\text{-}R7}$ was greater in MG 4, but was not translated into the highest ISGR and/or ISW for this cultivar MG. Our results suggest that in both environments, a FLI_{R1} 0.70 was required to

reach the highest yields, (Figure 2.2). At Lex-2016, a FLI_{R1} above 0.7 in MG 4 did not translate to higher yields. At Pri-2017, the FLI_{R1} was overall lower, and only MG 4 reached a value of 0.7 by the beginning of flowering. Interestingly, yields of MG 2 were relatively high despite their low FLI_{R1} (0.3-0.55), which could be explained by the gain in solar radiation intensity and more optimal temperatures during seed-fill compared with MG 4 cultivars at this environment. Similar yield between MG 4 and one of the MG 2 cultivars were found at Pri-2017. A possible explanation to this is that even though MG 2 cultivars reached R1 with the lowest FLI_{R1}, they grew under better environmental condition of solar radiation.

Our results did not indicate a yield gain associated to an increase in node number with later maturities. The number of nodes was greater in MG 4 cultivars compared to earlier maturities at Lex-2016, but this was not related to higher seed number and/or yield in this treatment. At Pri-2017 no differences in node number between MG cultivars were found.

Increasing SR from 40 to 54 seed m^{-2} increased yield and seed number by 5 and 4.5% on average across MG cultivars and environments (Table 2.4). The high SR treatment increased FLI_{R1} by 11% on average compared with the normal SR (Table 2.9). The cultivar within MG and environment also affected yield, but we did not find an interaction with SR (Table 2.4). Previous studies in Arkansas also found that increasing plant population in June-July planting dates increased yields under irrigated and non-irrigated conditions (Ball et al., 2000a). In Kentucky, high populations under rainfed condition also increased yields with planting dates that ranged from May to June (Lee et al., 2008). In contrast to our finding, other experiments conducted in the Mid-South found an interaction between soybean MG cultivar (ranging from MG 00 to 6) and plant population on yield with

planting dates in May (Edwards and Purcell, 2005). The lack of interaction between the SR treatments and MG cultivar in this study could be due to the relatively smaller range of MG cultivars compared to Edwards and Purcell (2005) and to the later planting dates (late June and early July) in our study.

Overall, yields were affected to a greater extent by the cultivar choice than by the SR treatment. At Lex-2016, MG 3 cultivars were the highest yielding, and MG 2 and 4 cultivars reduced yields by 14% (Table 2.4). At Pri-2017, the MG 4 cultivars and AG29X8 were the highest yielding, followed by P38T61R (9% yield reduction), and by cultivars P28T08R and AG3533 (21% yield reduction) (Table 2.4). In our study, seed number explained yield differences more than any of the other traits studied (r=0.68 at Lex-2016, and 0.94 at Pri-2017) (Table 2.11). The positive relationship between seed number and yield is well known (Board et al., 2003; Board and Modali, 2005; Nico et al., 2015; Rotundo et al., 2012; Santachiara et al., 2017a). Some studies have found a positive correlation between yield and ISW (Board, 2004; Board et al., 2003), while others have not (Kahlon et al., 2011). In our study, a positive correlation was found between yield and ISW (r: 0.45) in Lex-2016 (Table 2.11).

The analysis of physiological traits related to seed number determination in this study revealed that seed number was correlated to SA in both environments (r= 0.81-0.78). In addition, seed number was positively correlated with PC (r= 0.83), and negatively correlated with the $Days_{VE-R1}$ (r= -0.33) at Lex-2016 (Table 2.11). At Pri-2017, the ISGR (r= -0.32), $iPAR_{R1-R5}$ (r= 0.33), FLI_{R1} (r= 0.35) and $Days_{VE-R1}$ (r= 0.34) were also positively correlated with seed number (Table 2.11). In contrast to our results at Lex-2016, no relationship between seed number and PC was reported by Rotundo et al. (2012), across

soybean MGs and environments studied (United States and Argentina). At Lex-2016, cultivar P93Y92 was the highest yielding on average but had a lower seed number compared to cultivar P28T33R. Thus, cultivar P93Y92 was the highest yielding due to an intermediate seed number and heavy seeds, whereas cultivar P28T33R had the greatest seed number on average but the smallest seeds. These results indicate that there was a compensatory mechanism between seed number and ISW. Even though ISGR was not related to ISW, P93Y92 had the second highest ISGR (3.92 g seed^{-2} day^{-1}) which contributed to a higher ISW and the highest yield in this cultivar despite an intermediate seed number (Table 2.7).

At Pri-2017, MG 4 cultivars and AG29X8 were the highest yielding cultivars, explained by the high seed number production. In this environment, the lowest and highest yield cultivar (P28T08R and P47T36R) had the lowest and highest seed number, respectively (Table 2.4). The high seed number of AG29X8 at Pri-2017 was coincident with a high SA value (12.3 g seed m^{-2} day^{-1}) due to the highest ISGR and despite having one of the lowest FLI_{R1}. High seed number of MG 4 cultivars at Pri-2017 were coincident with a high SA value, as well as a high FLI_{R1} and the slowest ISGR. Relative yield had a linear relationship with $CumiPAR_{VE-R7}$ (R^2= 0.40) and FLI_{R1} (R^2= 0.26) in Pri-1017 (Figure 2.3). This could be due to the lower FLI_{R1} on average at this environment. At Pri-2017, the FLI_{R1} was more limiting for seed number determination, and later MGs were able to achieve more biomass and canopy cover by the start of reproductive stages since they had a longer cycle duration than MG 2 and 3 cultivars.

Crop growth rate was not significantly correlated with seed number in any environment (Table 2.11). These results do not agree with previous works, were a positive relationship

between seed number and CGR across different soybean cultivars, treatments (shade and/or extended photoperiod) and environments was found (Egli, 1993; Egli and Bruening, 2000; Egli and Yu, 1991; Kantolic et al., 2013). The lack of relationship between seed number and CGR in our study could be due to the small difference in CGR values within each environment, at Lex-2016 CGR values ranged from 30.7 to 34.8 g biomass m^{-2} day^{-1} while at Pri-2017 CGR values ranged from 9.2 to 15.5 g biomass m^{-2} day^{-1}. The lack of relationship could be also due to the different sampling dates across cultivars, that were based on dates of developmental stages.

Individual seed weight (ISW) is the second component of yield and is defined later in the growing season compared with seed number. Variation in ISW due to genetic factors is usually unrelated to yield due to a compensatory mechanism with seed number (Egli and Yu, 1991), while variation in ISW due to environmental factors can be related to yield (Egli, 1997). There are two main components that define ISW: ISGR and the duration of the EFP (Egli, 1998). In both environments studied we found a positive correlation of the ISW with the duration of the EFP (r= 0.43 and 0.40) (Table 2.11). The $Days_{R5\text{-}R7}$ was significant correlated (r= 0.41) with ISW only at Lex-2016, while the ISGR was not significant correlated with ISW in any environment (Table 2.11). Positive relations have been published between ISW and ISGR (Egli et al., 1981; Munier-Jolain and Ney, 1998). Individual seed weight was not affected by the SR effect in any of the two environments studied (Table 2.4). At Lex-2016, the EFP duration ranged from 37 to 56 days across cultivars while at Pri-2017 ranged from 32 to 37 days. At Lex-2016, the cultivar with the heaviest seed (P93Y92) had an intermediate EFP duration (40 days) (but high ISGR), while the cultivar with the lightest seed (P28T33R) had the shortest EFP duration (37 days). At

Pri-2017, the cultivar with the lightest seed also had the shortest EFP (32 days), and the heaviest seed an intermediate duration of the EFP (34 days) but relatively higher ISGR. A positive correlation between EFP and final seed size has been previously found across a wide range of cultivars (14 genotypes in 1981 and 59 genotypes in 1982) grown at Lexington, KY (r=0.6-0.71) (Egli et al., 1984). In our study, a longer EFP was also correlated with higher final seed weight. In addition, ISGR had a significant contribution to final seed size, with cultivars with the heaviest seed having ISGR in the high range within that environment. Despite the significant contribution of ISGR on ISW in our study, the lack of correlation between ISGR and ISW was probably due to a compensatory mechanism with seed number.

For example, P93Y92 had the second faster ISGR, probably associated to the heavy seed and low seed number compared with P28T33R that had the lowest ISGR, lightest seeds but highest seed number per area. (Table 2.4 and 2.7). At Pri-2017, cultivars within MG 4 had an EFP duration of 2 days longer than MG 2 and 3 (Figure 2.1b). Previous studies also reported longer EFP with long-season MG (Egli, 1993). In this environment, ISGR was very similar across soybean cultivars, the highest yielding and seeding number cultivar (P47T36R) had the smallest ISGR, hence the smallest seed. In addition, significant differences in ISGR were observed for high and normal SR, ISGR increased by 8.5% across soybean cultivars in environment 2 when growing under high SR compared with the normal SR.

CONCLUSIONS

Results from our study partially supported our hypothesis that under no water limitation, short-season MG cultivars at high seeding rate will reach reproductive stages under better environmental conditions and increase yield compared to full-season maturities. The short-season MG 2 reached reproductive stages 2 to 11 days earlier and with better environmental condition of solar radiation and temperature compared with the late-season MGs depending on the environment. However, the FLI_{R1} was reduced in MG 2 compared to later maturities and apparently limiting in one of the environments. Results from our study suggest that a fraction of light interception of approximately 0.70 by R1 might be required to achieve maximum yields. Overall, the yield of short-season MG (2) was not higher compared to the long-season MG, but it was similar to MG 4 cultivars at Lex-2016, and AG29X8 cultivar yield as much as the long season MGs 4 at Pri-2017. Maturity group 2 cultivars growing under high SR decreased yield by only 4 and 9 % on average compared to MG 4 cultivars growing under normal SR, at Lex-2016 and at Pri-2017, respectively. This relatively low yield penalty in short-season MG cultivars may be compensated by their earlier harvest that provides a wider window for harvest management operations, reduce the risk of late-season freezing temperatures, and could benefit from higher seed sell prices.

Chapter 2: Tables and Figures

Table 2.1. Location, planting date (PD), latitude and longitude and soil type.

Environment	Location	PD	Latitude - Longitude	Soil Type
Lex-16	Lexington	07/12/16	38º 2’ 53’’ N – 84º 30’ 6’’ W	UBlmU – ArA*
Pri-17	Princeton	06/26/17	37º 6’ 33’ N – 87º 52’ 55’’ W	UBlmU – ArA*

*UBlmB: Bluegrass-Maury silt loam, ArA: Armour silt loam and CrB2: Crider silt loam.

Table 2.2. Soybean maturity group (MG), cultivars name and growth habit (determinacy) of the commercial cultivars planted Lexington, 2016 (Lex-2016) and Princeton (Pri-2017)

Environment	Maturity group	Cultivars names	Growth habit
Lex-16	2	AG2733-P28T33R	Indeterminate
	3	AG3533-P93Y92	Indeterminate
	4	AG4336-AG4730	Indeterminate
Pri-17	2	P28T08R-AG29X8	Indeterminate
	3	AG3533-P38T61R	Indeterminate
	4	P41T33R-P47T36R	Indeterminate

Table 2.3. Average daily incident solar radiation and average temperature from R1 to R5 ($SolarRad_{R1\text{-}R5}$ and $Temp_{R1\text{-}R5}$) and from R5 to R7 ($SolarRad_{R5\text{-}R7}$ and $Temp_{R1\text{-}R5}$) by soybean maturity groups for each environment.

Maturity group	**$SolarRad_{R1\_R5}$**	**$SolarRad_{R5\_R7}$**	**$Temp_{R1\_R5}$**	**$Temp_{R5\_R7}$**
	MJ m^{-2} day^{-1}	MJ m^{-2} day^{-1}	ºC	ºC
Lexington 2016				
2	19.30	16.13	23.7	19.7
3	19.02	15.60	23.5	18.7
4	18.64	15.04	23.6	17.8
Princeton 2017				
2	19.80	18.08	24.7	21.8
3	19.71	17.48	23.7	21.7
4	19.66	16.67	23.6	21.5

Table 2.4. Mean values by environments for yield (kg ha^{-1}), seed number (seed m^{-2}), individual seed weight (ISW, mg seed^{-1}), harvest index (HI) and nodes number (nodes pl^{-1}). Values follow by different letter within an environment represent significant differences between soybean cultivars and seeding rate means ($p<0.05$). Probability and % sum of square in the model for the effect of environment, seeding rate, soybean maturity group, cultivars and their interaction from the analysis of variance (ANOVA) for yield, seed number, ISW, HI and nodes number.

Environment†	Cultivar (MG)	Yield	Seed number	ISW	Harvest index	Nodes
		Kg ha^{-1}	Seed m^{-2}	mg seed^{-1}		Nodes pl^{-1}
Lexington 2016						
Lex-2016	AG2733 (2)	4376 c	2592 bc	149.7 c	0.64 a	13.3 c
Lex-2016	P28T33R (2)	4403 c	3038 a	128.2 d	0.64 a	13.6 c
Lex-2016	AG3533 (3)	4935 ab	2801 ab	156.5 c	0.64 a	13.2 c
Lex-2016	P93Y92 (3)	5320 a	2657 bc	177.1 a	0.63 a	13.3 c
Lex-2016	AG4336 (4)	4575 bc	2453 c	165.1 b	0.63 ab	15.4 b
Lex-2016	AG4730 (4)	4283 c	2420 c	156.7 c	0.61 b	16.5 a
Princeton 2017						
Pri-2017	AG29X8 (2)	4822 ab	2459 ab	171.0 a	0.67 a	13.1
Pri-2017	P28T08R (2)	4005 d	2080 c	167.4 ab	0.65 b	13
Pri-2017	AG3533 (3)	4101 cd	2260 bc	158.0 c	0.67 a	13.7
Pri-2017	P38T61R (3)	4495 bc	2316 bc	168.8 a	0.65 b	13.8
Pri-2017	P41T33R (4)	4870 ab	2486 ab	170.6 a	0.65 b	13.5
Pri-2017	P47T36R (4)	5011 a	2708 a	161.2 bc	0.62 c	13.7
Seeding rate¥	**High (54 seed m^{-2})**	**4701 a**	**2572 a**	**161.5**	**0.65**	**14**
	Normal (40 seed m^{-2})	**4499 b**	**2473 b**	**160.2**	**0.64**	**14**

Continue Table 2.4

Fix factors	Degree of freedom	p - value (%SS)	p - value (%SS)	p - value (%SS)	p – value (%SS)	p - value (%SS)
Environment (env)	1	ns	** (14.1)	** (14.3)	** (17.1)	* (0.10)
Seeding rate (SR)	1	* (2.7)	* (1.8)	ns	ns	ns
Env*SR	1	ns	ns	ns	ns	ns
Maturity group (MG)	2	* (5.3)	ns	*** (12.0)	** (17.5)	*** (0.31)
Env*MG	2	*** (20.4)	*** (18.0)	*** (25.9)	ns	** (0.23)
SR*MG	2	ns	ns	ns	ns	ns
Env*SR*MG	2	ns	ns	ns	ns	ns
Cultivar(Env*MG)	6	** (11.9)	** (13.0)	*** (24.7)	*** (15.6)	ns
SR*Cultivar(Env*MG)	6	ns	ns	ns	ns	ns

† Env: Environment 1: Lex-2016 (Lexington, 2016), Environment 2: Pri-2017 (Princeton,2017)
¥ Seeding rate (SR): high (54 seed m^{-2}) and normal (40 seed m^{-2})
ns: Not significant (P≥0.05), * P≤ 0.05, ** P≤0.01 and *** P≤0.001

Table 2.5. Mean values by environment, soybean maturity groups (MG) and the MG x seeding rate interaction for crop growth rate (CGR, g biomass m^{-2} day^{-1}). Values follow by different letter represent significant differences between environments, MG and MG x seeding rate means ($p<0.05$). Probability of the interaction of time (DOY) with significant variables (environment. soybean MG and the MG x seeding rate interaction) for the analysis of covariance (ANCOVA) for CGR. Df: degrees of freedom.

Environment†	**Maturity Group**	**Seeding Rate**¥	**CGR** (g biomass m^{-2} day^{-1})	
Lex-2016			31.9	a
Pri-2017			12.9	b
	2		20.0	b
	3		27.8	a
	4		22.3	b
	2	High	20.3	ns
	2	Normal	19.7	ns
	3	High	24.6	ns
	3	Normal	25.2	ns
	4	High	24.6	a
	4	Normal	20.0	b
Fixed Factors	**Df**		**p-value**	
§DOY*Env	1		***	
DOY*MG	2		**	
DOY*SR*MG	3		*	

† Env: Environment 1: Lex-2016 (Lexington, 2016), Environment 2: Pri-2017 (Princeton,2017)
¥ Seeding rate (SR): high (54 seed m^{-2}) and normal (40 seed m^{-2})
§ DOY: days of the year, covariate factor
ns: Not significant ($P\geq0.05$), * $P\leq 0.05$, ** $P\leq0.01$ and *** $P\leq0.001$

Table 2.6. Mean values by environment and soybean maturity groups (MG) for RUE (radiation use efficiency, g biomass MJ^{-1}). Values follow by different letter represent significant differences between environments and MG means ($p<0.05$). Probability of the interaction of cumulative solar radiations (CumSrad) with significant variables (environment and MG) for the analysis of covariance (ANCOVA) for RUE. Df: degrees of freedom.

Environment†	**Maturity group**	**RUE** (g biomass MJ^{-1})
Lex-2016		1.76 a
Pri-2017		0.75 b
	2	1.09 b
	3	1.41 a
	4	1.26 ab
Fixed Factors	**Df**	**p-value**
§CumSrad* Environment	1	***
CumSrad*MG	2	*

† Env: Environment 1: Lex-2016 (Lexington, 2016), Environment 2: Pri-2017 (Princeton,2017)
§ CumSrad: cumulative solar radiation, covariate variable
ns: Not significant ($P\geq0.05$), * $P\leq 0.05$, ** $P\leq0.01$ and *** $P\leq0.001$

Table 2.7. Mean values by environment, environment x seeding rate and environment x cultivar for individual seed growth rate (ISGR, mg seed^{-1} day^{-1}). Values follow by different letter represent significant differences between environment, environment x seeding rate and environment x cultivar means ($p<0.05$). Probability of the interaction of time (DOY) with significant variables (environment, environment x seeding rate and environment x cultivar) for the analysis of covariance (ANCOVA) for ISGR. Df: degrees of freedom.

Environment†	**Seeding rate¥**	**Cultivar**	**ISGR** (mg seed^{-1} day^{-1})
Lex-2016			3.60 b
Pri-2017			4.80 a
Lex-2016	High		3.74
Lex-2016	Normal		3.37
Pri-2017	High		4.61 b
Pri-2017	Normal		5.00 a
Lexington 2016			
Lex-2016		AG2733	4.02 a
Lex-2016		P28T33R	3.34 d
Lex-2016		AG3533	3.84 b
Lex-2016		P93Y92	3.92 b
Lex-2016		AG4336	3.42 c
Lex-2016		AG4730	2.80 e
Princeton 2017			
Pri-2017		P28T08R	4.95 b
Pri-2017		AG29X8	4.97 a
Pri-2017		AG3533	5.00 a
Pri-2017		P38T61R	4.75 c
Pri-2017		P41T33R	4.70 d
Pri-2017		P47T36R	4.42 e
Fixed Factors		**Df**	**p-value**
§DOY*Environment (Env)		2	***
DOY*Env*Seeding rate		2	**
DOY*cultivar(Env)		10	***

† Env: Environment 1: Lex-2016 (Lexington, 2016), Environment 2: Pri-2017 (Princeton,2017)

¥ Seeding rate (SR): high (54 seed m^{-2}) and normal (40 seed m^{-2})

§ DOY: days of the year: covariance factor

ns: Not significant ($P\geq0.05$), * $P\leq 0.05$, ** $P\leq0.01$ and *** $P\leq0.001$

Table 2.8. Mean values by environments for partitioning coefficient (g seed g biomass^{-1}) and sink activity (g seed m^{-2}day^{-1}). Values follow by different letter within an environment represent significant differences between soybean cultivars x seeding rate means ($p<0.05$). Probability and % sum of square in the model for the effect of environment, seeding rate, soybean maturity group, cultivars and their interactions from the analysis of variance (ANOVA) for partitioning coefficient and sink activity.

		Partitioning coefficient		Sink activity	
		g seed g biomass^{-1}		g seed m^{-2}day^{-1}	
	Seed rate¥	**High**	**Normal**	**High**	**Normal**
Environment†	**Cultivar (MG)**				
Lexington 2016					
Lex-2016	AG2733 (2)	0.32 a	0.36 a	10.3 ab	10.5 a
Lex-2016	P28T33R (2)	0.37 a	0.29 ab	*11.8 a	8.6 b
Lex-2016	AG3533 (3)	0.36 a	0.28 ab	11.6 ab	10.0 ab
Lex-2016	P93Y92 (3)	0.34 a	0.28 ab	11.0 ab	9.8 ab
Lex-2016	AG4336 (4)	0.30 a	0.24 b	*10.1 b	6.7 c
Lex-2016	AG4730 (4)	0.20 b	0.24 b	6.6 c	6.9 c
Princeton 2017					
Pri-2017	AG29X8 (2)	Ψ1.42 a	1.24 a	12.4 a	12.1 ab
Pri-2017	P28T08R (2)	1.13 b	1.10 b	9.9 bc	10.7 b
Pri-2017	AG3533 (3)	0.73 c	0.73 e	11.9 a	10.7 b
Pri-2017	P38T61R (3)	Ψ0.57 d	0.88 c	*9.3 c	12.9 a
Pri-2017	P41T33R (4)	Ψ0.75 c	0.98 c	11.7 a	11.5 ab
Pri-2017	P47T36R(4)	Ψ0.73 c	1.06 bc	11.5 ab	12.5 a
lsd ($p<0.05$)		0.08		1.5	
Factors	**Degree of freedom**	**p - value (%SS)**		**p - value (%SS)**	
Environment (Env)	1	*** (75.4)		*** (23.6)	
Seeding rate (SR)	1	** (0.2)		* (1.2)	
Env*SR	1	*** (0.9)		*** (6.9)	
Maturity group (MG)	2	*** (9.4)		*** (7.6)	
Env*MG	2	*** (6.8)		*** (16.8)	
SR*MG	2	** (1.2)		ns	
Env*SR*MG	2	** (1.1)		ns	
Cultivar(Env*MG)	6	*** (1.5)		ns	
SR*Cultivar(Env*MG)	6	*** (1.2)		*** (13.5)	

† Env: Environment 1: Lex-2016 (Lexington, 2016), Environment 2: Pri-2017 (Princeton,2017)

¥ Seeding rate (SR): high (54 seed m^{-2}) and normal (40 seed m^{-2})

Ψ values are significant different between each other for that env x SR x cultivar (MG) interaction

ns: Not significant ($P\geq0.05$), * $P\leq 0.05$, ** $P\leq0.01$ and *** $P\leq0.001$

Table 2.9. Mean values by environments, for the fraction of light interception (FLI) at R1 and R5. Values follow by different letter within an environment represent significant differences between soybean cultivars x seeding rate means ($p<0.05$). Probability and % sum of square in the model for the effect of environment, seeding rate, soybean maturity group, cultivars and their interactions from the analysis of variance (ANOVA) for the fraction of light interception (FLI) at R1 and R5.

		FLI-R1		FLI-R5	
	Seed rate¥	**High**	**Normal**	**High**	**Normal**
Environment†	**Cultivar (MG)**				
Lexington 2016					
Lex-2016	AG2733 (2)	0.59 d	0.51 c	0.98	0.98
Lex-2016	P28T33R (2)	0.61 cd	0.54 c	0.99	0.99
Lex-2016	AG3533 (3)	0.73 bc	0.71 b	0.99	0.99
Lex-2016	P93Y92 (3)	0.67 bcd	0.70 b	0.99	0.99
Lex-2016	AG4336 (4)	0.76 ab	0.75 ab	0.99	0.99
Lex-2016	AG4730 (4)	0.87 a	0.82 a	1.00	1.00
Princeton 2017					
Pri-2017	AG29X8 (2)	*0.54 c	0.33 d	0.98	0.94
Pri-2017	P28T08R (2)	0.36 d	0.42 cd	0.97	0.94
Pri-2017	AG3533 (3)	*0.68 b	0.47 c	0.99	0.98
Pri-2017	P38T61R (3)	0.75 ab	0.66 ab	0.98	0.95
Pri-2017	P41T33R (4)	0.81 a	0.74 a	0.98	0.98
Pri-2017	P47T36R(4)	0.71 b	0.62 b	0.98	0.97
lsd ($p<0.05$)		0.098		ns	

Factors	**Df**	**p - value (%SS)**	**p - value (%SS)**
Environment (Env)	1	*** (9.6)	** (31.3)
Seeding rate (SR)	1	** (4.4)	* (6.0)
Env*SR	1	* (1.3)	* (6.3)
Maturity group (MG)	2	*** (52.0)	*** (10.3)
Env*MG	2	ns	*** (1.7)
SR*MG	2	ns	ns
Env*SR*MG	2	ns	ns
Cultivar(Env*MG)	6	*** (6.8)	ns
SR*Cultivar(Env*MG)	6	* (3.9)	ns

† Env: Environment 1: Lex-2016 (Lexington, 2016), Environment 2: Pri-2017 (Princeton,2017)
¥ Seeding rate (SR): high (54 seed m^{-2}) and normal (40 seed m^{-2})
ns: Not significant ($P\geq0.05$), * $P\leq 0.05$, ** $P\leq0.01$ and *** $P\leq0.001$

Table 2.10. Probability and % sum of square in the model for the effect of environment, seeding rate, soybean maturity group, cultivars and their interactions from the analysis of variance (ANOVA) for the duration of the vegetative phase ($Days_{VE-R1}$), seed-set phase ($Days_{R1-R5}$), seed-fill phase ($Days_{R5-R7}$) and effective filling period (EFP). Df: Degrees of freedom.

		$Days_{VE-R1}$	$Days_{R1-R5}$	$Days_{R5-R7}$	EFP
Fixed factors	**Df**	**p-value (%SS)**	**p-value (%SS)**	**p-value (%SS)**	**p-value (%SS)**
Enviroment (Env) †	1	* (2.14)	*** (67.5)	** (13.1)	*** (41.9)
Seeding rate (SR) ¥	1	ns	ns	ns	ns
Env*SR	1	ns	ns	ns	*** (4.1)
Maturity group (MG)	2	*** (70.3)	ns	*** (32.1)	*** (21.8)
Env*MG	2	** (6.7)	ns	** (9.4)	*** (11.0)
SR*MG	2	ns	ns	ns	*** (2.3)
Env*SR*MG	2	ns	ns	ns	*** (2.1)
Cultivar(Env*MG)	6	** (5.0)	ns	ns	*** (5.3)
SR*Cultivar(Env*MG)	6	ns	ns	ns	*** (6.9)

† Env: Environment

¥ Seeding rate (SR)

ns: Not significant (P≥0.05), * P≤ 0.05, ** P≤0.01 and *** P≤0.001

Table 2.11. Pearson Correlation values and probability (P-values) by environment of the relation of yield seed number and individual seed weight (ISW) with for the 17 physiological traits studied.

	Lexington, 2016			**Princeton, 2017**		
Variable	**Yield**	**Seed number**	**ISW**	**Yield**	**Seed number**	**ISW**
	correlation coefficient (r)					
	p-value					
Yield	1.00	0.68	0.45	1.00	0.94	0.16
kg ha^{-1}		***	**		***	ns
Seed number	0.68	1.00	-0.34	0.94	1.00	-0.17
seed m^{-2}	***		*	***		ns
ISW	0.45	-0.34	1.00	0.16	-0.17	1.00
mg $seed^{-1}$	**	*		ns	ns	
PC	0.62	0.83	-0.22	0.24	0.15	0.27
g seed g $biomass^{-1}$	***	***	ns	ns	ns	ns
CGR	0.27	-0.01	0.36	0.10	0.21	-0.34
g biomass m^{-2} day^{-1}	ns	ns	*	ns	ns	*
ISGR	0.34	0.17	0.22	-0.28	-0.32	0.10
mg $seed^{-1}$ day^{-1}	*	ns	ns	*	*	ns
SA	0.68	0.78	-0.08	0.78	0.81	-0.10
g seed m^{-2} day^{-1}	***	***	ns	***	***	ns
EFP	-0.04	-0.40	0.43	0.33	0.20	0.40
Days	ns	**	**	*	ns	**
HI	0.14	0.28	-0.17	-0.10	-0.14	0.08
	ns	ns	ns	*	ns	ns
RUE	0.24	0.13	0.15	0.16	0.26	-0.29
g biomass MJ^{-1}	ns	ns	ns	ns	ns	*
$iPAR_{R1-R5}$	0.20	-0.14	0.45	0.29	0.33	-0.11
MJ m^{-2} day^{-1}	ns	ns	**	*	*	ns
$CumiPAR_{VE-R7}$	0.19	-0.32	0.63	0.44	0.42	0.07
MJ m^{-2} day-1	ns	*	***	**	**	ns
FLI_{R1}	0.05	-0.24	0.38	0.35	0.35	-0.01
%	ns	ns	**	*	*	ns
FLI_{R5}	0.02	-0.23	0.31	0.11	0.19	-0.24
%	ns	ns	*	ns	ns	ns
$Days_{VE-R1}$	-0.14	-0.33	0.23	0.27	0.34	-0.21
Days	ns	*	ns	ns	*	ns
$Days_{R1-R5}$	-0.01	-0.07	0.08	-0.21	-0.16	-0.14
Days	ns	ns	ns	ns	ns	ns
$Days_{R5-R7}$	0.21	-0.14	0.41	0.42	0.39	0.10
Days	ns	ns	**	**	**	ns

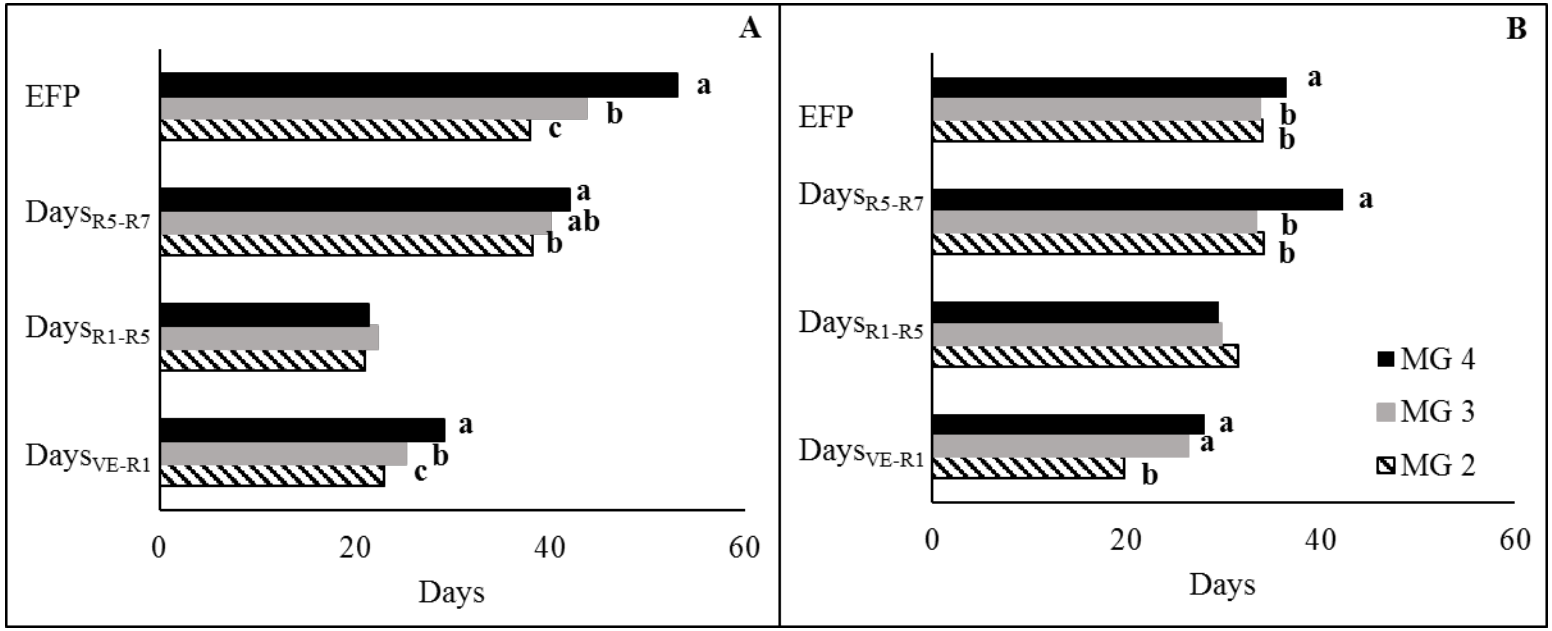

Figure 2.1. Mean values for the time measured from emergence to beginning of flower (Days$_{VE-R1}$), time measured from beginning of flower to beginning of seed (Days$_{R1-R5}$), time measured from the beginning of seed to maturity (Days$_{R5-R7}$) and the duration of the effective filling period (EFP), for (A) Lexington, 2016 and (B) Princeton, 2017. Bars follow with different letter represent significant differences ($p<0.05$) between maturity group means within a developmental stage duration and environment.

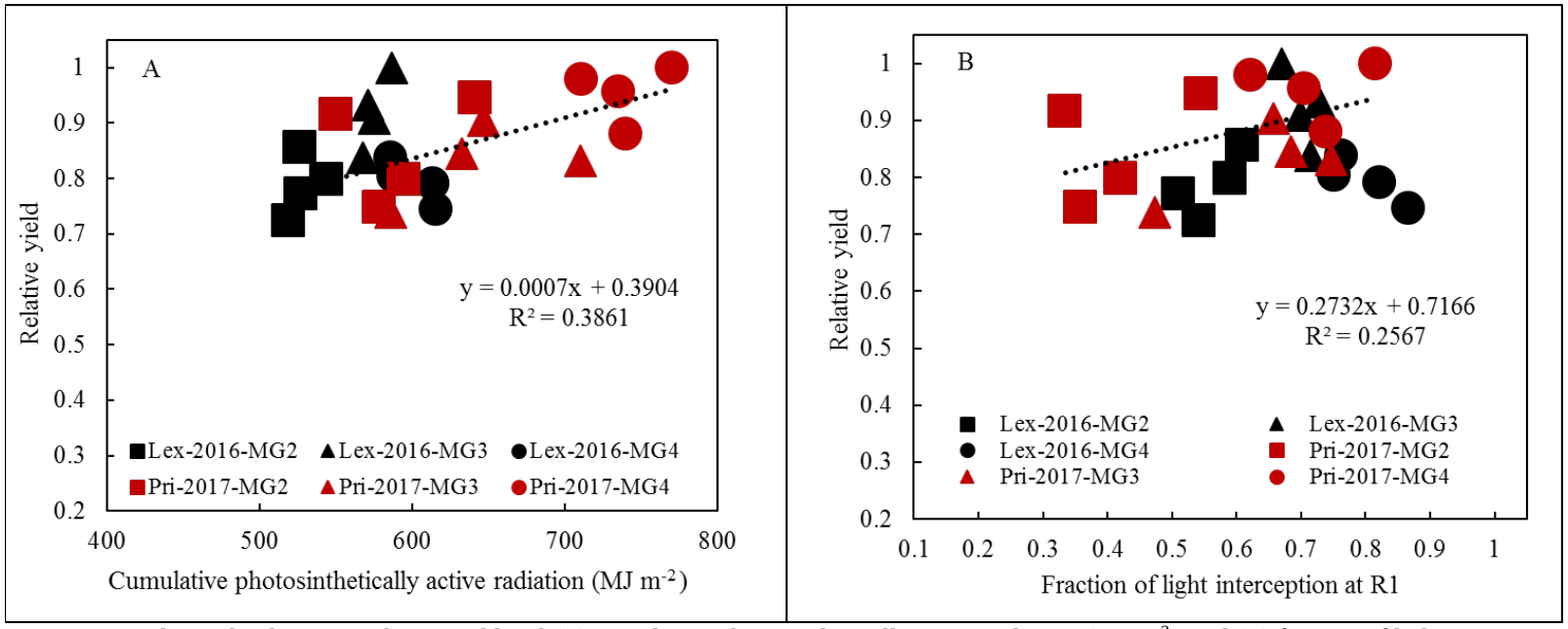

Figure 2.2. Relationship between relative yield and (A) cumulative photosynthetically active radiation (MJ m^{-2}), and (B) fraction of light interception at R1 by environments and soybean cultivars. Black symbols represented Lexington, 2016 (Lex-2016) while the red symbols represented Princeton, 2017 (Pri-2017). The different shape represents the soybean maturity groups, the linear relationship between relative yield and cumulative photosynthetically active radiation or fraction of light interception by R1 was only for Princeton, 2017.

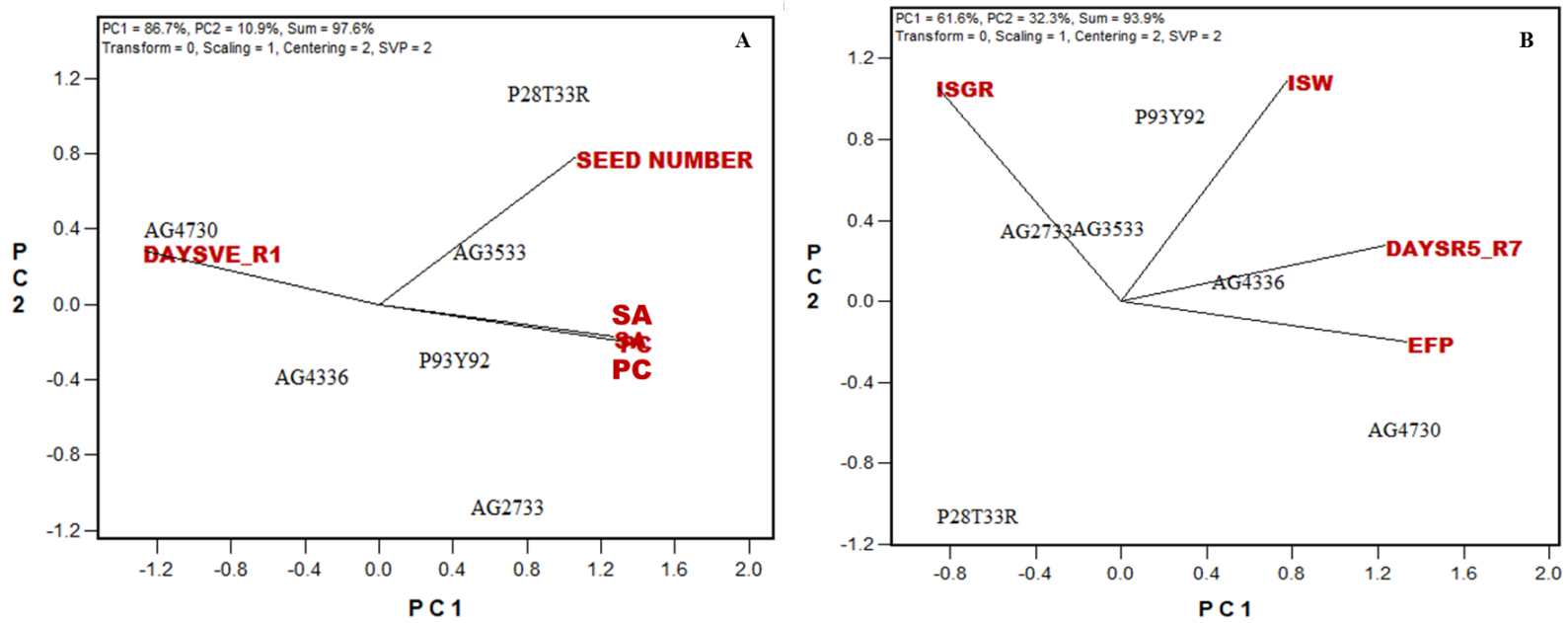

Figure 2.3. Cultivar by trait bi-plot model across soybean MGs based on principal component one (PC1) and two (PC2) in Lexington, 2016 (Lex-2016). (A) Model with seed number (SEED NUMBER) and physiological traits significantly related to seed number: PC: partitioning coefficient, SA: sink activity and $Days_{VE-R1}$: time measured from emergence to beginning of flower. (B) Model with individual seed weight (ISW) and physiological traits related to ISW, EFP: the duration of the effective filling period, ISGR: Individual seed growth rate and $Days_{R5-R7:}$ time measured from beginning seed to physiological maturity.

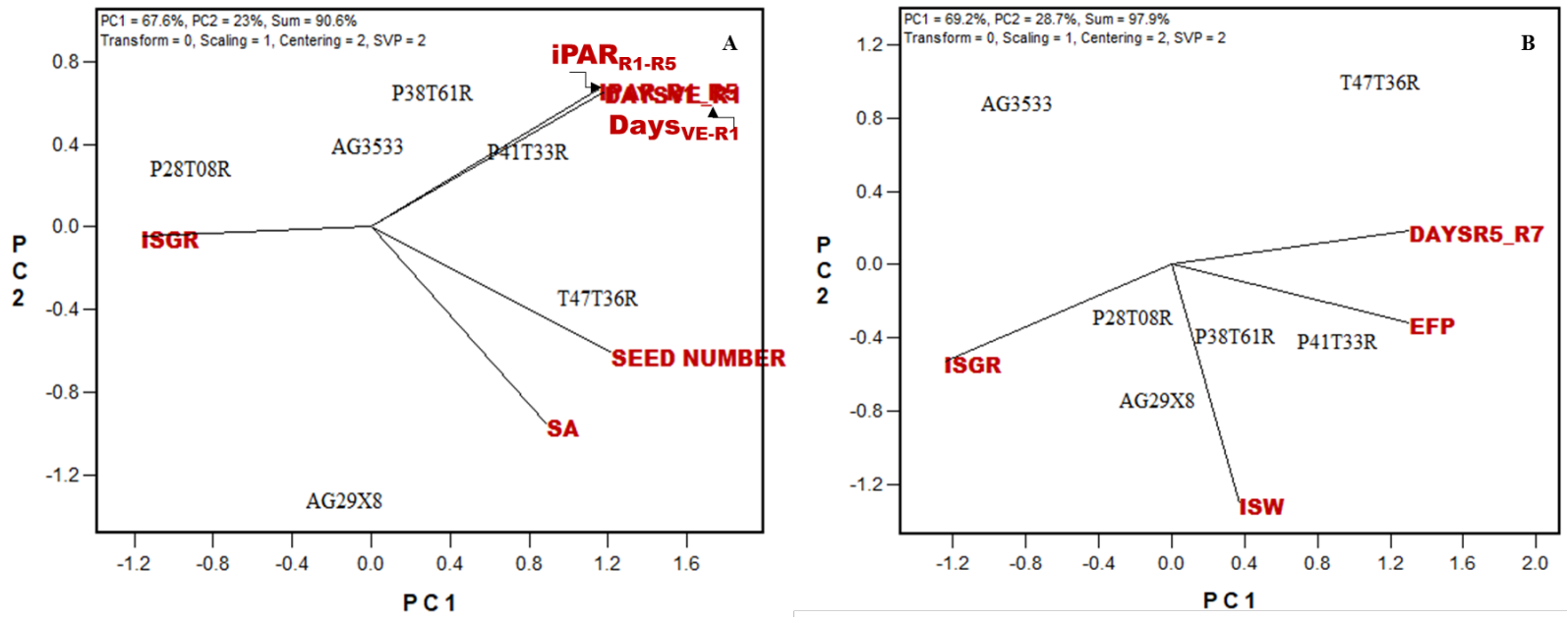

Figure 2.4. Cultivar by trait bi-plot model across soybean MGs based on principal component one (PC1) and two (PC2) in Princeton, 2017 (Pri-2017). (A) Model with seed number (SEED NUMBER) and physiological traits significantly related to seed number: SA: sink activity, ISGR: individual seed weight, $iPAR_{R1\text{-}R5}$: intercept solar radiation from R1 to R5 and $Days_{VE\text{-}R1}$: time measured from emergence to beginning of flower. (B) Model with individual seed weight (ISW) and physiological traits related to ISW, EFP: the duration of the effective filling period, ISGR: Individual seed growth rate and $Days_{R5\text{-}R7}$: time measured from beginning seed to physiological maturity.

CONCLUSIONS

In chapter 1, differences in the duration of the growth cycle were found between MG 2 to 5 (71 to 123 days). Overall, in all environments the highest yielding soybean maturity group were associated in a greater extend to high seed number (r= 0.89). The highest seed number maturity group soybean were positive correlated with the partitioning of biomass to grain (r= 0.97 and 071) in two out of three environments, negative correlated with individual seed growth (r= -0.63 and -0.60) in two out of three environments and negative related to crop growth rate (r= -0.70) in only one environment. Individual seed weight was mainly explained by the duration of the effective filling period (r= 0.26-0.43) across environments.

In chapter 2, short-season MG cultivars at high seeding rate will reach reproductive stages under better environmental conditions. However, the FLI_{R1} was reduced in MG 2 compared to later maturities and apparently limiting in one of the environments. Overall, the yield of short-season MG (2) was not higher compared to the long-season MG, but it was similar to MG 4 cultivars at Lexington, 2016, and AG29X8 cultivar yield as much as the long season MGs 4 at Princeton, 2017. Maturity group 2 cultivars growing under high SR decreased yield by only 4 and 9 % on average compared to MG 4 cultivars growing under normal SR, at Lexington, 2016 and at Princeton,2017, respectively.

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