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Title

Nutrient use efficiency in bioenergy cropping systems: Critical research questions

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Introduction

In the U.S., a major shift towards the use of cellulosic biomass is underway as the Energy Policy Act of 2005 mandates production of a minimum of 250 million gallons of renewable fuel per year using cellulosic biomass, starting in 2013. A critical component of biomass production sustainability will be the capacity to produce maximal plant biomass with minimal nutrient input under rain-fed conditions (Heaton et al., 2004a,b). Optimizing nutrient use efficiency in biomass production is essential to avoid increasing further the environmental damage associated with the global production and use of N, P, and K fertilizers. Additionally, lands currently considered too marginal for intensive food production may be considered suitable for biofuel production bringing highly erodible, nutrient-poor soils currently in conservation reserve programs back into intensive agriculture. In the Midwest, cropping systems may shift from the predominant maize - soybean base to a more varied array of species including novel perennial grasses for which little agronomic and environmental data exist. Sustainable biofuels production with the concomitant protection and improvement of air, soil and water resources requires a concerted effort by the scientific community to gain knowledge regarding the comparative production potentials and environmental impacts of candidate biofuel systems. Here we outline several critical challenges and/or unknowns for nutrient, especially N, use efficiency and fertilizer management in candidate bioenergy cropping systems. We also touch on the challenges for biotechnology to provide substantive improvements in crop nitrogen use efficiency (NUE).

Reactive N (Nr) in intensive U.S. agriculture

Achieving significant yield gains to meet calorie and fuel demands with concomitant reductions in Nr will require unprecedented gains in NUE from field to landscape scales. For the U.S., forecasts for future yield increases vary but projections for prime agricultural land area are constant indicating any significant productivity gains must come from higher yields per unit land area. In general, for plant species already improved for agriculture, physiological nutrient use scales with plant size, and, thus, future yield increases will necessarily require greater uptake of all plant nutrients including N (Brouder and Volenec, 2008). Meeting these higher plant nutrient demands requires either increased total nutrient availability and/or improved uptake efficiency; for N, the relative contributions of these factors will be mediated by soil C. Yet, soil C itself is a poorly understood function of N. Long-term studies have demonstrated but not sufficiently characterized the quantitative nature of the relationship between N fertilization and soil C storage (Larson et al., 1972; Rasmussen and Rhode, 1988; Robinson et al., 1996; Drinkwater et al., 1998). Historic soil C losses with intensive production observed at the long-term Morrow plots in IL (Odell et al., 1984) and the Sanborn plots in MO (Balesdent et al., 1988) and Ames, IA (Robinson et al., 1996) ceased when N fertilizers were first applied in the 1950s and subsequently stabilized or slowly increased with further N applications. Likewise, the higher N fertilizer rates in continuous when compared to rotational maize reflect a variety of factors including the amount and the quality of the residue of the preceding crop (Gentry et al., 2001; Anderson et al., 1997; Riedell et al., 1998) and do not represent a foregone, quantitative increase in Nr. Thus, N contributions to the ecological production function determining soil C levels, organic matter stability and related ecosystem services are bounded: too little N and soil C declines while too

much N may reduce soil C (Khan et al., 2007) with both cases resulting in reduced NUE with increased N_r release.

Given the agro-ecosystem specificity of soil C regulation (Jastrow and Miller, 1997), N quantities associated with tipping points in the balance between net productivity, soil C and minimized N_r can be expected to be specific to cropping systems and agro-ecozones. At present, these tipping points and their ecological production functions remain largely unknown. The inherent tension for intensive agriculture is that productivity and air, soil, and water quality exist in delicate balance and system shifts to enhance one ecosystem service may unwittingly disrupt another. Certainly the problem of high yields and environmental N_r are well known. In the eastern cornbelt, unfertilized native prairie loose little N_r to either surface waters or the atmosphere but net

primary productivity is low when compared to a maize-based system (Fig. 1). Less well understood and very poorly characterized are the tradeoffs that occur when crops are managed to mitigate one environmental N_r pool while maintaining high productivity. For example, with initial environmental concerns for agriculture focused more on water than air

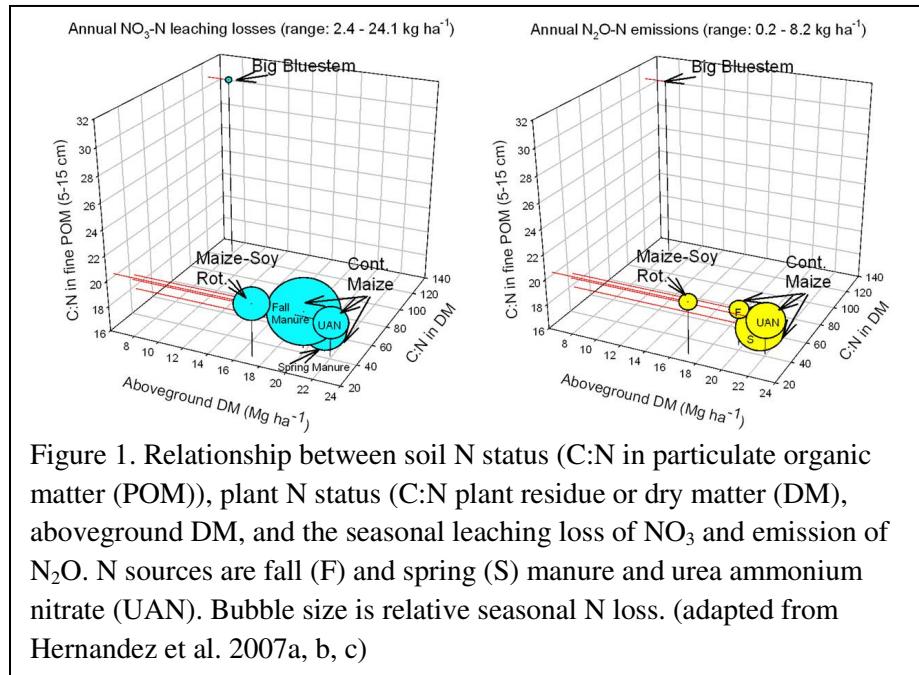


Figure 1. Relationship between soil N status (C:N in particulate organic matter (POM)), plant N status (C:N plant residue or dry matter (DM)), aboveground DM, and the seasonal leaching loss of NO₃ and emission of N₂O. N sources are fall (F) and spring (S) manure and urea ammonium nitrate (UAN). Bubble size is relative seasonal N loss. (adapted from Hernandez et al. 2007a, b, c)

quality, spring applications of manure were favored over fall as this timing reduces N loss to surface water in tile drains (Fig.1 (left)). However, one of the few multi-ecosystem service studies conducted to date demonstrates that the water quality benefit of a spring manure application occurs at a cost to air quality (Fig. 1 (right)). Likewise, it is reasonable to expect that controlled drainage currently advocated to stem N_r losses to surface water in the heavily tiled eastern cornbelt can be expected to increase denitrification and soil emission of N₂O. Doubtless, other established BMPs will have the same mixed result. At present, the scientific literature is dominated by 1 or 2 factor studies and lacks the comprehensive, system-level studies required to quantify tradeoffs and characterize the equivalency values of the different products of mass loss mechanisms.

NUE in perennial, candidate bioenergy crops

As for maize-based biofuel systems, a key factor in determining the net energy balance and environmental footprint of any potential biomass production scheme is the N economy of the system. While yield of grasses used for biomass production is clearly driven by N fertilization

(Fig. 2), use of exogenous N significantly reduces system net energy balance because of the high energy input into fertilizer N production (Hill et al., 2006; Lewandowski and Schmidt, 2006). To be viable, these authors indicated that biomass should be produced on agriculturally marginal lands with minimal fertilizer, pesticide, and fossil fuel inputs – agro-ecosystems where perennials and possibly sorghum (Pandey et al., 2001) are likely to outperform high-input annuals like maize both in terms of biomass production and NUE. The study of Tilman et al. (2006) represents a preliminary attempt at understanding the outside condition of this concept. The authors suggest that mixtures of native grassland perennials can sustainably produce significant quantities of biomass without fertilizer. However, growth of native grasses (e.g. big bluestem) is frequently N limited (Fig. 1, 2), and Russelle et al. (2007) challenge the Tilman et al. (2006) results maintaining inputs were underestimated.

Few other aspects of herbaceous biomass production are more unsettled and fragmented than are the current reports and recommendations pertaining to N fertilization of perennial grasses (Parrish and Fike, 2005). Response to N application varies with species (Cherney et al., 1991), and in time and space.

Lewandowski and Schmidt (2006) reported extremely high NUE ($350 \text{ g DM g}^{-1} \text{ N}$) for *Miscanthus* fertilized with $100 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, while the NUE of C_3 grasses were approximately $125 \text{ g DM g}^{-1} \text{ N}$. Heaton et al. (2004a,b) concluded that switchgrass responded to N better than *Miscanthus*, whereas other studies revealed no (Christian et al., 2001) or a highly varied (Brejda, 2000) response of switchgrass to N application.

Using ^{15}N to trace N movement in *Miscanthus*, Christian et al. (1997) determined that a modest portion of fertilizer N was sequestered in *Miscanthus* rhizomes, but that 40% of the applied N was completely lost from the plant-soil system. Ultimately, across all systems, the impact of production on the linked processes of N leaching and volatilization must be quantitatively compared. To date, numerous studies have focused on N leaching in maize-based systems but few, if any, studies on N leaching potentials in switchgrass, *Miscanthus*, and sorghum bio-fuel systems have been done. Likewise, studies of management system impacts on N_2O emission are either relatively sparse (e.g. maize) or virtually non-existent (e.g. sorghum, *Miscanthus*). Poor understanding of N_2O emission represents a critical knowledge void as the radiative forcing of 1 kg of N_2O is equivalent to 296 kg CO_2 ; Crutzen et al (2007) have hypothesized that N_2O release from agro-biofuel production may negate any expected benefits in global warming reduction associated with fossil fuel displacement. Indeed, N applied to perennials will be broadcast and therefore potentially subject to very high rates of volatilization.

Another untested concept is the potential for perennial plants to mobilize N from herbage to storage organs in fall, using this sequestered N pool as a source of N to initiate herbage growth the following spring (Beale and Long, 1997; Fike et al., 2006). If true, this attribute may not only

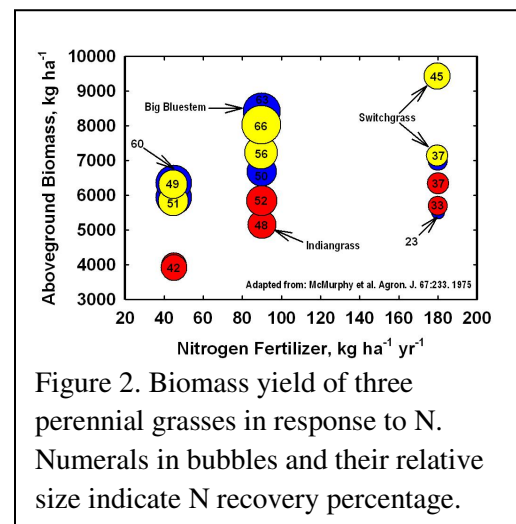


Figure 2. Biomass yield of three perennial grasses in response to N. Numerals in bubbles and their relative size indicate N recovery percentage.

reduce crop fertilizer N needs but also reduce N concentrations in biomass at harvest; a factor that is advantageous where harvested herbage N levels can have negative environmental consequences when combusted. Beale and Long (1997) examined biomass per unit tissue N at harvest for *Spartina* and *Miscanthus* and observed values of 250 and 180 g dry matter per g N, respectively. They remarked that literature values for maize (66 – 111 g g⁻¹), sorghum (130 g g⁻¹), wheat (53 – 81 g g⁻¹) and ryegrass (63 g g⁻¹) were substantially lower, indicating significantly reduced NUE for these common crops as compared to *Spartina* and *Miscanthus*. Because several studies have failed to demonstrate a yield response to fertilizer N, *Miscanthus* is now being advocated as a crop with high NUE, effective conservation of tissue N via seasonal shoot-rhizome cycling, low environmental N pollution potential, and high feedstock quality associated with low N₂O emission on tissue combustion (e.g. Christian et al., 2008). However, analysis of cropping system N balances suggests crop species such as *Miscanthus* may not have markedly better NUE; differences in harvest time alone can account for differences in N tissue concentration between *Miscanthus* and maize. When total plant N uptake is plotted as a function of total aboveground dry matter, values for *Miscanthus* harvested in February are consistent with those of maize harvested at physiological maturity (Fig. 3). Surprisingly, comparisons among crop species when whole-plant N accumulation is highest shows *Miscanthus* (July data) requires substantially more N per unit dry matter of yield than maize. Likewise, estimates derived from N fluxes between rhizomes and shoots indicate *Miscanthus* acquires similar amounts of exogenous N from soil as maize and can return to soil as much as 200 kg N ha⁻¹ in residues or leachate depending on harvest date. Thus, without closer analysis of N budgets and soil N losses, it appears premature to conclude any inherent advantages in NUE for *Miscanthus* and other less-studied cropping systems.

Genetic improvement of NUE

The convergence of commercial agriculture's interest in high yields and fertilizer cost reductions with the general public's interest in environmental stewardship has created an intense focus on strategies to enhance NUE. Expectations have been extremely high for biotechnology but, to date, targeted genetic solutions for improving traits controlling NUE appear elusive. In part, this may reflect the success of yield-focused breeding in indirectly optimizing the complex suite of traits that collectively confer high NUE. Twenty years ago, Eichelberger et al. (1989a,b) demonstrated with divergent selection for contrasting nitrate reductase activity that the commercial maize hybrids then in use were already optimized for nitrate assimilation. Eight

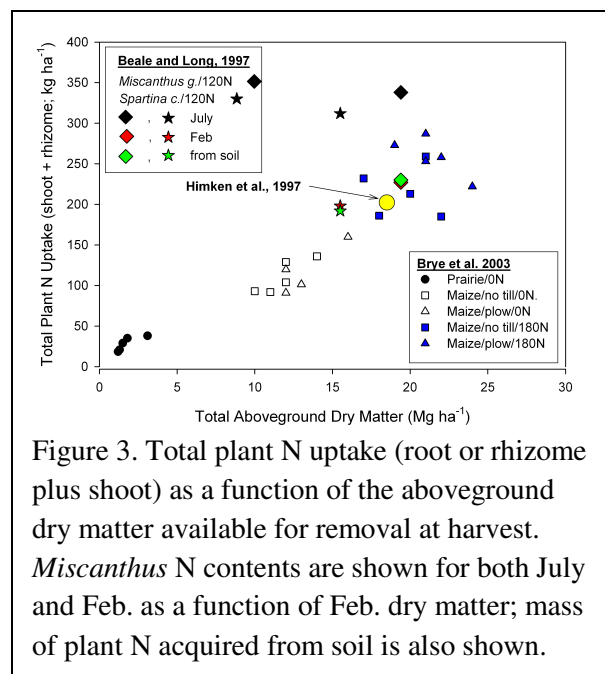


Figure 3. Total plant N uptake (root or rhizome plus shoot) as a function of the aboveground dry matter available for removal at harvest. *Miscanthus* N contents are shown for both July and Feb. as a function of Feb. dry matter; mass of plant N acquired from soil is also shown.

cycles of recurrent selection for high and low levels of post anthesis leaf lamina nitrate reductase activity resulted in a 3-fold difference amongst populations but failed to increase grain yield (Fig. 4a) or N uptake (Fig. 4b) irrespective of N fertility. However selection for low nitrate reductase activity reduced yield under a range of N fertility conditions; at high N levels, these yield reductions were associated with lower N uptake efficiency.

More recently, NUE studies have focused on limitations imposed by kinetic parameters and on the importance of gene expression for regulation of nutrient uptake across the cell membrane. Genes and complimentary DNA for dozens of high-affinity, nutrient-specific ion carriers have been cloned and characterized. Yet, as for selection of high nitrate reductase activity, these efforts have also not delivered enhanced NUE in commercial cultivars. Here, the explanation for lack of progress may again reflect that, in improved crops, this particular component of NUE has already been indirectly optimized. Moreover, mechanistic simulations of the N uptake process that consider both plant and soil parameters highlight the significant NUE limitations imposed by the root environment. Modeling work by Barber and Cushman (1981) initially suggested that maize N uptake was sensitive to changes in both root architecture and the maximum rate of N transport across the cell membrane but this study did not account for inter-root competition. In general, both initial concentration and diffusive flux of nitrate in soil tends to be several orders of magnitude higher than for other important but relatively immobile nutrients such as phosphorus. For example, a fertile soil can have a solution phase nitrate concentration of 5 mmol L⁻¹ and a soil diffusion rate of 2.5 x 10⁻⁶ cm² s⁻¹ while solution concentrations and diffusive flux for P are only about 1.4 x 10⁻² mmol L⁻¹ and 1.23 x 10⁻⁹ cm² s⁻¹, respectively (Barber, 1995). Simple simulations show adjacent, competing roots of the same plant can rapidly exhaust such a soil solution of its nitrate, and thus the finite supply of nitrate in the root zone is the factor most limiting plant uptake from a well-rooted volume of soil. True advances require systems-level thinking and integrated biotech-management solutions that encompass the multi-trait nature of plant-controlled aspects of NUE and the myriad of genotype x environment interaction that combine for a realized NUE.

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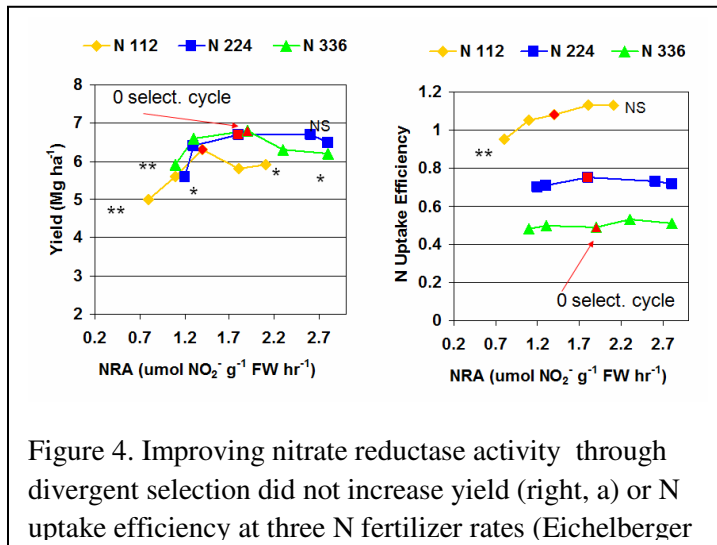


Figure 4. Improving nitrate reductase activity through divergent selection did not increase yield (right, a) or N uptake efficiency at three N fertilizer rates (Eichelberger

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