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RESEARCH

Physiological and Phenological Responses of Historical Soybean Cultivar Releases to Earlier Planting

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ABSTRACT

The trend toward earlier soybean [*Glycine max* (L.) Merr.] planting in the midwestern United States has interacted synergistically with genetic yield gain to provide improvement in on-farm yields. However, the impacts of earlier planting dates and their interaction with genetic gain in physiological and phenological traits remain unclear. The objectives of this study were to determine if a 30-d difference in planting date affected measured rates of genetic improvement in (i) total dry matter (TDM) production, (ii) harvest index (HI), and (iii) growth-stage duration in the north-central United States. Research was conducted at Arlington, WI, Urbana, IL, and Lafayette, IN during 2010 and 2011 using 59 Maturity Group (MG) II cultivars (released 1928–2008) at Wisconsin, and 57 MG III cultivars (released 1923–2007) at Illinois and Indiana, with targeted planting dates of 1 May and 1 June. A mixed-effect regression analysis was used to model genetic change in TDM, HI, and growth stage duration as impacted by planting date. Breeding efforts have increased TDM(R7), HI, seed-fill duration (SFD), and reproductive growth duration over time, as vegetative growth duration has been reduced. Early planting provided increased TDM(R7) and longer reproductive growth duration, but had no effect on HI or SFD. A synergistic planting date × year of release interaction existed for TDM(R7) in both maturity groups, but not for HI or SFD, suggesting that the higher yields in newer, early-planted cultivars resulted from greater TDM production, not improved HI or SFD.

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Abbreviations: DM, dry matter; HI, harvest index; MG, Maturity Group; SFP, seed-fill period; SFD, seed-fill duration; TDM, total dry matter.

Planting soybean [*Glycine max* (L.) Merr.] in late April and early May is currently recommended in the midwestern United States to achieve optimum grain yield and maximum economic return (De Bruin and Pedersen, 2008; Bastidas et al., 2008; Robinson et al., 2009). Average planting dates across the United States have gradually progressed to earlier calendar dates in the growing season over the past three decades (USDA–NASS, 2011), advancing approximately 12 d between 1981 and 2005 (Sacks and Kucharik, 2011). Rowntree et al. (2013) recently demonstrated that the interaction of earlier planting date with genetic yield gain had synergistically improved on-farm yields in the Upper Midwest in MG III cultivars, because of the greater positive yield response of newer cultivars to earlier planting. Yield is the product of TDM production and HI (Kumudini, 2002). Therefore, improvement in on-farm grain yield over time arising from on-farm inputs of genetic and/or agronomic technology has presumably resulted from an increase in either one, or both, of these components (Specht et al., 1999). The contribution of TDM and HI to genetic yield improvement has been evaluated among past cultivar releases

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in modern production environments (Kumudini et al., 2001; DeBruin and Pedersen, 2009), but little consideration has been given to the influence of advancements in agronomic practices over time (e.g., earlier planting) on the improvement of these traits. Synergistic interactions between planting date and the indirect improvement in TDM and HI, which have arisen from breeder focus on improving yield, would be useful information to understand the physiological basis for the greater yields achieved with newer, early-planted cultivars. However, no research to date has focused on those traits and their contribution to such interactions.

Improvements in TDM and HI have been shown to contribute to genetic yield gain, though these two traits are not direct selection targets by breeders per se. The relative contribution of each component is not equal. For example, Kumudini et al. (2001) reported that 78% of genetic yield gain in short-season cultivars (MG 00–MG 0) in Canada could be attributable to increased dry matter (DM) accumulation, with the remainder attributable to improved HI. Similarly, genetic yield improvement between old and new cultivars examined in Iowa was highly correlated with improved TDM in the newer cultivars, whereas HI remained unchanged over time (De Bruin and Pedersen, 2009). The improved ability of newer cultivars to produce greater TDM just before, and during, the SFP (R5 to R7), sustain higher crop growth rates in the later reproductive stages, and maintain leaf area further into the SFP are common characteristics of modern cultivars, and these factors promote increased carbon assimilation and likely provide a physiological foundation for the continuing genetic improvement in yield (Kumudini et al., 2001; De Bruin and Pedersen, 2009). Considering that soybean yields are most frequently optimized with earlier planting, it is not surprising that DM accumulation during the SFP can be maximized with early planting (Pedersen and Lauer, 2004b). Anderson and Vasilas (1985) reported increased DM accumulation from the VE to R1 growth stages (Fehr and Caviness, 1977) as planting was delayed, probably because of greater vegetative DM arising from warmer temperatures with June plantings, but these authors also noted greater DM accumulation during the R1 to R5 timeframe with May plantings.

Although not the predominant contributor to genetic yield improvement, HI in indeterminate soybean has been shown to be positively correlated with yield in some experiments (Morrison et al., 1999; Pedersen and Lauer, 2004a; Jin et al., 2010) and not correlated with yield in others (Schapaugh and Wilcox, 1980; Cregan and Yaklich, 1986). Published reports on HI as it relates to genetic yield improvement have either documented increases (Morrison et al., 1999; Kumudini et al., 2001; Jin et al., 2010) or no change (De Bruin and Pedersen, 2009) over time in experiments involving cultivars differing in year of release. Few studies to date have examined the impacts of earlier planting on HI. In Wisconsin, harvest indices were 2% greater in early-May than in late-May plantings (Pedersen and Lauer, 2004a). However, Wilcox and Frankenberger (1987) found no effect of planting date on HI among indeterminate and determinate cultivars in Indiana. Additional research efforts that utilize a large and comprehensive group of previously released cultivars may provide a more definitive conclusion on the genetic changes in HI over time and the response of HI to planting date.

Evidence exists to suggest that lengthening the duration of the SFP may provide an opportunity by which to improve yield (Gay et al., 1980). Increased SFD was documented in more recently released cultivars and those with higher yielding capabilities in previous research (Gay et al., 1980; McBlain and Hume, 1980; Boerma and Ashley, 1988). Due to the positive correlation between seed yield and SFD, it has been suggested that selection or direct screening of breeding lines for an increased SFD may be a useful tool to complement the selection of high-yielding cultivars in breeding programs (Dunphy et al., 1979; Egli et al., 1984; Smith and Nelson, 1986). Significant genotypic variation in SFD exists, but low heritability, significant genotype × environment interactions, and the complexity associated with precise measurement of the seed-fill trait make breeding decisions based on lengthening SFD challenging and not widely practiced (Egli, 2004). Planting date has been shown to have no effect on SFD (Egli et al., 1987). However, the choice of planting date may result in the probability and timing of environmental pressures within the growing season, including moisture and temperature stress, both of which have been shown to affect SFD (Egli and Wardlaw, 1980; Meckel et al., 1984).

Research evaluating the changes in physiological and phenological traits that may have occurred in concordance with genetic yield improvement over the past 75 yr would be useful. Such research would help to determine the degree to which those traits also changed with respect to agronomic improvements over time, and would be particularly useful with regard to understanding the contribution of those traits to the synergistic interaction between genetic × agronomic factors. Given that newer cultivars likely have the capacity to assimilate more carbon through increased DM accumulation, allocate a greater amount of assimilate to the seed through improved harvest indices, and extend the SFP compared to earlier released cultivars, exploration of genetic × agronomic interactions among these traits is a necessary next step in understanding how agronomic advancements can be synergistically coupled with genetic yield improvement over time. Earlier planting is one agronomic advancement that has interacted synergistically with genetic yield gain to provide higher yields (Rowntree et al., 2013), although the physiological changes that have facilitated these higher yields in newer, earlier planted cultivars must be elucidated.

Table 1. Experimental details with respect to test sites, soils, and dates of planting and harvest.

Location	Arlington, WI		Urbana, IL		Lafayette, IN	
Research site	Arlington Agricultural Research Station		Crop Sciences Research and Education Center		Throckmorton Purdue Agricultural Center	
	43°18′ N, 89°20′ W		40°3′ N, 88°14′ W		40°17′ N, 86°54′ W	
Soil series	Plano silt loam		Flanagan silt loam and Drummer silty clay loam		Throckmorton silt loam	
Soil family	fine-silty, mixed, mesic Typic Argiudoll		fine-silty, mixed, mesic Typic Endoaquoll and fine, smectitic, mesic Aquic Argiudoll		fine-silty, mixed, mesic mollic Oxyaquic Hapludalf	
Soil fertility						
Phosphorus (mg kg^{-1})	44–56		23–34		39–66	
Potassium (mg kg^{-1})	166–173		122		138–146	
pH	6.9–7.1		5.8–6.1		6.0–6.1	
Organic matter (g kg^{-1})	3.2		3.6–4.1		2.9–3.0	
Field operations	**2010**	**2011**	**2010**	**2011**	**2010**	**2011**
Planting date (May PD treatment)	4 May	5 May	15 May	12 May	10 May	17 May
Planting date (June PD treatment)	1 June	6 June	14 June	8 June	4 June	12 June
Harvest date (May PD treatment)	8 Oct.	17 Oct.	7 Oct.	11 Oct.	24 Sept.	11 Oct.
Harvest date (June PD treatment)	13 Oct.	17 Oct.	7 Oct.	11 Oct.	4 Oct.	11 Oct.
Planting date difference (d)	28	32	30	27	25	26

To examine the interactions between planting date and the measured rates of genetic improvement in physiological and phenological traits over time, a comprehensive study involving a total of 116 MG II and MG III public and proprietary cultivars released over eight decades was designed and implemented. We hypothesized that the higher yields observed with early planting of newer cultivars may have been the result of positive, synergistic interactions with early planting and the genetic improvement in one or more of the following traits that impact seed yield: TDM, HI, and SFD. To understand the effects of earlier planting on TDM, HI, and growth-stage duration in MG II and MG III cultivars in the north-central United States, the objectives of our study were to determine, for each of the three foregoing traits: (i) the impact of planting date on the trait, (ii) the modeling of genetic variation in the trait vs. cultivar year of release to assess trait change over time that may have been correlated responses accompanying breeder selection for higher seed yield, and (iii) the degree to which changes in the trait arising from a differential in planting date *interacted* with changes in the trait arising from a correlated response to the successive release of ever-higher yielding cultivars over time. The foregoing objectives were the primary ones, though there was interest in additional main effects and interactions derivable from the collected set of trait data.

MATERIALS AND METHODS

Research was conducted in 2010 and 2011 at Arlington, WI, Urbana, IL, and Lafayette, IN. Location-specific information and soil characteristics for the three sites can be found in Table 1. In both years of the experiment, soybean followed corn (*Zea mays* L.) harvested for grain at the Illinois and Indiana locations, whereas soybean followed corn harvested for silage at the Wisconsin location. All locations were fall-chiseled, and prepared in the spring with field cultivation (Wisconsin, Indiana) or mulch tillage (Illinois). Fertility and pest management at each location was performed according to the local university management recommendations. At each location, cultivars were seeded at two planting dates, with 1 May and 1 June as the desired target dates. The 1 May planting date (early) was selected to represent planting dates growers currently use, whereas the 1 June (late) planting was selected to represent planting dates used more commonly in the past (USDA–NASS, 2011). In both years, weather and soil moisture conditions resulted in planting occurring later than the target dates, though a 25- to 32-d differential in planting date was still achieved (Table 1).

At the Wisconsin location, 59 MG II soybean cultivars released over eight decades, from 1928 to 2008 were planted, whereas at the Illinois and Indiana locations, 57 MG III soybean cultivars released from 1923 to 2007 were planted. The cultivars used in the experiment, along with the plant introduction number and pedigree information, are provided in Table 2. Each cultivar used in the experiment was unique, novel, or widely grown during the time period of introduction. Cultivars included plant introductions grown about 80 yr ago, along with public and proprietary cultivars derived from subsequent cycles of selection and breeding since then. The soybean seed used for the experiment originated from public and private seed sources, with seed increases of all cultivars occurring during the 2009 and 2010 growing seasons. Seed of the MG II cultivars was increased at the University of Nebraska-Lincoln (Lincoln, NE), whereas seed of the MG III cultivars was increased at the University of Illinois at Urbana-Champaign (Urbana, IL). To provide an estimate of experimental error, 13 of the 59 MG II cultivars and 15 of the 57 MG III cultivars utilized were replicated twice within each planting date, for a total of 72 plots per planting date treatment at each maturity group. A limited number of cultivars were chosen for replication due to limited seed supply and field space constraints. Replicated cultivars within each maturity group were intentionally chosen to be evenly distributed across years of release. The experiment was replicated by environment, defined as location within year, for each maturity group.

Table 2. List of cultivars, year of release, maturity group, plant introduction (PI) number, and pedigree.

Cultivar	Year of release	Maturity Group	PI No.†	Pedigree‡
Dunfield§	1923	III	PI548318	P.I. 36846 (NE China)
Illini§	1927	III	PI548348	Selection from A.K. in 1920
Korean§	1928	II	PI548360	From China
AK (Harrow)§	1928	III	PI548298	Selection from A.K. (by 1928)
Mukden§	1932	II	PI548391	P.I. 50523 (NE China)
Mandell	1934	III	PI548381	Selection from Manchu in 1926
Richland§	1938	II	PI548406	P.I. 70502-2 (NE China)
Mingo	1940	III	PI548388	Selection from Manchu in 1924
Lincoln§	1943	III	PI548362	Mandarin × Manchu
Hawkeye§	1947	II	PI548577	Mukden × Richland
Adams	1948	III	PI548502	Illini × Dunfield
Harosoy§	1951	II	PI548573	Mandarin (Ottawa) (2) × A.K. (Harrow)
Lindarin	1958	II	PI548589	Mandarin (Ottawa) × Lincoln
Shelby	1958	III	PI548574	Lincoln (2) × Richland
Ford	1958	III	PI548562	Lincoln (2) × Richland
Ross	1960	III	PI548612	Monroe × Lincoln
Harosoy 63	1963	II	PI548575	Harosoy (8) × Blackhawk
Hawkeye 63	1963	II	PI548578	Hawkeye (7) × Blackhawk
Wayne§	1964	III	PI548628	L49-4091 × Clark
Adelphia	1964	III	PI548503	C1070 × Adams
Amsoy	1965	II	PI548506	Adams × Harosoy
Corsoy§	1967	II	PI548540	Harosoy × Capital
Beeson	1968	II	PI548510	C1253 (Blackhawk × Harosoy) × Kent
Calland§	1968	III	PI548527	C1253 × Kent
Amsoy 71§	1970	II	PI548507	Amsoy (8) × C1253
Williams§	1971	III	PI548631	Wayne × L57-0034 (Clark × Adams)
Wells	1972	II	PI548630	C1266R (Harosoy × C1079) × C1253
Woodworth§	1974	III	PI548632	Wayne × L57-0034
Harcor	1975	II	PI548570	Corsoy × OX383 (Corsoy × Harosoy 63)
Private 2-7	1977	II	n/a	n/a
Private 2-8	1977	II	n/a	n/a
Wells II	1978	II	PI548513	Wells (8) × Arksoy
Vickery	1978	II	PI548617	Corsoy (5) × (L65-1342 and Anoka × Mack)
Private 3-1§	1978	III	n/a	n/a
Cumberland	1978	III	PI548542	Corsoy × Williams
Oakland	1978	III	PI548543	L66L-137 (Wayne × L57-0034) × Calland
Corsoy 79	1979	II	PI518669	Corsoy (6) × Lee 68
Beeson 80	1979	II	PI548511	Beeson (8) × Arksoy
Century§	1979	II	PI548512	Calland × Bonus
Amcor	1979	II	PI548505	Amsoy 71 × Corsoy
Pella	1979	III	PI548523	L66L-137 × Calland
Williams 82§	1981	III	PI518671	Williams (7) × Kingwa
Private 2-11	1982	II	n/a	n/a
Private 3-15	1983	III	n/a	n/a
Century 84	1984	II	PI548529	Century (5) × Williams 82
Elgin	1984	II	PI548557	F_4 selection from AP6 population
Zane	1984	III	PI548634	Cumberland × Pella
Harper	1984	III	PI548558	F_4 selection from an unknown diallel-cross population
Preston	1985	II	PI548520	Schechinger S48 × Land O'Lakes Max
Private 2-15	1985	II	n/a	n/a
Chamberlain§	1986	III	PI548635	A76-304020 × Land O'Lakes Max
Private 3-2	1986	III	n/a	n/a
Resnik	1987	III	PI534645	Asgrow A3127(4) × L24
Pella 86	1987	III	PI509044	From backcross of Pella(5) × Williams 82
Burlison	1988	II	PI533655	F_4 selection from K74-113-76-486 × Century
Private 2-9	1988	II	n/a	n/a
Elgin 87	1988	II	PI518666	Elgin (5) × Williams 82
Conrad§	1988	II	PI525453	A3127 × Tri-Valley Charger
Jack§	1989	II	PI540556	Fayette × Hardin

Plots were mechanically seeded in four rows, spaced 76 cm apart, at a rate of 370,650 untreated seeds ha^{-1}. Planted plot dimensions at all locations were 3.1 m wide by 4.6 m long. Determination of TDM production for MG II and MG III required destructive sampling at the Wisconsin and Illinois locations, respectively. To facilitate in-season biomass sampling at these locations, plots proposed for destructive sampling also had dimensions of 3.1 by 4.6 m and were planted adjacent to the nondestructive yield plots, so the total plot size was 6.2 by 4.6 m for each cultivar. To determine TDM production at various seasonal time points, a 0. 76-m^2 area was randomly selected and hand-harvested (clipped at the soil surface) from each destructive plot at the R1, R4, and R7 growth stages. The collected aboveground biomass from each plot was dried at 60°C to a constant weight using a forced-air drying oven. Samples were weighed and TDM was recorded at R1 [labeled as TDM(R1)], R4 [as TDM(R4)], and R7 [as TDM(R7)].

Apparent HI, as described by Schapaugh and Wilcox (1980), was determined at R8 at each of the locations by dividing the weight of grain (seed) collected by the total weight of aboveground biomass (seeds, pods, and stems). The HI data from Illinois in 2011 were not included in the analysis due to harvesting issues. Lodging scores were recorded on a visual scale of 1 to 5 (1 = erect; 5 = fully lodged) when all plots had attained stage R8. The growth stage of each plot was recorded twice weekly throughout the growing season from emergence

Table 2. Continued.

Cultivar	Year of release	Maturity Group	PI No.†	Pedigree‡
Kenwood	1989	II	PI537094	Elgin × A1937
Private 2-1	1989	II	n/a	n/a
Private 3-9	1989	III	n/a	n/a
Private 2-2	1990	II	n/a	n/a
Private 3-10	1990	III	n/a	n/a
RCAT Angora	1991	II	PI572242	B152 × T8112
Private 2-6	1991	II	n/a	n/a
Private 3-16	1991	III	n/a	n/a
Dunbar	1992	III	PI552538	Platte × A3127
Thorne	1992	III	PI564718	A80-344003 × A3127BC3F2-1
Private 3-17	1992	III	n/a	n/a
Private 2-5	1993	II	n/a	n/a
Private 3-18	1993	III	n/a	n/a
Private 2-10	1994	II	n/a	n/a
Private 2-16	1994	II	n/a	n/a
Private 3-19	1994	III	n/a	n/a
IA 2021	1995	II	n/a	Elgin 87 × Marcus
Macon§	1995	III	PI593258	Sherman × Resnik
IA 3004	1995	III	n/a	Northrup King S23-03 × A86-301024
Savoy	1996	II	PI597381	Burlison × Asgrow A3733
Private 2-12	1996	II	n/a	n/a
Maverick	1996	III	PI598124	LN86-4668 (Fayette × Hardin) × Resnik(3)
Private 3-4	1996	III	n/a	n/a
Private 3-11	1996	III	n/a	n/a
Dwight§	1997	II	PI597386	Jack × A86-303014
Private 2-18	1997	II	n/a	n/a
Pana	1997	III	PI597387	Jack × Asgrow A3205
Private 3-5	1997	III	n/a	n/a
Private 3-12	1997	III	n/a	n/a
IA 2038	1998	II	n/a	Pioneer 9301 × Kenwood
Private 3-6	1998	III	n/a	n/a
IA 3010	1998	III	n/a	Jaques J285 × Northrup King S29-39
Private 3-7§	1999	III	n/a	n/a
IA 2050	2000	II	n/a	Northrup King S24-92 × A91-501002
IA 2052	2000	II	n/a	Northrup King S24-92 × Parker
Private 3-20	2000	III	n/a	n/a
Loda§	2001	II	PI614088	Jack × IA 3003
Private 2-4	2001	II	n/a	n/a
Private 2-17	2001	II	n/a	n/a
U98-311442	2001	III	n/a	A94-773014 × Bell
IA 3014	2001	III	n/a	LN90-4366 × IA3005
Private 3-8§	2002	III	n/a	n/a
IA 2068	2003	II	n/a	AgriPro P1953 × LN94-10470
IA 3023	2003	III	n/a	Dairyland DSR-365 × Pioneer P9381
Private 2-3	2004	II	n/a	n/a
NE3001	2004	III	n/a	Colfax × A91-701035
Private 3-13§	2004	III	n/a	n/a
IA 3024	2004	III	n/a	A97-553017 × Pioneer YB33A99
IA 2065	2005	II	n/a	n/a
Private 2-19	2005	II	n/a	n/a
Private 2-20	2005	II	n/a	n/a
IA 2094	2006	II	n/a	AgriPro X0121B74 × A00-711036
Private 3-22	2006	III	n/a	n/a
Private 3-23	2006	III	n/a	n/a
Private 3-14	2007	III	n/a	n/a
Private 2-13	2008	II	n/a	n/a
Private 2-14§	2008	II	n/a	n/a

† n/a, not applicable.

‡ n/a, not available.

§ Cultivars replicated within location.

to maturity (VE to R8). The number of days after planting were recorded for each plot when 50% of the plants had reached a given growth stage. The recording of vegetative growth stages terminated when plants reached beginning flower (R1). The duration of vegetative and reproductive growth periods were calculated based on the number of days between V1 to R1 and R1 to R7, respectively. The SFD was determined based on the number of days between R5 and R7.

All data were subjected to a mixed-effect regression analysis using the PROC MIXED procedure in SAS Version 9.2 (SAS Institute Inc., Cary, NC). Models were constructed for maturity groups separately. The main effects of planting date, cultivar year of release, and the planting date × year of release interaction were treated as fixed effects. Environment and cultivar, along with the planting date × environment, planting date × cultivar, and planting date × environment × cultivar interactions were considered to be random effects. Cultivar was treated as a random effect because those selected for the experiment were chosen from a larger group of cultivars available over the eight decades. Fixed effects were tested for significance ($P < 0.05$) using the appropriate F test. Final models were a function of the model fit statistics (AIC, BIC, −2 Res Log Likelihood), as well as biological interpretation. Simple correlation coefficients were calculated using the PROC CORR procedure in SAS Version 9.2 (SAS Institute Inc., Cary, NC). The TDM, HI, and growth stage duration data were regressed over year of release to evaluate the change in these traits associated with the breeder selection for yield over the 80 yr of genetic yield improvement at each planting date. There was no evidence to suggest that a nonlinear model provided a more appropriate fit to the observed trends in TDM, HI, or growth

Table 3. Mean monthly air temperature and total monthly precipitation at Arlington, WI, Urbana, IL, and Lafayette, IN during the 2010 and 2011 growing seasons, and during the past 30 yr.

	Arlington, WI			Urbana, IL			Lafayette, IN		
	2010	2011	30 yr	2010	2011	30 yr	2010	2011	30 yr
Air temperature (°C)									
April	10.4	6.2	7.1	15.1	11.9	11.1	14.9	11.6	10.7
May	15.3	13.4	13.2	18.3	16.9	16.9	18.1	17.1	16.6
June	19.7	19.6	18.7	23.8	22.8	22.3	23.3	22.6	21.8
July	22.9	24.0	20.8	25.2	26.8	23.8	24.4	26.0	23.4
August	22.2	21.0	19.6	25.1	24.1	23.0	24.3	22.7	22.4
September	15.6	14.5	15.2	19.7	17.5	19.0	19.4	17.1	18.8
Precipitation (mm)									
April	107.5	106.4	88.9	48.5	214.6	93.5	72.9	192.6	86.6
May	88.9	55.4	93.7	78.5	121.9	124.2	72.6	113.4	117.9
June	169.4	98.8	118.9	198.6	106.7	110.2	95.0	92.8	115.6
July	222.8	64.3	105.7	90.7	39.9	119.4	66.3	45.5	103.6
August	114.0	39.9	99.1	40.1	44.7	99.8	42.2	26.3	100.1
September	50.5	96.5	89.9	76.7	70.9	79.5	24.1	82.8	71.2

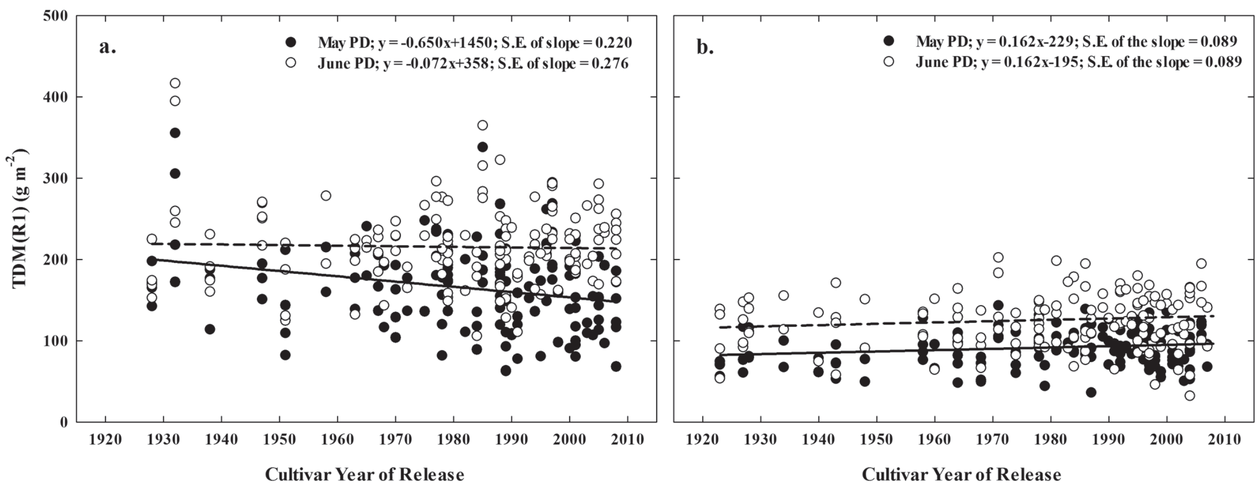

Figure 1. Regression of (a) Maturity Group (MG) II and (b) MG III total dry matter at growth stage R1 [TDM(R1)] (g m^{-2}) over soybean cultivar year of release at May (solid) and June (dashed) planting dates (PD) in 2010 and 2011.

stage duration over year of release, so a linear rather than nonlinear model was chosen to describe the relationships.

RESULTS AND DISCUSSION

Environment

Except for the month of July, average air temperatures were lower in 2011 than 2010 at all locations (Table 3). At the Wisconsin location, 2010 could be characterized as an above-average rainfall year, whereas 2011 was a year with very low midseason (July–August) rainfall and less than normal early- and late-season rainfall. In Wisconsin, the combination of above-average temperature and precipitation in 2010 led to record state soybean yields. At the Illinois and Indiana locations, early-season precipitation (April–May) was greater in 2011 than in 2010. Midseason (July–August) precipitation at both Illinois and Indiana was well below the 30-yr average for both years, with drier conditions prevailing in 2011 than in 2010. Excess soil moisture was the most important factor resulting in actual planting dates not matching the targeted dates.

Total Dry Matter Production

In both maturity groups, breeder selection for higher yield over the course of 80 yr of cultivar release had little concordant impact ($P > 0.05$) on TDM(R1) (Fig. 1), which suggests that the amount of vegetative DM accumulated before R1 is of little relevance when selecting for higher yielding cultivars. These findings confirm previous research results, in which old and new cultivars were shown to produce similar amounts of TDM during vegetative growth (Kumudini et al., 2001; De Bruin and Pedersen, 2009). June-planted cultivars produced significantly greater ($P < 0.05$) TDM(R1) than did cultivars planted in May in MG II (Fig. 1a); however, planting date had no effect on TDM(R1) in MG III (Fig. 1b). Bastidas et al. (2008) noted the warmer temperatures that prevail after planting in June are conducive to a faster rate of DM accumulation which can more than compensate for the shorter amount of time spent in vegetative growth before R1, and the faster daily rate of DM accumulation observed with

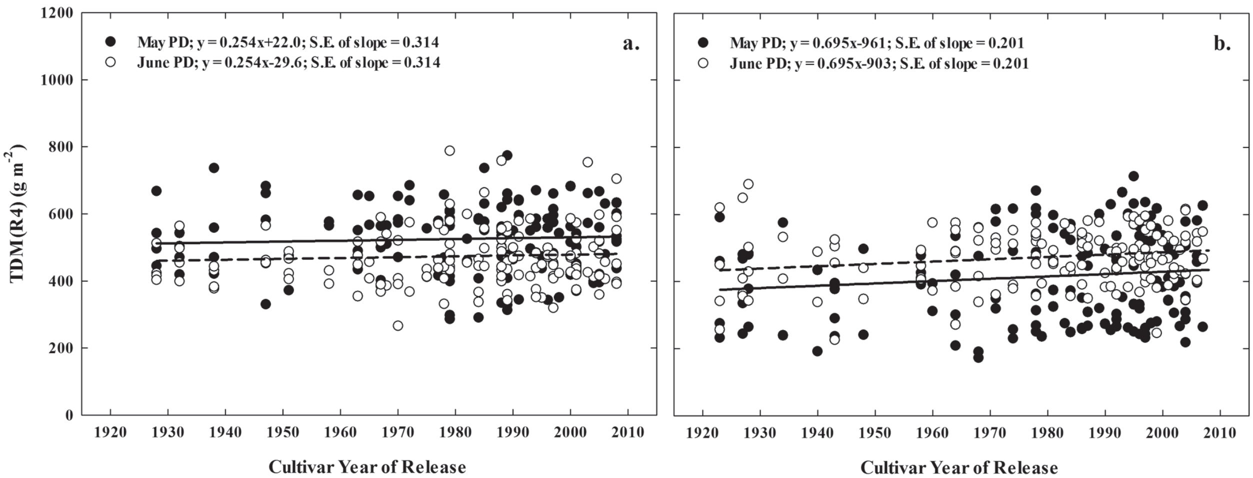

Figure 2. Regression of (a) Maturity Group (MG) II and (b) MG III total dry matter at growth stage R4 [TDM(R4)] (g m^{-2}) over soybean cultivar year of release at May (solid) and June (dashed) planting dates (PD) in 2010 and 2011.

late planting in MG II in the present study corroborated similar results reported by Anderson and Vasilas (1985).

A planting date × year of release interaction existed ($P < 0.01$) for TDM(R1) in MG II only (Fig. 1a). The divergence in the modeled trend lines for TDM(R1) in MG II was the result of a decrease of 0.65 (± 0.22) g m^{-2} yr^{-1} in newer, May-planted cultivars, relative to the statistically unchanged trend of −0.07 (± 0.28) g m^{-2} yr^{-1} observed in June-planted cultivars, a pattern that may be partially explained by the observed trends in vegetative growth duration in the same set of MG II cultivars (discussed later). These differing responses to planting date and cultivar year of release between maturity groups were likely attributable to a combination of both environmental differences between locations and the genotypic differences between maturity groups.

TDM(R4) in MG II remained unchanged over the course of eight decades of breeder-mediated improvement in cultivar yield over year of release (Fig. 2a), while TDM(R4) in MG III has observably risen over this same period, to the extent that TDM(R4) was greater ($P < 0.01$) in newer cultivars than in earlier released cultivars (Fig. 2b). Newer MG III cultivars were able to accumulate more DM from R1 to R4, a reproductive period that overlaps with the V6 and later phases of vegetative development (Bastidas et al., 2008). The annual increase of 0.70 (± 0.20) g m^{-2} yr^{-1} in TDM(R4) for MG III was small relative to the annual increase in TDM production after R4 in the same set of cultivars (discussed next). Planting date did not affect the amount of TDM(R4) produced in either maturity group, and in the same manner, the interaction between the main effects of planting date and year of release were not significant (Fig. 2). The failure to detect a planting date × year of release interaction suggested that TDM(R4) could not be enhanced in newer cultivars by advancing planting date by approximately 30 d.

Kumudini et al. (2001) found TDM levels to be similar between old and new cultivars until the R4 growth stage, but thereafter, newer cultivars were able to accumulate more DM than earlier released cultivars. Similarly, De Bruin and Pedersen (2009) reported no significant differences in TDM among old and new cultivars when TDM was measured at 85 d after emergence (approximately R4); however, newer cultivars were able to accumulate significantly more DM by 105 d after emergence (approximately R5.5) and during the SFP. Taking into consideration the results from the present study and from previous research, R4 appears to be approximately the point during seasonal soybean growth and development at which newer cultivars begin to accumulate greater amounts of DM than earlier released cultivars. This slightly higher accumulation rate subsequently accelerates and continues during SFP.

Recently released cultivars produced significantly greater ($P < 0.001$) TDM(R7) than did cultivars from earlier years of release in both maturity groups (Fig. 3). The improved ability of newer cultivars to accumulate more DM during the SFP and subsequently translate the accumulated DM into greater seed yield has been well documented (Kumudini et al., 2001; Pedersen and Lauer, 2004b; De Bruin and Pedersen, 2009). Planting date had an appreciable impact on TDM(R7) in both MG II ($P < 0.05$) and MG III ($P < 0.001$) cultivars (Fig. 3). May-planted cultivars were able to accumulate significantly more DM by R7 than cultivars planted approximately 30 d later. The TDM(R7) results in the present study complement the results of Pedersen and Lauer (2004b), who observed increased TDM in early- vs. late-May planting at the R6 stage. In this study, a significant interaction between planting date and cultivar year of release ($P < 0.05$) for TDM(R7) was detected in MG II, whereas the relationship in MG III cultivars was weak ($P = 0.052$) (Fig. 3). These results indicate that TDM(R7) in newer MG II and MG III cultivars can be enhanced more than what is possible with older cultivars

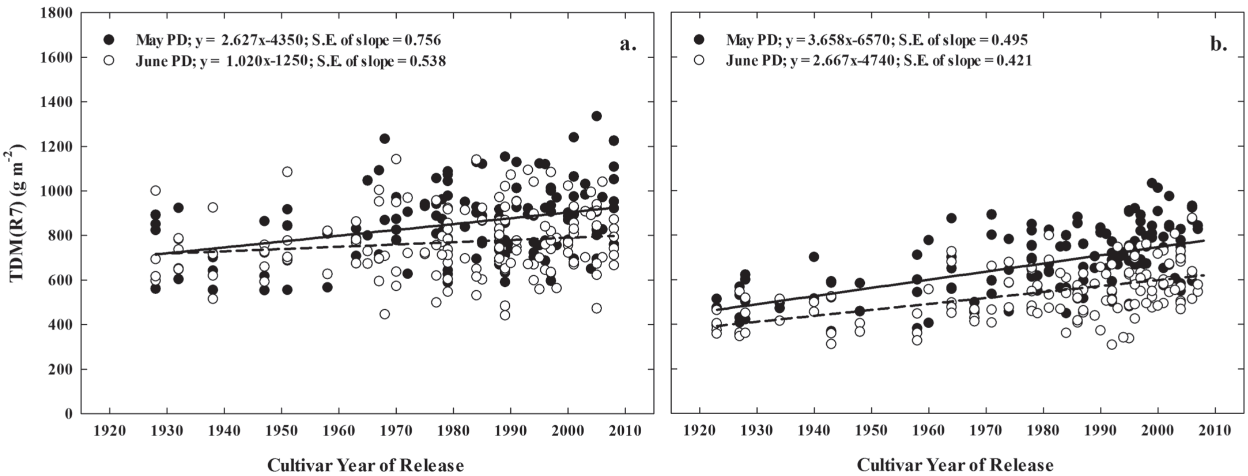

Figure 3. Regression of (a) Maturity Group (MG) II and (b) MG III total dry matter at growth stage R7 [TDM(R7)] (g m^{-2}) over soybean cultivar year of release at May (solid) and June (dashed) planting dates (PD) in 2010 and 2011.

when the planting date is advanced from June to May. This synergistic interaction, which results in significantly higher TDM(R7) in early-planted, newly released cultivars, offers a physiological foundation for the concordant synergism of early planting with newer MG III cultivar releases relative to seed yield that was recently documented by Rowntree et al. (2013).

Clearly, the ability of newer cultivars to accumulate more DM after R4, and especially during the SFP, has facilitated breeder selection for higher yielding, recent cultivar releases and thus has contributed to genetic yield improvement. Greater assimilation of carbon and improved DM accumulation during the SFP among newer cultivars is the result of an increased duration of leaf area and improved crop growth rates (De Bruin and Pedersen, 2009). Researchers have speculated that the improved lodging resistance in newer cultivars also may allow for greater assimilate supply and canopy photosynthesis because of improved light interception (Specht et al., 1999). In the present study, lodging scores (1 = erect, 5 = fully lodged) in both maturity groups decreased nearly identically ($P < 0.001$) over cultivar year of release at a rate of 0.027 (± 0.003) scoring units yr^{-1} (data not shown), confirming similar findings of other researchers (Luedders, 1977; Specht and Williams, 1984; Voldeng et al., 1997). There was no effect ($P > 0.05$) of planting date, or a planting date × year of release interaction, on lodging resistance in either maturity group.

Harvest Index

Many inconsistencies regarding the degree of genetic improvement, if present at all, in HI have been reported in the literature. These inconsistencies have been speculated to stem from differences in experimental techniques across studies, such as the methods used in calculating growth parameters, the timing and techniques used in sampling, and the genotypic background of the cultivars evaluated (Kumudini, 2002). Furthermore, much of the research evaluating HI with respect to cultivar year of release has been based on the use of a limited number of cultivars (approximately 4—6) within a given maturity group (Gay et al., 1980; Frederick et al., 1991; Kumudini et al., 2001; DeBruin and Pedersen, 2009). Although research on soybean HI is obviously resource intensive, determining the degree of genetic change in HI (and other physiological traits) requires the evaluation of HI in a large sample of historical cultivar releases, so that the regression of HI over year of release will accurately reflect the annualized degree of change over time. With a larger sample, the risk of drawing inappropriate conclusions from limited number of cultivars that may not be historically representative will be mitigated, and the scope of inference will be substantively expanded.

Newer cultivars exhibited greater HIs than earlier released cultivars ($P < 0.001$), improving at a rate of 0.089% (± 0.021) yr^{-1} for MG II and 0.094% (± 0.013) yr^{-1} for MG III (Fig. 4). The genetic improvement in HI over cultivar year of release detected in the present study (approximately 0.09% yr^{-1}) confirms previous results reported for shorter-season MG 00 to MG 0 cultivars in China (0.10% yr^{-1}) (Jin et al., 2010) and Canada (0.12% yr^{-1}) (Morrison et al., 1999). However, no differences in HI between old and new cultivars have been detected by other researchers (Frederick et al., 1991; De Bruin and Pedersen, 2009), which might be due to the fewer number of cultivars used in those studies compared the number used in the present study. Planting date had no impact on HI in both maturity groups, and thus the report by Pedersen and Lauer (2004a) of a 2% higher HI in early-May- vs. late-May-planted soybean in Wisconsin was not confirmed in the present study. The lack of a HI response to earlier planting is in agreement with the Spaeth et al. (1984) postulation of HI stability across a range of environmental conditions, including latitudinal variation in photoperiod and soil moisture availability (Spaeth et al.,

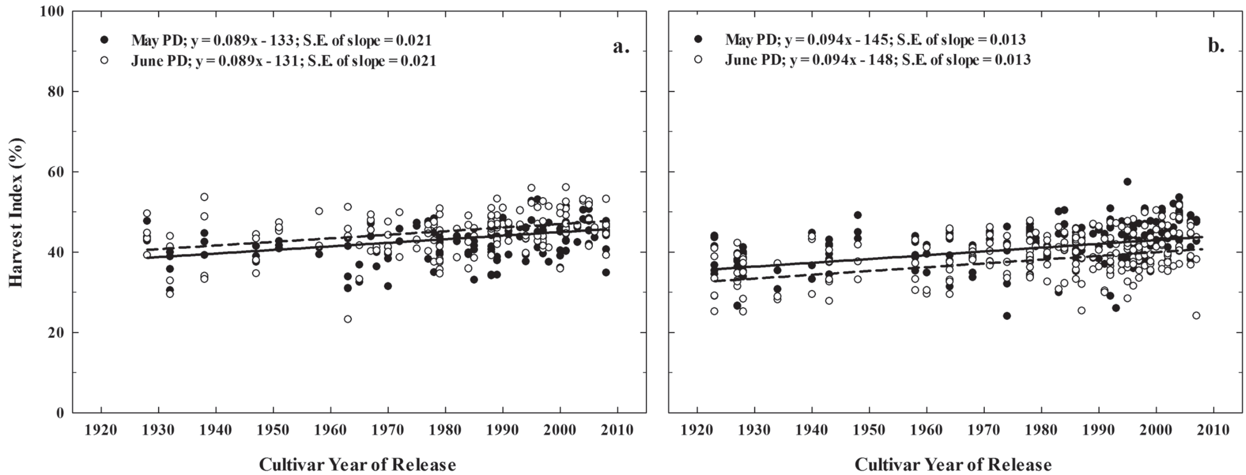

Figure 4. Regression of (a) Maturity Group (MG) II and (b) MG III harvest index (%) over soybean cultivar year of release at May (solid) and June (dashed) planting dates (PD) in 2010 and 2011.

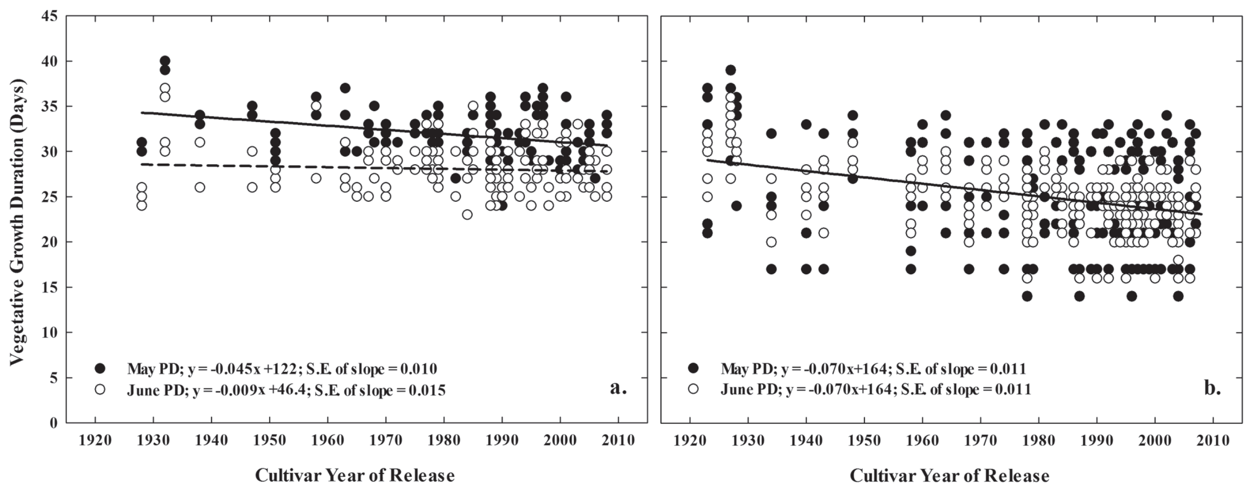

Figure 5. Regression of (a) Maturity Group (MG) II and (b) MG III vegetative growth duration (days from V1 to R1) over soybean cultivar year of release at May (solid) and June (dashed) planting dates (PD) in 2010 and 2011.

1984), though Purcell and Specht (2004) noted that HI in soybean cultivars can be reduced if subjected to a drought.

The planting date × year of release interaction was not statistically significant for either maturity group (Fig. 4), reflecting the similar response of HI to planting date among old and new cultivars. Because a significant planting date × year of release interaction existed for TDM(R7) and not for HI, it appears that increased TDM, not HI, has been responsible for the synergistic role that earlier planting plays in optimizing the magnitude of the annualized genetic yield gain. Simply put, the higher yield possible when newer cultivars are planted early is likely attributable to the greater TDM arising from the interplay of better genetics *and* better agronomics.

Growth-Stage Duration

Determining whether SFD had been altered by long-term breeder selection for higher yield, and within that context, whether SFD differed in response to planting date, were two of the primary goals in the evaluation of soybean phenology in this historical set of soybean cultivars planted 30 d apart. Also of interest was the impact of any indirect consequences of long-term yield selection on the lengths of vegetative (V1–R1) and reproductive growth (R1–R7) periods and what those data might reveal in terms of SFP.

The duration of V1 to R1 vegetative growth decreased ($P < 0.001$) over cultivar year of release in MG III cultivars at a rate of 0.070 (± 0.010) fewer days per year, but there was no effect of planting date or a planting date × year of release interaction in this set of cultivars. The duration of vegetative growth in MG II cultivars was not shown to change over year of release ($P = 0.064$); however, a significant interaction ($P < 0.001$) between the main effects of planting date and cultivar year of release existed in MG II cultivars, suggesting that the rate of change in vegetative growth duration was not the same for each planting date (Fig. 5). Vegetative growth duration in the May planting decreased at a rate of 0.036 (± 0.010) d yr^{-1} compared to the unchanged duration between V1 and R1 in the June planting, which was a similar pattern to the trends in TDM(R1)

Table 4. Simple linear correlation coefficients (*r*) between yield, total dry matter at growth stages R1, R4, and R7 [TDM(R1), TDM(R4), TDM(R7)], harvest index (HI), vegetative growth duration (VGD), reproductive growth duration (RGD), seed-fill period (SFP) and cultivar year of release for Maturity Group (MG) II and MG III cultivars at May and June planting dates (PD) during 2010 and 2011.

	TDM(R1)	TDM(R4)	TDM(R7)	HI	VGD	RGD	SFP	Year of release
MG II, May PD								
Yield	-0.14	-0.06	0.34***	0.24**	-0.21*	0.30***	0.28***	0.72***
TDM(R1)	–	0.08	-0.11	-0.21**	0.59***	-0.25**	-0.08	-0.26**
TDM(R4)	–	–	0.14	-0.18*	-0.03	0.23**	0.18*	-0.03
TDM(R7)	–	–	–	0.01	-0.14	0.40***	0.38***	0.35***
HI	–	–	–	–	-0.31***	-0.33***	-0.35***	0.30***
VGD	–	–	–	–	–	-0.26**	-0.02	-0.32***
RGD	–	–	–	–	–	–	0.94***	0.21*
SFP	–	–	–	–	–	–	–	0.16
MG II, June PD								
Yield	-0.01	0.34***	0.43***	0.11	0.21*	0.50***	0.53***	0.62***
TDM(R1)	–	0.04	0.09	-0.25**	0.55***	-0.15	-0.01	-0.03
TDM(R4)	–	–	0.33***	-0.18*	0.36***	0.49***	0.48***	0.11
TDM(R7)	–	–	–	-0.13	0.37***	0.45***	0.48***	0.15
HI	–	–	–	–	-0.50***	-0.36***	-0.39***	0.36***
VGD	–	–	–	–	–	0.41***	0.55***	-0.06
RGD	–	–	–	–	–	–	0.96***	0.11
SFP	–	–	–	–	–	–	–	0.16
MG III, May PD								
Yield	0.27**	-0.25**	0.82***	0.34***	-0.24***	0.39***	0.36***	0.67***
TDM(R1)	–	0.22**	0.34***	-0.14	-0.04	0.19*	0.07	0.20*
TDM(R4)	–	–	-0.20*	0.17	-0.20*	0.44***	0.09	0.13
TDM(R7)	–	–	–	0.35**	-0.09	0.33***	0.40***	0.58***
HI	–	–	–	–	-0.44***	0.28***	0.23***	0.32***
VGD	–	–	–	–	–	-0.59***	-0.05	-0.33***
RGD	–	–	–	–	–	–	0.61***	0.62***
SFP	–	–	–	–	–	–	–	0.57***
MG III, June PD								
Yield	-0.18*	-0.04	0.83***	0.44***	-0.25***	0.17**	0.20***	0.68***
TDM(R1)	–	0.57***	-0.25**	0.13	-0.18*	0.46***	0.32***	0.07
TDM(R4)	–	–	-0.03	0.35**	-0.18*	0.46***	0.30***	0.14
TDM(R7)	–	–	–	0.47***	-0.06	-0.06	0.09	0.52***
HI	–	–	–	–	-0.27***	0.04	0.17*	0.32***
VGD	–	–	–	–	–	-0.49***	-0.18**	-0.53***
RGD	–	–	–	–	–	–	0.76***	0.57***
SFP	–	–	–	–	–	–	–	0.46***

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the <0.001 probability level.

in MG II cultivars. Simple correlation coefficients for vegetative growth duration and TDM(R1) ranged from 0.55 to 0.59 (Table 4). The main effect of planting date on this phase of soybean phenology was significant ($P < 0.001$), but it is important to recognize that earlier planted cultivars spent a longer amount of time in the V1 to R1 period than did later planted cultivars, largely because of the cooler temperatures during May. However, as noted, early-planted cultivars still produced less TDM(R1) than late-planted cultivars. V1 to R1 growth response was unique to the cultivar genetics within a maturity group, as well as the moisture and temperature regimes at each location.

The observed reduction in the duration of vegetative growth corresponded well with the observed enhancement ($P < 0.001$) in reproductive growth duration over cultivar year of release in both maturity groups (Fig. 6). Early-planted cultivars also had a greater duration of reproductive growth than late-planted cultivars, although the planting date effect was not as strong in MG III ($P = 0.063$) as it was in MG II ($P < 0.05$). May-planted MG II cultivars exhibited a rate of improvement in the duration of reproductive growth (0.089 [± 0.015] d yr^{-1}) that was nearly twice the rate of improvement (0.046 [± 0.016] d yr^{-1}) in June-planted cultivars, leading to a significant interaction ($P < 0.01$) between

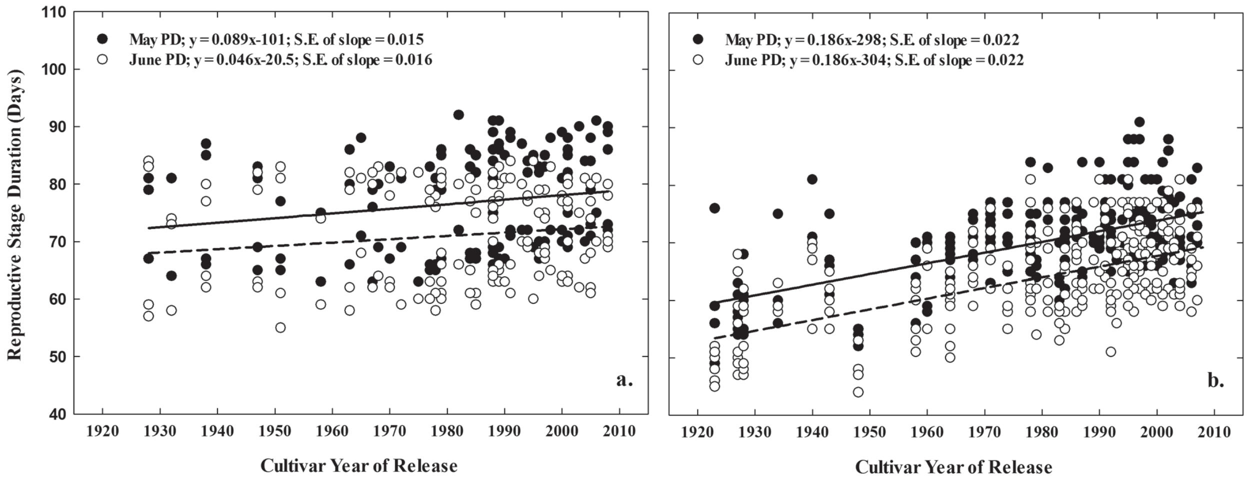

Figure 6. Regression of (a) Maturity Group (MG) II and (b) MG III reproductive growth duration (days from R1 to R7) over soybean cultivar year of release at May (solid) and June (dashed) planting dates (PD) in 2010 and 2011.

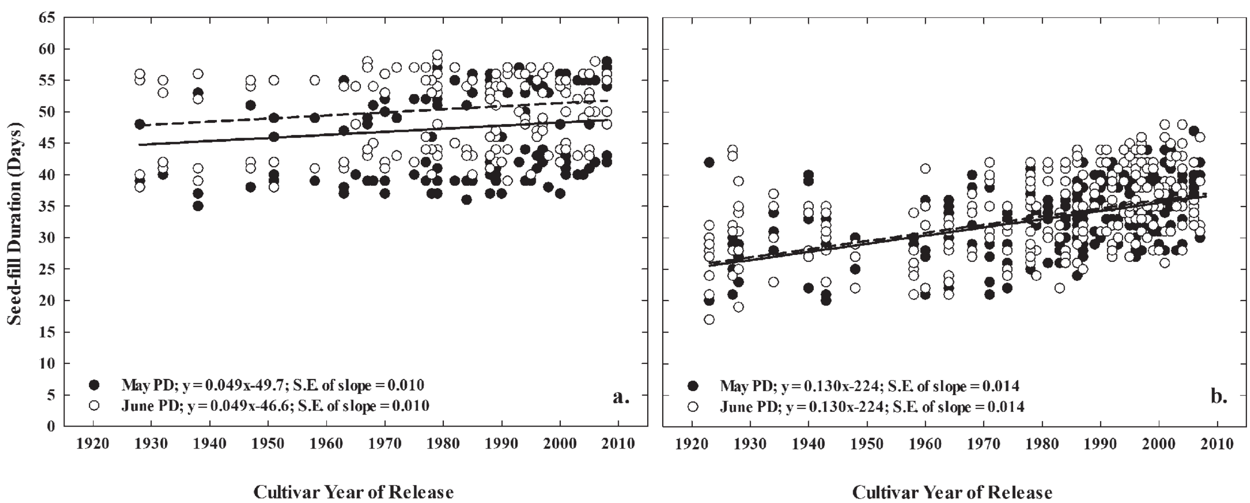

Figure 7. Regression of (a) Maturity Group (MG) II and (b) MG III seed-fill duration (days from R5 to R7) over soybean cultivar year of release at May (solid) and June (dashed) planting dates (PD) in 2010 and 2011.

the annualized rate of change in reproductive growth duration and planting date. In MG III, there was not a discernible difference ($P > 0.05$) in the rate of annual improvement in reproductive growth duration between the two planting dates. In short, breeders have indirectly selected for cultivars that begin anthesis somewhat sooner after emergence, which has increased the duration of the R1 to R7 reproductive growth period in newer cultivar releases.

Newer cultivars exhibited a longer ($P < 0.001$) SFP (R5–R7) than did earlier released cultivars in both MG II (0.049 [± 0.010] d yr^{-1}) and MG III (0.13 [± 0.014] d yr^{-1}) (Fig. 7). The annual improvement in SFD is consistent with previous research that reported a positive correlation between longer SFPs and higher yields when cultivars were evaluated for both (Gay et al., 1980; McBlain and Hume, 1980; Boerma and Ashley, 1988). Planting date had no effect ($P > 0.05$) on SFD in either maturity group in the present study. Similar results also were reported by Egli et al. (1987) at two planting dates, albeit with a limited number of cultivars. In addition, the interaction of planting date with cultivar year of release was not significant in either maturity group, which suggested that SFD among old and new cultivars was not influenced by the practice of earlier planting utilized in more modern production systems.

Very low soil moisture availability during the SFP has generally been shown to reduce SFD (Meckel et al., 1984), primarily because a drought can significantly hasten the onset of soybean plant senescence (Specht et al., 2001). Moisture availability in Wisconsin was very limited during the SFP in 2011 (primarily August) and resulted in a shorter SFD than what was observed in 2010, when adequate moisture conditions prevailed. At all MG III locations, soil moisture availability was very limited during the SFP in both 2010 and 2011. Environmental conditions varied between years of the experiment in both maturity groups, and those conditions were frequently influential in the determination of SFD.

CONCLUSIONS

Based on the measurements made in the present study, the genetic yield improvement in MG II and MG III cultivars that was achieved by long-term breeder selection, as reported by Rowntree et al. (2013), seems to have resulted in coordinately greater DM accumulation and a higher HI. Genetic improvement in TDM production was largely the result of greater DM accumulation during the later stages of reproductive growth (R4–R7) and not during vegetative growth. Early-planted cultivars produced greater TDM(R7) than did late-planted cultivars, but planting date had no detectable effect on HI. A synergistic interaction of planting date with cultivar year of release in TDM(R7) revealed that newer cultivars respond more positively to early planting by accumulating more DM after R4 and during the SFP. However, an interaction of planting date with cultivar year of release was not observed in HI. Therefore, the synergism attained in yield when newer MG III cultivars are planted earlier, which was recently documented by Rowntree et al. (2013), likely arises, not from greater HI, but from the greater TDM production possible with this on-farm input of technological innovation in both genetics *and* agronomics.

As yields have improved, breeder focus on selecting for high yield has led to indirect selection for a coordinate decrease in the duration of V1 to R1 vegetative growth *and* an increase in the duration of R1 to R7 reproductive growth. The observed rate of SFD increase over cultivar year of release corresponded well with the annual improvement in yield observed in MG II and MG III cultivars. Given the indeterminate nature of MG II and MG III cultivars, the annual improvement in both the duration of reproductive growth and SFD may provide an increased period of time during the growing season through which newer cultivars can take advantage of positive weather events and produce higher yields. Planting date did not affect SFD, nor did the response of SFD over cultivar year of release differ between planting dates. Thus, the on-farm trend toward earlier planting in the midwestern United States has had no significant impact on the length of the SFP, despite the observable trend toward a longer SFP in newer cultivars. Due to the low heritability of SFD and lack of positive SFD response to production systems that favor higher yields (i.e., earlier planting), the data in the present study would suggest that SFD does not deserve much attention in soybean breeding programs. However, breeders that utilize early-planting trials in selection programs have an advantage in the sense of exploiting the synergistic interaction between earlier planting and the selection of high-yielding breeding lines as potential cultivar releases. Indeed, given that greater TDM production is likely the physiological foundation for current and future genetic yield improvement, breeders should consider coupling early-planting test environments with other agronomic management options that might optimize TDM.

Acknowledgments

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