RESEARCH PAPER

Historical gains in soybean (Glycine max Merr.) seed yield are driven by linear increases in light interception, energy conversion, and partitioning efficiencies

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Abstract

Soybean (Glycine max Merr.) is the world’s most widely grown leguminous crop and an important source of protein and oil for food and feed. Soybean yields have increased substantially throughout the past century, with yield gains widely attributed to genetic advances and improved cultivars as well as advances in farming technology and practice. Yet, the physiological mechanisms underlying the historical improvements in soybean yield have not been studied rigorously. In this 2-year experiment, 24 soybean cultivars released between 1923 and 2007 were grown in field trials. Physiological improvements in the efficiencies by which soybean canopies intercepted light (ε_i), converted light energy into biomass (ε_c), and partitioned biomass into seed (ε_p) were examined. Seed yield increased by 26.5 kg ha⁻¹ year⁻¹, and the increase in seed yield was driven by improvements in all three efficiencies. Although the time to canopy closure did not change in historical soybean cultivars, extended growing seasons and decreased lodging in more modern lines drove improvements in ε_i. Greater biomass production per unit of absorbed light resulted in improvements in ε_c. Over 84 years of breeding, soybean seed biomass increased at a rate greater than total aboveground biomass, resulting in an increase in ε_p. A better understanding of the physiological basis for yield gains will help to identify targets for soybean improvement in the future.

Key words: Energy conversion efficiency, harvest index, light interception efficiency, partitioning efficiency, radiation use efficiency, yield potential.

Introduction

Soybean (Glycine max) yields have steadily increased throughout the past century from advances made in breeding, improved management practices, and increased atmospheric carbon dioxide concentrations (Specht et al., 1999; De Bruin and Pederson, 2008; Rowntree et al., 2013). However, the current rate of gain is insufficient to meet the United Nations target of doubling crop yields by 2050 in order to meet the needs of a growing population (Tilman et al., 2011; Ray et al., 2013). While soybean yields have been increased through traditional breeding efforts, the physiological mechanisms underlying past yield gains in the USA are largely unknown. An understanding of the physiological basis of past improvements in soybean yield could help identify strategies for increasing future production.

Yield potential (Y_p) is defined as the maximum yield achieved when a crop is grown in absence of biotic and abiotic stresses (Evans and Fischer, 1999). Y_p can be parameterized by different efficiencies in the following equation adapted from Monteith (1977):

\[ Y_p = 0.487 S_i \times \varepsilon_i \times \varepsilon_c \times \varepsilon_p \]
In this equation, $S_i$ is total incident solar radiation during the growing season of which ~48.7% is photosynthetically active. Light interception efficiency ($\epsilon_i$) is determined by the speed and duration of canopy closure along with canopy size and architecture. Energy conversion efficiency ($\epsilon_c$), or radiation use efficiency, is determined by the amount of solar energy that is transformed into biomass through the balance of photosynthesis and respiration. Partitioning efficiency ($\epsilon_p$), or harvest index, is determined by the amount of biomass energy allocated to vegetative versus reproductive structures (Zhu et al., 2010). The Monteith equation tracks energy transfer from the sun to the seed and provides insight into the physiological mechanisms that ultimately govern yield potential. As a result, the Monteith equation has been used to assess which parameters are at their theoretical maxima and which could be improved further to advance yield (Gifford et al., 1984; Loomis and Amthor, 1999; Reynolds et al., 2000; Reynolds et al., 2010; Zhu et al., 2010; Ainsworth et al., 2012).

The extent to which soybean breeding strategies have improved $\epsilon_i$, $\epsilon_c$, and $\epsilon_p$ in US soybean germplasm has not been investigated. In Chinese and Canadian soybean germplasm, negative correlations between plant height and lodging score with cultivar year of release (YOR) have been reported (Jin et al., 2010; Morrison et al., 2000). These changes in height and lodging improved the standing power of the crop and are hypothesized to increase $\epsilon_i$ (Zhu et al., 2010). Improved $\epsilon_p$ with YOR in Chinese and Canadian germplasm was attributed to increased seed biomass with little or no increase in total aboveground biomass (Jin et al., 2010; Morrison et al., 1999). There is some evidence that $\epsilon_c$ also has been improved by breeding because leaf-level photosynthetic carbon assimilation increased with YOR (Jin et al., 2010; Morrison et al., 1999). However, $\epsilon_c$ is the season-long balance between C gain and C loss, and changes in carbon utilization and respiration can offset changes in photosynthesis. Additionally, a direct correlation between leaf-level photosynthesis and crop yield is not consistently apparent (Kumudini, 2002). Therefore, it is not known how decades of soybean breeding have altered $\epsilon_c$.

It has been suggested that modern cultivars in high-yielding environments achieve theoretical maximum efficiencies of $\epsilon_i$ (0.9) and $\epsilon_p$ (0.6), while $\epsilon_c$ is far below the theoretical C$_3$ maximum (0.094; Zhu et al., 2010). However, there has not been a comprehensive study that parameterizes the Monteith equation across US soybean cultivars with a range of release dates in order to assess how decades of breeding have altered the efficiencies in the field. Further, there is insufficient knowledge about whether elite germplasm are reaching their theoretical maximum efficiencies. Therefore, in order to elucidate the physiological mechanisms of yield improvement in historical soybean germplasm, this study parameterizes the Monteith equation in US soybean cultivars released from 1923–2007. It has been hypothesized that: (1) breeding has increased canopy duration and decreased lodging, therefore $\epsilon_i$ will increase with cultivar YOR; (2) breeding has improved net C balance in soybean, therefore $\epsilon_c$ will increase with cultivar YOR; and (3) seed yield has been increased by traditional breeding while vegetative biomass has not been affected, therefore $\epsilon_p$ will increase with YOR.

**Materials and methods**

**Experimental design**

Research was conducted at the Crop Research and Education Center in Urbana, IL (40° N 88° 14′W) in 2012 and 2013. Twenty-four indeterminate, maturity group III soybean cultivars were chosen to represent 84 years of past yield gains (Table 1). The publicly developed cultivars were obtained from the USDA Soybean Germplasm Collection, Urbana, IL, courtesy of Dr Randall Nelson. Nonpublic selections were obtained from Pioneer Hi-Bred, Syngenta, and Monsanto and were coded as private entries. Cultivars were chosen to minimize differences in maturity date and to maximize evenness of distribution across the years of study. Seed of all cultivars were produced in a common environment in Illinois the year prior to each experiment. Each year of the experiment was arranged in a randomized complete block design with three replicates. In one block, the cultivars were each grown in large plots (3.05 × 12.20 m with 16 rows in 2012 and 3.05 × 9.44 m with 12 rows in 2013) and in the two remaining blocks, cultivars were grown in smaller plots (3.05 × 3.05 m with four rows in both years). The smaller plots were used to determine seed yield at maturity as well as lodging while the larger plots were used for destructive physiological measurements, tissue sampling, as well as yield determination at maturity. Experimental plots were planted at a row width of 0.76 m and thinned after emergence to a uniform density (Table 2) after unequal stand density was observed in 2011 in a preliminary experiment (Supplementary Fig. S1A available at JXB online). Unequal stand density was caused by differences in germination rates (Supplementary Fig. S1B). Daily meteorological data, including $S_i$ (Fig. 1A, B), temperature (Fig. 1C, D), and precipitation (Fig. 1E, F), were collected ~1.5 km from the field site by the Illinois Climate Network monitoring station (Angel, 2009). Plots were irrigated using drip-line tubing four times during the 2012 season to prevent water stress (Fig. 1E). Drip-line tubing was not laid in 2013 because of ample precipitation early in the growing season.

**Table 1.** List of maturity group III soybean cultivars grown with year of release and plant introduction number

| Cultivar | YOR   | PI no.       |
|----------|-------|--------------|
| Dunfield | 1923  | PI648318     |
| Illini   | 1927  | PI648348     |
| AK (Harrow) | 1928 | PI648298     |
| Mandell  | 1934  | PI648381     |
| Lincoln  | 1943  | PI648362     |
| Adams    | 1948  | PI648502     |
| Ford     | 1958  | PI648562     |
| Shelby   | 1958  | PI648574     |
| Ross     | 1960  | PI648612     |
| Adelphia | 1964  | PI648503     |
| Wayne    | 1964  | PI648628     |
| Calland  | 1968  | PI648527     |
| Williams | 1971  | PI648631     |
| Woodworth| 1974  | PI648632     |
| Zane     | 1984  | PI648634     |
| Private 3-2 | 1986 | na           |
| Resnik   | 1987  | PI634645     |
| Private 9 | 1989 | na           |
| Private 19 | 1994 | na           |
| Private 11 | 1996 | na           |
| IA 3010  | 1998  | na           |
| IA 3023  | 2003  | na           |
| Private 3-13 | 2004 | na           |
| Private 3-14 | 2007 | na           |
Measurements of $\epsilon_i$ were made once or twice per week throughout the growing season. The photosynthetically active radiation (PAR) was measured above ($I_a$) and below ($I_b$) the canopy in two undisturbed areas in each large plot between 11:00 and 14:00 on clear-sky days with a 0.87-m line quantum sensor (AccuPAR LP-80, Decagon Devices, Pullman, WA, USA). $\epsilon_i$ was estimated from two measurements of PAR directly above the canopy and eight measurements

### Table 2. Summary of meteorological conditions, plant density, and planting and harvest dates in the 2 years of study

| Year | Planting date | Harvest date | Final plant density (plants ha$^{-1}$) | Precipitation (mm) | Mean maximum temperature ($^\circ$C) | Radiation (MJ m$^{-2}$) |
|------|---------------|--------------|---------------------------------------|-------------------|------------------------------------|------------------------|
| 2012 | 12 May        | 30 Oct       | 386,421                               | 483$^a$           | 30.6                               | 2944                   |
| 2013 | 16 May        | 14 Oct       | 379,325                               | 315               | 28.1                               | 2130                   |

$^a$Precipitation plus irrigation.

**Fig. 1.** Meteorological data for the 2012 and 2013 experimental growing seasons (planting date to 30 September): daily total solar radiation (A and B), daily maximum, mean, and minimum temperatures (C and D), and rainfall and irrigation events and accumulated precipitation across the growing season (E and F).
below the canopy. Below-canopy measurements were made ~2.5 cm above the ground across a 0.76 m transect between rows. \( \varepsilon_i \) was then calculated as 1 – \( \frac{I_{f,i}}{I_{f}} \) (Nobel et al., 1993). The season-long mean \( \varepsilon_i \) was calculated using all measurements taken throughout the season. \( \varepsilon_i \) measurements were stopped and assumed to be 0 once the plot reached growth stage R7 defined by pod maturity (Fehr et al., 1971), by which time most of the remaining foliage had senesced.

Aboveground biomass accumulation per unit area was measured every 2 weeks. Avoiding the edges of the plot (0.5 m), a 1-m length of row was harvested at 2.5 cm above the ground. Plants were counted and separated into leaf, stem (including petioles and petioles), and pod sections. Plant material was then dried for 1 week at 70 °C and weighed. In order to convert total biomass into energy equivalents, seeds, leaves, and stems were ground and analysed for total energy content using adiabatic bomb calorimetry (model 1261, Parr Instrument, Moline, IL, USA) with benzoic acid as a standard (Supplementary Figs S2 and S3). Biomass measurements were made in parallel with \( \varepsilon_i \) measurements. Cumulative intercepted radiation (PAR, \( \varepsilon_i \)) at the time of each biomass harvest was calculated by multiplying the accumulated PAR by the linearly interpolated \( \varepsilon_i \) estimated for each period of time between biomass harvests. For calculation of season-long \( \varepsilon_i \), cumulative PAR, (MJ m\(^{-2}\)) was plotted against cumulative biomass energy (MJ m\(^{-2}\)) until peak biomass was observed. The slope of the linear fit was used to estimate \( \varepsilon_i \) (Monteith, 1972) and it was assumed that \( \varepsilon_i \) was 0 on the day of crop emergence.

### Statistical analysis

A significant correlation between yield, Monteith efficiencies, and cv YOR was tested using least-squares regressions (PROC MIXED procedure, SAS version 9.2, SAS Institute, Cary, NC, USA) or first-order linear regression (SigmaPlot, Systat Software, Richmond, CA, USA). A t-test was used to determine if linear regressions slopes were significantly different among years. A two-segment linear regression model (PROC NL MIXED procedure, SAS version 9.2) was also fit to the data and compared to the linear fit using the Akaike information criterion coefficient.

### Results

#### Yield increased linearly with cv YOR

There was a linear improvement in soybean yields with cultivar YOR, with increases of 32.1 kg ha\(^{-1}\) year\(^{-1}\) in 2012 and 20.8 kg ha\(^{-1}\) year\(^{-1}\) in 2013 (Fig. 2A, B). The rate of yield gain in 2012 was significantly greater than in 2013 (\( P<0.005 \)). Older cultivars showed less year-to-year variation in seed production, with yield differences of ~145 kg ha\(^{-1}\) between years, while the newest cultivars yielded ~800 kg ha\(^{-1}\) more in 2012 compared to 2013 (Fig. 2A, B). Newer cultivars (Private 3–14, Private 3–13, and IA3023) were consistently among the highest yielding and older cultivars (Dunfield and Illini) were the lowest in both years of the experiment.

#### \( \varepsilon_i \) increased with cv YOR

Season-long \( \varepsilon_i \) increased with YOR in both 2012 and 2013 (Fig. 2C, D), and the slopes in the trends were not significantly different between years (\( P=0.24 \)). Increases in season-long \( \varepsilon_i \) with cultivar YOR were driven by a longer growing season, with more recent cultivars maturing later (Fig. 3). The growing season was ~10 d longer in lines released from the 1980s to the 2000s, compared to the lines released from the 1920s to the 1940s (Fig. 3). There was difference in the rate of canopy closure in older or newer cultivars, and most cultivars approached 90% closure by ~60 d after planting (Fig. 3). Lodging, which negatively affects \( \varepsilon_i \) at the end of the growing season, also decreased with YOR (Supplementary Fig. S4).

#### \( \varepsilon_p \) increased with cv YOR

\( \varepsilon_p \) was calculated as the ratio of seed biomass to total aboveground biomass and also expressed in terms of energy content of the seed to the energy content of total aboveground biomass at full maturity (R8; Fehr et al., 1971). Total seed and stem biomass was measured as for described, except 2 m of row were harvested for calculation of \( \varepsilon_p \). Lodging scores were determined in all three experimental plots using a 0–10 scale according to the following system: most main stems were completing vertical at 0° (0), 45° (5), completely horizontal at 90° (10). When the cultivars had reached maturity, yield was determined by harvesting two centre rows from each of the three yield plots with a 2-row combine and estimates were adjusted to 13% seed moisture content.

#### Statistical analysis

A significant correlation between yield, Monteith efficiencies, and cv YOR was tested using least-squares regressions (PROC MIXED procedure, SAS version 9.2, SAS Institute, Cary, NC, USA) or first-order linear regression (SigmaPlot, Systat Software, Richmond, CA, USA). A t-test was used to determine if linear regressions slopes were significantly different among years. A two-segment linear regression model (PROC NL MIXED procedure, SAS version 9.2) was also fit to the data and compared to the linear fit using the Akaike information criterion coefficient.

#### Results

### Yield correlations with Monteith efficiencies

In 2012, all three Monteith efficiencies (\( \varepsilon_i, \varepsilon_c, \text{and} \varepsilon_p \)) were significantly correlated with yield (Fig. 6), and \( \varepsilon_c \) and \( \varepsilon_p \) were correlated with one another (Fig. 6). However, \( \varepsilon_i \) was not correlated with \( \varepsilon_c \) or \( \varepsilon_p \) in 2012. In 2013, \( \varepsilon_c \) and \( \varepsilon_p \) were significantly correlated with yield (Fig. 7) but \( \varepsilon_i \) was not (Fig. 7). \( \varepsilon_i \) was more strongly correlated to yield in 2013 (Fig. 7), a year with ~30% less total solar radiation over the growing season compared to 2012. \( \varepsilon_p \) is autocorrelated with seed yield and
therefore it showed very high correlation coefficients in both years (Figs 6 and 7).

Discussion

In field trials of US soybean cultivars released over the past 84 years, seed yield significantly increased with YOR. When separating yield into its physiological efficiencies, there were consistent increases in the efficiencies by which canopies intercepted solar energy, converted it into biomass, and partitioned biomass into yield. In a highly productive agricultural area in the midwest USA, peak $\varepsilon_i$ is >90% and $\varepsilon_p$ is reaching the theoretical maxima value (60%) in recently released soybean cultivars. However, there is still room for further improvement in $\varepsilon_i$ in modern soybean cultivars.

This study of historical soybean cultivars estimated rates of soybean yield gain of 1.8% year$^{-1}$ in 2012 and 1.1% year$^{-1}$ in 2013. These rates are in line with the annual percentage gains reported in a literature review by Specht et al. (1999) and are similar to rates reported in a recent study of 60 cultivars with a similar range of YOR dates that also included the 24 cultivars grown in this present study (Rowntree et al.,...
While Rincker et al. (2014) found the data were better described by a two-segment linear fit with different slopes before and after 1964, the rates of yield gain in this study were better described by a single linear fit, perhaps because there was less power in this study to detect differences in the rate of yield gain before and after 1964. The gains in soybean yield reported here are also similar to improvements reported for other major crops including maize (Zea mays; Duvik and Cassman, 1999; Richards, 2000), rice (Oryza sativa; Peng et al., 2000), and wheat (Triticum aestivum; Reynolds et al., 1999; Shearman et al., 2005). The greater rates of yield gain observed in 2012 compared to 2013 were likely caused by differences in environmental factors and irrigation. The experimental site experienced hot, dry growing conditions in 2012, so plots were irrigated to reduce water stress. The 2013 growing season had lower maximum temperatures, less incoming solar radiation, and ample water early in the season. However, drought conditions occurred after the canopy closed and when seeds were filling, which likely contributed to the lower rate of gain in seed yield in 2013. When comparing the 2 years of the study, it was also notable that more recently released cultivars consistently outperformed older cultivars in all environments, they may have greater environmental sensitivity. These results are consistent with Rincker et al. (2014), who found greater rates of soybean yield gain in high-yielding environments and lower yield stability in more recently released cultivars.

The effective capture of solar radiation across the growing season determines how much solar energy is available for conversion into biomass and therefore yield. In this study, εi increased with cultivar YOR similarly across both years, with soybean canopies intercepting approximately 50–75% of the growing season’s PAR. Peak εi in all soybean cultivars was >90%, consistent with previous reports (Dermody et al., 2008). However, the seasonal εi measured in this study is lower than the theoretical maximum εi for soybean of ~90% (Zhu et al., 2010) and lower than previously reported levels of 89% (Dermody et al., 2008). This may be because the current study used wider row spacing than Dermody et al. (2008) and because the current study took more measurements early in the growing season when the canopy was still developing. There was no difference in time to canopy closure among new and old soybean varieties, but rather an increase in the duration of a photosynthetically active canopy allowing greater capture of St. This was in part because more recent cultivars have later maturity dates (Rowntree et al., 2013) but also because lodging significantly decreased with YOR, which lengthened the duration of an active canopy. Other studies in soybean have reported similar improvements in lodging score over years of breeding (Specht et al., 1999; Morrison et al., 2000; Jin et al., 2010). There are very few direct estimates of εi in soybean, but leaf area index (LAI) is commonly measured and used to indicate εi. A decreasing trend in LAI with YOR has been reported (Morrison et al., 1999; Jin et al., 2010), indicating that newer cultivars with lower LAI may have reduced capacity for intercepting light. However, while LAI can be a good indicator of light interception at the early stages of canopy closure, at an LAI of 3.5–4.0 light interception exceeds 95% (Board and Harville, 1992). Therefore, LAI values above ~4.0 reveal very little about εi. Improvement strategies for light interception in major crops tend to focus primarily on extending the growing season and/or engineering for optimal crop canopy architecture (Reynolds et al., 2000; Parry et al., 2010; Zhu et al., 2010), which would increase the total St for the crop to intercept. In rice, for example, each day added to the growing season translated into a 180 kg ha⁻¹ increase in yield (Akita, 1988).
Energy conversion efficiency and its improvement has been the focus of many yield improvement strategies (Amthor, 2010; Zhu et al., 2010; Parry et al., 2010; Raines, 2011; Ainsworth et al., 2012). Yet the extent of how $\epsilon_c$ has been improved through historical breeding is not well understood. In this study, $\epsilon_c$ increased with YOR in both 2012 and 2013, leading to a $\sim$36% improvement over the 84 years covered in this study ($\sim$0.43% year$^{-1}$). A similar increase in $\epsilon_c$ in wheat cultivars released from the 1970s to the 1990s has been reported (Shearman et al. 2005); however, earlier studies of different wheat cultivars failed to report a similar trend (Slafer et al., 1990; Calderini et al., 1997). In the current study, $\epsilon_c$ was 29% higher in 2013 compared to 2012, with a maximum $\epsilon_c$ of 2.9% in 2012 and 4.3% in 2013. These rates are higher than the rates of field-grown C$_3$ crops (2.4%) previously reported by Zhu et al., (2008) but still well below the theoretical maximum of 9.4% (Zhu et al., 2010). The exclusion of root biomass in the calculation of $\epsilon_c$ also underestimates the efficiency (Sinclair and Muchow, 1999), although it is not known how traditional breeding has affected root biomass allocation. $\epsilon_c$ is estimated from the linear relationship between biomass accumulation and intercepted light, and gains in $\epsilon_c$ in recently released soybeans came from increased biomass production for a given amount of intercepted light (Fig. 4). Changes in respiration or photosynthesis could underpin this trend in $\epsilon_c$, and previous work in Canadian and Chinese germplasm suggests that leaf-level photosynthesis has improved with YOR (Jin et al., 2010; Morrison et al., 1999). However, future studies are needed to determine the mechanisms driving improvements in $\epsilon_c$ in these maturity group III historical lines. $\epsilon_c$ in 2012 was lower than in 2013, because although the crop intercepted 33% more PAR in 2012 than in 2013, because although the crop intercepted 33% more PAR in 2012 than in 2013, peak biomass was only 13% greater in 2012 than in 2013. Photosynthesis saturates at $\sim$50% full sunlight and plants are not able to utilize all the intercepted solar radiation, which results in decreased efficiencies of energy conversion (Sinclair and Muchow, 1999; Ort, 2001). A recent meta-analysis by Slattery et al. (2013) found in shading experiments that $\epsilon_c$ increased by 18% when

**Fig. 4.** Accumulated aboveground biomass versus cumulative PAR in 2012 (A) and 2013 (B). Lines represent least-squared regression between dry biomass versus cumulative PAR. The slope of each line ($m$) is $\epsilon_c$. Each point represents the biomass and cumulative PAR for the five oldest cultivars and the five most recently released cultivars.
**Fig. 5.** Determinants of partitioning efficiency (ε) versus YOR at growth stage R8 plotted against cultivar YOR in 2012 and 2013: seed biomass (A and B) and total biomass (C and D). Lines represent significant least-squares regression (** P<0.001).

**Fig. 6.** 2012 correlation matrix of yield and Monteith efficiencies. ε is expressed in terms of biomass (g seed/g total aboveground biomass). Scatterplots and correlation coefficients are plotted in a matrix where lines represent significant least-squares regression. Bold indicates significant results.
Physiological basis for historical yield improvement in soybean

Plants were grown in shaded conditions compared to full sunlight. Consistent with the meta-analysis, $\varepsilon_c$ of soybean was greater in a year with less solar radiation; however, despite the increased efficiency in 2013, 2012 resulted in higher absolute seed yields. Although the plants were less efficient in the amount of C fixed per MJ of light in 2012, the plants had higher rates of incident solar radiation throughout the growing season which more than compensated for the loss of efficiency and led to the increase in peak biomass.

Consistent increases in $\varepsilon_p$ with YOR were observed in 2012 and 2013. The range of $\varepsilon_p$ based on biomass for both years was similar (0.3–0.55), and the most recently released cultivars approached the theoretical maximum of 0.60 (Figs 6 and 7). The improvement of $\varepsilon_p$ with YOR was achieved through tripling seed biomass per area but only doubling total biomass per area (Fig. 5). The rate of gain in $\varepsilon_p$ in Chinese soybean germplasm was similar at 0.40% year$^{-1}$ (Jin et al., 2010). In Canadian soybean germplasm, historical improvements in $\varepsilon_p$ were only due to increases in seed weight and not total biomass (Morrison et al., 1999). In other major food crops, particularly small grains, improvements in $\varepsilon_p$ largely drove improvements in yield from 1900 to 1980 (Hay, 1995). In wheat, linear increases in $\varepsilon_p$ were found with YOR in the UK and Mexico and were achieved through increased grain yield with no increase in total biomass (Austin et al., 1989; Sayre et al., 1997). More recently, Shearman et al. (2005) reported that $\varepsilon_p$ levelled off at ~0.5 when they looked at cultivars of wheat that were released from 1970 to 1995. Historically, rice showed improvements in $\varepsilon_p$ until it reached a maximum of around 0.6 in the 1980s when increases in yield were then attributed to greater rates of biomass production (Hay, 1995; Peng et al., 2000). The $\varepsilon_p$ of maize was already high (~0.45) in the early 1930s and therefore gains in maize yield were made through increases in total biomass (Hay, 1995; Richards, 2000). While the data presented here support a linear increase in $\varepsilon_p$ with YOR in soybean (i.e. the data are not reaching a plateau), $\varepsilon_p$ in the most recently released lines is approaching the theoretical maximum.

In conclusion, several physiological changes have accompanied the impressive gains in soybean yield over the past 80 years. First, soybean canopies of more recently released cultivars have greater season-long canopy interception efficiencies owing to longer growing seasons and improved resistance to lodging. Second, modern soybean cultivars have better efficiencies of converting light energy into aboveground biomass and produce 9–17% more aboveground biomass energy in a growing season than cultivars released before 1950. Third, the partitioning of biomass to seeds has been...
maximized in modern soybean lines. Where is there room for future improvement in soybean yield? Longer growing seasons would enable already efficient soybean canopies to harvest more light (Rowntree et al., 2013), but there appears to be little room for improving $\varepsilon_p$. On the other hand, $\varepsilon_c$ is still well below the theoretical maximum, even in the most recently released cultivars, and therefore it is an important target for future improvement.

**Supplementary material**

Supplementary data are available at *JXB* online.

- **Supplementary Fig. S1.** Plant density and seed germination versus YOR in 2011.
- **Supplementary Fig. S2.** Leaf and stem energy content versus YOR.
- **Supplementary Fig. S3.** Seed composition versus YOR in 2012 and 2013.
- **Supplementary Fig. S4.** Lodging score versus YOR in 2012 and 2013.

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