



## Nutrient partitioning and stoichiometry in soybean: A synthesis-analysis



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### ABSTRACT

On-farm attainable soybean yields are primarily limited by nutrient and water supply. High-yielding soybeans is related to high nutrient uptake. A proposed theoretical framework underpinning yield formation includes plant nitrogen (N) uptake, N harvest index (NHI), and N seed concentration (%N<sub>seeds</sub>). The objectives of this study were focused on (i) investigating the effect of NHI and %N<sub>seed</sub> on yield-to-uptake relation for N, and (ii) analyzing dry mass and N partitioning and extending this analysis to phosphorous (P) and potassium (K) uptake and (iii) studying the influence of specific seed:stover ratios on the relationship of N with P, and K uptake. Metadata on yield, nutrient uptake and specific-organ nutrient concentration (%nutrient) was summarized from experiments located in three different environments: Indiana, Kansas (both US), and Argentina (herein termed as IN, KS, and ARG, respectively). The main outcomes from this research were: 1) the yield-to-uptake relation for N was primarily explained by NHI; 2) the algebraic model proposed by Sinclair (1998), that includes each specific-organ %nutrient explained consistently nutrient (N, P or K) HI as a function of HI with different trend, and 3) plant nutrient ratios were primarily governed by vegetative %nutrient (stover fraction), acting as a nutrient reservoir or supply depending on the demand of nutrient in the seed. Further research on the nutrient and biomass partitioning should focus on examining the NHI:HI relationship under varying genotype x environment x management interaction.

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### 1. Introduction

Nitrogen (N) is essential for plant growth and seed production (Lawlor, 2002). In soybean, N demand is satisfied by biological N fixation (BNF) and by soil N supply. A historical review performed by Salvagiotti et al. (2008) documented a linear response for the yield-to-uptake relation for N with a 13 kg yield per unit (kg) of N taken up by the crop. Soybean N internal efficiency (slope, yield-to-uptake relation for N) is smaller relative to other crops due to the

*Abbreviations:* N, nitrogen; P, phosphorus; K, potassium; HI, harvest index; NHI, N harvest index; PHI, P harvest index; KHI, K harvest index; %N<sub>seed</sub>, seed N concentration; %N<sub>stover</sub>, stover N concentration; %P<sub>seed</sub>, seed P concentration; %P<sub>stover</sub>, stover P concentration; %K<sub>seed</sub>, seed K concentration; %K<sub>stover</sub>, stover K concentration.

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high oil and protein content in seeds that demands large amounts of N uptake and remobilization from vegetative tissues (Sinclair and de Wit, 1975). A minimum N concentration (%N) in plant is needed to maintain optimum photosynthetic rate (and therefore biomass production), since most of leaf N is a constituent element of the protein ribulose 1,5-bisphosphate carboxylase involved in the photosynthesis process (Sinclair and Horie, 1989). To accomplish this demand, BNF should supply a large proportion of N during a substantial portion of the growing season (from early vegetative stages until the end of seed-filling period).

Changes in seed yield can be understood by studying its relationship with total plant N uptake and via dissecting N uptake-related components. Total plant N uptake, N harvest index (NHI, seed N-to-plant N content ratio) and N concentration in seeds (%N<sub>seed</sub>) may explain seed yield generation in crops as described in Eq. (1):

$$\text{Seed yield}(\text{kg ha}^{-1}) = (\text{Total plant N uptake} \times \text{NHI}) / \%N_{\text{seed}} \quad (1)$$

Total plant N uptake, NHI, and %N<sub>seed</sub> are all influenced by the complex genotype x environment x management practices interaction (Below, 2002; Masclaux-Daubresse and Chardon, 2011). Using the framework proposed in Eq. (1), Rotundo et al. (2014) reported, for a large set of genotypes evaluated in several environments, that plant N uptake was the main component in high-yielding soybean genotypes. Despite the genotypic variability in NHI and %N<sub>seed</sub> found in this study, the relative influence of NHI and %N<sub>seed</sub> has not been studied. Sadras (2006) found an equal contribution from both traits to seed yield and plant N uptake relationship when different legumes species were evaluated.

Eq. (1) indicates the importance of N partitioning to seed from non-seed tissues, i.e. NHI (Hay, 1995) which depends on biomass partitioning to seeds in crops, i.e. harvest index (HI), seed yield-to-plant biomass (Donald and Hamblin, 1976). Increases in HI are usually positively correlated with NHI, since greater biomass accumulation in seeds results in an N adjustment in terms of partitioning between organs in the plant (Sinclair, 1998). This correlation has been also observed in other legumes as common bean (Araújo and Teixeira, 2003) and in cereals as wheat and corn (Ciampitti and Vyn, 2012; Loffler et al., 1984). For the same authors, the NHI:HI relationship has been studied as a linear response regardless of other plant traits. For instance, in soybean, NHI and HI may also vary as a function of seed protein concentration because of different biomass and N partitioning during the seed-filling period (Salado-Navarro et al., 1985), and also may be modified by residual %N present in the stover fraction (herein termed as %N<sub>stover</sub>) and their N stoichiometry ratio (“seed:stover N stoichiometry”) with seed N concentration (herein termed as %N<sub>seed</sub>). This approach has been summarized algebraically in a formula proposed by Sinclair (1998):

$$\text{NHI} = \frac{[\%N_{\text{seed}} \times \text{HI}]}{[\text{HI} \times (\%N_{\text{seed}} - \%N_{\text{stover}}) + \%N_{\text{stover}}]} \quad (2)$$

Lawn (1989) suggested that improvements in HI are constrained by NHI, and indirectly by both %N<sub>seed</sub> and %N<sub>stover</sub>. This author proposed a theoretical framework for the NHI and HI relationship (Eq. (2)), suggesting a curvilinear response in crops with high %N<sub>seed</sub> and low %N<sub>stover</sub>, and being almost linear when %N<sub>seed</sub> approaches %N<sub>stover</sub>. The latter situation would be reflected in crops such as maize and sorghum where the N concentration in grain and stover are closer (ca. 1:2 ratio; Jones, 1983).

Both approaches explaining the NHI:HI relationship has not been documented for a specific crop species with data from field studies. Additionally, to the extent of our knowledge, this theoretical approach was only evaluated for the NHI:HI relationship but not for other macronutrients.

Nitrogen should be in balance with other macronutrients such as phosphorus (P) and potassium (K) in order to maximize seed yield. An approach for understanding these balances can be pursued by analyzing plant nutrient stoichiometric ratios (e.g., N:P and N:K ratios). For example, as biomass increases during the plant growth cycle, plant N:P ratio tended to decrease because of changes in plant nutrient concentrations in the plant (Greenwood et al., 2008). This occurs because of the differentiation of tissues (e.g., leaves, stem, roots) during the crop cycle, with each tissue having different proportions of nutrients according to its function (Greenwood et al., 2008). Variability in N:P and N:S ratios for legumes species and more specifically for soybean have been previously documented (Sadras, 2006; Salvagiotti et al., 2012). However, previous research studies did not consider the influence of the variation in nutrient concentration related to specific plant organs. Moreover, characterization for P and K stoichiometry in modern soybean cultivars over a wide range of genotypes and environmental conditions has not yet been reported in literature.

The aims of this study were to 1) provide evidence about the relative effect of NHI and %N<sub>seed</sub> on yield-to-uptake relation for N; 2) implement the mathematical framework proposed by Sinclair (1998) for NHI:HI relationship in soybean and extend it to P and K, and 3) study the influence of seed:stover ratios on the relationship of N with P, and K uptake.

## 2. Materials and methods

### 2.1. Experimental data

Data from experiments carried out in Argentina (herein term as ARG) and the US (Kansas, KS, and Indiana, IN) were used, including different genotypes, environments and management practices (Table 1). The final database included: 1) seed yield (dry basis), 2) %N, %P and %K in seeds and stover, and 3) seed, stover, and total biomass.

Eight site-years were summarized from 2009 to 2014 seasons, comprising 167 data points (including replications) for all plant traits evaluated. At all site-years, the experimental layout was a complete randomized block (CRB) design with three (ARG, IN) and five (KS) replications. Planting dates, seeding rates and crop protection practices were in accordance with local farmer practices. Plots were between four (KS and ARG) to eight (IN) rows width and 4 to 5 m long. Row spacing differed by region with 0.52 m spacing in ARG, 0.76 and 0.38 m in KS, and 0.76 m in IN.

### 2.2. Crop measurements

Phenological stages were recorded during all seasons and biomass was sampled in R7 for ARG and KS, and in R8 for IN (Fehr and Caviness, 1977) in representative rows of each plot. For all site-years biomass sampling included leaves in standing biomass except for IN. Differences in sampling time across all environments should not affect final nutrient content since maximum nutrient content is achieved at or right before those growth stages (Bender et al., 2015).

Seed yield was measured by harvesting a representative area of each plot. Samples were weighed and adjusted to dry basis. Aboveground biomass (BM) was collected by cutting plants at the ground-level in a 1 m<sup>2</sup> area (KS and ARG) and in a 0.76 m<sup>2</sup> area (IN). Plants collected from each plot were separated in non-seed (herein term “stover”) and seed biomass fractions and dried at 65 °C until constant weight was attained. Samples were ground to determine total nutrient concentration (%nutrient, N, P and K) via combustion method for N (AOAC, 2000) in KS and IN, and Kjeldahl in ARG. For P and K concentration was made via the inductively coupled plasma (ICP) spectrometry method (AOAC, 2000).

Nutrient uptake for each plant fraction was calculated as the product of %nutrient multiplied by the specific-organ mass (dry basis). Plant nutrient uptake was calculated as the sum of stover and seed nutrient content [Eq. (1)].

$$\text{Plant Nutrient Uptake}(\text{kg ha}^{-1}) = [\% \text{Nutrient}_{\text{stover}} \times \text{BM}_{\text{stover}}(\text{kg ha}^{-1})] + [\% \text{Nutrient}_{\text{seed}} \times \text{BM}_{\text{seed}}(\text{kg ha}^{-1})] \quad (3)$$

Harvest index (HI) and nutrient HIs (NHI, PHI, KHI) where determined as the seed to aboveground biomass (BM) or nutrient content ratio [Eqs. (4); (5)].

$$\text{HI} = \frac{\text{Seed}(\text{kg ha}^{-1})}{\text{BM}(\text{kg ha}^{-1})} \quad (4)$$

$$\text{Nutrient HI} = \frac{\text{Seed Nutrient Uptake}(\text{kg ha}^{-1})}{\text{Plant Nutrient Uptake}(\text{kg ha}^{-1})} \quad (5)$$

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