



Physiological and management factors contributing to soybean potential yield



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ABSTRACT

The largest reported soybean grain yield is approximately three-fold more than the highest reported U.S. average yield. An understanding of yield determination is needed to identify avenues for increasing yield and for defining the yield potential of soybean. To illustrate physiological traits important for yield determination, we used a framework that models yield as the product of seed number (seed m^{-2}) and individual seed mass (mass_{seed}). Developmentally, seed m^{-2} is determined first and is proportional to the biomass accumulation rate (BAR, $g\ m^{-2}\ d^{-1}$) and the fraction of assimilate allocated to reproductive structures. Seed m^{-2} is inversely proportional to the individual seed growth rate (ISGR, $mg\ seed^{-1}\ d^{-1}$) where the ISGR represents the minimum amount of assimilate necessary to prevent a flower or pod from aborting. Hence, seed m^{-2} can be increased by optimizing conditions for crop growth (e.g., radiation interception, stress-free environment, high soil fertility levels) and having a low ISGR. Determination of mass_{seed} occurs later during ontogeny than seed m^{-2} and can be expressed as the product of the ISGR and the effective seedfilling period (EFP, d). Variation among genotypes for ISGR is quite large and is generally not affected greatly by the environment. There is also genotypic variation in the EFP, but the EFP is decreased by a variety of biotic and abiotic stresses. Our analysis indicates that reaching the potential yield of soybean depends upon high BAR and extending the EFP, and a key factor affecting both of these variables is ensuring non-limiting crop nutrition, especially nitrogen. Strategies for increasing soybean maximum yield include early planting (which extends the EFP), optimizing crop nutrition, minimizing biotic and abiotic stresses, and developing breeding programs tailored for high yield environments. Characterizing physiological traits important for yield with genetic markers offers tools for combining favorable traits for high-yield environments.

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1. Introduction—Current yield levels and records

United States average soybean [*Glycine max* L. (Merr.)] grain yields have increased from the earliest record of 739 $kg\ ha^{-1}$ in 1924 to a high of 2956 $kg\ ha^{-1}$ in 2009 (USDA-NASS, 2013). While this increase in soybean yield over time is substantial, both researchers and growers have documented yields much greater than the

reported nationwide averages (Table 1). In converted rice paddies in Japan, Spaeth et al. (1987) reported yields of 6490 $kg\ ha^{-1}$. In New Jersey, Flannery (1989) recorded a soybean yield of 7923 $kg\ ha^{-1}$ in 1983 and a 5-yr average irrigated yield of 6921 $kg\ ha^{-1}$. In 1982, Cooper (2003) was able to achieve yields of 6817 $kg\ ha^{-1}$ in research in Ohio. In Queensland, Australia yields up to 8604 $kg\ ha^{-1}$ were reported (Cooper, 2003; Lawn et al., 1984). Researchers in China recorded yields up to 9200 $kg\ ha^{-1}$ (Isoda et al., 2010), but yields were based on only a small number of individual plants (14 to 28). Without further details and without a more representative yield sample, this report remains questionable. Physiological experiments in Argentina extended the photoperiod by 2 h in field experiments from 1 to 35 days after R3 (Fehr and Caviness, 1977) and reported yields up to 8957 $kg\ ha^{-1}$ (Kantolic and Slafer, 2007).

A few soybean growers have also achieved exceptional soybean yields. In 1968, the winner of the United States National Soybean Yield Contest did so with 7310 $kg\ ha^{-1}$ (Cooper, 2003). In 1997,

Abbreviations: BAR, biomass accumulation rate; BM, biomass; DMAC, dry matter allocation coefficient; EFP, effective filling period; HI, harvest index; HI_{act}, actual harvest index; HI_{app}, apparent harvest index; IR, intercepted radiation; ISGR, individual seed growth rate; mass_{seed}, mass per seed; MG, maturity group; P_{max}, maximum photosynthetic rate; RUE, radiation use efficiency; SLW, specific leaf weight; QTLs, quantitative trait loci.

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Table 1

Summary of location, soil series, maximum yield and management comments from peer-reviewed high yield soybean research.

Location	Soil series	MG	Maximum Yield (kg ha ⁻¹)	Management comments	Reference
Adelphia, NJ	Freehold sandy loam	3	7955	Drip fertigation, 156 kg N, 252 kg P ₂ O ₅ , 336 kg K ₂ O ha ⁻¹ and 12 Mg ha ⁻¹ biennial dairy manure, planted near 1 May in 15 to 36-cm rows Irrigated as needed. Planted 9 November in 35-cm rows. Photoperiod extended by 2 h after R3 from 1 to 35 days	Flannery (1989)
Buenos Aires, Argentina	Vertic Argiudol	5	8957	Drip irrigation, 240 kg N, 300 kg P ₂ O ₅ , 195 kg K ₂ O ha ⁻¹ yr ⁻¹ from 15 Mg ha ⁻¹ poultry manure, planted 29 Apr. in alternate 30 and 60-cm rows	Kantolic and Slafer (2007)
Shihezi, China	nr [†]	nr	9200 [‡]	Converted rice paddy, rainfed, 25 kg N, 76 kg P ₂ O ₅ , 93 kg K ₂ O ha ⁻¹ , planted between 18 and 24 May in 75-cm rows	Isoda et al. (2006, 2010)
Shinjo, Japan	clayey, humic andosol	3	6490	Overhead irrigation, poultry manure, planted 24 Apr. to 30 May in twin rows 24-cm apart, centered on 76 cm	Spaeth et al. (1987)
Stark City, MO	Newtonia silt loam	4–5	7953	Overhead irrigation, 222 kg N, 202 kg P ₂ O ₅ , 403 kg K ₂ O ha ⁻¹ yr ⁻¹ , 17.5-cm rows	Van Roekel and Purcell (2014)
Wooster, OH	Wooster silt loam	3	7050		Cooper (2003)

[†] Not reported.[‡] Yields were based on 14 to 28 plants per plot and are, therefore, questionable.

a grower achieved yields near 6719 kg ha⁻¹ in the Nebraska irrigated contest category (Specht et al., 1999). In 2008, the winner of the Missouri Soybean Association's non-irrigated contest category had a yield of 7324 kg ha⁻¹ in southeast Missouri (Steever, 2008). And finally, the highest soybean yields reported from yield contests were from the Missouri Soybean Association Yield Contest with yields of 9339 kg ha⁻¹ (2006), 10,388 kg ha⁻¹ (2007), and 10,791 kg ha⁻¹ (2010) (Cubbage, 2010). Van Roekel and Purcell (2014) reported yields from these same fields in southwest Missouri in 2011 to 2013, and each year individual cultivars had yields between 6979 and 7953 kg ha⁻¹.

The high yields reported in yield contests have created some controversy and skepticism because of the lack of supportive, quantitative data that would provide a mechanistic explanation. Additional concerns are associated with the uncertainty in what constitutes the potential yield of soybean. Potential yield is defined as the “yield of a crop cultivar when grown with water and nutrients non-limiting and biotic stress effectively controlled” (Van Ittersum et al., 2013). This becomes an issue when attempting to estimate future prospects for yield increases via yield-gap analyses using current farmer average yields and the potential yield (Egli and Hatfield, 2014; Lobell et al., 2009). High potential yield estimates will often result in large yield gaps; however, attaining such potential yields are likely not economically or sustainably possible (Egli and Hatfield, 2014). Potential yield also varies geographically due to changes in climate. Furthermore, non-irrigated production systems may be consistently constrained by water supply and a water-limited potential yield may be more realistic in those production systems (Van Ittersum et al., 2013). However, the focus of this discussion will be on the ultimate potential yield of soybean when water supplies are non-limiting. To provide an estimate of the potential yield of soybean, it is crucial to first examine the processes that determine soybean grain yield.

Our objective was to review mechanistic frameworks for determining the primary two components of soybean yield: seed number (seed m⁻²) and individual seed mass (mass_{seed}, g seed⁻¹). The determination of soybean seed number and mass revolve around a few key growth characteristics that can be quantified as the above-ground biomass accumulation rate, individual seed growth rate, and the effective seedfilling period. We will discuss how these physiological processes are affected by environmental, management, and genetic factors to better understand the combination of factors that lead to expression of soybean potential yield.

2. Theoretical framework for soybean yield

2.1. Seed number determination

Soybean grain yield is determined by the seed per unit area and mass of individual seeds:

$$\text{Yield (g m}^{-2}\text{)} = (\text{seed m}^{-2}) * (\text{mass}_{\text{seed}}) \quad (1)$$

During soybean ontogeny, seed number determination occurs first, followed by seed weight determination (Board and Kahlon, 2011). Of these two variables, seed m⁻² has a greater influence on yield compared with seed weight (Board, 1987; De Bruin and Pedersen, 2008; Kokubun and Watanabe, 1983; Robinson et al., 2009; Shibles et al., 1975; Singer et al., 2004). One theory regarding seed m⁻² determination was proposed by W.G. Duncan (Egli et al., 1978b) whereby “the number of seed produced by a soybean community is set at a level such that the sum of their individual growth rates essentially equals the ability of the soybean canopy to support seed growth”. In other words, seed m⁻² is a function of the total crop canopy photosynthate production and the rate of photosynthate utilization by the individual seed. Charles-Edwards (1984) theorized that “each growing point on a plant requires a minimum flux of assimilate for growth to continue.” These concepts were applied to the determination of seed m⁻² by Charles-Edwards et al. (1986):

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

In Eq. (2), N_g represents the number of developing grain ∇_F represents the daily canopy net photosynthesis, γ represents the partitioning coefficient of daily canopy net photosynthesis to reproductive growth, and A_g is the minimum amount of assimilate required to prevent developing grain from aborting. Eq. (2) indicates that seed m⁻² may be increased by lowering the photosynthate requirement per grain, allowing the total crop photosynthate production to be divided among additional reproductive units. Alternative or supplemental avenues to increase the seed m⁻² would be to increase the amount of photosynthate produced during the flowering and podset periods or to increase the proportion of photosynthate allocated to seeds.

This model was evaluated by Egli and Zhen-wen (1991) who used seed m⁻² as an estimate for N_g and experiments employing shade treatments to vary ∇_F . Net canopy photosynthesis production was estimated as the above-ground biomass accumulation rate (BAR; g m⁻² d⁻¹) during flowering and podset (R1 to R5; Fehr

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