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Comparative Nitrogen Uptake and Distribution in Corn and Velvetleaf (*Abutilon theophrasti*)

John L. Lindquist, Darren C. Barker, Stevan Z. Knezevic, Alexander R. Martin, and Daniel T. Walters*

Weeds compete with crops for light, soil water, and nutrients. Nitrogen (N) is the primary limiting soil nutrient. Forecasting the effects of N on growth, development, and interplant competition requires accurate prediction of N uptake and distribution within plants. Field studies were conducted in 1999 and 2000 to determine the effects of variable N addition on monoculture corn and velvetleaf N uptake, the relationship between plant N concentration ([N]) and total biomass, the fraction of N partitioned to leaves, and predicted N uptake and leaf N content. Cumulative N uptake of both species was generally greater in 2000 than in 1999 and tended to increase with increasing N addition. Corn and velvetleaf [N] declined with increasing biomass in both years in a predictable manner. The fraction of N partitioned to corn and velvetleaf leaves varied with thermal time from emergence but was not influenced by year, N addition, or weed density. With the use of the [N]–biomass relationship to forecast N demand, cumulative corn N uptake was accurately predicted for three of four treatments in 1999 but was underpredicted in 2000. Velvetleaf N uptake was accurately predicted in all treatments in both years. Leaf N content (N_L , g N m⁻² leaf) was predicted by the fraction of N partitioned to leaves, predicted N uptake, and observed leaf area index for each species. Average deviations between predicted and observed corn N_L were < 88 and 12% of the observed values in 1999 and 2000, respectively. Velvetleaf N_L was less well predicted, with average deviations ranging from 39 to 248% of the observed values. Results of this research indicate that N uptake in corn and velvetleaf was driven primarily by biomass accumulation. Overall, the approaches outlined in this paper provide reasonable predictions of corn and velvetleaf N uptake and distribution in aboveground tissues.

Nomenclature: Velvetleaf, *Abutilon theophrasti* Medic. ABUTH; corn, *Zea mays* L. ‘Pioneer 33A14’.

Key words: Growth analysis, functional equilibrium, leaf area index, nitrogen nutrition, N use efficiency.

Corn yield loss because of velvetleaf competition is highly variable (Lindquist et al. 1996). Lindquist and Mortensen (1999) argued that velvetleaf causes corn yield loss primarily through competition for light, suggesting that leaf area and plant height are important canopy characteristics that determine the outcome of corn–velvetleaf competition. Both plant height and leaf area development can be influenced by the availability and competition for belowground resources (Bonifas et al. 2005; Bonifas and Lindquist 2006; McCullough et al. 1994; Radin 1983; Zhou et al. 1997). Nitrogen (N) addition has a positive effect on both corn and velvetleaf growth, but velvetleaf height, leaf area index (LAI), and biomass tend to respond more to N addition than corn (Barker et al. 2006). Therefore, Barker et al. (2006) suggested that when corn and velvetleaf emerge simultaneously in a mixture, velvetleaf competitiveness increases with increasing N supply.

Plants grown in mixture generally do not directly influence the physiological status of neighboring plants (with the exception of parasitic or allelopathic plants). However, plants do have a direct effect on the resources available in their immediate environment. Therefore, weeds cause crop loss indirectly through their influence on the resources required for crop growth (Goldberg 1990). Each species has a unique response to the quantity of resources available within an environment. The outcome of interplant competition is driven by the physiological mechanisms that regulate the effect of each species on a given resource and the response to the quantity of that resource available to the plant. Therefore, improving our understanding of the mechanisms of interplant competition requires detailed study of plant response to each

resource in the absence of the confounding effects of interspecific interactions (Lindquist 2001a).

Several models have been used to describe and predict N uptake by two general approaches (e.g., Baldwin et al. 1973; ten Berge et al. 1994, 1997; Graf et al. 1990; Hasegawa and Horie 1996; Jeuffroy et al. 2002; Kropff 1993; Lindquist 2001a; Nye and Tinker 1977; Sinclair and Muchow 1995). The first approach comes from solute transport theory, in which nutrient uptake is determined primarily by the predicted solute concentration at the root surface (Baldwin et al. 1973; Nye and Tinker 1977). The only plant-driven components of this approach are the root radius, root length density, and the “root absorbing power,” a term that essentially describes solute movement across the root surface (intake) as measured on excised root segments. Aboveground biomass has no effect on uptake by this approach. The second approach is more plant centered and predicts N uptake as the minimum of (1) the daily N demand and (2) the quantity of N available for plant uptake (ten Berge et al. 1997). A number of models are available for predicting the quantity of N available for uptake (e.g., Benbi and Richter 2002; de Willigen 1991), but these are outside the scope of this research.

Nitrogen demand is not well defined, so its prediction is typically based on the limitations in N uptake on the basis of the current status of plant growth. We follow ten Berge et al. (1994) and Sheehy et al. (1998) and suggest that daily N demand can be predicted as the minimum of four critical limiting factors,

$$N_{\text{demand}} = \min(U_N, U_M, U_D, U_P) \quad [1]$$

where U_N is maximum observed N uptake rate (g N m⁻² d⁻¹); U_P is the potential rate of N accumulation (g N m⁻² ground d⁻¹); U_M is the maximum uptake rate (g N m⁻² d⁻¹) as limited by maximum N fraction per unit new dry matter (Equation 2),

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$$U_M = q_N dW/dt \quad [2]$$

where q_N (g N g^{-1}) is the maximum ratio of daily N uptake to measured daily growth rate and dW/dt ($\text{g m}^{-2} \text{d}^{-1}$) represents a potential growth rate; and U_D is the N uptake rate ($\text{g N m}^{-2} \text{d}^{-1}$) as limited by the difference between potential and actual amount of N in existing biomass on any given day (Equation 3),

$$U_D = W_a[N] - N_a = N_p - N_a \quad [3]$$

where W_a is aboveground biomass (g m^{-2}) of the species, $[N]$ (g N g^{-1}) is potential N concentration (wt/wt), N_p is the potential N content of the species (g N m^{-2} ground), and N_a is actual N content of the species (g N m^{-2} ground). The potential N concentration ($[N]$) can be predicted as a function of total aboveground biomass of the species (W_a , g m^{-2}) (Greenwood et al. 1990),

$$[N] = aW_a^{-b} \quad [4]$$

where a is maximum $[N]$ (5.7 and 4.1% [w/w] for C_3 and C_4 species, respectively) and b is a shape coefficient (0.5 for both C_3 and C_4 species). Both a and b have been determined empirically for some crop species, but not for weeds (although Coleman et al. [1993] presented evidence suggesting this relationship is accurate for velvetleaf). Equation 4 can be rewritten in terms of the total potential amount of N accumulated in aboveground biomass (N_p , g N m^{-2} ground area; Equation 5) (Sheehy et al. 1998).

$$N_p = (a/100)W^{(1-b)}, \quad (W \geq 100 \text{ g m}^{-2}) \quad [5]$$

Sheehy et al. (1998) argued that the potential rate of N accumulation (U_p , $\text{g N m}^{-2} \text{ground d}^{-1}$) in aboveground biomass can then be predicted by differentiating Equation 5,

$$U_p = dN_p/dt = [(1-b)a/100]W^{-b} dW/dt, \quad [6]$$

$$(W \geq 100 \text{ g m}^{-2})$$

and

$$U_p = dN_p/dt = (a/100)dW/dt + W da/dt, \quad [7]$$

$$(W \leq 100 \text{ g m}^{-2})$$

where we assume that $[N] = a$ when $W \leq 100 \text{ g m}^{-2}$ (therefore, $W da/dt = 0$). To get dW/dt , we need to know the relationship between total aboveground biomass and time (d; or thermal time, GDD), which can be measured or simulated.

A correlation between CO_2 assimilation and leaf N content (N_L , g N m^{-2} leaf) has frequently been observed (Hasegawa and Horie 1996; Lawlor 2002; Lindquist 2001b; Sinclair and Horie 1989) because the majority of the N in plant leaves is found in photosynthetic proteins (Sage and Percy 1987a). C_3 plants use ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) to initially fix CO_2 , whereas C_4 plants use phosphoenolpyruvate (PEP) carboxylase (Ehleringer and Monson 1993). Because less N is associated with PEP carboxylase than Rubisco (Brown 1978) and because C_4 plants contain less Rubisco than C_3 plants, their overall leaf N content is generally lower. Nevertheless, C_4 plants maintain equal or higher photosynthetic rates than C_3 plants, which means that photosynthetic N use efficiency, or the ratio of photosynthetic rate to N investment in the leaf, is greater in

C_4 plants than in C_3 plants (Brown 1978, 1985; Lawlor 2002; Sage and Percy 1987a, 1987b; Sage et al. 1987).

Because interplant competition is dependent on the relative growth rate (RGR) of each competing species (Davis and Liebman 2001; Grime 1979; Harbur and Owen 2004; Tilman 1990) and RGR is dependent on the rate of photosynthesis within their tissues, the photosynthetic efficiency of each species (along with the quantity of photosynthetic tissue) is critical to the outcome of interplant competition. Therefore, the quantity of newly acquired N partitioned to leaves and leaf N content (N_L , g N m^{-2} leaf) is important in determining potential plant productivity (Gastal and Lemaire 2002). Although Equation 4 can be used to determine the expected N concentration of the entire canopy, these equations do not account for the partitioning of N to leaves once it is taken up. Assuming that the N content of leaves is proportional to the N content of total aboveground biomass, the fraction of N taken up that is partitioned to leaves at any given time or stage of growth simplifies to Equation 7,

$$P_L = \frac{N_{\text{leaf}}}{N_a} \quad [7]$$

where N_{leaf} and N_a are the N content in leaves (g N m^{-2} ground area) and in total aboveground tissues (g N m^{-2} ground area), respectively. The empirical relationship between P_L and time can then be used to predict the N content of leaves at any time t ($N_{L,t}$, g N m^{-2} leaf) using (Sinclair and Muchow 1995),

$$N_{L,t} = \frac{P_L N_{a,t}}{\text{LAI}_t} \quad [8]$$

where $N_{a,t}$ is the predicted total aboveground N content (g N m^{-2}) and LAI_t is the leaf area index ($\text{m}^2 \text{leaf m}^{-2}$ ground), both at time t .

An overall goal of our research on corn and velvetleaf is to accurately predict the effects of N supply on plant growth and N utilization. The specific objectives of this research were to quantify and compare the influence of variable N addition on monoculture-grown corn and velvetleaf N uptake, the relationship between plant N concentration and total biomass, the fraction of N partitioned to leaves over time, and the predicted N uptake and $N_{L,t}$ obtained from Equations 1 through 8, as well as the biomass and leaf area relationships presented in Barker et al. (2006).

Materials and Methods

Field Experiment. Field experiments were conducted at the Agricultural Research and Development Center near Mead, NE, in 1999 and 2000. Soil at the site was a Sharpsburg silty clay loam (fine, smectitic, mesic, Typic Argiudoll) with pH 6.7 to 6.8 and 3.3% soil organic carbon (SOC). Phosphorus (P) was broadcast applied as 0-46-0 at a rate of 48 kg P ha⁻¹ in 1999 on the basis of a soil test. No P or potassium was required in 2000. To obtain an initial estimate of the soil-available N in each experimental unit (EU), two 1.2-m soil cores were pulled and partitioned into four 30-cm depth increments. Each depth increment was homogenized and analyzed for soil nitrate and SOC content at the

University of Nebraska Soil and Plant Analysis Laboratory by the cadmium reduction method (Brown 1998).

The experiment was designed as a randomized complete block with four N addition treatments. The highest N level was determined on the basis of a 12.5-Mg ha⁻¹ corn yield goal and residual soil N as determined by soil tests. Nitrogen was applied as ammonium nitrate at rates of 0, 45, 90, and 180 kg N ha⁻¹ and 0, 60, 120, and 240 kg N ha⁻¹ in 1999 and 2000, respectively. Plants were grown in monoculture at a density of 65,800 corn plants per hectare and either 26,300 (2 plants m⁻¹ row) or 131,600 velvetleaf plants per hectare (10 plants m⁻¹ row). An EU was 6 by 9 m and 3 by 9 m for corn and velvetleaf, respectively, in 1999, and 6 by 10.5 and 3 by 10.5, respectively, in 2000.

Corn 'Pioneer 33A14' and velvetleaf were seeded in rows spaced 0.76 m apart on May 3 in both 1999 and 2000. Irrigation was not available in 1999, but was provided throughout the growing season in 2000, with approximately 51 mm of water applied once every 2 to 3 wk. Additional cultural practices were reported in Barker et al. (2006).

Data Collection. Destructive plant samples were periodically taken in each EU to quantify crop and weed growth and canopy dynamics. The first sample was taken on May 24, 1999, and May 15, 2000. Sampling continued weekly for the next 10 wk and thereafter every other week, when samples were staggered among treatments (the high and low N application treatments were taken one week and the two middle N treatments the next). Plants within a 1-m section of row were sampled from the second, third, sixth, or seventh row of each EU of the corn treatments, or from the second, third, or fourth row of each velvetleaf density treatment. At least 1 m of row and the adjacent row were left intact between each sample area to ensure no edge effects of sampling. Development stage and plant height were determined for each plant within the sampled area before clipping plants at the soil surface. Plants were then separated into stems, leaves, dead leaves, and reproductive tissues, and green leaf area was determined with an area meter.¹ Tissues were then dried at 60 C to constant weight. Dry tissue samples were then ground to a maximum fineness of 1 mm and a representative sample was sent to the University of Nebraska Soil and Plant Analysis Laboratory to determine percent N concentration² of each sample.

Data Analysis. Actual N content (g N m⁻² ground) of an organ group (leaves, dead leaves, stems, reproductive tissues) was calculated as the product of the biomass of that organ group (g m⁻²) on a given sampling date and its [N]. Total aboveground N content (N_a, g N m⁻²) was calculated as the sum of the N content of the organ groups. Therefore, N_a calculated over time is equivalent to the cumulative N uptake (U_a, g N m⁻² ground), which was defined as a function of days after emergence (DAE) with the logistic function of Equation 9,

$$U_a = \frac{U_{\max}}{1 + \exp(c - d \text{ DAE})} \quad [9]$$

where U_{max} is maximum N uptake and *c* and *d* are shape coefficients. Equation 9 was fitted to measured uptake from each EU with the nonlinear regression analysis of SAS³ PROC NLIN to estimate values for U_{max}, *c*, and *d* for each EU. The ratio *d/d*, which defines the time of maximum absolute N

uptake, and maximum absolute N uptake rate (U_N = U_{max}*d*/4) were also calculated for each EU. Resulting estimates of U_{max}, *c*, *d*, *d/d*, and U_N were subjected to ANOVA with PROC MIXED³ to test the difference between N treatments for corn and between N and density treatments for velvetleaf. PROC MIXED was used to compute least squares means, standard errors, and the difference between least squares means with an LSD-like pairwise *t* test to test for treatment differences at the α = 0.05 level. Estimates of q_N([dU_a/dt]/[dW_a/dt]) (Equation 2) were calculated as the ratio between the derivative of Equation 9 with respect to time and the derivative of the same equation fit to cumulative biomass over time (DAE) and plotted as a function of time (DAE). An overall maximum value was identified for each species and used as an estimate of q_N.

Nitrogen concentration ([N]) of corn and velvetleaf in total aboveground tissue as a function of total aboveground biomass was compared to that proposed by Greenwood et al. (1990) by comparing the residual mean square error (rmse) for the fit of Equation 4 on observed [N] as a function of observed total aboveground biomass with the residual mean square error (rmse1) for the difference between observed [N] and the Greenwood et al. (1990) curve. rmse1 = (O - P)²/n, where O is the actual observed N concentration in tissues at a given sampling date; P is the predicted N concentration in tissue for that date obtained by Equation 4, with a = 410 and 570 for corn and velvetleaf, respectively; b = 0.5 for both species; and n is the sample size. The two rmse values were compared with an F test, where F = rmse1/rmse (Montgomery 1991). A significant F value indicates that rmse1 > rmse or that the Greenwood et al. (1990) relationship does not adequately predict the observed [N].

To determine N partitioning to leaves (P_L), the ratio between N content of leaves and N content of total aboveground tissue (Equation 7) was plotted against thermal time (GDD), and the relationships were compared among N treatments and plant density (for velvetleaf). If no differences were observed among treatments, a single equation was fit to all data for each species.

Corn and velvetleaf cumulative potential N demand was predicted by Equation 1, where U_N was the maximum N uptake rate (U_N = U_{max} *d*/4, g N m⁻² d⁻¹) obtained from the fit of Equation 9 on cumulative N uptake over time (Tables 1 and 2); U_M was calculated from the derivative of Equation 9, fit to cumulative biomass (dW/dt) over time (d) and q_N values obtained as described above; U_D was calculated from Equation 3, where N_p was obtained from Equation 5 and N_a was calculated as the predicted N content from the previous day (as would occur in any simulation model); and U_P was calculated from Equation 6, with the Greenwood et al. (1990) parameter values for *a* and *b* and the derivative of Equation 9 fit to cumulative biomass (dW/dt) over time (d). We used time in days for this analysis, but thermal time (GDD) for the analysis of fraction N partitioning, because although most simulation models are driven by thermal time, they function on a daily time step. Therefore, rate parameters used to limit N demand on a given day will necessarily be reported in units of d⁻¹, whereas the fraction of N in leaves will naturally vary with development stage, which is driven by thermal time. From these calculations, predicted N uptake is equivalent to predicted N demand, assuming that the quantity of N available for uptake is always sufficient to meet that demand. This certainly might not be the case, but we did not

Table 1. Estimates of parameters from the fit of Equation 9 (maximum N uptake [U_{max}], c , d , time of maximum N uptake [d/d], and maximum absolute N uptake rate [U_N] to observed corn N uptake over time [days after emergence]) and their variation among N addition treatments (N_{trt}) in 1999 and 2000.^a

Year	N_{trt} kg N ha ⁻¹	U_{max} g N m ⁻²	c	d	d/d d	U_N g N m ⁻² d ⁻¹	rmse (v) ^b	F^c
1999	0	9.39 d	7.89 a	0.187 a	47 a	0.438 b	6.065 (49)	1.25
	45	11.60 c	4.85 bc	0.114 c	43 c	0.327 c	8.301 (49)	1.03
	90	14.13 b	5.35 b	0.139 b	38 d	0.486 ab	9.029 (49)	1.19
	180	21.67 a	4.22 c	0.098 d	45 b	0.515 a	7.244 (49)	2.99*
2000	0	21.68 bc	3.08 a	0.066 ab	50 a	0.340 a	5.499 (29)	2.32*
	60	20.83 c	3.22 ab	0.075 a	49 a	0.359 a	8.891 (29)	2.40*
	120	23.70 ab	2.90 b	0.059 b	51 a	0.336 a	8.193 (29)	3.19*
	240	25.26 a	2.90 b	0.056 b	52 a	0.353 a	15.854 (29)	2.97*

^a Within columns and years, means followed by different letters are significantly different at $P < 0.05$.

^b rmse, residual mean square error; v, degrees of freedom.

^c $F = \text{rmse1}/\text{rmse}$, where $\text{rmse1} = (O - P)^2/n$, in which O is the actual observed N in tissues at a given sampling date, P is the predicted N in tissue for that date obtained by Equation 1, and n is the sample size, and rmse is the residual mean square error for the fit of Equation 9 to observed cumulative N uptake over time.

* Values are significant at $P < 0.05$, indicating that $\text{rmse1} > \text{rmse}$.

observe N availability throughout the growth period in this study. Accuracy of the predicted N uptake was evaluated by comparing the residual mean square error for predicted N uptake (rmse1) with that for the fit of Equation 9 on cumulative uptake with an F test as described previously (Montgomery 1991).

Corn and velvetleaf leaf N content ($N_{L,t}$, g N m⁻² leaf) was predicted by Equation 8, where P_L was obtained from the observed P_L relationship, $N_{a,t}$ was calculated from Equation 1, and LAI was the observed value for a given EU. Normalized deviations [$(P - O)/O$] between predicted (P) and observed (O) leaf N content (N_L , g N m⁻² leaf) were then plotted as a function of observed N_L for corn and velvetleaf in 1999 and 2000. The average of these normalized deviations (average error) provides an estimate similar to a coefficient of variation.

Results and Discussion

Cumulative corn N uptake varied with N treatment in each year of the study (Table 1). Corn maximum N uptake (U_{max})

at zero N was 43% of that at 180 kg N ha⁻¹ treatment in 1999 (Table 1). Cumulative N uptake was generally greater in 2000 compared with 1999, but the change across N treatments was not as consistent as in 1999 (Figure 1). Similar trends were observed for total aboveground biomass, in which biomass was greater in 2000 compared with 1999 and maximum biomass increased with increasing N supply in 1999 but not in 2000 (Barker et al. 2006). Nitrogen uptake is reduced when soil water is limiting (Burns 1980; Wallace 1990). Adequate soil water was available in both years early in the growing season, but periods of drought occurred after anthesis in 1999 when no irrigation was available. This might have led to less N uptake in the lower N treatments in 1999 compared with 2000.

Cumulative velvetleaf N uptake varied with N addition, velvetleaf density treatment, and their interaction in each year (Table 2). Maximum accumulated velvetleaf N uptake (U_{max}) was greater in the high compared with low plant densities in both years. The greater uptake is due to a greater aboveground biomass at the higher weed density (Barker et al. 2006).

Table 2. Estimates of parameters from the fit of Equation 9 (maximum N uptake [U_{max}], c , d , time of maximum N uptake [d/d], and maximum absolute N uptake rate [U_N] to observed velvetleaf N uptake over time [days after emergence]) and their variation among velvetleaf density in monoculture (Vd, plants m⁻¹ row) and N addition treatments (N_{trt}) in 1999 and 2000.^a

Year	Vd	N_{trt} kg N ha ⁻¹	U_{max} g N m ⁻²	c	d	d/d d	U_N g N m ⁻² d ⁻¹	rmse (v) ^b	F^c
1999	2	0	25.32 a	5.86 c	0.053 c	104 a	0.366 b	6.016 (30) ^d	1.10
		45	10.78 d	9.68 a	0.148 a	68 c	0.352 b	5.206 (41)	1.08
		90	15.71 c	9.42 a	0.133 a	76 b	0.379 ab	14.074 (41)	0.97
		180	19.16 b	7.33 b	0.109 b	68 c	0.483 a	22.171 (41)	1.17
	10	0	23.61 a	8.44 a	0.119 a	80 a	0.498 a	6.793 (30)	1.07
		45	11.89 d	7.21 b	0.127 a	58 bc	0.342 c	8.570 (41)	1.44
		90	15.92 c	6.28 c	0.115 a	55 c	0.446 b	12.730 (41)	0.99
		180	20.94 b	6.98 bc	0.128 a	61 b	0.529 a	23.209 (41)	1.05
2000	2	0	8.60 c	9.49 a	0.175 b	58 b	0.385 b	7.364 (25)	1.52
		60	14.21 a	7.85 b	0.118 c	78 a	0.332 b	6.970 (25)	0.99
		120	10.98 b	10.80 a	0.219 a	53 bc	0.553 a	9.322 (25)	1.03
		240	12.98 a	9.73 a	0.191 ab	51 c	0.600 a	8.476 (25)	1.24
	10	0	16.56 c	7.49 a	0.133 a	69 a	0.397 b	10.279 (25)	1.08
		60	13.74 d	5.25 b	0.097 ab	56 b	0.330 b	6.481 (25)	0.97
		120	20.88 b	4.47 b	0.080 b	58 b	0.394 b	14.751 (25)	1.14
		240	23.59 a	4.89 b	0.084 b	60 b	0.482 a	13.613 (25)	1.54

^a Within columns, years, and density treatment, means followed by different letters are significantly different at $P < 0.05$.

^b rmse, residual mean square error; v, degrees of freedom.

^c $F = \text{rmse1}/\text{rmse}$, where $\text{rmse1} = (O - P)^2/n$ (where O is the actual observed N in tissues at a given sampling date, P is the predicted N in tissue for that date obtained using Equation 1 and n is the sample size) and rmse is the residual mean square error for the fit of Equation 9 to observed cumulative N uptake over time. An asterisk following the F value indicates it is significant at $p < 0.05$, indicating that $\text{rmse1} > \text{rmse}$.

^d The degrees of freedom for the 0 N treatment was smaller in 1999 because one replicate was lost.

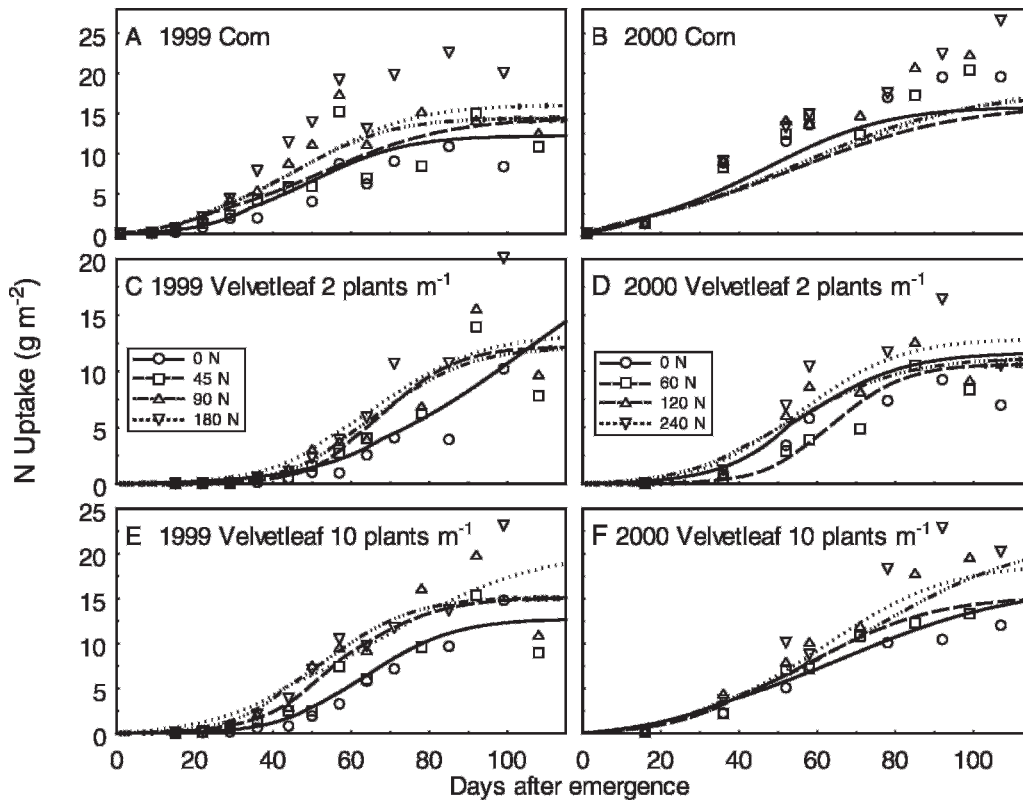


Figure 1. Effect of nitrogen (N) addition on corn and velvetleaf cumulative N uptake in aboveground tissues (g N m^{-2} ground) as a function of days after emergence. Symbols represent the mean observed value at a given sampling date. Solid lines represent the cumulative predicted N demand according to Equation 1, wherein U_N was the maximum observed N uptake rate as shown in Tables 1 and 2; U_M was calculated from the derivative of the fit of Equation 9 on cumulative biomass and q_N values of 0.032 and 0.04 for corn and velvetleaf, respectively; U_D was calculated from Equation 3, in which N_p was obtained from Equation 5 and N_a was the predicted N content from the previous day (as would occur within a simulation model); and U_P was calculated from Equation 6.

Cumulative velvetleaf N uptake generally increased with increasing N addition in both years (Table 2; Figure 1). Differences in cumulative N uptake among N treatments are similar to observed differences in cumulative aboveground biomass (Barker et al. 2006).

The potential corn N uptake rate (U_N) was greatest ($0.52 \text{ g N m}^{-2} \text{ d}^{-1}$) in the 180 kg N ha^{-1} treatment in 1999 but did not differ among N treatments ($0.35 \text{ g N m}^{-2} \text{ d}^{-1}$) in 2000 (Table 1). In addition, corn potential uptake rate was observed later in 2000 (49–52 DAE) compared with 1999 (38–47 DAE). Potential velvetleaf N uptake rate was similar to that of corn and was greatest in the highest N treatments in both years but did not vary across years (Table 2).

Calculation of U_M (Equation 2) includes a parameter (q_N) that defines the maximum ratio of daily N uptake to measured daily growth rate. To obtain estimates of q_N , we calculated the ratio between the derivative of Equation 9 as fit to observed N uptake over time and the derivative of the same equation fit to biomass accumulation over time. A plot of the results (data not shown) showed that q_N generally declined with time, and the maximum value for corn and velvetleaf was about 0.032 and 0.040 g N g^{-1} , respectively, which are within the ranges reported by ten Berge et al. (1997).

Corn and velvetleaf [N] declined with increasing aboveground biomass in both 1999 and 2000 (Figure 2). Estimates of parameters (a and b) from the fit of Equation 4 on observed corn and velvetleaf [N] in aboveground tissues varied with N and velvetleaf density treatments in both years (Tables 3 and 4). Estimates of a for corn increased with increasing N addition in both years, whereas the estimate for

b declined in 1999 but did not vary with N addition in 2000. Estimates of a for velvetleaf generally increased with increasing N addition and velvetleaf density, whereas estimates of b varied inconsistently with N addition and tended to be greater in the higher density treatment. Estimates of a indicate that early season corn N concentration ranged from 50 to 65 mg N g^{-1} , which is larger than that shown for corn in Greenwood et al. (1990), whereas velvetleaf [N] ranged from 42 to 55 mg N g^{-1} , which is smaller than the values proposed for C_3 species. On the other hand, estimates of the b parameter for both corn and velvetleaf were smaller than those proposed in Greenwood et al. (1990). Greenwood et al. (1990) proposed their relationship on the basis of observed [N] values after total aboveground biomass exceeded 1 Mg ha^{-1} (100 g m^{-2}). Therefore, our different estimates of a and b are likely the result of the different units used (mg N g^{-1} vs. fraction N and g m^{-2} vs. Mg ha^{-1}) and the large number of observations $< 100 \text{ g m}^{-2}$ that were included in our analysis. Results of an F test indicate that corn [N] predicted with the Greenwood et al. (1990) relationship was less accurate than the regression of Equation 3 on observed [N] only for one treatment in 1999 (Table 3). However, except for the highest N addition treatment in 2000, predicted velvetleaf [N] was consistently overpredicted with the Greenwood et al. (1990) curve (Table 4; Figure 2).

Predicted corn N uptake varied less across N treatments than observed N uptake (Figure 1). Results of the F test indicate that the predicted N uptake by Equation 1 was less accurate than the regression of Equation 9 on observed N uptake over time only in the greatest N addition treatment in

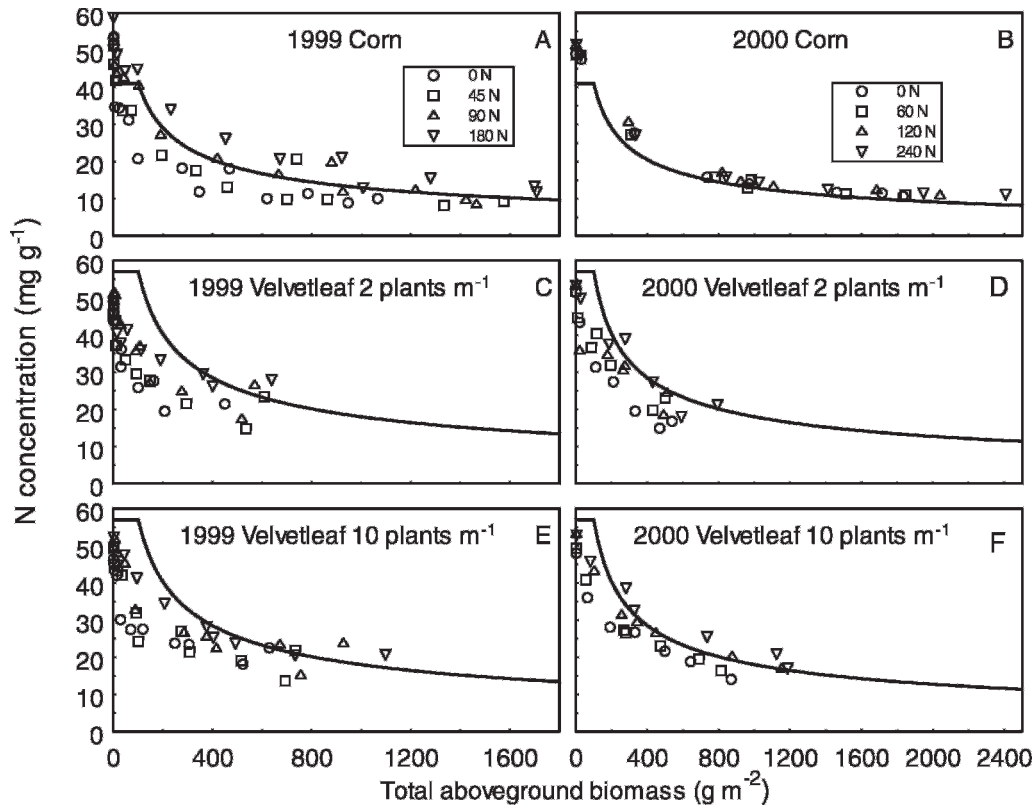


Figure 2. Effect of nitrogen (N) addition on corn and velvetleaf N concentration [N] (mg g^{-1}) in aboveground tissue as a function of total aboveground biomass. Symbols represent the mean observed [N] and biomass values at a given sampling date. Solid lines represent the Greenwood et al. (1990) relationship (Equation 4, wherein $a = 410$ and 570 for corn and velvetleaf, respectively, and $b = 0.5$ for both species).

1999 (Table 1), in which N uptake was substantially underpredicted (Figure 1). Corn N uptake was underpredicted in all treatments in 2000 (Figure 1). Velvetleaf N uptake was more accurately predicted across N addition treatments than corn (Figure 1). Results of the F test indicate that predicted velvetleaf N uptake was never less accurate than the regression of observed velvetleaf N uptake over time (Table 2; Figure 1).

Predicted N demand obtained from Equation 1 was typically limited by U_M from emergence until aboveground

biomass of both species reached about 100 g m^{-2} and thereafter was limited by U_p (Equation 6, results not shown). This result suggests that the Greenwood et al. (1990) parameters underestimate actual corn [N] in aboveground tissues and, subsequently, predicted N demand, whereas velvetleaf [N] was more accurately predicted. If the Greenwood et al. (1990) relationship is intended to be the upper limit of [N] for the species, then Figure 2 shows that corn [N] was indeed underestimated by the Greenwood et al. (1990) parameters. However, velvetleaf [N] was either overpredicted during early growth (i.e., $< 200 \text{ g m}^{-2}$) in 1999 or actual [N] was lower than expected even in the highest N addition treatment in that year.

Fraction of N in corn and velvetleaf leaves declined with thermal time from emergence, but was not influenced by year, N addition, or velvetleaf density (Figure 3). Velvetleaf partitioned a slightly larger fraction of N to leaves than corn (intercepts = 0.84 vs. 0.80 , respectively) early in the season and maintained that higher fraction of N in leaves slightly longer. Although the initial value in Figure 3 is considerably greater than the constant value of 0.6 assumed in the corn growth model of Sinclair and Muchow (1995), the average over the season (0.5 from 0 to $1,450 \text{ GDD}$ after emergence) is smaller, which might partially explain why their model tended to overpredict corn $N_{L,t}$.

Whole-plant corn leaf N content ($N_{L,t}$) ranged from about 0.7 to 3.0 g N m^{-2} leaf and increased with increasing N addition in 1999 (Figure 4). However, $N_{L,t}$ ranged from 1.2 to 3.0 g N m^{-2} leaf and did not vary among N treatments in 2000. Nitrogen addition and velvetleaf density did not influence velvetleaf $N_{L,t}$ in either year (results not shown).

Table 3. Estimates of parameters from the fit of Equation 4 (a and b) on observed corn N concentration ([N]) in aboveground tissues in relation to total aboveground biomass in 1999 and 2000.^a

Year	N_{irr} kg N ha ⁻¹	a	b	rmse (v) ^b	F^c
1999	0	49.5 d	0.187 a	41.41(50)	2.79*
	45	51.4 c	0.173 b	55.85(50)	0.97
	90	56.7 b	0.161 c	76.26(50)	0.55
	180	61.9 a	0.150 d	64.64(50)	1.01
2000	0	60.4 c	0.1844	54.26(30)	0.39
	60	61.2 c	0.1844	52.00(30)	0.45
	120	62.9 b	0.1844	55.77(30)	0.65
	240	64.5 a	0.1844	50.03(30)	0.68

^a Within columns and years, means followed by different letters are significantly different at $P < 0.05$.

^b rmse, residual mean square error; v, degrees of freedom.

^c $F = \text{rmse1}/\text{rmse}$, where $\text{rmse1} = (O - P)^2/n$ (where O is the actual observed [N] at a given sampling date, P is the predicted [N] for that date obtained by Equation 4 with $a = 4.1$ and 5.7% for corn and velvetleaf, respectively; $b = 0.5$ for both species; and n is the sample size) and rmse is the residual mean square error for the fit of Equation 4 to observed [N] over time.

* Values are significant at $P < 0.05$, indicating that $\text{rmse1} > \text{rmse}$.

Table 4. Estimates of parameters from the fit of Equation 4 (*a* and *b*) on observed velvetleaf nitrogen concentration ([N]) in aboveground tissues in relation to total aboveground biomass in 1999 and 2000.^a

Year	N _{trt}	<i>a</i>		rmse (v) ^b	<i>F</i> ^c	<i>b</i>		rmse (v) ^b	<i>F</i> ^c
		2 Plants m ⁻¹				10 Plants m ⁻¹			
		kg N ha ⁻¹							
1999	0	42.3 c	0.091 b	41.72 (31) ^d	9.53*	49.3 d	0.129 b	27.16 (31)	12.05*
	45	43.3 c	0.093 b	58.79 (42)	5.01*	53.9 c	0.144 a	43.76 (42)	5.83*
	90	52.0 a	0.108 a	69.75 (42)	2.76*	58.8 b	0.136 ab	41.25 (42)	2.89*
	180	46.2 b	0.067 c	58.75 (42)	3.69*	61.8 a	0.131 b	46.09 (42)	1.80*
2000	0	50.5 b	0.140 a	47.68 (26)	5.49*	60.1 c	0.165 a	30.49 (26)	5.57*
	60	49.7 b	0.097 c	65.36 (26)	2.29*	58.8 c	0.150 b	37.11 (26)	2.33*
	120	51.1 b	0.108 b	26.72 (26)	5.40*	65.0 b	0.145 b	34.53 (26)	1.00
	240	55.3 a	0.105 bc	63.81 (26)	0.66	68.5 a	0.145 b	41.64 (26)	0.70

^a Within columns and years, means followed by different letters are significantly different at *P* < 0.05.

^b rmse, residual mean square error; v, degrees of freedom.

^c *F* = rmse1/rmse, where rmse1 = $(O - P)^2/n$ (where *O* is the observed [N] at a given sampling date; *P* is the predicted [N] for that date obtained by Equation 4, with *a* = 4.1 and 5.7% for corn and velvetleaf, respectively, and *b* = 0.5 for both species; and *n* is the sample size) and rmse is the residual mean square error for the fit of Equation 4 to observed [N] over time.

^d Degrees of freedom for the zero N treatment was smaller in 1999 because one replicate was lost.

* Values are significant at *P* < 0.05, indicating that rmse1 > rmse.

Average velvetleaf $N_{L,t}$ was greater than that of corn in both years, which was expected because *C*₃ species maintain greater [N] in the leaves than *C*₄ plant species. Muchow and Sinclair (1994) suggested that corn yield is optimized when $N_{L,t} > 1.5$ g N m⁻² leaf. Corn $N_{L,t}$ fell below the 1.5 g N m⁻² threshold during much of the 1999 growing season in the low N addition treatments. However, corn $N_{L,t}$ rarely fell below 1.5 g N m⁻² in 2000. Therefore, corn appears to have been substantially more N stressed in 1999 than 2000. These results help explain the strong response of corn biomass and leaf area index to N addition in 1999, but not in 2000 (Barker et al. 2006).

Deviation between predicted and observed corn and velvetleaf leaf N content ($N_{L,t}$) showed a tendency toward

overprediction when $N_{L,t}$ was small, but became more accurate as $N_{L,t}$ increased (Figure 4). The average of those deviations is similar to a coefficient of variation and was small for corn in 2000 (-0.12 or closer to zero) but larger in 1999, ranging from 0.34 to 0.88 (Table 5). The average of those deviations for velvetleaf $N_{L,t}$ was larger than that for corn in both years, but also tended to be smaller in 2000 than in 1999 (Table 5).

Results of this research indicate that corn and velvetleaf N uptake is driven primarily by biomass accumulation, and that [N] in tissue changes with aboveground biomass in a predictable manner. Use of the Greenwood et al. (1990) [N]-biomass relationship as altered by Sheehy et al. (1998) to predict N uptake resulted in accurate predictions of corn and

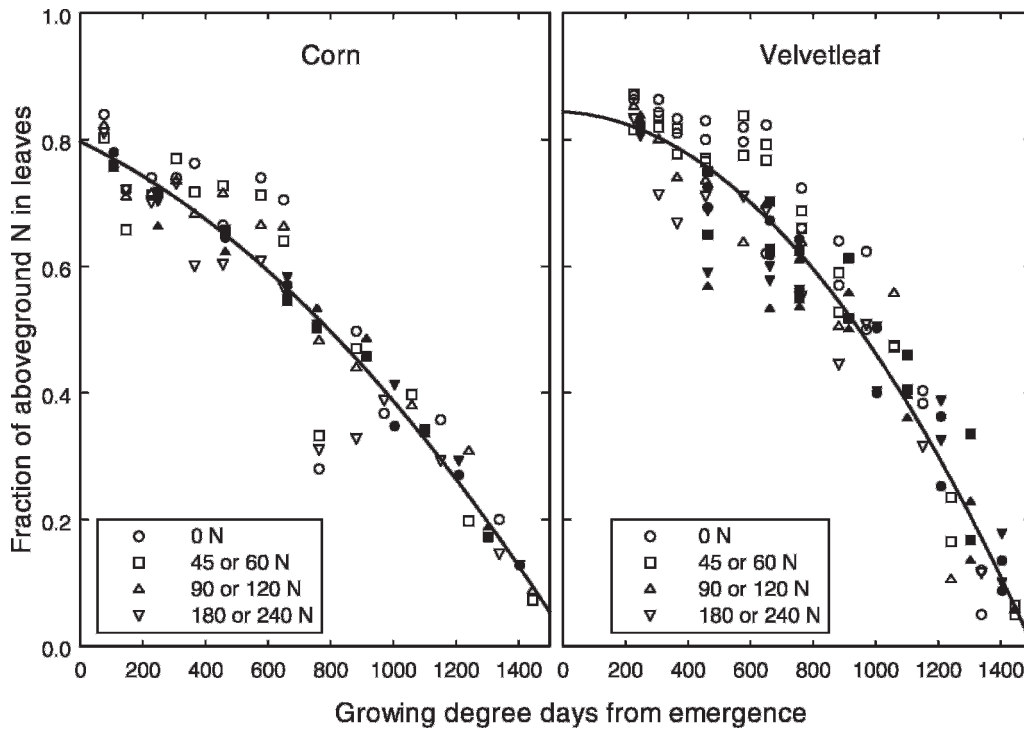


Figure 3. Corn and velvetleaf fraction of nitrogen (N) in leaves as a function of thermal time from emergence. Fraction of N in leaves (P_L , Equation 7) did not vary among N or velvetleaf density treatments, so the relationship is represented by a single equation across all treatments and years for each species. Open and closed symbols represent data from 1999 and 2000, respectively. $P_{L,corn} = 0.79688 - 0.00023747GDD - 0.00000017229GDD^2$, $r^2 = 0.84$; $P_{L,velvetleaf} = 0.84403 - 0.00002452GDD - 0.000000357407GDD^2$, $r^2 = 0.85$.

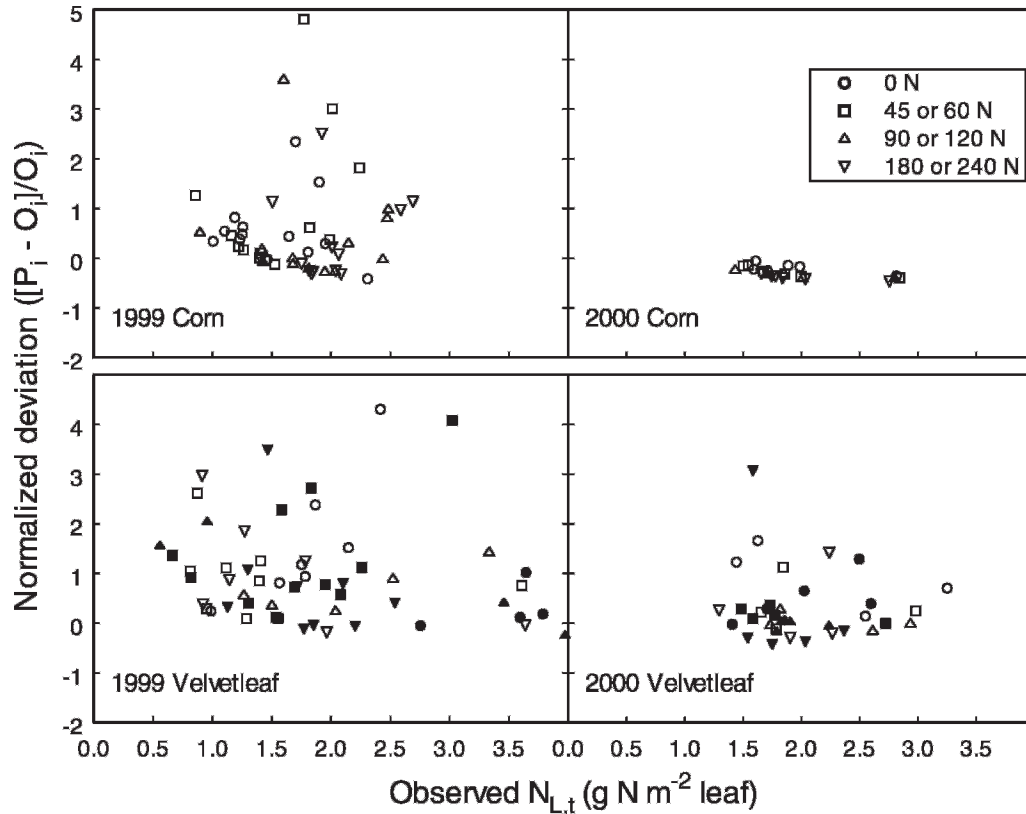


Figure 4. Normalized deviations between predicted and observed leaf nitrogen content (N_L , g N m^{-2} leaf) plotted as a function of observed N_L for corn and velvetleaf in 1999 and 2000. Predicted N_L was calculated by Equation 8, wherein P_L was obtained from the relationship shown in Figure 3, $N_{a,r}$ was calculated from Equation 1, and LAI was the observed value. In the velvetleaf plots, open and closed symbols represent velvetleaf grown at 2 and 10 plants m^{-1} row, respectively.

velvetleaf N uptake in most cases, although the corn [N]–biomass relationship might need to be altered to better reflect the higher corn [N] observed here. The fraction of above-ground N found in leaves in relation to thermal time was remarkably stable across years and treatments for both species. This is useful because it appears that a single function can be used to predict the partitioning of N to leaves of each of these species regardless of N supply or plant density. Average deviations between predicted and observed corn N_L were < 88 and 12% of the observed values in 1999 and 2000, respectively. Velvetleaf N_L was less well predicted, with

average deviations ranging from 39 to 248% of the observed values. Overall, the approaches to predicting N demand and distribution outlined here appear to be accurate for corn and velvetleaf. Further research is needed to incorporate these approaches into an ecophysiological model for interplant competition and to evaluate the entire model against independent experiments on corn–velvetleaf competition for N and light.

Table 5. Average of the normalized deviations $[(P - O)/O]$ between predicted (P) and observed (O) leaf N content ($N_{L,t}$) of monoculture-grown corn and velvetleaf. Predicted $N_{L,t}$ was obtained by Equation 8, where P_L was obtained from Figure 3, $N_{a,r}$ was calculated by Equation 1, and LAI was the observed value for a given experimental unit.

Year	N_{trt}^a kg N ha $^{-1}$	Average deviation		
		Corn	Velvetleaf	
			2 Plants m^{-1} row	10 Plants m^{-1} row
1999	0	0.58	2.48	0.63
	45	0.88	1.09	1.19
	90	0.35	1.24	1.22
	180	0.34	1.77	1.32
2000	0	-0.12	1.68	1.11
	60	0.06	0.41	0.94
	120	0.05	1.50	0.65
	240	-0.01	1.13	0.39

^a N_{trt} , N addition treatment.

Sources of Materials

¹ LI-3000 area meter, LiCor, 4421 Superior Street, Lincoln, NE 68504-0425.

² LECO CHN-2000, LECO Corporation, 3000 Lakeview Avenue, St. Joseph, MI 49085-2396.

³ SAS Institute Inc., 100 SAS Campus Drive, Cary, NC 27513-2414.

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