

Soybean Yield Partitioning Changes Revealed by Genetic Gain and Seeding Rate Interactions

Justin J. Suhre, Nicholas H. Weidenbenner, Scott C. Rowntree, Eric W. Wilson, Seth L. Naeve, Shawn P. Conley, Shaun N. Casteel, Brian W. Diers, Paul D. Esker, James E. Specht, and Vince M. Davis*

ABSTRACT

Soybean [*Glycine max* (L.) Merr.] yield has increased during the past century; however, little is understood about the morphological parameters that have contributed most to yield gain. We conducted field studies to determine relationships between genetic gain of soybean yield and seeding rate. The hypothesis was newer cultivars would express higher yield than older cultivars when grown in higher plant populations. A total of 116 soybean cultivars equally representing Maturity Groups (MGs) II and III released over the last 80 yr were evaluated at high and low seeding rates in Wisconsin, Minnesota, Illinois, and Indiana. Seeding rates were 445,000 and 148,000 seeds ha⁻¹ resulting in 311,000 and 94,000 plants ha⁻¹ (high and low, respectively). Seed yield was greater for the high seeding rate vs. low seeding rate throughout all cultivars and years of release, but the difference was larger in newer cultivars. The differences observed primarily came from an increased number of pods and seeds plant⁻¹. However, newer cultivars grown in low seeding rates increased per plant yield linearly by $0.118 (\pm 0.02)x - 208.0$ g plant⁻¹, where x = year-of-release, which was three times greater than at the high seeding rate. The greater yield trend came from seeds produced on plant branches. Therefore, newer cultivars produce more compensatory yield on plant branches under lower plant populations than older cultivars, so over the last 80 yr there has been a diminishing response to the expected yield penalty from reduced plant density.

Soybean yield has increased over the last century. The rate at which yield has increased, however, can be calculated in a variety of ways over different segments of time. Hartwig (1973) stated that soybean yield had continually increased dating back to the early 1900s. The USDA began recording the national average yield of soybean in 1924. Regression of yield on year indicated that yield has improved 23.4 kg ha⁻¹ yr⁻¹ between 1924 and 2011 (USDA-ERS, 2011). Voldeng et al. (1997) proposed that in Canada, yield gain from genetic improvement could be fit to a quadratic function, which indicated that genetic yield improvement before 1976 was nil. In the United States, Specht et al. (1999) reported a linear soybean yield increase of 22.6 kg ha⁻¹ yr⁻¹ between 1924 and 1998, but a 31.4 kg ha⁻¹ yr⁻¹ linear increase trend between 1972 and 1997.

Soybean yield is produced as a phenotypic expression through the combination of genetic potential, agronomic practices, and environmental conditions. Therefore, the improvement in genetics due to breeding efforts and biotechnology (Sleper and Shannon, 2003), coupled with improvements in agronomic management practices, have contributed some proportion of the yield increase over time. The exact proportions contributed by each, however, are not well understood. Specht and Williams (1984) estimated the relative contribution of genetic improvement in the United States was 12.5 kg ha⁻¹ yr⁻¹ among MG IV or earlier hybridized cultivars released after 1940. Later, Specht et al. (1999) summarized several other yield gain studies (Luedders, 1977; Boerma, 1979; Wilcox et al., 1979; Specht and Williams, 1984; Voldeng et al., 1997) and reported the average annual increase in soybean yield due to improved genetics ranged from 10 to 30 kg ha⁻¹ yr⁻¹.

Specht et al. (1999) estimated that roughly half of the increasing yield trend is from improved genetics, and the remaining half is the result of improved agronomic practices such as earlier planting, narrower rows, better weed control, and reduced harvest losses. Geneticists and agronomists both routinely recognize that phenotypic expression comes from interactions arising from genetics $\times$ environment ($G \times E$), thus we are precisely interested in the interactions of genetic improvement $\times$ seeding rate ($GI \times SR$). A variety of agronomic practice changes have been hypothesized to improve soybean yield including (i) earlier planting dates (Johnson, 1987; Specht et al., 1999; Heatherly and Elmore, 2004; Bastidas et al., 2008), (ii) narrower row spacing (Voldeng et al., 1997; Specht et al., 1999; Heatherly and Elmore, 2004), (iii) higher seeding rates

J.J. Suhre and B.W. Diers, Dep. of Crop Sciences, Univ. of Illinois, Urbana, IL 61801; N.H. Weidenbenner and S.L. Naeve, Dep. of Agronomy and Plant Genetics, Univ. of Minnesota, St. Paul, MN 55108; S.C. Rowntree, V.M. Davis, and S.P. Conley, Dep. of Agronomy, Univ. of Wisconsin, Madison, WI 53706; E.W. Wilson and S.N. Casteel, Dep. of Agronomy, Purdue Univ., West Lafayette, IN 47907; P.D. Esker, Dep. of Plant Pathology, Univ. of Wisconsin, Madison, WI 53706, current address: Escuela de Agronomía, Universidad de Costa Rica, San Jose, Costa Rica; J.E. Specht, Dep. of Agronomy and Horticulture, Univ. of Nebraska, Lincoln, NE 68583. Received 3 Jan. 2014. *Corresponding author (vmdavis@wisc.edu).

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Abbreviations: MG, maturity group.

(Voldeng et al., 1997; Cober et al., 2005; De Bruin and Pedersen, 2009), (iv) improved weed control from herbicide use (Luedders, 1977; Voldeng et al., 1997; Specht et al., 1999), (v) increased soil fertility arising from fertilization of alternate-year crops (Luedders, 1977), and (vi) reduced harvest losses (Specht et al., 1999; Ustun et al., 2001). Certainly, some of these improvements arise from the reduction of stresses on the plants during growth, and Pathan and Sleper (2008) stated that increasing resistance to biotic and abiotic stress is the overall goal of plant breeding. As agronomic and genetic changes have co-occurred over time, it is plausible that agronomic improvement has led to production environments that now allow *more* of the intrinsic genetic yield potential currently available in modern era soybean cultivars to be expressed. By testing a historic array of cultivars in diverse production environments, it can be determined if genetic yield gain is similar (i.e., parallel trends) or different (i.e., intersecting regression trends). If the regression trends are parallel but the genetic trend line is more elevated in one environment vs. the other, it would reflect the agronomic effect is independent of the genetic gain. In contrast, if the divergent genetic yield gain rates are observed in different production environments (i.e., regression interaction), it would reflect a synergistic interaction over time between the yield improvement mediated by genetics and that mediated by agronomics.

One stress soybean plants must overcome in any typical production environment is interplant competition for needed resources like light and soil-provided nutrients (Weiner and Thomas, 1986). Of interest, though, is the fact that many field research experiments have established that soybean can produce relatively similar yields from large changes in plant density (Carpenter and Board, 1997a, 1997b; Board, 2000; Edwards and Purcell, 2005; Harder et al., 2007; Lee et al., 2008). Previous research has documented that 95% of observed maximum yields were obtained with a seeding rate that was either as low as 73,000 or as high as 815,000 seeds ha^{-1} (Egli, 1988; Oplinger and Philbrook, 1992; Elmore, 1998; De Bruin and Pedersen, 2008; Cox and Cherney, 2011). However, current University Extension recommendations in the region of these experiments suggest harvest plant populations need to be at least 247,000 plants ha^{-1} to expect maximum yield (Conley and Gaska, 2010; Davis, 2010; Pedersen, 2009; Robinson and Conley, 2007).

It is likely that not all the mechanisms responsible for the ability of soybean plants to produce compensatory seed yield like branch initiation, leaf area expansion, reduced flower and pod abortion, additional seeds produced per pod, additional seed mass, or others are fully understood when soybean are grown at low densities. However, one very important mechanism is the ability for plants to produce seed yield on branches, in addition to the main stems (Lehman and Lambert, 1960; Herbert and Litchfield, 1982; Carpenter and Board, 1997a; Frederick et al., 2001). In general, the interception of solar radiation, and the utilization of radiant energy for plant biomass are the main processes in generating crop growth and yield. Therefore, achieving plant growth early in the season is important to maximize yield (Bullock et al., 1998; Edwards et al., 2005; Bastidas et al., 2008). Maximum yields are most likely produced from environments when complete canopy coverage is accomplished by the beginning of pod developmental reproductive stages (R3); however, soybean has a significant reduction in yield if complete canopy does not occur by the beginning of seed fill (R5) (Purcell et al., 2002; Edwards et al., 2005; Bastidas et al., 2008; Lee et al., 2008). Board and Settini (1986) determined

two-thirds of plant growth from branches occurs between R1 and R5. Therefore, higher population densities may be more important early in the growing season to maximize light interception (Purcell et al., 2002). On the contrary, the initiation of branches occurs very early in vegetative development, and cultivars with an improved ability to produce branches to maximize light interception during the critical stages of reproductive growth could have an advantage of producing compensatory yield in lower density environments (Carpenter and Board, 1997a). Knowledge of whether partitioning yield between stems and branches over time as influenced by the cultivars released over time will give credence to the fact this point is important.

To maximize the potential for continually increasing soybean yield in the future, a much better understanding of the yield gain contributions due to genetic improvement, agronomic practices, and/or associated synergistic effects could help direct breeders and agronomists to better target their improvement efforts. Few previous research reports have clearly elucidated the differential contributions of agronomic vs. genetic advancements to soybean yield gains, particularly as it relates to yield components like branching ability as influenced by management decisions like seeding rate. We report here an experiment aimed at identifying potential interaction between two seeding rates and the rate of genetic yield gain. The latter was estimated by evaluating the agronomic performance of a historic set of cultivars planted at low and high seeding rates. Our null hypothesis was that newer cultivars would express higher yield potential than older cultivars when grown in higher plant densities showing a greater ability to withstand interplant competition. Previous experiments have examined this relationship and found newer cultivars to plateau yield at higher plant densities than older cultivars suggesting newer genetics can better withstand plant competition (Cober et al., 2005; De Bruin and Pedersen, 2009) using different maturity groups and/or different experimental designs. Our study examines a larger number of cultivars. Moreover, given that compensatory yield production on soybean plant branches is known to be important, it is a major focus of this research because we are not aware of any reports documenting the change in yield partitioning over genetic years of release previous to this experiment. Therefore, in addition to the foregoing hypothesis, we tested whether modern cultivars differ from obsolete cultivars with respect to the way they partition seed production between main stems and branches when the planting density is changed.

MATERIALS AND METHODS

Field trials were conducted to determine the interaction between stand density and genetic yield gain in soybean. This experiment was conducted using the same cultivars and locations as Rowntree et al. (2013) and Wilson et al. (2014). There were 59 MG II cultivars grown in Arlington, WI, and Waseca, MN; and there were 57 MG III cultivars grown in Urbana, IL, and Lafayette, IN (Table 1). Cultivars were seeded once at 445,000 seeds ha^{-1} (high) and 148,000 (low) seeds ha^{-1} in plots randomly located in a block, and there were 13 MG II cultivars and 15 MG III cultivars with two replications also randomly located in the block to provide an estimate of experimental error in the regression models for a total of 144 plots. Planted plot dimensions at all locations were 3.1 m wide by 4.6 m long which consisted of four 76-cm wide rows. Location information and soil characteristics for the four locations are presented in Table 2. There was one field

trial at each location and year for a total of 8 site-years. Plant stands were recorded at harvest to evaluate the relationship between the plant stand target goal and the plant stand that was observed in each of the two seeding rates. Harvest stands, when averaged over the experiment were 311,000 (70% of target) and 94,000 (64% of target) plants ha⁻¹ for the high and low seeding rate treatments, respectively. An analysis of variance indicated that the observed stands for the two treatments were significantly different at $P < 0.05$ at all locations (data not shown). Stands in every plot were not manually thinned or adjusted to achieve identical plant densities for each cultivar, so all data analyses presented herein use the two seeding density target values as the two classification levels.

To provide evidence of genetic gain for the high and low seeding rates over the year-of-release, 1 m of row from one of the center two rows was hand harvested at maturity at the Urbana and Waseca locations. Plants were cut at the soil surface using a hand-held clipper, the total number of plants hand-harvested was recorded, and plant branches were separated from main stems in the field. Stems and branches were processed separately thereafter. Samples were dried with a forced air dryer at 60°C for 7 d to obtain consistent moisture. Dried stem and branch samples were weighed, and heights of main stem were measured from the cut base to the top of the uppermost reproductive node for MG III cultivars. Nodes on main stems and branches were also counted. Pods were also counted for the entire meter of row and divided by the number of plants in the sample to determine pods stem⁻¹. Subsequently, pods node⁻¹ was calculated by dividing total pods by total stem nodes. Pods were threshed by hand and seeds were separated from pod hulls and other unwanted plant debris using a series of standard seed sieves. All seeds for the entire meter of row were counted using a computerized seed counter (Agriculture, Guelph, ON, Canada) and weighed to determine the mass seed⁻¹.

Harvest index was determined and expressed as a percentage of total stem + branch seed weight plot⁻¹ to total dried plant biomass weight plot⁻¹ without accounting for dropped leaves from the Waseca and Urbana locations. The remaining plants in the center two rows of each plot from those two locations, as well as Arlington and Lafayette locations, were harvested with a plot combine for seed yield. Final seed yield was adjusted to a moisture content of 130 g kg⁻¹.

The experimental data were subjected to a mixed-effect regression analysis using the PROC MIXED procedure in SAS Version 9.2 (SAS Institute, 2009). Prior research has expressed genetic yield gain trends linearly (Specht et al., 1999) or quadratically (Voldeng et al., 1997) over cultivar year-of-release. A linear mixed-model provided the best fit for this experiment, and was used here. Seed yield ha⁻¹ (kg), seed yield plant⁻¹ (g), stem seed yield plant⁻¹ (g), branch seed yield plant⁻¹ (g), stem height plant⁻¹ (cm), nodes stem⁻¹ plant⁻¹ (n), pods stem⁻¹ node⁻¹ (n), seeds stem⁻¹ pod⁻¹ (n), seeds branch⁻¹ pod⁻¹ (n), and harvest index (%) were analyzed. Seeding rate, year-of-release, maturity group and their respective interactions were considered fixed effects. Variables were removed from the model if deemed insignificant by the -2 log likelihood method to present a simplified model for analyzed data when possible. Environment and cultivar, along with environment × seeding rate, cultivar × seeding rate, and environment × cultivar × seeding rate were considered random effects. Cultivar was assigned as a random effect due to the fact that those selected

for the experiments were chosen from a larger group of cultivars available over the eight decades represented. Maturity group was examined as a classification variable to determine if there were any seed yield (kg ha⁻¹) differences between MG II and MG III cultivars. The seeding rate × year-of-release interaction was examined to determine if differences in the rate of yield gain existed between the seeding rates, and yield data and morphological parameters were regressed over year-of-release to evaluate change over time for each of the two seeding rates.

RESULTS AND DISCUSSION

Influence of Maturity Group

The effect of MG, and its interactions, that is, MG × year-of-release, MG × seeding rate and MG × year-of-release × seeding rate interactions were not significant for yield ($P = 0.61$), seed yield plant⁻¹ ($P = 0.39$), stem nodes plant⁻¹ ($P = 0.33$), stem pods node⁻¹ ($P = 0.13$), branch seeds pod⁻¹ ($P = 0.73$), stem seed weight plant⁻¹ ($P = 0.36$), branch seed weight plant⁻¹ ($P = 0.37$) or harvest index ($P = 0.95$). Stem seeds pod⁻¹ was not affected by MG × year-of-release × seeding rate, MG × year-of-release, or MG ($P = 0.76$). The interaction of MG × year-of-release for stem seeds pod⁻¹ was significant ($P = 0.01$), but it also was excluded from the final model since all other factors analyzed for MG were insignificant. Plant height was not measured for MG II cultivars, so no interactions between plant height and MG could be evaluated. The MG was not expected to influence these results; however, we examined this possibility as MG is a common and important divisor for different sets of cultivars grown in the different geographies where these experiments were located. Moreover, in a similar set of experiments maturity has been found to be later in more recently released cultivars (Rinker et al., 2014). Due to the lack of differences observed, a reduced model excluding MG and its interactions was used for all other dependent variables examined.

Seed Yield

More recently released cultivars produced higher seed yield ha⁻¹ than previously released cultivars ($P < 0.001$) for both seeding rates (Fig. 1), and yield was also always greater in the higher seeding rate ($P = 0.0002$). More importantly, there was an interaction between seeding rate and cultivar year-of-release ($P < 0.0001$). The genetic yield gain rate in the historic cultivar set, when planted at a higher seeding rate was estimated to be 24.1 ± 1.2 kg ha⁻¹ yr⁻¹, but was only 19.3 ± 1.3 kg ha⁻¹ yr⁻¹ when those same cultivars were planted at a lower seeding rate (Fig. 1).

An increase in genetic yield gain over time has been well documented by other researchers (Luedders, 1977; Specht et al., 1999; Wilcox, 2001; Cober et al., 2005; De Bruin and Pedersen, 2008, 2009; Kahlon et al., 2011; Rowntree et al., 2013). In the present case, we must conclude that the interaction between genetic yield improvement and agronomic improvement (seeding rate) is synergistic, given the 4.8 kg ha⁻¹ yr⁻¹ greater yield gain observed at the higher seeding densities. The ability of newer genetics to withstand more plant competition than older genetics has also been reported by (a) Cober et al. (2005) who observed genetic yield gain of newer cultivars plateaued at higher plant densities than did older ones in a historic set of 34 Canadian cultivars of MG 00 and 0 released between 1934 and 1996 subjected to five seeding rates equidistantly spaced between 25 and 200 seeds m⁻²,

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

Cultivar	Year of release	Maturity Group	PI no.†	Pedigree‡	Cultivar	Year of release	Maturity Group	PI no.‡	Pedigree§
Korean§	1928	II	PI548360	From China	Dunfield§	1923	III	PI548318	P.I. 36846 (NE China)
Mukden§	1932	II	PI548391	P.I. 50523 (NE China)	Illini§	1927	III	PI548348	Sel. from A.K. in 1920
Richland§	1938	II	PI548406	P.I. 70502-2 (NE China)	AK (Harrow)§	1928	III	PI548298	Sel. from A.K. (by 1928)
Hawkeye§	1947	II	PI548577	Mukden × Richland	Mandell	1934	III	PI548381	Sel. from Manchu in 1926
Harosoy§	1951	II	PI548573	Mandarin (Ottawa)(2) × A.K. (Harrow)	Mingo	1940	III	PI548388	Sel. from Manchu in 1924
Lindarin	1958	II	PI548589	Mandarin (Ottawa) × Lincoln	Lincoln§	1943	III	PI548362	Mandarin × Manchu
Harosoy 63	1963	II	PI548575	Harosoy (8) × Blackhawk	Adams	1948	III	PI548502	Illini × Dunfield
Hawkeye 63	1963	II	PI548578	Hawkeye (7) × Blackhawk	Shelby	1958	III	PI548574	Lincoln (2) × Richland
Amsoy	1965	II	PI548506	Adams × Harosoy	Ford	1958	III	PI548562	Lincoln (2) × Richland
Corsoy§	1967	II	PI548540	Harosoy × Capital	Ross	1960	III	PI548612	Monroe × Lincoln
Beeson	1968	II	PI548510	C1253 (Blackhawk × Harosoy) × Kent	Wayne§	1964	III	PI548628	L49-4091 × Clark
Amsoy 71§	1970	II	PI548507	Amsoy (8) × C1253	Adelphia	1964	III	PI548503	C1070 × Adams
Wells	1972	II	PI548630	C1266R (Harosoy × C1079) × C1253	Calland§	1968	III	PI548527	C1253 × Kent
Harcor	1975	II	PI548570	Corsoy × OX383 (Corsoy × Harosoy 63)	Williams§	1971	III	PI548631	Wayne × L57-0034 (Clark × Adams)
Private 2-7	1977	II	na	na	Woodworth§	1974	III	PI548632	Wayne × L57-0034
Private 2-8	1977	II	na	na	Private 3-1§	1978	III	na	na
Wells II	1978	II	PI548513	Wells (8) × Arksoy	Cumberland	1978	III	PI548542	Corsoy × Williams
Vickery	1978	II	PI548617	Corsoy (5) × (L65-1342 and Anoka × Mack)	Oakland	1978	III	PI548543	L66L-137 (Wayne × L57-0034) × Calland
Corsoy 79	1979	II	PI518669	Corsoy (6) × Lee 68	Pella	1979	III	PI548523	L66L-137 × Calland
Beeson 80	1979	II	PI548511	Beeson (8) × Arksoy	Williams 82§	1981	III	PI518671	Williams (7) × Kingwa
Century§	1979	II	PI548512	Calland × Bonus	Private 3-15	1983	III	na	na
Amcor	1979	II	PI548505	Amsoy 71 × Corsoy	Zane	1984	III	PI548634	Cumberland × Pella
Private 2-11	1982	II	na	na	Harper	1984	III	PI548558	F4 sel. from an unknown diallel-cross pop.
Century 84	1984	II	PI548529	Century (5) × Williams 82	Chamberlain§	1986	III	PI548635	A76-304020 × Land O Lakes Max
Elgin	1984	II	PI548557	F4 selection from AP6 population	Private 3-2	1986	III	na	na
Preston	1985	II	PI548520	Schechinger S48 × Land O' Lakes Max	Resnik	1987	III	PI534645	Asgrow A3127(4) × L24
Private 2-15	1985	II	na	na	Pella 86	1987	III	PI509044	From backcross of Pella(5) × Williams 82
Burlison	1988	II	PI533655	F4 selection from K74-113-76-486 × Century	Private 3-9	1989	III	na	na
Private 2-9	1988	II	na	na	Private 3-10	1990	III	na	na
Elgin 87	1988	II	PI518666	Elgin (5) × Williams 82	Private 3-16	1991	III	na	na
Conrad§	1988	II	PI525453	A3127 × Tri-Valley Charger	Dunbar	1992	III	PI52538	Platte × A3127
Jack§	1989	II	PI540556	Fayette × Hardin	Thorne	1992	III	PI564718	A80-344003 × A3127BC3F2-1
Kenwood	1989	II	PI537094	Elgin × A1937	Private 3-17	1992	III	na	na
Private 2-1	1989	II	na	na	Private 3-18	1993	III	na	na
Private 2-2	1990	II	na	na	Private 3-19	1994	III	na	na
RCAT Angora	1991	II	PI572242	B152 × T8112	Macon§	1995	III	PI593258	Sherman × Resnik
Private 2-6	1991	II	na	na	IA 3004	1995	III	na	Northrup King S23-03 × A86-301024
Private 2-5	1993	II	na	na	Maverick	1996	III	PI598124	LN86-4668 (Fayette × Hardin) × Resnik(3)
Private 2-10	1994	II	na	na	Private 3-4	1996	III	na	na

Continued next page.

Table 1 (continued).

Cultivar	Year of release	Maturity Group	PI no.†	Pedigree‡	Cultivar	Year of release	Maturity Group	PI no.‡	Pedigree§
Private 2-16	1994	II	na	na	Private 3-11	1996	III	na	na
IA 2021	1995	II	na	Elgin 87 × Marcus	Pana	1997	III	PI597387	Jack × Asgrow A3205
Savoy	1996	II	PI597381	Burlison × Asgrow A3733	Private 3-5	1997	III	na	na
Private 2-12	1996	II	na	na	Private 3-12	1997	III	na	na
Dwight§	1997	II	PI597386	Jack × A86-303014	Private 3-6	1998	III	na	na
Private 2-18	1997	II	na	na	IA 3010	1998	III	na	Jaques J285 × Northrup King S29-39
IA 2038	1998	II	na	Pioneer 9301 × Kenwood	Private 3-7§	1999	III	na	na
IA 2050	2000	II	na	Northrup King S24-92 × A91-501002	Private 3-20	2000	III	na	na
IA 2052	2000	II	na	Northrup King S24-92 × Parker	U98-311442	2001	III	na	A94-773014 × Bell
Loda§	2001	II	PI614088	Jack × IA 3003	IA 3014	2001	III	na	LN90-4366 × IA3005
Private 2-4	2001	II	na	na	Private 3-8§	2002	III	na	na
Private 2-17	2001	II	na	na	IA 3023	2003	III	na	Dairyland DSR-365 × Pioneer P9381
IA 2068	2003	II	na	AgriPro P1953 × LN94-10470	NE3001	2004	III	na	Colfax × A91-701035
Private 2-3	2004	II	na	na	Private 3-13§	2004	III	na	na
IA 2065	2005	II	na	na	IA 3024	2004	III	na	A97-553017 × Pioneer YB33A99
Private 2-19	2005	II	na	na	Private 3-22	2006	III	na	na
Private 2-20	2005	II	na	na	Private 3-23	2006	III	na	na
IA 2094	2006	II	na	AgriPro X0121B74 × A00-711036	Private 3-14	2007	III	na	na
Private 2-13	2008	II	na	na					
Private 2-14§	2008	II	na	na					

† na, not applicable.

‡ na, not available.

§ Cultivars replicated within location.

Table 2. Experimental details with respect to test sites, soils, and dates of planting and harvest.

Location	Arlington, WI		Waseca, MN		Urbana, IL		Lafayette, IN	
Research Site	Arlington Agricultural Research Station 43°18' N, 89°20' W		Southern Research and Outreach Center 44°4' N, 93°31' W		Crop Sciences Research and Education Center 40°3' N, 88°14' W		Throckmorton Purdue Agricultural Center 40°17' N, 86°54' W	
Soil Series	Plano silt loam		Webster-Nicollet clay loam		Flanagan silt loam and Drummer silty clay loam		Throckmorton silt loam	
Soil Family	fine-silty, mixed, mesic Typic Argiudoll		fine-loamy, mixed, mesic Typic Endoaquoll and Aquic Hapludoll		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		32–37		23–34		39–66	
Potassium, mg kg ⁻¹	166–173		165–185		122		138–146	
pH	6.9–7.1		5.9–7.1		5.8–6.1		6.0–6.1	
Organic matter, g kg ⁻¹	3.2		5.4–6.3		3.6–4.1		2.9–3.0	
	<u>2010</u>	<u>2011</u>	<u>2010</u>	<u>2011</u>	<u>2010</u>	<u>2011</u>	<u>2010</u>	<u>2011</u>
Field operations								
Planting date	4 May		5 May		15 May		12 May	
Harvest date	8 Oct.		7 Oct.		15 Oct.		14 Oct.	
					7 Oct.		11 Nov.	
							10 May	
							24 Sept.	
							10 Oct.	

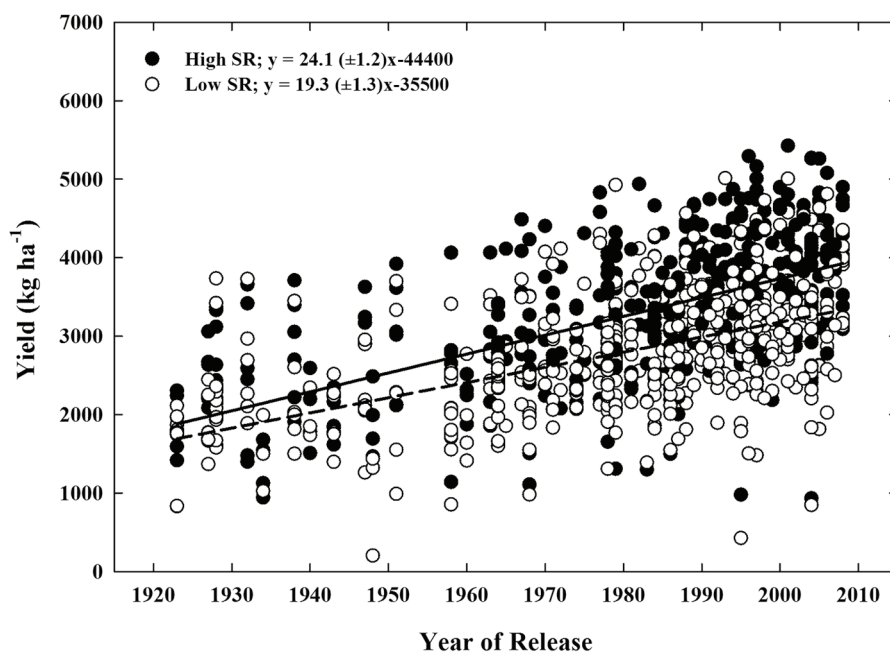


Fig. 1. Regression of seed yields (kg ha^{-1}) of 116 Maturity Groups (MGs) II and III soybean cultivars on the year of cultivar release, ($P = 0.0001$) in production systems that had a high seeding rate (solid) or low seeding rate (dashed) of 445,000 and 148,000 seeds ha^{-1} , respectively. Data points are means over replicates and years (2010 and 2011) and the standard error of the slope is in parentheses presented in each equation.

and (b) De Bruin and Pedersen (2009) who reported a similar result in Iowa when four MG II cultivars (two pre-1948 releases and two post-2005 releases) were planted for five target densities of 4.9, 14.8, 24.7, 34.6, and 44.5 plants m^{-2} . Because of the greater number of cultivars used in our study, it provides firm support for those earlier reported results (Cober et al., 2005; De Bruin and Pedersen, 2009) wherein fewer cultivars were used. Therefore, it appears newer cultivars are genetically better adapted to produce higher yield in stands with higher interplant competition compared to cultivars released in earlier years, which

conclusively supported the notion of synergism of modern genetics with a modern agronomic practice. Cultivars released more recently also produced greater seed yield plant^{-1} ($P < 0.001$) than did previously released cultivars (Fig. 2). In terms of main effect, seed yield plant^{-1} was always greater in the low seeding rate than in the high seeding rate ($P < 0.001$). However, the two factor interaction was significant ($P = 0.001$) (Fig. 2). Over time (i.e., release year), the positive rate of seed yield plant^{-1} change was $0.118 \pm 0.02 \text{ g yr}^{-1}$ in the low plant density, but was only $0.038 \pm 0.02 \text{ g yr}^{-1}$ in the high plant density (Fig. 2).

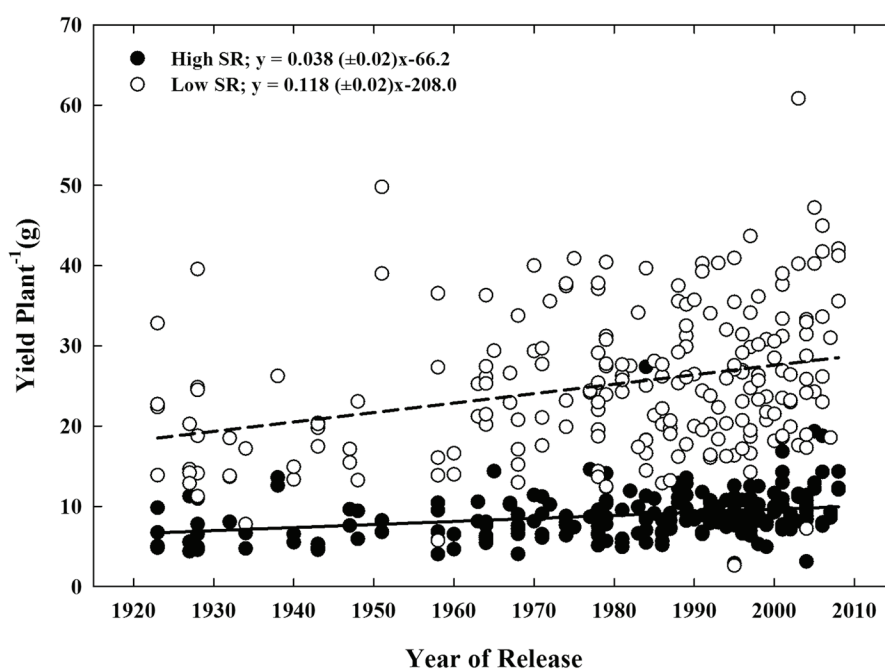


Fig. 2. Regression of yield (g plant^{-1}) of 116 Maturity Groups (MGs) II and III soybean cultivars on the year of cultivar release, ($P = 0.0015$) in production systems that had a high seeding rate (solid) or low seeding rate (dashed) of 445,000 and 148,000 seeds ha^{-1} , respectively. Data points are means over replicates and years (2010 and 2011) and the standard error of the slope is in parentheses presented in each equation.

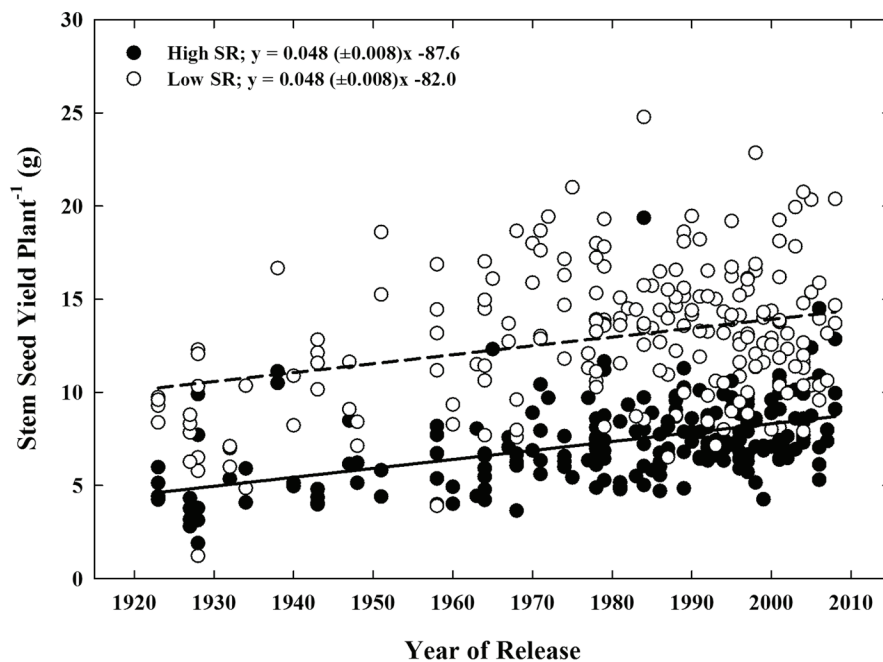


Fig. 3. Regression of stem seed yield (g plant^{-1}) of 116 Maturity Groups (MGs) II and III soybean cultivars on the year of cultivar release, ($P < 0.0001$) in production systems that had a high seeding rate (solid) or low seeding rate (dashed) of 445,000 and 148,000 seeds ha^{-1} , respectively. Data points are means over replicates and years (2010 and 2011) and the standard error of the slope is in parentheses presented in each equation.

Partitioning of Seed Yield in Stems and Branches

Seed yield and yield components were not only examined on a plant^{-1} basis, but plant productivity was also segmentally examined on a plant stem and plant branch basis. Cultivars in the low seeding rate produced more seed yield $\text{stem}^{-1} \text{ plant}^{-1}$ compared to cultivars in the high seeding rate, but no interaction was detected. In both seeding rate scenarios, the rate of genetic gain in plant stem yield over time was the same, that is, 0.048 g yr^{-1} seed yield $\text{stem}^{-1} \text{ plant}^{-1}$ (Fig. 3). As expected, branch yield plant^{-1} was

greater for the low seeding rate ($P < 0.001$). However, the interaction between seeding rate and year-of-release for branch seed yield plant^{-1} was significant ($P < 0.001$), in that the rate of genetic gain in plant branch yield over time was 0.071 g yr^{-1} when plant density was low, but reduced by 0.003 g yr^{-1} when plant density was high (Fig. 4).

It is of interest to contemplate the biological significance of the foregoing findings. In summary, seed yield plant^{-1} increased for all cultivars in both the high and low seeding rates; however, seed

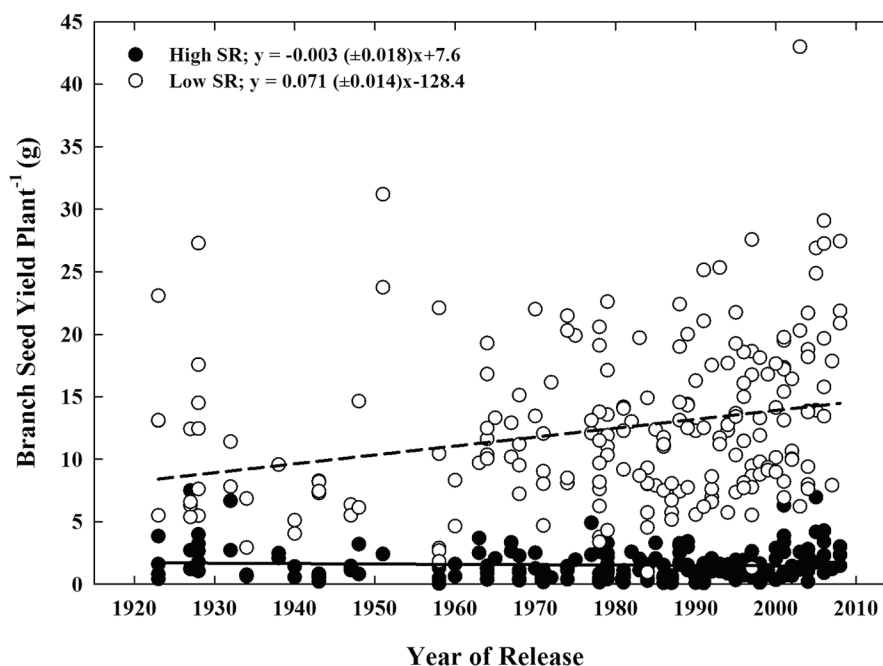


Fig. 4. Regression of branch seed yield (g plant^{-1}) of 116 Maturity Groups (MGs) II and III soybean cultivars on the year of cultivar release, ($P = 0.0001$) in production systems that had a high seeding rate (solid) or low seeding rate (dashed) of 445,000 and 148,000 seeds ha^{-1} , respectively. Data points are means over replicates and years (2010 and 2011) and the standard error of the slope is in parentheses presented in each equation.

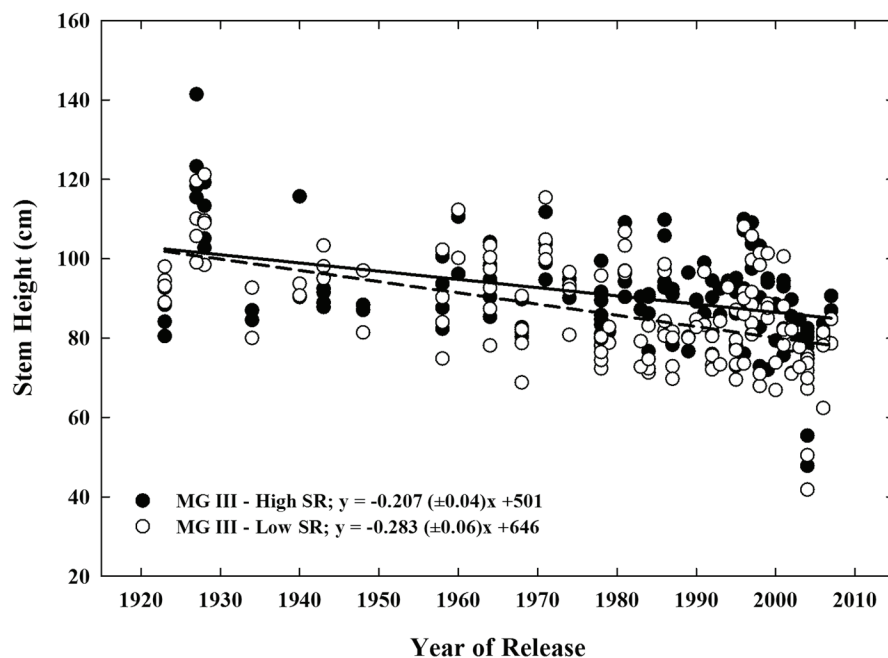


Fig. 5. Regression of stem height (cm) of 57 Maturity Group (MG) III soybean cultivars on the year of cultivar release, ($P = 0.0438$) in production systems that had a high seeding rate (solid) or low seeding rate (dashed) of 445,000 and 148,000 seeds ha^{-1} , respectively. Data points are means over replicates and years (2010 and 2011) and the standard error of the slope is in parentheses presented in each equation.

yield plant^{-1} increased three times faster over the last 80 yr when plant densities were low instead of high, resulting in a significant interaction. Analysis of seed yield plant^{-1} (Fig. 2), when parsed into a stem seed yield plant^{-1} (Fig. 3) and branch seed yield plant^{-1} (Fig. 4), revealed a key finding. There was no $\text{GI} \times \text{SR}$ interaction with respect to stem yield (i.e., in both densities, the upward trending lines from old to new cultivars were parallel). In contrast, there was such an interaction with respect to branch yield-branching was substantively suppressed in the high density in both old and new cultivars leading to a flat trend line, but

at low densities the degree to which branching contributed to seed yield appreciably increased as newer cultivars replaced older cultivars. It is thus clear that the ability of modern era cultivars to produce threefold more seed yield plant^{-1} in low densities in comparison to older cultivars is specifically attributable to greater ability to produce seed yield on branches. It is well known that branching increases with decreases in seeding rates (Lehman and Lambert, 1960; Carpenter and Board, 1997a), but documenting that propensity to branch more profusely over years of cultivar release is a novel discovery.

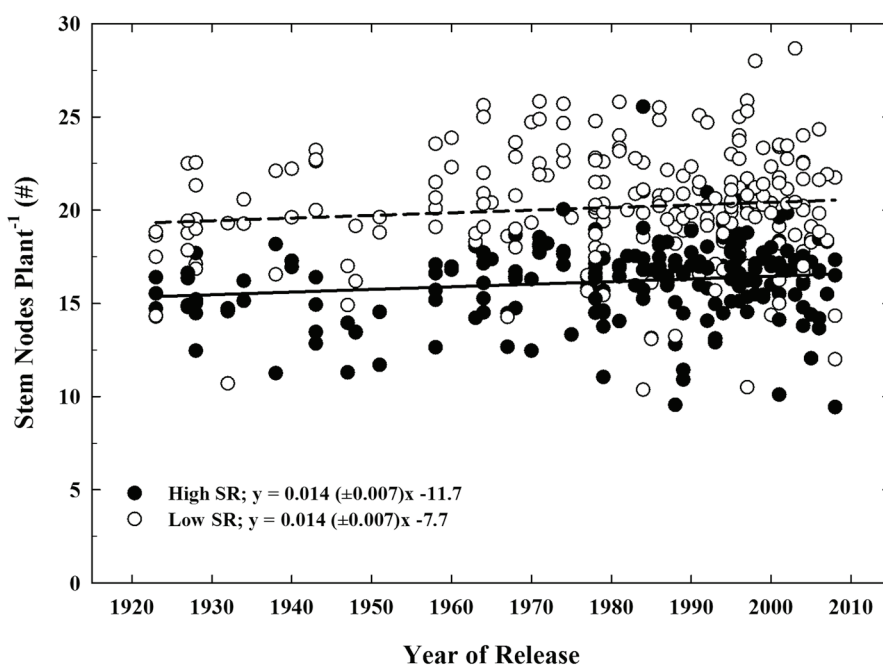


Fig. 6. Regression of stem nodes plant^{-1} of 116 Maturity Groups (MGs) II and III soybean cultivars on the year of cultivar release, ($P = 0.0405$) in production systems that had a high seeding rate (solid) or low seeding rate (dashed) of 445,000 and 148,000 seeds ha^{-1} , respectively. Data points are means over replicates and years (2010 and 2011) and the standard error of the slope is in parentheses presented in each equation.

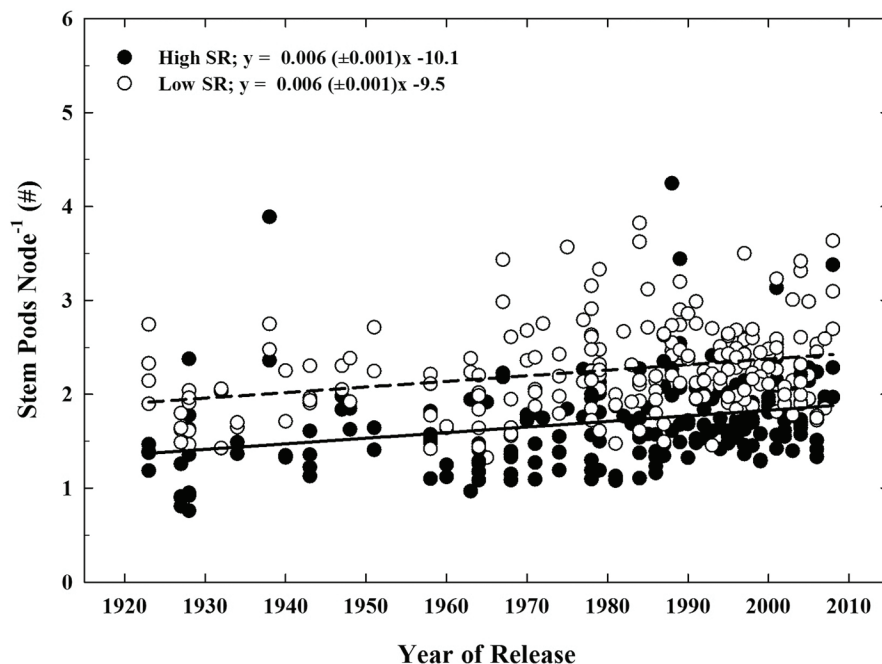


Fig. 7. Regression of stem pods node⁻¹ of 116 Maturity Groups (MGs) II and III soybean cultivars on the year of cultivar release, ($P < 0.0001$) in production systems that had a high seeding rate (solid) or low seeding rate (dashed) of 445,000 and 148,000 seeds ha⁻¹, respectively. Data points are means over replicates and years (2010 and 2011) and the standard error of the slope is in parentheses presented in each equation.

Morphological Parameters

Stem height was only recorded for the MG III cultivar set. Stem height decreased for the high and low seeding rates across year-of-release at a rate of 0.21 and 0.28 cm yr⁻¹, respectively (Fig. 5). Seeding rate per se did not have an effect on stem height ($P = 0.051$), but remains in the final model because the interaction between seeding rate and year-of-release was significant ($P = 0.044$) (Fig. 4). As mentioned above, plant height decreased at a slightly faster pace over year-of-release in the low seeding rate

vs. the high seeding rate. At first, this might seem surprising, but as noted earlier modern cultivars tend to branch more than older ones at low densities, and the diversion of dry matter from stems to branches might be a foundational reason for this. Stem height results here are similar to those reported by Ustun et al. (2001), and indicate that breeders have achieved shorter plants to prevent lodging, therefore improving yield. Plant height is one of the most important morphological parameters in yield potential as plants can lodge from becoming too tall causing lower ability

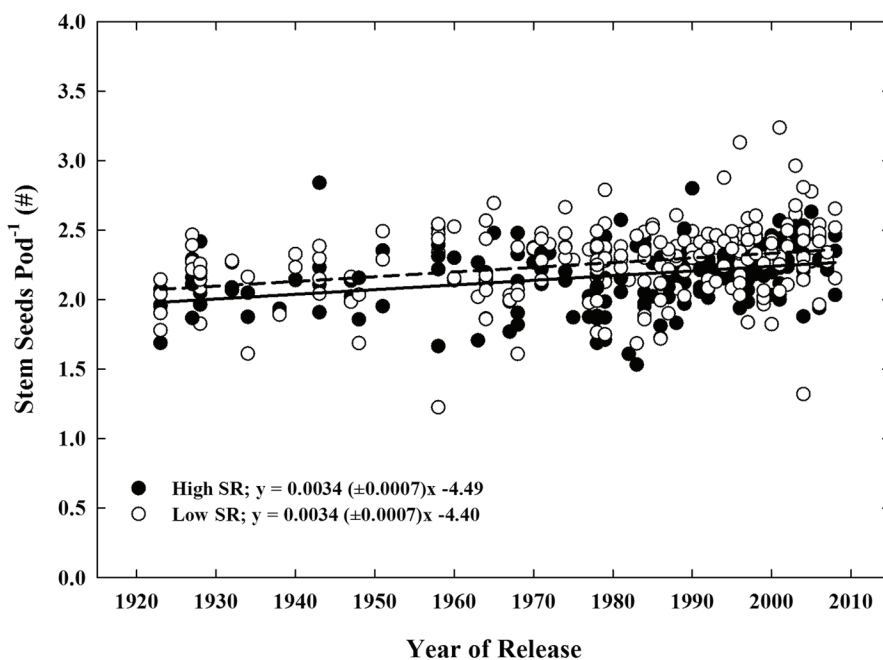


Fig. 8. Regression of stem seeds pod⁻¹ of 116 Maturity Groups (MGs) II and III soybean cultivars on the year of cultivar release, ($P < 0.0001$) in production systems that had a high seeding rate (solid) or low seeding rate (dashed) of 445,000 and 148,000 seeds ha⁻¹, respectively. Data points are means over replicates and years (2010 and 2011) and the standard error of the slope is in parentheses presented in each equation.

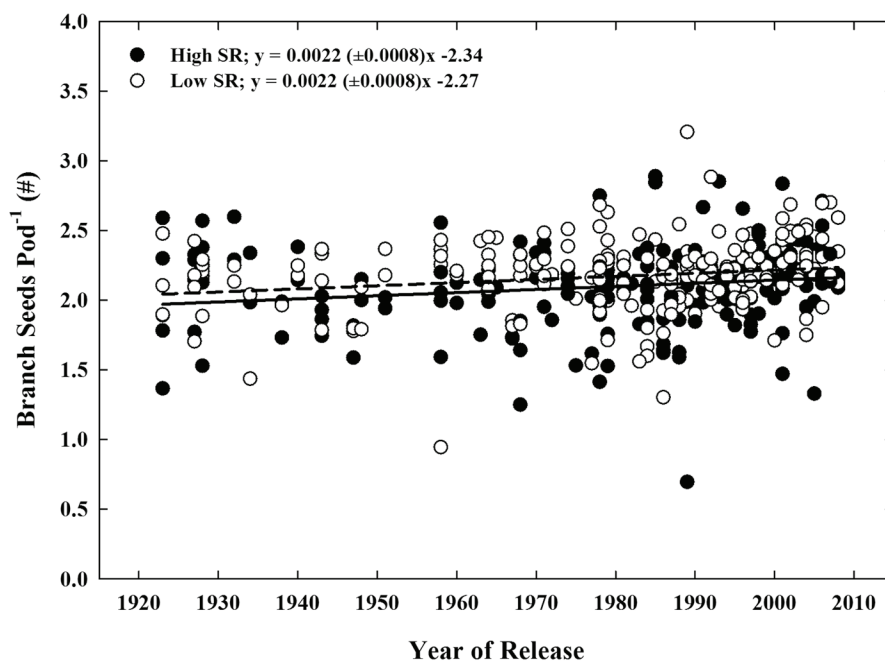


Fig. 9. Regression of branch seeds pod⁻¹ of 116 Maturity Groups (MGs) II and III soybean cultivars on the year of cultivar release, ($P = 0.0064$) in production systems that had a high seeding rate (solid) or low seeding rate (dashed) of 445,000 and 148,000 seeds ha⁻¹, respectively. Data points are means over replicates and years (2010 and 2011) and the standard error of the slope is in parentheses presented in each equation.

to photosynthesize, mechanical harvest losses and disease pressure (Ustun et al., 2001). Despite decreased overall stem height, nodes stem⁻¹ plant⁻¹ increased by 0.014 nodes yr⁻¹ in both the high and low seeding rate scenarios across year-of-release (Fig. 6). The lack of interaction led to its exclusion from the final model. However, there was a seeding rate effect ($P = 0.022$) observed as the low seeding rate averaged four more nodes stem⁻¹ plant⁻¹ than the high seeding rate over cultivar year-of-release, therefore stem pods plant⁻¹ for low seeding rate was higher since the rate of gain was similar. We believe this is also a novel finding not previously reported in the current literature.

The low seeding rate also produced an average of 0.6 more stem pods node⁻¹ over the high seeding rates ($P < 0.001$), but with no interaction between year-of-release and seeding rate since both seeding rates showed the same response across cultivars (Fig. 7). There was a similar increase in stem pods node⁻¹ for both the high and low seeding rates over cultivar year-of-release at a rate of 0.006 pods node⁻¹ yr⁻¹. Stem seeds pod⁻¹ increased at a rate of 0.0034 seeds pod⁻¹ yr⁻¹ (Fig. 8) and branch seeds pod⁻¹ (Fig. 9) increased 0.0022 seeds pod⁻¹ yr⁻¹ at both seeding rates. More seeds pod⁻¹ were produced on the stems and branches of plants in the low seeding rate, specifically 0.09 and 0.07 more seeds pod⁻¹, respectively. Since the stem height decreased and number of stem nodes increased, one must make the inference that internode length has been shortened by breeding efforts over time.

Stem pods node⁻¹ also increased with newer cultivars. Since there was an increased number of nodes stem⁻¹ plant⁻¹, pod number increased at a higher rate when viewed on a plant⁻¹ basis rather than node⁻¹ (data not shown). At lower plant populations, plants can produce more seed plant⁻¹ to compensate yield due to lessened neighboring competition for resources, and this is often accomplished by producing more pods plant⁻¹ generated from reproductive nodes (Pandey and Torrie, 1973; Kahlon et al., 2011).

The slight increase in the number of pods node⁻¹ and the increase in the number of nodes stem⁻¹ plant⁻¹ indicate more total pods are now produced per plant in newer cultivars. The increase in stem and branch seeds pod⁻¹ coupled with an inferred increase in total pods plant⁻¹ provides evidence that newer cultivars have the ability to develop more seed plant⁻¹ compared to older cultivars.

Harvest Index

Seeding rate per se did not influence harvest index, however, harvest index increased across year-of-release for high and low seeding rate at $0.114 \pm 0.013\% \text{ yr}^{-1}$ (Fig. 10). Since harvest index is described as the measure of the weight of a harvested product (seeds) as a percentage of the total plant weight, higher harvest index indicates better partitioning of plant energy resources. Harvest index measurements in this study did not account for leaf weight and therefore further detail study in this aspect might be warranted. However, harvest index as measured in this study without the inclusion of leaf weight has improved over years of successful soybean breeding, but appears to be un-influenced by plant population.

CONCLUSION

Research and on-farm documentation have provided evidence that soybean breeders have continuously developed higher yielding soybean cultivars over time. The implementation of optimum management practices has also helped these improved soybean cultivars express their maximum yield potential. The optimum seeding rate is one management practice that growers can easily manipulate to strive for higher yields and greater profit margins. Unfortunately, even if a seeding rate that is most appropriate for any given production system is planted, many biotic and abiotic factors like equipment malfunction, seedling disease, soil crusting, early-season

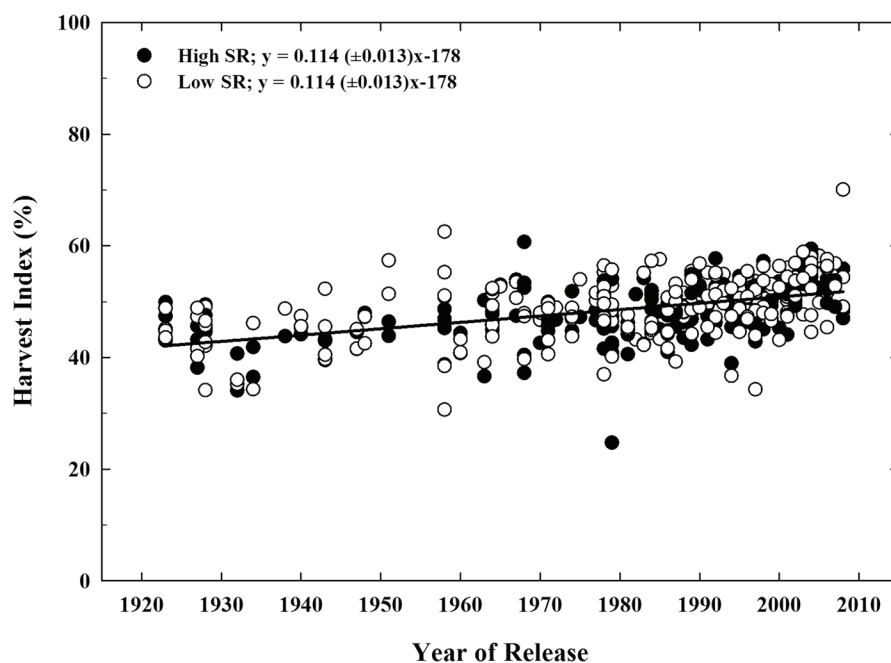


Fig. 10. Regression of harvest index (%) of 116 Maturity Groups (MGs) II and III soybean cultivars on the year of cultivar release, ($P < 0.0001$) in production systems that had a high seeding rate (solid) or low seeding rate (dashed) of 445,000 and 148,000 seeds ha^{-1} , respectively. Data points are means over replicates and years (2010 and 2011) and the standard error of the slope is in parentheses presented in each equation.

hail events, and other detrimental circumstances, can lessen the number of plants established in a crop stand.

In our research the high seeding rate provided better yields compared to the low seeding rate across all cultivar years of release. Yield expressed by year of release increased over time for both the high and low seeding rates; however, the yield increases for the high seeding rate were greater than for the low seeding rate. The yield increases observed for both seeding rates provides evidence that soybean breeders have successfully improved soybean traits to provide greater yield in both high and low density stands.

Seed yield plant^{-1} increased in the low seeding rate at 0.118 g yr^{-1} while it only increased 0.038 g yr^{-1} at the high seeding rate. Interestingly, the increase in stem seed yield plant^{-1} progressed at the same rate (0.048 g yr^{-1}) for both the high and low seeding rates; therefore, the improved increase in seed yield plant^{-1} over cultivar year-of-release at low seeding rates was due to additional seed yield plant^{-1} produced on branches where the low seeding rate increased 0.071 g yr^{-1} compared to the high rate which decreased -0.003 g yr^{-1} . From these data, we conclude that it is evident extensive soybean breeding has developed soybean cultivars with better branching ability and a greater capacity to compensate yield when plant stands are lower than optimal.

It is evident that soybean breeders are continuing to increase the soybean yield trend over time. Newer cultivars have reduced height and increased nodes $\text{stem}^{-1} \text{ plant}^{-1}$, stem pods node^{-1} and stem and branch seeds pod^{-1} . Harvest index has also improved suggesting that newer soybean cultivars are more efficient converting plant available energy to seed compared to older cultivars. Most interesting was the finding that soybean plants in the high seeding rate produced a majority of seed on the main stem while those in the low seeding rate compensated lower plant stands by producing relatively equal seed on the stems and branches. Moreover the yield produced on branches is substantially higher on newer cultivars. Though this was not true at higher seeding rates (Fig. 4), it must be

kept in mind that producers are tending to use lower seeding rates these days because of soybean seed costs.

While this research demonstrated that soybean breeders have selected cultivars over time for increased yield production in higher plant density environments (increased inter-plant competition), it more importantly demonstrated that newer cultivars have vastly improved ability to produce compensatory seed yield in suboptimal densities. The cause of this shift may be due to breeders inadvertently selecting cultivars that demonstrate greater yield stability in low densities during the selection and advancement process in breeding programs or the happenstance that higher yielding cultivars in normal densities also take better advantage of lessened competition for resources in low densities. While this benefit may have resulted inadvertently, the benefit of this additional compensatory yield in newer cultivars in suboptimal stand densities has likely been an un-noticed, hidden yield advantage of newer cultivars responsible for producing a significant but immeasurable amount of soybean yield throughout the last many decades of soybean production. These results may support research in other crops like corn (*Zea mays* L.), and the suggestions made by some breeders, that agronomic design can be manipulated to quicken the selection of higher yielding plant genetics with density neutral responses so farmers have greater risk tolerance of adverse conditions (Fasoula and Tollenaar, 2005; Fasoula, 2013). Soybean breeders moving forward should consider evaluating how newer cultivars perform in different plant stand densities to capitalize on this knowledge as growers will continually strive to choose seeding rates that best optimize both agronomic yield potential and economic returns.

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