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Nutrient Uptake, Partitioning, and Remobilization in Modern Soybean Varieties

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ABSTRACT

The absence of recent data regarding the nutritional needs of modern soybean [*Glycine max* (L.) Merr.] production systems necessitates a greater comprehensive understanding of nutrient uptake, partitioning, and remobilization. The objective of this study was to evaluate macro- and micronutrient accumulation and partitioning in current soybean cultivars. Across 3 site-years, plants were sampled at seven growth stages and divided into four plant tissue fractions for quantification of nutrient uptake. Accumulation (per ha) of 275 kg N, 21 kg P (48 kg P_2O_5), 172 kg K (207 kg K_2O), 113 kg Ca, 50 kg Mg, 19 kg S, 335 g Zn, 371 g Mn, 325 g B, 849 g Fe, and 63 g Cu were required to produce approximately 3500 and 9500 kg ha^{-1} of grain and total biomass, respectively. Supplemental fertility modestly increased biomass and yield (2%), but did not alter nutrient partitioning or harvest index. Nutrients with high harvest index (i.e., percentage of total nutrient accumulation partitioned to grain) values included P (81%), N (73%), Cu (62%), and S (61%), which may serve as a limitation to high yield. Seasonal patterns of nutrient accumulation suggested that K and Fe were acquired primarily during late vegetative growth while the uptake of N, P, Ca, Mg, S, Zn, Mn, B, and Cu were more equally distributed between vegetative and seed-filling growth phases. These results document the rate and duration of macro- and micronutrient accumulation in soybean, and highlight the importance of adequate nutrient availability during key crop growth periods.

Soybean yields in the United States have averaged around 2500 kg ha^{-1} for the last decade, which represents an approximate fourfold increase since 1924 (USDA-NASS, 2013b). Over this same time, U.S. maize [*Zea mays* (L.)] yields have increased nearly sevenfold (USDA-NASS, 2013a). While there are a number of possible explanations for the slower rate of gain observed with soybean relative to maize, inadequate fertility may be a contributing factor. During a 30-yr period from 1977 through 2006, national soybean yields increased by more than 40%, compared to an increase in P and K fertilizer usage rates for soybean production of only 2 and 33%, respectively (USDA-NASS, 2013b; USDA-ERS, 2013). Inadequate fertilization of soybean during the past three decades may also have contributed to the decline of P, K, S, and Zn soil test levels in important soybean growing regions of the United States (Fixen et al., 2010). Continued soybean yield improvements, especially in production systems with marginal fertility management, necessitate a greater understanding of soybean's season-long nutritional needs.

Patterns of nutrient uptake, partitioning, and remobilization in soybean were studied during the 1930s through 1970s in an effort to better understand the physiology of nutrient accumulation (Borst and Thatcher, 1931; Hammond et al., 1951; Hanway and Weber, 1971a; Harper, 1971). Of these studies, only one assessed micronutrients. More importantly, however, is that cultivars and management practices have changed since the 1970s. For example, some historical soybean production methods included the use of solid seed drills (Borst and Thatcher, 1931) resulting in more narrow row spacing (e.g., 20 cm between rows) and relatively high planting densities with low yield and total biomass production (Table 1; Borst and Thatcher, 1931; Hammond et al., 1951; Hanway and Weber, 1971b). Present, higher yielding soybean production systems typically use lower planting densities and in some cases wider row spacing (e.g., 76 cm) with improved fertilizer source and placement technologies. Grain producers have also realized gains in biomass production and in some cases yield resulting from insecticide and fungicide use (Bradley and Sweets, 2008; Bradshaw et al., 2008; Swoboda and Pedersen, 2009). These more commonly used agronomic practices accompanied by improved varieties may favor nutrient uptake during different key growth stages than originally thought.

Soybean was originally introduced and adapted to U.S. agriculture to serve as a leguminous forage crop (Morse et al., 1950), and as a result, parameters including total biomass production were likely of greater value than dry weight harvest index (i.e., proportion of total dry weight represented by grain

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Abbreviations: CEC, cation exchange capacity; HI, harvest index; RM, relative maturity; SOM, soil organic matter.

Table 1. Agronomic management practices and measured total nutrient uptake in soybean, compiled from select nutrient accumulation studies during the past 80 yr. All units are expressed on a dry weight basis (i.e., 0% moisture).

Agronomic parameters	Borst and Thatcher, 1931	Hammond et al., 1951†	Hanway and Weber, 1971a, 1971b‡
Row spacing, cm	20	97	102
Plant density, 1000's plants ha^{-1}	667–890	445	388
Productivity, Mg ha^{-1}			
Grain yield	1.2	2.0	2.7
Biomass yield	4.7	6.2	8.6
Nutrient uptake, kg ha^{-1}			
N	125	164	265
P	15	14	23
P_2O_5	34	31	52
K	38	51	86
K_2O	46	61	104
Ca	45	96	–
Mg	33	47	–

† Productivity and nutrient uptake data were averaged across two soil types.

‡ Productivity data was estimated from Hanway and Weber (1971b) and nutrient uptake data from Hanway and Weber (1971a).

tissues) and seed yield. Consequently, biomass production of soybean increased markedly during the past 80 yr (Table 1). Although soybean dry weight is highly sensitive to environmental factors (e.g., water and temperature stress) that contribute to intra-seasonal variations in plant growth, rates of dry matter accumulation over 450 kg ha^{-1} d^{-1} have been documented in maximum yield research studies (Sadler and Karlen, 1995). Dry matter accumulation rates from earlier research were as low as 90 to 110 kg ha^{-1} d^{-1} (Hanway and Weber, 1971b; Hammond et al., 1951) but have increased to more than 250 kg dry matter ha^{-1} d^{-1} (Sadler and Karlen, 1995) in more recent studies. The rate and duration of biomass accumulation also influence plant dry weight partitioning, especially during seed development (i.e., after R4). Across a range of varieties, approximately one-third of total aboveground dry weight is partitioned to the mature seeds, with the remaining distributed among leaf (22%), stem (22%), petiole (10%), and pod (14%) tissues (Hanway and Weber, 1971b). It is unknown how current varieties and agronomic management practices in more intensive agricultural production systems have changed soybean dry weight accumulation and partitioning.

Nutrient accumulation in soybean is largely influenced by dry weight accumulation (Hanway and Weber, 1971a), and despite lower seed yield, total uptake of key nutrients in soybean may exceed a high yielding maize crop (Flannery, 1986; Bender et al., 2013). A maximum yield research study by Flannery (1986) reported soybean nutrient accumulation totals of 614 kg N ha^{-1}, 65 kg P ha^{-1} (148 kg P_2O_5 ha^{-1}), and 403 kg K ha^{-1} (485 kg K_2O ha^{-1}), as much as two- to threefold greater than a maize crop yielding 12.0 Mg ha^{-1} (Bender et al., 2013). Regardless of yield level, nutrient accumulation in soybean occurs during three distinct phases: (i) a slow rate of acquisition for approximately 30 d following emergence, (ii) maximum rates of nutrient uptake between R2 (full bloom) and R5 (beginning seed), and (iii) reduced rates of nutrient accumulation during late reproductive (e.g., seed maturation) growth (Harper, 1971; Usherwood, 1998). Maximal daily rates of nutrient accumulation were quantified for N (4.5 kg N ha^{-1}), P (0.4 kg P ha^{-1} or 0.9 kg P_2O_5 ha^{-1}) and K (1.5 kg K ha^{-1} or 1.8 kg K_2O ha^{-1}), which also occurred during pod development and seed-filling stages (Hanway and Weber, 1971a). A fundamental difference in soybean and maize nutrient partitioning is that the seed of soybean serves as a more highly concentrated nutrient sink (Hammond et al., 1951). Despite reduced rates of nutrient acquisition during late reproductive growth, accelerated rates of nutrient remobilization are necessary to supply nearly one-half of N, P, and K to developing grain tissues (Hanway and Weber, 1971a). Understanding nutrient accumulation, partitioning, and remobilization is essential for optimal soybean production, but comprehensive research studies that also include secondary macronutrients and micronutrients are limited (Table 1).

The most recent literature describes nutrient accumulation in soybean from the 1930s through the 1970s (Table 1). No recent data exist, however, which document the cumulative effect of improved soybean varieties, fertilizer source and placement technologies, and plant health/plant protection advancements on the rate and duration of nutrient accumulation in soybean. Studies routinely include mineral elements of N, P, and K, with little information regarding secondary macronutrients and micronutrients. Furthermore, it is unknown if current fertilizer recommendations are adequate in supporting soybean nutritional needs at biomass and seed yield levels that are greater than ever before. The objective of this research was to determine the mineral nutrition needs of soybean by quantifying season-long nutrient uptake, partitioning, and remobilization.

MATERIALS AND METHODS

Agronomic Practices

Field experiments were conducted in 2012 and 2013 near the Northern Illinois Agronomy Research Center in DeKalb, IL, on a Drummer (fine-silty, mixed, superactive, mesic Typic Endoaquoll)–Elburn (fine-silty, mixed, mesic Aquic Argiudoll) silty clay loam and at the Department of Crop Sciences Research and Education Center in Champaign, IL, on a Drummer–Flanagan (fine, smectitic, mesic Aquic Argiudoll) silty clay loam. Pre-planting soil properties (0–15-cm depth) at DeKalb measured 53 g kg^{-1} organic matter, cation exchange capacity (CEC) of 22.3 cmol kg^{-1}, 23 mg kg^{-1} P, 164 mg kg^{-1} K, 737 mg kg^{-1} Mg, and 2788 mg kg^{-1} Ca. At Champaign, pre-planting soil properties included 43 g kg^{-1} organic matter, CEC of 20.3 cmol kg^{-1}, 54 mg kg^{-1} P, 164 mg kg^{-1} K, 391 mg kg^{-1} Mg, and 2246 mg kg^{-1} Ca. The minerals P, K, Mg, and Ca were extracted using Mehlich III solution with additional soil testing procedures as per Brown (1998). Maize was the previous crop at each site. Individual experimental plots were comprised of eight rows, 12.2 m in length with 0.76 m spacing. Two rows were used to collect yield data, two rows were designated for in-season destructive plant sampling, and four rows were positioned to provide adequate border space.

Treatment combinations were arranged as a randomized complete block design with six replications. Plots were planted on 15 May 2013 (DeKalb), 7 June 2013 (Champaign), and 12 June 2012 (DeKalb) reaching an approximate final plant stand of 358,000 plants ha^{-1}. Two locally adapted and randomly selected varieties were planted at each location and included Pioneer 92Y80 (2.8 RM, 2012 only), Asgrow AG2831 (2.8 RM), or Asgrow AG3432 (3.4 RM). Weed control consisted of a pre-emergence application of saflufenacil {*N*′-[2-chloro-4-fluoro-5-(3-methyl-2,6-dioxo-4-(trifluoromethyl)-3,6-dihydro-1(2H)-pyrimidinyl) benzoyl]-*N*-isopropyl-N-methylsulfamide}, imazethapyr {2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1*H*-imidazol-2-yl]-5-ethyl-3-pyridinecarboxylic acid}, and dimethenamid-P {(S)-2-chloro-*N*-[(1-methyl-2-methoxy)ethyl]-*N*-(2,4-dimethyl-thien-3-yl)-acetamide}, and a post-emergence application of glyphosate {*N*-(phosphonomethyl)glycine} at the V3 growth stage. Contrasting fertilization regimes were used to identify differences in the potential for nutrient accumulation between an unfertilized control and those fertilized using a balanced nutrition approach for a targeted yield level of 5000 kg ha^{-1} (Salvagiotti et al., 2008). Immediately before planting, fertilized plots received 37 kg P ha^{-1} (84 kg P_2O_5 ha^{-1}) as MicroEssentials SZ (12–40–0–10S–1Zn) (The Mosaic Company, Plymouth, MN) in a band approximately 15-cm below the soil surface which supplied an additional 25 kg N ha^{-1}, 21 kg S ha^{-1}, and 2.1 kg Zn ha^{-1}. Fertilized plots also received a pre-plant broadcast application of muriate of potash (0–0–60) at a rate of 56 kg K ha^{-1} (67 kg K_2O ha^{-1}) during 2013. At approximately R3 (beginning pod development; Pedersen, 2009), all plots received a fungicide application of azoxystrobin {Methyl (*E*)-2-{2-[(6-(2-cyanophenoxy)pyrimidin-4-yl)oxy]phenyl}-3-methoxyacrylate} and propiconazole {1-[[2-(2,4-dichlorophenyl)-4-propyl-1,3-dioxolan-2-yl]methyl]-1*H*-1,2,4-triazole} and an insecticide application of lambda-cyhalothrin { [1a(S*),3a(Z)]-cyano(3-phenoxyphenyl)methyl-3-(2-chloro-3,3,3-trifluoro-1-propenyl)-2,2-dimethylcyclopropanecarboxylate} and thiamethoxam {4H-1,3,5-oxadiazinan-4-imine, 3-((2-chloro-5-thiazolyl)methyl)-tetrahydro-5-methyl- N-nitro} at the labeled rate (2013 only).

Biomass Sampling and Tissue Nutrient Analysis

Seasonal biomass and nutrient accumulation was determined using a repeated measures approach by sampling plots at the V4 (fourth trifoliate), V7 (seventh trifoliate), R2 (full bloom), R4 (full pod), R5 (beginning seed), R6 (full seed), and R8 (full maturity) growth stages (Pedersen, 2009). When approximately 50% of plants exhibited the respective growth stage, 10 plants per plot were sampled. Wooden biomass collection crates (0.76 by 0.91 by 0.15 m) were centered over the row shortly after emergence, and used to retain senesced leaf, petiole, and pod tissues, which occurred during reproductive development. Each plant was separated into stem (stems and petioles), leaf (individual leaves), reproductive (flowers and pods), and grain tissue components. Stem, leaf, and reproductive tissues were dried at 70°C to a 0% moisture concentration for dry weight determination. Grain nutrient content at R5 and R6 was determined from hand-sampled plants while grain yield and nutrient uptake at R8 was measured using combine-harvested grain.

Stem, leaf, reproductive, and grain tissues were ground to pass through a 2-mm mesh screen for nutrient concentration analysis. All samples were analyzed for N, P, K, Ca, Mg, S, Zn, Mn, B, Fe, and Cu (A&L Great Lakes Laboratories, Inc., Fort Wayne, IN). Nitrogen was analyzed using a combustion method, and other nutrients analyzed using a two-part process of acid-microwave digestion followed by Inductively Coupled Plasma (ICP) Spectrometry (Horwitz and Latimer, 2011). Tissue nutrient concentrations and dry weight were used to algebraically derive nutrient content. Nutrient harvest indices were calculated as the content of nutrients in the grain relative to total aboveground nutrient uptake.

Statistical Analysis

Total nutrient uptake, grain nutrient content, and harvest index were analyzed using PROC MIXED (SAS Institute, 2009). Site-year, variety, and fertility regime were included in the model as fixed effects and replication nested within site-year was included as a random effect. A nonlinear β growth regression function (Yin et al., 2003) was used to predict nutrient accumulation as a function of days after planting (DAP). Additional regression output included the maximum total nutrient accumulation and the rate of nutrient accumulation according to Yin et al. (2003).

The primary objective of this research was to document nutrient uptake, partitioning, and utilization, and as a result, growth stage was used to graphically illustrate differences. Figures that document season-long nutrient accumulation patterns were prepared using SigmaPlot (SigmaPlot v12.3; Systat Software, Inc., San Jose, CA), and mimic the approach previously used for maize by Bender et al. (2013). Means from statistical analysis were imported into SigmaPlot and figures were then generated using the simple spline curve option with smoothed data points. All units are expressed on a dry weight (0% moisture) basis.

RESULTS AND DISCUSSION

Weather

In 2012 above-average temperatures and periods of limited rainfall were observed (Table 2). During May and July, for example, temperatures were approximately 3°C higher than normal. The season-long precipitation deficit at DeKalb primarily occurred during June and July, presumably during late vegetative and early reproductive growth. Locations in 2013 experienced below-average temperatures during vegetative development in contrast to late reproductive growth, which experienced higher than average temperatures with minimal rainfall (Table 2). Although intra-seasonal weather fluctuations may temporarily influence nutrient accumulation (Sadler and Karlen, 1994, 1995), the data from this study represent a range of growing conditions, germplasm, and agronomic practices.

Biomass Accumulation, Dry Matter Partitioning, and Grain Yield

Total biomass accumulation and grain yield were significantly influenced by site-year, variety, and fertility treatment (Table 3). Averaged across 3 site-years and corresponding treatment combinations, mean biomass accumulation and grain yield were 9524 and 3480 kg ha^{-1}, respectively (Table 4). These data

Table 2. Average monthly weather data between 1 May and 30 September for Champaign (2013) and DeKalb, IL (2012 and 2013), obtained from Illinois State Water Survey (2014). The average daily temperature, Tavg °C, is for the corresponding month. Precipitation (cm) is the average monthly accumulated rainfall. Values in parentheses are the deviations from the 20-yr average (1993–2012).

Location	Month				
	May	June	July	August	September
DeKalb, 2012					
Tavg, °C	18.4 (+2.6)	21.6 (+0.7)	24.8 (+2.5)	20.9 (−0.1)	15.7 (−1.0)
Precipitation, cm	8.1 (−1.8)	1.8 (−7.8)	6.2 (−2.3)	6.1 (−3.8)	3.8 (−3.7)
Champaign, 2013					
Tavg, °C	18.1 (+0.8)	21.8 (−0.6)	22.8 (−1.5)	22.9 (−0.3)	20.6 (+1.6)
Precipitation, cm	11.9 (+0.5)	13.6 (+3.2)	8.8 (−1.2)	1.2 (−8.8)	1.2 (−6.9)
DeKalb, 2013					
Tavg, °C	16.6 (+0.8)	19.9 (−1.1)	21.3 (−1.1)	21.2 (+0.2)	17.6 (+0.9)
Precipitation, cm	9.2 (−0.7)	19.8 (+10.2)	4.3 (−4.3)	11.0 (+1.1)	3.5 (−4.0)

Table 3. Analysis of variance for grain yield, total biomass, and nutrient uptake at physiological maturity (R8) for varieties grown at DeKalb (2012 and 2013) and Champaign (2013). Site-year, variety nested within site-year, and fertility regime were included in the model as fixed effects and replication nested within site-year was included as a random effect.

Parameter	Site-year (S)	Variety (S)	Fertility	Fertility × S	Fertility × Variety (S)
	$P > F$				
Grain yield	0.022	<0.001	0.022	0.341	0.011
Biomass	<0.001	0.012	0.001	0.916	0.628
N	<0.001	0.113	0.001	0.922	0.380
P	<0.001	0.236	<0.001	0.019	0.239
K	<0.001	0.013	<0.001	0.406	0.677
Ca	<0.001	<0.001	0.001	0.062	0.293
Mg	<0.001	0.047	0.003	0.356	0.350
S	<0.001	0.011	<0.001	0.421	0.212
Zn	0.006	0.030	0.028	0.070	0.441
Mn	<0.001	0.049	<0.001	0.092	0.106
B	<0.001	<0.001	0.019	0.826	0.772
Fe	0.018	0.403	0.133	0.572	0.392
Cu	0.017	0.062	0.040	0.635	0.153

Table 4. The effect of fertility treatment on biomass and nutrient accumulation parameters associated with producing, on average, 3480 kg ha^{-1} soybean grain. Total uptake at physiological maturity, removal with grain, and harvest index (percentage of total nutrient uptake present in the grain) of macro- and micronutrients were averaged over varieties at DeKalb (2012 and 2013) and Champaign (2013). All values are reported on a dry weight basis (0% moisture) and were estimated using mean values measured at R8 (physiological maturity). Mean values are followed by the standard deviation and are reported in the same units as the mean.

Parameter	Total uptake			Removal with grain			Harvest index		
	Unfertilized	Fertilized	Average	Unfertilized	Fertilized	Average	Unfertilized	Fertilized	Average
	kg ha^{-1}						%		
Biomass	9126 ± 704	9923 ± 1008	9524 ± 866	3429 ± 157	3531 ± 155	3480 ± 155	38 ± 3.7	36 ± 2.9	37 ± 3.3
N	267 ± 15	284 ± 21	275 ± 18	198 ± 11	205 ± 12	201 ± 11	74 ± 2.9	72 ± 2.5	73 ± 2.7
P	20 ± 1.8	22 ± 1.9	21 ± 1.8	16 ± 1.4	18 ± 1.2	17 ± 1.3	82 ± 3.0	80 ± 3.1	81 ± 3.0
P_2O_5	45 ± 4.1	51 ± 4.3	48 ± 4.2	37 ± 3.2	40 ± 2.7	39 ± 2.9	82 ± 3.0	80 ± 3.1	81 ± 3.0
K	135 ± 14	151 ± 17	142 ± 15	63 ± 3.3	66 ± 3.2	64 ± 3.2	48 ± 5.1	45 ± 4.2	46 ± 4.6
K_2O	162 ± 17	181 ± 20	172 ± 19	76 ± 4.0	79 ± 3.8	78 ± 3.9	48 ± 5.1	45 ± 4.2	46 ± 4.6
Ca	105 ± 15	120 ± 18	113 ± 17	9 ± 0.7	10 ± 0.5	10 ± 0.6	9 ± 1.5	9 ± 1.4	9 ± 1.4
Mg	48 ± 5.7	53 ± 7.6	50 ± 6.7	9 ± 0.6	9 ± 0.5	9 ± 0.5	19 ± 2.7	18 ± 2.2	18 ± 2.4
S	17 ± 1.2	20 ± 1.7	19 ± 1.5	11 ± 0.7	12 ± 0.6	11 ± 0.6	60 ± 4.4	63 ± 3.8	61 ± 4.1
	g ha^{-1}						%		
Zn	318 ± 45	351 ± 56	335 ± 50	135 ± 7.6	145 ± 9.7	140 ± 8.7	45 ± 8.2	44 ± 8.2	44 ± 8.2
Mn	326 ± 54	416 ± 68	371 ± 61	87 ± 8.4	97 ± 5.9	92 ± 7.2	29 ± 3.7	26 ± 3.8	28 ± 3.7
B	315 ± 31	336 ± 34	325 ± 32	111 ± 10	112 ± 11	111 ± 10	35 ± 4.0	33 ± 3.0	34 ± 3.5
Fe	817 ± 153	881 ± 171	849 ± 161	241 ± 21	251 ± 19	246 ± 20	30 ± 5.3	30 ± 5.1	30 ± 5.1
Cu	61 ± 5	65 ± 8	63 ± 6	39 ± 3.1	39 ± 4.0	39 ± 3.5	63 ± 4.3	61 ± 3.8	62 ± 4.1

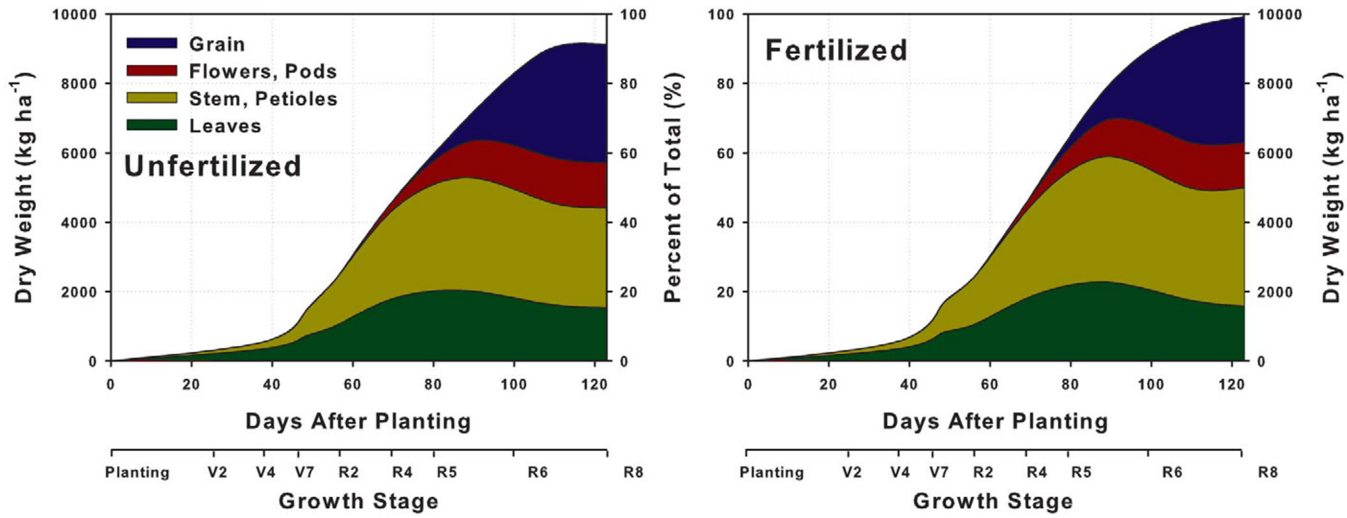

Fig. 1. The effect of fertility treatment on the seasonal accumulation and partitioning of dry weight averaged over two soybean varieties at 3 site-years during 2012 and 2013. All parameters were measured on a dry weight basis (i.e., 0% moisture) and produced an averaged grain yield of 3429 kg ha^{-1} (unfertilized) and 3531 kg ha^{-1} (fertilized).

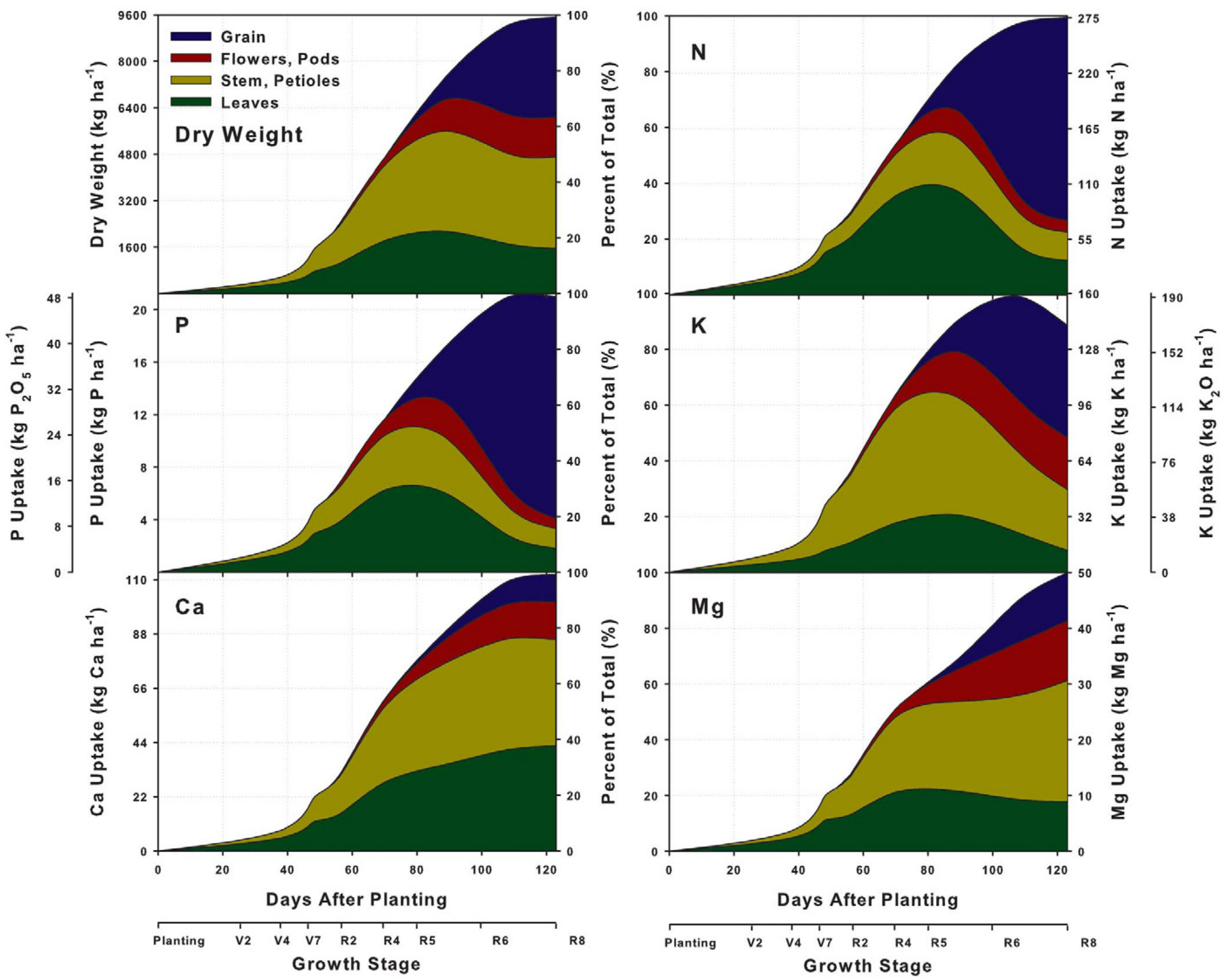

Fig. 2. The seasonal accumulation and partitioning of dry weight, N, P, K, Ca, and Mg averaged over two soybean varieties and fertility regimes at 3 site-years during 2012 and 2013. All parameters were measured on a dry weight basis (i.e., 0% moisture) and produced an average grain yield of approximately 3480 kg ha^{-1}.

Table 5. Maximum total uptake and rate of nutrient accumulation derived using a beta growth function (Yin et al., 2003) measured across variety and fertility treatments at DeKalb (2012 and 2013) and Champaign (2013). At each of seven sampling periods the days after planting were recorded and used to estimate the corresponding growth stages at each location. All values are reported on a dry weight basis (0% moisture) for macronutrients (kg ha^{-1}) and micronutrients (g ha^{-1}).

Parameter	Location, Year†	Maximum total accumulation				Maximum accumulation rate	
		Mean		95% CL	Growth stage‡	Mean	Growth stage
		kg ha^{-1}				kg ha^{-1} d^{-1}	
Biomass	DeKalb, 2012	10,586	±	339	R7	161	R4
	Champaign, 2013	9,539	±	214	R6.5	175	R5
	DeKalb, 2013	9,201	±	280	R6.5	151	R5
	Average	9,775	±	278	R7	162	R4
N	DeKalb, 2012	318	±	10.0	R6.5	4.8	R3
	Champaign, 2013	259	±	6.1	R6.5	4.7	R4
	DeKalb, 2013	277	±	8.2	R7	4.3	R4
	Average	285	±	8.1	R6.5	4.6	R4
P	DeKalb, 2012	25.4	±	0.79	R6.5	0.38	R2
	Champaign, 2013	19.5	±	0.48	R6	0.35	R4
	DeKalb, 2013	20.4	±	0.92	R7	0.30	R4
	Average	21.8	±	0.74	R6.5	0.34	R4
P_2O_5	DeKalb, 2012	58.2	±	1.8	R6.5	0.87	R2
	Champaign, 2013	44.8	±	1.1	R6	0.80	R4
	DeKalb, 2013	46.7	±	2.1	R7	0.69	R4
	Average	49.9	±	1.7	R6.5	0.79	R4
K	DeKalb, 2012	192	±	8.0	R6.5	3.1	R1
	Champaign, 2013	140	±	4.7	R6	2.6	R4
	DeKalb, 2013	161	±	6.6	R6	2.7	R4
	Average	164	±	6.5	R6	2.8	R3
K_2O	DeKalb, 2012	231	±	9.6	R6.5	3.7	R1
	Champaign, 2013	169	±	5.7	R6	3.1	R4
	DeKalb, 2013	194	±	8.0	R6	3.3	R4
	Average	198	±	7.8	R6	3.4	R3
Ca	DeKalb, 2012	115	±	4.8	R6.5	1.8	R2
	Champaign, 2013	147	±	19.7	R8	2.1	R5
	DeKalb, 2013	101	±	4.1	R6.5	1.7	R4
	Average	121	±	9.5	R7	1.9	R4
Mg	DeKalb, 2012	51.6	±	2.7	R8	0.68	R1
	Champaign, 2013	60.0	±	9.5	R8	0.81	R5
	DeKalb, 2013	41.9	±	2.0	R8	0.59	R4
	Average	51.2	±	4.7	R8	0.69	R4
S	DeKalb, 2012	21.3	±	0.7	R7	0.31	R2
	Champaign, 2013	17.6	±	0.6	R6.5	0.32	R4
	DeKalb, 2013	17.7	±	0.7	R7	0.25	R4
	Average	18.9	±	0.7	R7	0.29	R4

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suggest that the significant yield improvements of soybean production during the past 80 yr (Table 1) resulting from genetic advancements (Specht et al., 1999) and agronomic improvements may have concomitantly increased plant nutritional requirements.

Differences in potential for biomass accumulation associated with varieties appeared to be related to the relative maturity (RM), which included a 2.8 and 3.4 RM variety at each location. Regardless of location, the longer RM variety consistently produced greater biomass (+378 to +1,001 kg ha^{-1}) relative to the shorter RM variety; however, the presumably more adapted variety (i.e., 2.8 RM in DeKalb and 3.4 RM in Champaign) out yielded its less-adapted counterpart in each comparison. An increase in biomass (+797 kg ha^{-1}; $P = 0.001$) and grain yield (+102 kg ha^{-1}; $P = 0.022$) was also observed with the fertility treatment (Table 4). These differences were a consequence of an increased rate of dry weight accumulation during late reproductive growth (i.e., R6 to R8) of the fertility treatment compared to the control (i.e., 26.5 vs.

Table 5. (continued).

Parameter	Location, Year†	Maximum total accumulation				Maximum accumulation rate	
		Mean		95% CL	Growth stage‡	Mean	Growth stage
		g ha^{-1}				g ha^{-1} d^{-1}	
Zn	DeKalb, 2012	–	±	–	–	–	–
	Champaign, 2013	292	±	11.5	–	3.57	–
	DeKalb, 2013	288	±	19.9	R8	3.99	R4
	Average	290	±	15.7	R8	3.78	R4
Mn	DeKalb, 2012	431	±	19.1	R7	6.65	R4
	Champaign, 2013	476	±	72.3	R8	6.23	R4
	DeKalb, 2013	216	±	13.6	R7	2.95	R4
	Average	374	±	35.0	R7	5.28	R4
B	DeKalb, 2012	364	±	11.7	R6.5	5.50	R3
	Champaign, 2013	346	±	27.0	R8	5.26	R5
	DeKalb, 2013	296	±	10.0	R6.5	4.78	R4
	Average	335	±	16.2	R7	5.18	R4
Fe	DeKalb, 2012	904	±	55	R6.5	14.3	R2
	Champaign, 2013	899	±	61	–	8.5	–
	DeKalb, 2013	814	±	47	–	6.4	–
	Average	872	±	54	R6.5	9.7	R2
Cu	DeKalb, 2012	58.1	±	2.3	R6.5	0.87	V6
	Champaign, 2013	69.3	±	12.1	R8	0.89	R5
	DeKalb, 2013	63.8	±	3.1	R8	0.85	R4
	Average	63.7	±	5.8	R8	0.87	R3

† Zinc data from DeKalb (2012) were omitted due to Zn concentration outliers.

‡ Missing parameters represent those of inadequate fit with the beta growth function, necessitating the use of a linear regression function.

11.6 kg ha^{-1} d^{-1}, respectively). The relative partitioning of dry weight to plant tissues, however, was markedly similar between fertility regimes (e.g., treatment differences were within 1% of the trial mean for each plant tissue and growth stage) during both vegetative and reproductive growth (Fig. 1). Although greater biomass accumulation provides the foundation for increased nutrient accumulation, differences in dry weight partitioning largely regulate nutrient allocation (Marcelis, 1996; Engels et al., 2012). Because dry weight allocation and nutrient partitioning to these plant tissues were similar across fertility regimes, nutrient accumulations were averaged across fertility treatments in the figures.

The estimated maximum biomass accumulation ranged from 9201 to 10,586 kg ha^{-1} across 3 site-years and was predicted to occur at approximately R7 (Table 5). Even with the use of biomass collection crates, the slight reduction in biomass between R7 and R8 was likely a consequence of incomplete leaf and petiole collection (Borst and Thatcher, 1931; Hammond et al., 1951; Hanway and Weber, 1971b; Harper, 1971; Sadler and Karlen, 1995). The partitioning of biomass at maturity was distributed across leaf (16%), stem (33%), pod (14%), and grain (37%) tissues (Fig. 2). The improvement of dry weight harvest index represents a fundamental shift in germplasm use and agronomic production during the last 80 yr (Table 1). For example, current data (Table 4) exhibits a twofold increase in biomass production compared to Borst and Thatcher (1931) and a near threefold improvement in grain yield during the same time period (Specht et al., 1999).

Total Nutrient Uptake and Removal

Total nutrient accumulation was algebraically derived at maturity (Table 4) and also predicted using a β growth function (Table 5). Predicted values in Table 5 represent theoretical maximum levels of nutrient accumulation in-season and thus exceed means determined at crop maturity (Table 4). Total nutrient uptake was significantly influenced by the main effect of site-year (Table 3) as differences in the potential for maximum nutrient accumulation were realized within each environment (Table 5). The fertility treatment significantly increased accumulation of fertilized (N, P, K, S, Zn) and unfertilized (Ca, Mg, Mn, B, and Cu) nutrients ($P < 0.05$; Table 4). Increased nutrient accumulation did not always lead to greater nutrient removal, particularly for nutrients with low harvest index (HI) values such as Mg, B, and Fe. Combined with dry weight data, these findings suggest that supplemental fertilization in this study was used as a strategy to maintain greater nutrient availability, leading to increased nutrient uptake, total biomass production, and ultimately grain yield.

Regardless of fertility regime, agronomic production practices and soil conditions with a capacity to supply nutrients at the listed quantities in Table 4 would be expected to meet soybean nutritional needs for an average yield level of approximately 3480 kg ha^{-1}. While the potential for nutrient accumulation in soybean has increased by two to threefold during the past 80 yr as a result of increased dry matter production and grain yield (Borst and Thatcher, 1931; Table 1), the rate of increase for some nutrients appears to have slowed during the most recent 40 yr (Hanway and Weber, 1971a, 1971b; Table 1). Nutrient uptake values in the current study are considerably lower than those published by Flannery (1986), who measured nutrient accumulation of N (614 kg ha^{-1}), P (65 kg P or 148 kg P_2O_5 ha^{-1}), and K (403 kg K or 485 kg K_2O ha^{-1}) in a maximum yield research study producing 18,615 kg biomass ha^{-1}. Mean grain yield values presented in this study are approximately 30 to 40% greater than the current U.S. average (USDA-NASS, 2013b), however, and presented nutrient accumulation information may serve as a resource for the anticipated improvement in soybean yield.

Quantification of the factors affecting grain nutrient accumulation and removal is imperative, as this parameter influences soil test levels, plant nutrient utilization, and the grain as a potential feed source. On a per kg basis, grain nutrient concentrations were measured for N (57.8 g), P (4.8 g), K (18.5 g), Ca (2.8 g), Mg (2.5 g), S (3.2 g), Zn (40.2 mg), Mn (26.3 mg), B (31.9 mg), Fe (70.7 mg), and Cu (11.3 mg) (data not shown). Murrell (2005) compiled and summarized soybean nutrient removal data from numerous university and extension publications, providing removal coefficients for each macronutrient. Although grain nutrient concentrations in this study tended to be slightly lower than those reported by Murrell (2005), updated values are necessary to accurately estimate nutrient removal.

Grain nutrient HI values are a relative indicator of nutrient partitioning to soybean grain tissues, quantified as the ratio of grain nutrient removal to total nutrient accumulation. On average, more than 80% of accumulated P was removed via harvested soybean grain tissues compared to N, S, and Cu; all of which measured >60%. Unlike that observed in maize (Bender et al., 2013), the micronutrient with the greatest HI value in this soybean study was Cu, which supports the potential role of Cu

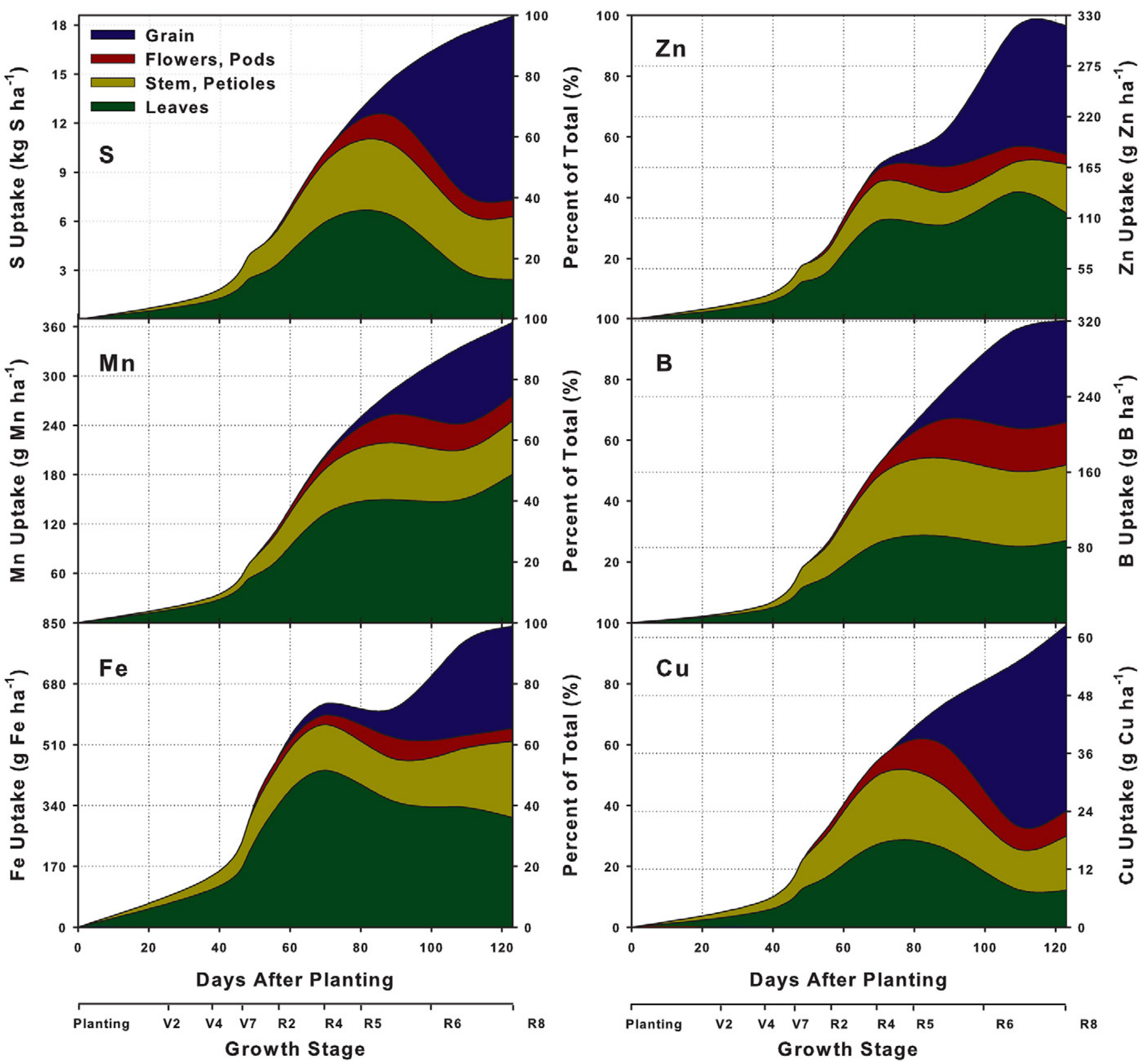

Fig. 3. The seasonal accumulation and partitioning of S, Zn, Mn, B, Fe, and Cu averaged over two soybean varieties and fertility regimes at 3 site-years during 2012 and 2013. All parameters were measured on a dry weight basis (i.e., 0% moisture) and produced an average grain yield of approximately 3480 kg ha^{-1}.

in pollen viability and seed formation (Broadley et al., 2012). Harvest index values for N, P, S, and Mg are similar to those presented by Hanway and Weber (1971a) and Hammond et al. (1951). Potassium HI values have decreased considerably (Table 4; 46%), compared to those of Hammond et al. (1951; 69%) and Hanway and Weber (1971b; 56%), with concomitant increases in dry weight HI during the same time period.

Time and Rate of Nutrient Acquisition

Seasonal patterns of nutrient accumulation document the time and rate of nutrient uptake for soybean yielding approximately 3500 kg ha^{-1} (Fig. 2 and 3). Although vegetative growth temporarily coincides with the initiation of reproductive development among indeterminate varieties of the northern United States, the completion of growth stage R4 was selected as a reference point to distinguish the onset of seed-filling (Pedersen, 2009). Results suggested that the rate and time of acquisition varied among nutrients and were associated with specific vegetative or reproductive growth periods. Nearly three-quarters of K and Fe uptake, for example, occurred before the onset of seed filling (Fig. 2 and 3; Table 6). In contrast, the uptake of N, P, Ca, Mg, S, Zn, Mn, B, and Cu was more evenly distributed during vegetative and seed-filling growth phases (Fig. 2 and 3; Table 6). Compared to the rapid uptake of mineral nutrients directly before the onset of pollination in maize (Bender et al., 2013), nutrient uptake in soybean more closely coincides with dry matter accumulation producing a steady, season-long approach to nutrient assimilation (Fig. 2 and 3).

Nutrient uptake patterns closely resemble those published during the last 80 yr (Borst and Thatcher, 1931; Hammond et al., 1951; Hanway and Weber, 1971a), although in modern cultivars, the proportion of total nutrient accumulation acquired during seed filling has increased over time (Table 6). The differences are especially apparent for N, P, Ca, and Mg, which have increased by as much as 18% during this reproductive period. Increased dry matter production as a result of improved soybean yields and greater dry matter HIs achieved through more efficient dry matter partitioning may have contributed to the greater demand for mineral nutrient accumulation during seed filling.

Maximum rates of biomass and nutrient accumulation were measured for parameters at each site-year and the approximate growth stage during which they occurred. Dry matter accumulation peaked at 162 kg ha^{-1} d^{-1} (during R4; Table 5) across site-years with a near-constant rate, which occurred from approximately V6 to R6 (Fig. 2). In a comparison of five soybean nutrient uptake studies conducted by Sadler and Karlen (1995), it was concluded that the potential for steady rates of biomass and nutrient accumulation exist despite intra-seasonal variation in response to soil moisture and temperature stresses. Measured maximum accumulation rates (Table 5) are lower than theorized maximum values presented by Sadler and Karlen (1995), but similar to or greater than those published by Borst and Thatcher (1931), Hammond et al. (1951), and Hanway and Weber (1971a). Collectively, these findings suggest that the improved potential for dry matter production has concomitantly increased the potential for nutrient accumulation. With the exception of K and Fe, maximum rates of nutrient uptake were consistent across macro- and micronutrients and tended to occur during a brief period that bracketed R4 (Table 5). These data confirm those published by Harper (1971) who estimated the period of maximal nutrient accumulation occurs between R2 and R5 in a non nutrient-limiting hydroponics study.

Nutrient Remobilization

Nutrient harvest indices represent the relative proportion of grain nutrient content to total nutrient accumulation and were >60% for P, N, Cu, and S (Table 4). Physiological processes that increase grain nutrient content include nutrient accumulation after the onset of seed filling with direct partitioning to developing grain tissues, or nutrient remobilization from leaf, stem, or flower and pod tissues (Bender et al., 2013). To supply grain N over one-half of total N accumulation occurred after the onset of seed filling (Table 6) in addition to remobilization of 65 and 32% of leaf and stem N contents, respectively, measured near the beginning of seed fill (Fig. 2). A similar pattern occurred for P where more than 45% of P was accumulated during seed filling (Table 6) with approximately two-thirds of measured leaf and stem contents remobilized to developing seed tissues (Fig. 2). Consistent with N and P translocation tendencies published in previous soybean nutrient accumulation studies (Borst and Thatcher, 1931; Hanway and Weber, 1971a), the quantity of

Table 6. Percentage of total nutrient accumulation after the completion of R4 estimated from select nutrient accumulation studies during the past 60 yr. Days after planting (DAP) was used to estimate the length of time spent during specific phases of crop growth across studies. No micronutrient data was available from Hammond et al. (1951) and Hanway and Weber (1971a).

Parameter	Hammond et al., 1951†	Hanway and Weber, 1971a, 1971c‡	Current study
	Growth season information		
Planting date	22 May	4 May–16 May	15 May–12 June
DAP to R4	80 d	75 d	70 d
DAP to R8	135 d	126 d	123 d
Approximate days during seed filling	55 d	51 d	53 d
	Percent of total nutrient accumulation after the completion of R4		
Biomass	34	42	51
N	37	40	46
P	35	43	45
K	29	42	28
Ca	36	–	45
Mg	31	–	49

† Percentage of nutrient accumulation after R4 was estimated using harvest date number nine.

‡ Biomass data was estimated from Hanway and Weber (1971c) and nutrient uptake data from Hanway and Weber (1971a).

grain N and P obtained from remobilization was as much as fourfold greater from leaf vs. stem tissues. These data reinforce the importance of season-long nutrient accumulation and the utility of existing plant tissues as reservoirs to accommodate intra-seasonal periods of elevated nutrient demand.

Additional nutrients with notable remobilization tendencies included K and Cu (Fig. 2 and 3). Despite the lower HI of K (46%) relative to N and P, nutrient translocation was still necessary where approximately twice the quantity of K was remobilized from existing stem compared to leaf tissues. Although leaf tissues served as the primary source of remobilized N and P, these results suggest that plant stem tissues may serve as temporary storage for some nutrients. The magnitude of K remobilization from existing stem tissues had not been previously documented (Sale and Campbell, 1986). Unlike the micronutrients Zn, Mn, B, and Fe, only Cu exhibited remobilization characteristics where more than one-half of leaf Cu was translocated to grain tissues (Fig. 3). With a seed HI of 62%, uptake during seed filling was required to supplement the remobilization of Cu to the seed. These results also imply that if a temporal plant or leaf deficiency of Cu exists, a foliar application of Cu may relieve the deficiency while simultaneously supplying the grain with needed Cu.

Implications for Soybean Production

Intensified agronomic production practices and improved germplasm have contributed to greater average soybean yields than ever before (Table 1; Specht et al., 1999). Increases in the potential for biomass production provide the driving force for greater nutrient accumulation, especially for macronutrients such as P and K. From a historical perspective, routine fertilizer applications of K were likely necessary to maximize total biomass, especially during the introduction and popularization of soybean as a forage legume in the United States (Borst and Thatcher, 1931). In a comparison of current data to initial soybean nutrient uptake research (Borst and Thatcher, 1931), the modernization of soybean varieties selected for high seed yield has increased historical HI values for dry weight (from 26 to 37%) and P (from 68 to 81%) with a simultaneous reduction in K HI (from 58 to 46%). Altered dry weight and nutrient harvest indices with substantial increases in the percentage of total nutrient accumulation occurring during seed fill (Table 6) necessitates precise nutrient management for current production systems. For example, total P accumulation measured approximately one-half that of a maize crop yielding 12.0 Mg ha^{-1} (Table 4; Bender et al., 2013), though similar P HI values of nearly 80% suggest a potential for rapid soil P decline given inadequate nutrient replacement. Conversely, the partitioning of K in soybean has different agronomic implications. Total K accumulation in soybean yielding 3.5 Mg ha^{-1} was similar to that of maize yielding 12.0 Mg ha^{-1} with near equal partitioning of total K among plant tissues (Fig. 2; Bender et al., 2013). Over 50% of total K in stem and petiole biomass was remobilized to soybean grain tissues, representing approximately two-thirds of grain K. The 78 kg K ha^{-1} (94 kg K_2O ha^{-1}) partitioned to non-grain biomass (i.e., stem, leaf, and pod tissues) would presumably serve as a major K source for the following crop.

Although Fixen et al. (2010) found that a growing number of soybean-producing regions decreased soil test levels for P, K, and S, removing non-grain soybean residues would accelerate soil nutrient decline. Nearly two-thirds of the total aboveground biomass, or 6044 kg dry weight ha^{-1}, remained in leaf, stem, and reproductive tissues at physiological maturity (Table 4) and normally return to the soil after harvest. Agronomic production practices which harvest non-grain plant tissues for animal bedding or feed sources, commonplace in key cattle-producing regions, would remove up to an additional 74 kg N, 4 kg P (9 kg P_2O_5), 78 kg K (94 kg K_2O), 103 kg Ca, 41 kg Mg, 8 kg S, 195 g Zn, 279 g Mn, 214 g B, 603 g Fe, and 24 g Cu per hectare (Table 4). The quantity of nutrients retained in non-grain tissues can vary considerably according to soil test levels and fertility management practices, especially as it relates to the potential for luxury consumption of basic cations such as K, Ca, and Mg (Hammond et al., 1951; Fageria, 2001).

Soybean assimilates a substantial amount of N during its growth due to the high protein concentration of the grain (Egli, 1998). Although the current study did not distinguish between N acquired from the soil vs. N resulting from symbiotic N_2 fixation, past literature suggests that, on average, the soybean plant obtains approximately 50% of its N from N_2 fixation (Salvagiotti et al., 2008). Given the presented yield level of 3480 kg ha^{-1} accumulating a total of 275 kg N ha^{-1}, we can assume that approximately one-half, or 137.5 kg N ha^{-1}, was obtained from N_2 fixation (Table 4). Harvesting the soybean grain removed 201 kg N ha^{-1} and would thus result in a soil depletion and a negative N balance for the following crop of nearly 63.5 kg N ha^{-1} if only considering the contribution from N_2 fixation.

Because the entire N requirement of the soybean plant does not come from fixation, the implication is that a greater total amount of N must be supplied by soil and other sources as the yield potential increases. For example, a 5000 kg ha^{-1} soybean crop (approximately double the current U.S. average) will require nearly 350 kg N ha^{-1} for its production, and approximately 175 kg N ha^{-1} must be supplied by the soil or other nutrient sources (Salvagiotti et al., 2008). While N mineralization from organic matter varies across environments and weather conditions, projection of soil N supply can be estimated with soil organic matter and organic N conversions. Assuming that 5% of soil organic matter is organic N and that 2% is mineralized on an annual basis (Fernández et al., 2012), each percent of soil organic matter will supply an estimated 22.5 kg N ha^{-1} yr^{-1} in the upper 17 cm of the soil profile. Because most Illinois soils contain 3 to 5% soil organic matter, it can be assumed that only 67.5 to 112.5 kg N ha^{-1} yr^{-1} may be supplied from soil N mineralization to NH_4^+ forms with the remainder supplied from other sources. Given these assumptions, the result would be a net N deficit by as much as 107.5 kg N ha^{-1} when producing 5000 kg ha^{-1}. This information is in general agreement with Salvagiotti et al. (2008), who suggested that yields exceeding 4000 to 4500 kg ha^{-1} will likely require supplemental N applications because of limitations in biological N fixation and soil organic matter mineralization.

CONCLUSIONS

The primary objective of this research was to quantify nutrient uptake, partitioning, and remobilization using current soybean varieties in modern soybean production systems. Improved biomass production, grain yield, and harvest indices have occurred during the last 80 yr, resulting in concurrent increases in nutrient accumulation. Patterns of biomass production and nutrient accumulation are presented for an average yield of approximately 3500 kg ha^{-1} and are most suitable for producers targeting this yield level. Although nutrient acquisition was most rapid between R3 to R4 for measured nutrients, patterns of nutrient accumulation highlighted intra-seasonal differences in the timing of nutrient acquisition. Uptake of K and Fe primarily occurred during late vegetative and early reproductive growth in contrast to uptake of N, P, Ca, Mg, S, Zn, Mn, B, and Cu, which was more evenly distributed throughout the entire growing season. As a result, agronomic practices that also ensure nutrient availability during late-season reproductive growth would be expected to meet soybean fertility needs for these nutrients.

During seed filling, grain tissues required remobilization and season-long nutrient accumulation. Four nutrients had HI values >60% including P (81%), N (73%), Cu (62%), and S (61%), and may cause a yield limitation given inadequate soil or plant availability during reproductive growth. Incorporation of current findings, such as when and where nutrients are accumulated in soybean, may contribute to existing agronomic recommendations and help ensure plant fertility needs are met with season-long nutrient availability.

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