

Multi-Compartmental Modeling of Nitrogen Translocation in Sorghums Differing in Nitrogen Use Efficiency

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ABSTRACT

Some cultivars of sorghum [*Sorghum bicolor* (L.) Moench] are more efficient than others in using nitrogen (N) from the soil to produce grain. A study was conducted to test the hypothesis, that the processes involved in the translocation of N differed between two sorghum lines, China 17, a N-efficient genotype, and Tx623, a less efficient genotype, during their ontogenetic development. Both cultivars were grown in the field and periodically sampled to determine the amount of N in above-ground parts of the plants, i.e. stalk, leaves, and grain. Compartmental modeling, which is based on sets of differential equations that describe the flow of material through compartments, was used as the basis for analysis of the rates and rate constants of N which had moved among parts of the plant. Compartmental models are relatively simple, systematic mathematical representations that can be used to aid in understanding how different plant parts influence plant-N dynamics. China 17's rate constants between upper parts of the stalk and between the upper stalk and grain were larger in the earlier part of the season and became smaller toward the end than Tx623 meaning that China 17 was more capable of moving N to the upper parts of the plant earlier in the season than was Tx623. However, no differences in rate constants were detected for stalk to leaves and within leaves rate constants, meaning that the N-movement processes in the leaves were essentially the same between the two genotypes. The model also detected pseudo-compartments associated with the upper leaves in both genotypes which indicated that

Received 6 January 2008; accepted 7 August 2008.

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there are several processes or other rate-controlling factors associated with N flow in the leaves. A multi-compartmental model, based on rather simple assumptions and which only required N for each plant part over time, was used to describe N translocation between plant parts for two different sorghum genotypes. The model was able to detect fundamental differences between the genotypes in terms of N translocation processes, however more work is needed to understand the physiological processes underlying the results.

Keywords: nitrogen flux, nutrient movement, compartmental analysis, dynamic model

INTRODUCTION

Nature can never be completely described, for according to the ancient Chinese sage, Lao Tzu in Tao Teh King, such a description of Nature would have to duplicate Nature (Baum, 1958). Leonardo da Vinci observed, regarding science, that there is no certainty where one cannot apply at least one branch of mathematics, or where the science is not united with mathematics (Marinoni, 1952). Since the early 1970s, mathematical modeling of crops has played an increasing role in education, understanding genetic regulation and physiological processes in plants, assisting in crop improvement, and supporting decision-making (Rose and Charles-Edwards, 1981; Hammer et al., 2002). The present paper describes differences among two genotypes of sorghum (*Sorghum bicolor* (L.) Moench) using a formal (Cooper et al., 2002), mathematical system that is based on morphological characteristics. This system is a model of the movement of nitrogen between various above-ground parts of a sorghum plant and is a simplification of a more complex natural system.

Of approximately 350,000 plant species which have been identified by botanists, about 50 crop species are of major importance, both economically and for the nutrition of humans, poultry, and livestock. Cereals as a group supply about 65% of dry matter and over 50% of the protein consumed in the world (Dambroth and El Bassam, 1990). Sorghum is a significant cereal in the semi-arid tropics, because it can produce grain in marginal environments and because it is the dietary staple of more than 500 million people in more than 30 countries (National Research Council, 1996).

Nitrogen use efficiency (NUE) is an indicator of efficiency by which plants utilize nitrogen (N), and NUE can be measured in various ways (Maranville et al., 1980; Moll et al., 1982; Onken et al., 1985; Cassman et al., 1998; Raun and Johnson, 1999). In the present study, we use the definition of biomass N use efficiency (NUE_1) of Maranville et al. (1980), namely total biomass production per unit total above-ground plant N. In a study of genotypes of sorghum differing in nitrogen-use-efficiency, Buah et al. (1998) characterized sorghum inbred Tx623 as responsive to N fertilizer, but with low NUE_1 . Subsequently, Maranville and Madhavan (2002) compared Tx623 and a high NUE_1 line of sorghum, China

17, by comparing their assimilation efficiency index. The assimilation efficiency index gives an estimate of carbon dioxide (CO_2) assimilation activity by photosynthetic tissue; this index is the slope of A/C_i , where the initial slope value of CO_2 assimilation (A) by a sample of photosynthetic tissue is plotted against internal leaf CO_2 concentration (C_i). Maranville and Madhavan (2002) found that when subjected to N stress in the greenhouse, the high- NUE_1 China 17 genotype had a higher assimilation efficiency index than Tx623 at both low and high soil N levels. Moreover, China 17 retained a higher phosphoenolpyruvate carboxylase (PEPcase) activity than the less NUE_1 Tx623, suggesting that PEPcase and enzymes associated with phosphoenolpyruvate synthesis may be factors in maintaining relatively high photosynthesis under N stress.

While the model of the present study does not include aspects of metabolism such as photosynthesis, the research by Maranville and Madhavan (2002) indicates that differences in movement of N among morphological parts of the above-ground parts of the two genotypes studied may be affected by differences in photosynthetic processes in the two genotypes. The higher rates of accumulation of N in the above-ground parts of the China 17 plants and their earlier and greater loss of N from vegetative parts of the shoot to the grain, compared to Tx623, are associated with higher NUE_1 of China 17. Further research is needed regarding the relationships between photosynthesis and N flow among the vegetative and reproductive parts of the sorghum shoot to determine how the differences in photosynthesis are related to movement of N among plant parts during the vegetative and reproductive phases of growth.

Nitrogen is translocated from other parts of the sorghum plant to the grain as it develops (Warrick, 2001). Studies of translocation of N in maize (Crawford et al., 1982) and wheat (Harper et al., 1987) indicate that even when N is available to the plant during the reproductive phase of growth, N accumulates in the grain from sources both outside the plant (the soil) and from vegetative organs (e.g., stems and leaves).

Dynamic rates of translocation of N in maize during the reproductive phase of growth have been estimated by Crawford et al. (1982) using first derivatives of linear polynomial regression equations estimating the amount of N in different plant tissues during the reproductive phase of growth. In a similar manner, effects of manganese (Mn) deficiency, sufficiency, and toxicity on net fluxes of seven mineral nutrients, water, and carbohydrate for compartments representing different tissues of the plant as a function of time were estimated using first derivatives of non-linear regression equations (Crawford et al., 1989; Crawford et al., 1990).

Most previous studies on N translocation rates have been somewhat limited by the use of statistical models that fail to consider the plant as an entire system with the consequence of not understanding how different plant parts influence rates of movement of N between the plant parts. Multi-compartmental systems analysis is an effective way of modeling N flow through the plant, taking into

account rates of N movement between the components of the system. A multi-compartmental system of this type consists of a finite number of subsystems, called compartments that interact with each other by processes of transportation and diffusion (Jacquez, 1985). Usually, a compartment is assumed to be a physical entity through which a substance flows where the material in the compartment is well-mixed and homogeneous. The mathematical framework of compartmental systems is based on sets of differential equations that describe the flow of material through compartments (Burghes and Borrie, 1981). Compartmental models are abundant in medicine, physiology, ecology, and other disciplines (Lasser and Walcher, 2002) and have been used to study the movement of ^{14}C through interconnected "pools" in plants (Pearlman and Lawlor, 1981) and the transport of ^{32}P in grape plants (Tsukerman and Dorokhov, 1991) and to model the movement of organic chemical contaminants in plants (Paterson, et al., 1994; Trapp, 1995; Trapp and Matthies, 1998; Fryer and Collins, 2003).

This study was conducted to use compartmental systems analysis to model nitrogen flow among morphological parts of the shoot (above-ground parts) of two sorghum lines, a low-NUE₁ sorghum inbred Tx623 and a higher-NUE₁ sorghum landrace, China 17, and to test for differences between genotypes regarding the translocation of N among different above-ground plant parts during their ontogenetic development. Examining the fluxes of N during the vegetative and reproductive phases of growth was undertaken to better understand the differences of nitrogen translocation between the grain and other parts of the shoot of the plant for these two genotypes which have been shown by Maranville and Madhavan (2002) to have marked biochemical and physiological differences which may contribute to their differences in nitrogen use efficiency.

MATERIALS AND METHODS

A field experiment was conducted at the University of Nebraska Agricultural Research and Development Center near Mead, Nebraska. Seeds of two genotypes of sorghum [*Sorghum bicolor*], China 17 and Tx623, were planted in a randomized complete block design with two genotypes per block and four blocks on June 7, 1999. The soil, a Sharpsburg silty clay loam (fine, smectitic, mesic Typic Argiudoll Typic Argiudoll) was fertilized with 90 kg N per hectare applied broadcast as ammonium nitrate and incorporated. The plants were rain-fed and were not irrigated. The sorghum was thinned shortly after emergence to 70,000 plants per hectare in 75 cm row spacing.

Samples of the parts of the plants (described below) above the surface of the soil were taken at the following number of weeks after emergence: 2, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 15, 16, and 17. Because of the wide range of the amount of above-ground biomass per plant during the ontogenetic development of the

plants from emergence to grain fill, it was impossible to sample identical plant parts at each sampling date. The purpose of sampling as many morphologically distinct, above-ground parts of the plant as possible at different stages of growth was to enable subsequent comparison of estimates of rates of movement of nitrogen among different morphological parts of the plants of the two genotypes. Because of the small amount of above-ground biomass per plant during the earliest stage of growth, the number of plants sampled per replicate at week 2 was five. At week 3, two plants were sampled per replicate, and at all subsequent samplings, three plants per replicate were sampled. Because of the small amount of biomass per replicate at weeks 2 and 3, the total amount of above-ground biomass per replicate was sampled and measured. At weeks 4 and 5 when the plants were still relatively small, the biomass of each plant above the ground was divided into “lower plant” and “upper plant,” dividing the shoot between the lower four leaves and the upper four leaves. At weeks 6 and 7, samples were taken of the stalk, 1st four leaves, 2nd four leaves, and 3rd four leaves, counting from the base of the plant. Once the plants were larger at week 8, the plants were sampled thusly: 1st section (lowermost quarter) of stalk, 2nd section (next highest quarter) of stalk, 3rd section (next highest quarter) of stalk, and 4th section (highest quarter) of stalk, 2nd four leaves, 3rd four leaves, and 4th four leaves. This sampling scheme for the stem and leaves was continued through the final sampling at week 17. The head was sampled on China 17 plants, if present, at weeks 10 and 11. By week 12, the head was sampled on all replicates of both China 17 and Tx623 genotypes. Grain was sampled once it appeared, first on China 17 at week 12, then beginning at week 13, grain was evident and sampled on all plants of both genotypes. All plant samples were air dried to constant weight and total N was determined using the Kjeldahl method (AOAC, 1960). For the head, only seed N data were used for subsequent mathematical analyses.

We used multi-compartmental modeling to describe the N flows and to compare differences in timing and rates of N translocation in the two sorghum genotypes. The dynamics of a compartmental system is derived from mass balance considerations and differential equations (Jacquez, 1985). Figure 1 gives the behavior of one compartment with all possible N flows where y_i denotes the amount of N in compartment i at a point in time; while the outflow, or efflux, of N from compartment i to any compartment j is F_{ji} whereas the influx

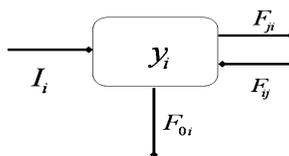


Figure 1. Inflows and outflows for a single compartment.

from compartment j to compartment i is F_{ij} . The influx of N to compartment i not from another compartment, but from outside the system, is I_i , and the efflux from compartment i not to another compartment, to outside the system is F_{0i} . All the flows are assumed to be nonnegative. Mass balance considerations yield the equation:

$$\dot{y}_i = \frac{\partial y_i}{\partial t} = \sum_{i \neq j} (F_{ij} - F_{ji}) + I_i - F_{0i} \quad (1)$$

Based on first-order kinetics, we assume that the flow from a compartment at any particular time, is directly proportional to the amount of N in the compartment at that time, or more specifically, $F_{ji} = k_{ji} \cdot y_i$ where k_{ji} is the rate constant. The first-order kinetics model is a model of growth and decay which has been used to represent many situations in many disciplines. The model has been used to represent a wide range of phenomena such as drug absorption, dating of archaeological samples, water cooling and alcohol absorption, and this differential equation has been applied to population modeling, energy demand forecasting, continuously compounding interest and murder time detection (Burghes and Borrie, 1981).

For n compartments, the system of n differential equations may be stated as: $\dot{\mathbf{Y}} = \mathbf{K} \mathbf{Y} + \mathbf{I}$. Where $\dot{\mathbf{Y}}$ is a vector of derivatives \dot{y}_i from equation (1), \mathbf{K} is called the system matrix containing the rate constants and \mathbf{I} contains the initial conditions of the system. When k_{ji} is constant, the system is linear and the usual estimation approach is to (1) mathematically solve the system for each y_i as a function of the k_{ji} and time and (2) use nonlinear least-squares to estimate the k_{ji} . In this work, it was necessary to specify some k_{ij} as nonlinear functions of other parameters and time. Thus it was not possible to find an analytic solution to the system and we used numerical methods to estimate the rate constants. We solved the system using a numerical ordinary differential equation subroutine (ODE), fit the model to the mean N values averaged over plots for each genotype, estimated the rate constants using the Levenberg-Marquardt least-squares subroutine (NLPLM) and we estimated standard errors with approximated derivatives using a finite differences subroutine (NLPFDD) from SAS PROC IML (SAS, 1995). The derivatives were used later for calculating the variances and covariances for the rate constant estimates.

The initial model (Figure 2) for each sorghum line was composed of six compartments: Y_0 , the lower half of the plant, including the two lower parts of the stem and two lower sets of leaves; Y_1 , the lower half of the upper half of the stalk; Y_2 , the leaves attached to the lower half of the upper half of the stalk; Y_3 , the upper half of the upper half of the stalk; Y_4 , the leaves attached to the upper half of the upper half of the stalk; and Y_5 , the grain. To find a model with an adequate fit for each sorghum line, we fit a sequence of compartmental models to measured amounts of N from week 8 through week 17 after emergence. The

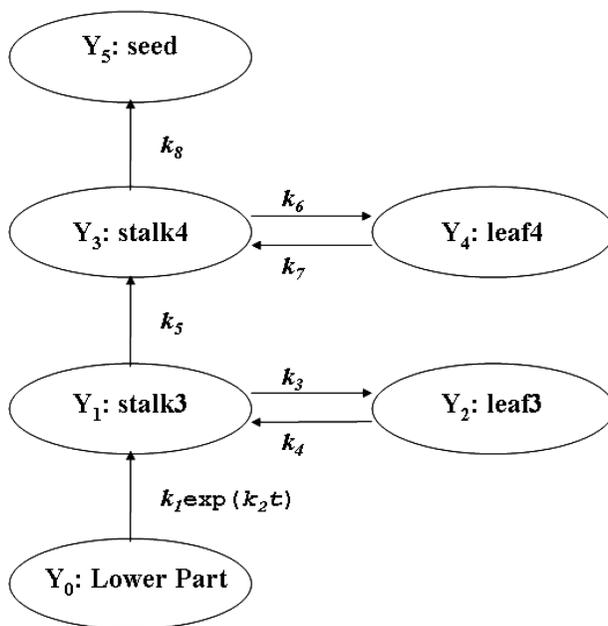


Figure 2. Initial compartmental system for two sorghum lines.

N amounts in the upper plant parts before week 8 were small with large relative variation and considered negligible. To simplify the model and to focus on grain and plant parts in the top portion of the plant, N from the lower half of the plant was aggregated into one compartment Y_0 . In addition, since there were no measurements of the root or soil N, we assumed that N available to the lower plant parts was essentially unlimited. We also assumed that the rate constant from the lower part of the plant (Y_0) to Y_1 was $k_1 \exp(k_2 t)$ due to the rapid growth of the top half of the plant during weeks 8 through 17 and that the N requirements of these upper plant parts will change rapidly as the plant grows. We assessed the fit of each model using the squared correlation between the actual and predicted N for each compartment (R^2) and with figures of predicted and actual values over time. If the fit was inadequate, we modified the model by adding pseudo-compartments and/or by specifying some rate constants to be functions of time. Pseudo-compartments are unmeasured compartments useful for modeling heterogeneity in the original compartments, in this case the leaf or stalk parts, that can account for several factors affecting N-fluxes in the leaves or stalk (Jacquez, 1985). Allowing some rate constants to change over time is biologically reasonable since it is likely that N-flow rates between plant parts will change as the plant develops. Significance of rate constant estimates for the final models were assessed using t statistics, i.e., the ratio of the estimate to its standard error. The statistical comparison of the rate constants of China 17

and Tx623 was performed using approximate t -tests (Cochran and Cox, 1957) using the estimated rate constants and standard errors for the two lines. For all models, we assumed that N flow was from the lower to the upper parts of the plant, that grain was a sink for the N and that any loss of N from the system as a whole was negligible.

RESULTS AND DISCUSSION

For both sorghum lines, the initial model (Figure 2) fit poorly for all compartments, except grain. One reason for the poor fits could have been due to heterogeneity of some compartments. Heterogeneous compartments may be modeled by adding pseudo-compartments to the system (Figure 3). We specified several different models by adding pseudo-compartments to the stalk, leaf and grain compartments. For both lines, a substantial improvement of fit resulted by adding pseudo-compartments (Y_6 and Y_7) in each set of leaves (Y_2 and Y_4) and by assuming the rate constant into and out of the pseudo-compartments were identical for each set of leaves as shown in Figure 3. The restriction of assuming equal rate constants in and out of the pseudo-compartments reduced the number of unknown estimates without degrading the fit.

Although the fits with the pseudo-compartments were improved, the model was still predicting N levels substantially lower than the means of measured amounts in the lower leaf compartment, particularly with China 17. To

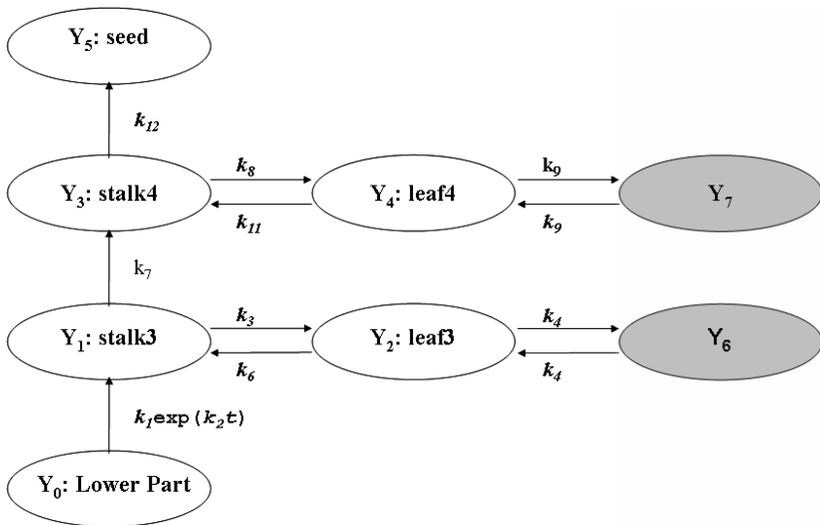


Figure 3. Model with pseudo-compartments added to leaves.

Table 1
Estimates of rate constants for final model—China 17

Rate Constant	Estimate	Std. Error
k_1	0.000257	0.000782
k_2	1.030606 ^{*,x}	0.386841
k_3	4.977946	6.433529
k_4	0.169528	0.319367
k_6	3.754795	4.934768
k_{71}	3.006902 [*]	0.683099
k_{72}	0.264792 ^{*,y}	0.080052
k_8	1.69398 [*]	0.928825
k_9	0.10542	0.253589
k_{11}	2.55578 [*]	1.466072
k_{121}	0.772019 ^{*,z}	0.067483
k_{122}	0.320447 ^{*,z}	0.081572

^{*}Significantly different from 0, $p < 0.05$.
^xSignificantly different from Tx623 k_2 , $p < 0.05$.
^ySignificantly different from Tx623 k_7 , $p < 0.05$.
^zSignificantly different from Tx623 k_{12} , $p < 0.05$.

improve the fit and to gain a better understanding of the differences between the genotypes, we estimated several models with selected rate constants as discrete functions of time t . Specifically, the rate constants k_7 and k_{12} from the model in Figure 3 were modified to change at 9 and 12 weeks, respectively:

$$k_7 = \begin{pmatrix} k_{71} & \text{if } t \leq 9 \\ k_{72} & \text{if } t > 9 \end{pmatrix} \quad k_{12} = \begin{pmatrix} k_{121} & \text{if } t \leq 12 \\ k_{122} & \text{if } t > 12 \end{pmatrix}. \tag{2}$$

We found the fit to improve considerably for China 17. Rate constant estimates of this final model for China 17 are given in Table 1. The R^2 for China 17 for each compartment were: stalk3, 0.83; leaves3, 0.95; stalk4, 0.94; leaves4, 0.89; grain, 0.91.

The fit for Tx623 was not improved by specifying rate constants as discrete functions of time which may have been caused by very little total head biomass in Tx623 before week 12 due to its slower development than China 17. The final estimates for Tx623 for the model in Figure 3 are given in Table 2. Except for the grain compartment, the fit for Tx623 was not as good as China 17 as indicated by the R^2 values of each compartment for Tx623: stalk3 0.17; leaves3 0.75; stalk4 0.82; leaves4 0.68; grain 0.96.

Comparison of the rate constants of the two lines revealed significant differences for stalk-stalk constants (k_7 and k_{12}), but no significant difference between lines for stalk-leaves rate constants (e.g., k_3 , k_6 etc) or within leaves rate constants (Table 1). Rate constant k_2 differed between lines ($p < 0.05$)

Table 2
Estimates of rate constants for final model—Tx623

Rate Constant	Estimate	Std. Error
k_1	0.381826	1.078565
k_2	0.000000	0.379867
k_3	8.529696	8.131288
k_4	0.943209	1.54533
k_6	2.565308	2.678755
k_7	2.790043*	1.227382
k_8	5.149132	7.575213
k_9	0.159161	0.590499
k_{11}	2.667376	4.177569
k_{12}	0.557649*	0.079798

*Coefficient is significantly different from 0.

where China 17 showed a positive relationship with time while Tx623 did not. China 17 k_{72} was significantly less ($p < 0.05$) than k_7 for Tx623 indicating that after nine weeks the N flux from stalk 3 to stalk 4 was slower for China 17 than Tx623 for a given N level in stalk 3. A similar phenomenon occurred for stalk 4 to grain rate constants. The China 17 rate constant from stalk 4 to grain before week 12 was larger than that for Tx623 ($k_{121} > k_{12}$; $p < 0.05$) but smaller after week 12 ($k_{122} < k_{12}$; $p < 0.05$). Considering that all these differences between lines from the lower plant to stalk 3 (k_2), from stalk 3 to stalk 4 (k_7 , k_{71} and k_{72}) and from stalk 4 to grain (k_{12} , k_{121} and k_{122}), China 17's rate constants changed over time while those for Tx623 did not. In addition, China 17's rate constants for N flux in the stalk were larger in the earlier part of the season and became smaller toward the end. However, no difference in rate constants were detected for stalk to leaves and within leaves rate constants.

To provide additional insight into the differences in N translocation, differential rates (dy/dt) were approximated for each time by obtaining predictions from the model and approximating rates of change for each time point based on these predictions (Figures 4 and 5). In addition, dates of the maximum and minimum N flux rates are given in Table 3. For all plant parts, China 17 reached a maximum rate of accumulation of N before Tx623. Moreover, the loss of N from the lower part of the shoot was faster for China 17 than for Tx623. Since the environmental conditions were essentially identical for the two genotypes, these prominent differences in timing and fluxes for the same plant parts indicate that there are genetic controls which are manifest differently between the two genotypes. Further research is needed to elucidate the genetic basis for these differences between the two genotypes.

The final models for both genotypes are biologically meaningful. China 17's larger stalk N rate constants earlier in the season, when compared to Tx623

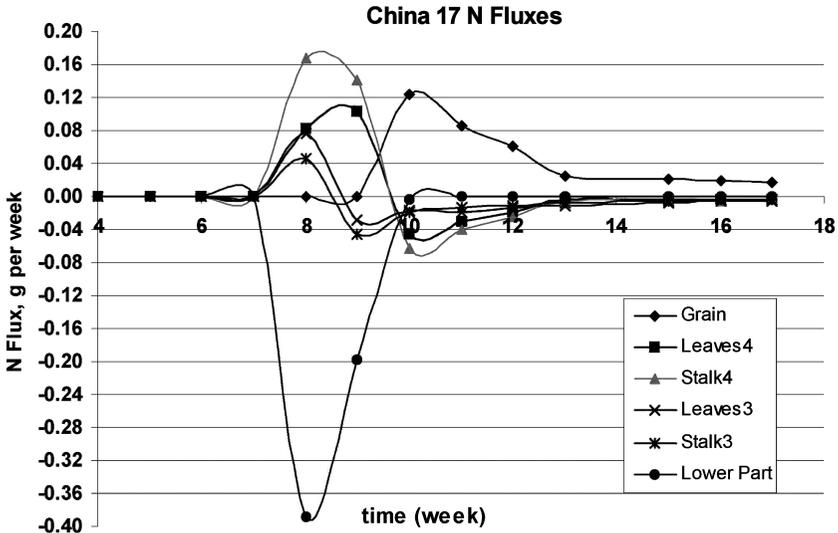


Figure 4. N Flux rates for China 17 sorghum vs time (week after emergence).

provide insight into the findings by Maranville and Madhavan (2002) that China 17 has a higher assimilation efficiency index and NUE_1 than Tx623 and that the two genotypes differed in movement of N among morphological aboveground parts. The upper leaves and stalk of China 17 sorghum accumulated N earlier

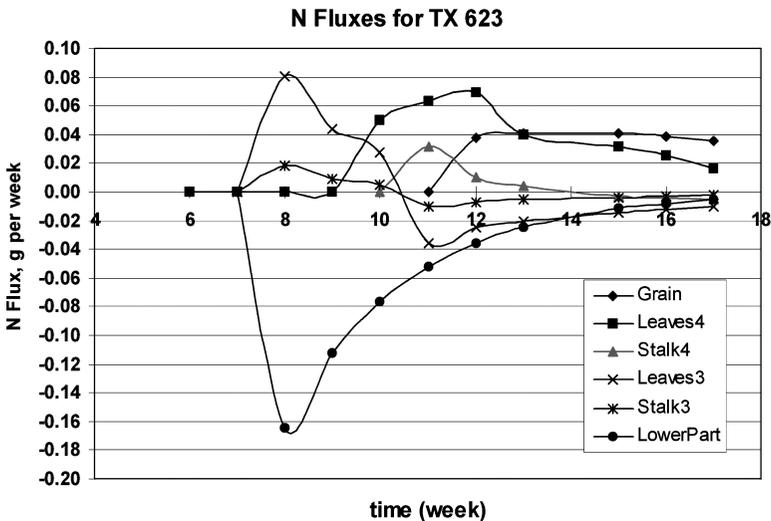


Figure 5. N Flux Rates for TX 623 sorghum vs time (week after emergence).

Table 3
Days to achieve the extreme differential rates for China 17 and Tx623

Sorghum Line	Plant Part	Maximum days	Minimum days
China 17	Stalk3	55	64
China 17	Leave3	56	64
China 17	Stalk4	58	72
China 17	Leave4	62	72
China 17	Grain	71	n/a
Tx623	Stalk3	58	78
Tx623	Leave3	58	78
Tx623	Stalk4	78	n/a
Tx623	Leave4	78	n/a
Tx623	Grain	86	n/a

and more rapidly and lost N to the grain earlier and more rapidly during grain filling, compared to Tx623.

The presence of pseudo-compartments in the leaves appears to indicate that the compartmental model approach can detect several processes or other rate-controlling factors associated with N flow in the leaves. Heterogeneity of leaf compartments could be caused by any number of physiological processes. Since nitrate is the predominant form of N available to plants (Hageman, 1986), processes affecting assimilation of nitrate-N that may account for heterogeneity in the leaf compartments could include differences in transport of unreduced (nitrate) and reduced forms of N; biosynthesis of enzymes and storage proteins; remobilization, or hydrolysis and transport, of nitrogenous compounds from vegetative tissues to other sinks (Wardlaw, 1976; Schrader, 1978). Heterogeneity of the leaf compartments may also be influenced by the fact that 50 to 60 percent of N in the leaves is associated with chloroplasts (Hageman, 1986) or the presence in the leaves of both labile N and less-labile (or non-labile) N. In addition, several processes may occur in the photosynthetic tissue of sorghum in such a way as to have distinctly different or heterogeneous, effects on the amount and rate of N movement into and out of the compartments (Maranville and Madhavan, 2002). The pseudo-compartments of the model may also reflect different net effects of concurrent anabolic and catabolic processes, hormonal control of these processes, or the anatomical differences between the xylem and phloem in the leaves. In his discussion of metabolic control, Raven (1981) states that the evolution of selective porters in the membrane of cells permitted control of the entry of substrates and effectors and the exclusion of toxic solutes while allowing the retention of genes, enzymes, and intermediates. These porters, according to Raven catalyze transport fluxes, are subject to 'coarse' and 'fine' control, and permit the cell to select which exogenous solutes it takes up and what it subsequently does with them. Further research is needed

to understand mechanisms suggested by the pseudo-compartments of our model.

There are several practical observations that can be made. Our results suggest that if one is to harvest a sorghum crop only for the grain in order to maximize the harvest of nitrogenous substances (e.g., amino acids, proteins), plant breeders should develop sorghums with the ability to strongly remobilize N from the vegetative organs. On the other hand, if both the grain and stover are to be harvested for a staple and feed for animals, sorghums which exhibit relatively less remobilization of N from vegetative organs to the grain may be preferable. Finally, compartmental systems analysis based on rather simple assumptions, can be productively used to model nutrient flow in developing plants. This approach is possible without using tracers or special methods and is available to a wide audience of researchers who can measure nutrient amounts in various plant parts and have access to readily available software.

ACKNOWLEDGMENTS

We thank D. Scoby for his technical assistance and J. Henao, J. Lindquist and G. Hammer for their critical comments regarding the manuscript. The research was partially funded by grant LAG-G-00-96-90009-00 of the U.S. Agency for International Development.

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