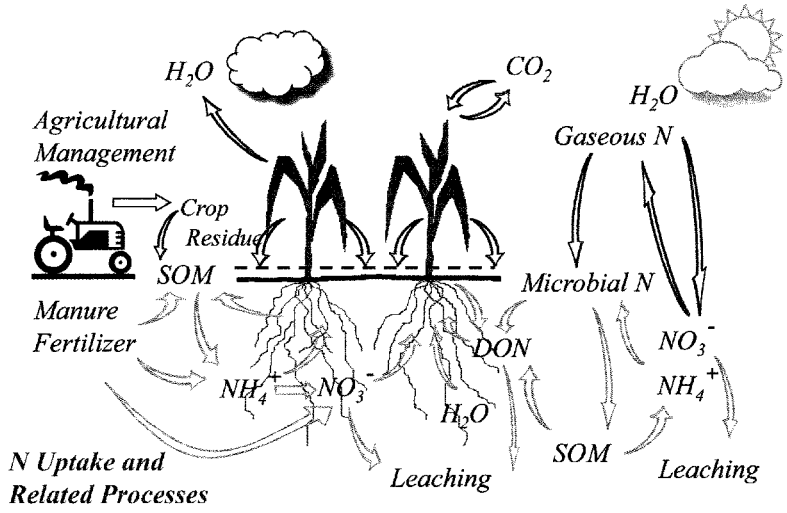
Quantifying and Understanding Plant Nitrogen Uptake for Systems Modeling



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10 Simulation of Nitrogen Demand and Uptake in Potato Using a Carbon-Assimilation Approach

Dennis Timlin, Mikhail Kouznetsov, David Fleisher, Soo-Hyung Kim, and V. R. Reddy

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10.1 INTRODUCTION

Nitrogen (N) is an important nutrient for plant growth but is present in soil in limited amounts for non-N-fixing agricultural crops. For this reason, soil amendment with N fertilizer is needed to obtain economic crop yields. The amendments, however, have to be carefully managed because N is highly mobile in soils and can become a pollutant when excess amounts move to groundwater.

Crop simulation models have become important tools for quantifying N dynamics, with the goal of managing N application with respect to specific soil, crop, and environmental conditions (Ahuja et al. 2002). An advantage of crop simulation models is that they can account for the relationships among environmental conditions, plant growth rate, N demand, and N availability in the soil on a dynamic basis. In order to simulate N uptake, these models, need to accurately account for carbon assimilation, N demand, and mechanisms of N uptake.

There is ample empirical evidence from experiments that the rate of growth of plants is proportional to N availability (Rodgers and Barneix 1988; Schenk 1996; Grindlay 1997). Long-term growth responses to N appear to be mainly a function of the effect of N on the increase of leaf area and resultant light interception (Grindlay 1997). Since dry-matter increase and canopy expansion (leaf area) are related via leaf growth, it is important to keep in mind that the relationships between N concentration in the plant and growth rate or biomass are largely empirical and correlative (Verkroost and Wassen 2005).

The effects of limited N on energy conversion to produce dry matter are believed to be minimal. Because leaf area controls light capture and carbon (C) assimilation, in order to utilize N, sufficient C must be available for leaf growth. In a greenhouse study, NO_3^- flux rates declined as cloud cover reduced radiances by as much as 75% (Clement et al. 1978). These results suggest that there are both feed-forward and feedback relationships between C assimilation and N uptake. This results in correlations among %N, growth rate, and dry matter (Grindlay 1997). When plant growth is limited by N supply, there is still accumulation of C compounds, resulting in reduced N percentage in the tissues (McDonald et al. 1986). This is consistent with an analysis of net primary productivity and light utilization efficiency, where Dewar (1996) concluded that N did not affect light utilization efficiency directly. This suggests that it is not photosynthesis that is ultimately limiting but, rather, the utilization of photosynthates for growth (McDonald et al. 1986; Grindlay 1997). Root sugar levels, for example, have been found to be responsible for expression of genes related to nitrate uptake (Matt et al. 2001).

There are still questions as to what determines the critical N concentration in plants (Grindlay 1997; Verkroost and Wassen 2005) and the physiological mechanisms the plant uses to regulate N uptake (Miller and Cramer 2005). This is complicated by the complex role of N in plant metabolism. Nitrogen can operate as a signaling mechanism as well as a structural component (Miller and Cramer 2005). There are numerous transporter systems in plant roots that depend on the form and concentration of N in the soil (Miller and Cramer 2005). These function under different circumstances and are subject to complex regulation. Nitrogen is also a primary component of the enzymes that control growth and development processes.

Hence, N uptake in plants involves complex processes that depend on C-assimilation rates, N demand by the plant, transpiration rate, root density and distribution, the form of N, and N concentration and water distribution in the soil.

The relationship between C assimilation and N uptake is further complicated by atmospheric CO_2 concentrations and the effects on C-assimilation rate and partitioning. Recent research with elevated CO_2 has shown that plants grown at elevated CO_2 have lower N contents than those grown at ambient levels (Kimball et al. 2002). There is still some uncertainty as to the reason for these differences. This suggests that there is not a simple relationship between C assimilation and N uptake, but within a given CO_2 level, C-assimilation rates will impact N demand.

Despite this complexity, simulation of N uptake in crop models is usually abstracted as two components: calculation of how much N the plant needs (demand), and uptake (supply) processes (see Gayler et al. 2002 for an application). According to Jeuffroy et al. (2002), there is a wide range in how crop models treat demand and uptake, and they are often simplified and combined into one process. The use of a critical N percentage is common in crop models to model N demand (Jeuffroy et al. 2002). Nitrogen limitation is calculated from the percentage of demand that can be met given maximum and minimum values of critical N. This value is expressed as a ratio from 0 to 1 and is used to adjust growth rate or radiation use efficiency. This mimics the effects of N deficiency rather than the mechanism. Nitrogen deficiency may also be used to adjust the C-assimilation rate (Verkroost and Wassen 2005) or leaf photosynthetic rate (see Jeuffroy et al. 2002).

Experimentally determined relationships between growth rate and N content have led to functional approaches to modeling N demand and uptake. One approach is to use an allometric relationship between N and biomass (Lemaire and Salette 1984; Plénet and Lemaire 1999). Another approach is the use of critical N contents in plants (Gastal and Lemaire 2002; Hirose 1988). Each plant component has a critical N content that may vary by growth stage and age. This provides a method to relate N availability to growth rate. As described in Gastal and Lemaire (2002), functional relationships between N content and growth stage are impacted by the effect of N on plant processes such as leaf photosynthesis. Nitrogen distribution in the canopy and leaf expansion rate also affects light interception, which, in turn, impacts C assimilation.

To better understand the processes of growth and N uptake, Verkroost and Wassen (2005) developed a model of N response under limited N using an N-allocation approach. Here they modeled the rate of formation of photosynthetic proteins (mainly RuBisCO, ribulose-1,5-bisphosphate carboxylase/oxygenase) as a function of N uptake. They also considered degradation of N-containing photosynthetic proteins through a first-order kinetic process. Carbon assimilation and resultant growth rate were a function of photosynthetic capacity. This model replicated linear growth rate responses to N seen in the literature, with a negative intercept (representing a growth cost for N utilization). The method of allocating N to photosynthetic proteins and allowing degradation (in which case N is recycled) was found to be a promising approach to simulation of N demand. They concluded that, when N is limited, it appeared to be allocated so as to maintain a constant photosynthetic efficiency, where N uptake and formation of photosynthetic N are balanced by degradation of photosynthetic proteins in order to maintain the highest possible C-assimilation rates.

This was a conceptual model in which light interception was not explicitly modeled. Verkroost and Wassen (2005) did show that, in N-limited situations, productivity based on N uptake is balanced between N needed to maintain photosynthesis and N left over for biomass production. However, photosynthetically active N could be an analog for leaf area. This would suggest that (under N-limiting conditions) any increase in photosynthetically active leaf area would have a cost that reduces total biomass due to the need to use C to build photosynthetically active proteins. Thus there would be an upper limit on N demand based on diminishing efficiency as N uptake increases. This concept may also be useful to model N demand as a function of $[CO_2]$, since it has been reported that the concentration of photosynthetically active proteins are reduced under elevated CO_2 (Stitt and Krapp 1999).

An important component of simulating N dynamics in plants is the quantification of N uptake. Nitrogen is present as a solute in the soil water in the forms of both ammonium (NH_4^+) and nitrate (NO_3^-), and as a result it is taken up in the transpiration stream, a process sometimes referred to as "passive uptake." This mode of uptake, however, is not completely passive, as the nutrient is required to pass through an impermeable membrane at the root surface, and an ionic balance must be maintained in the roots. It is likely that it is largely unregulated, however. The effect of transpiration rate on passive uptake may be more related to translocation from roots to the shoot than it is to the uptake process itself. In a study on the effect of transpiration rate on sodium uptake, Smith and Middleton (1980) reported that transpiration rate was more closely related to sodium translocated from the roots than total sodium content in the plant.

Plants can also actively take up N through diffusion by inducing an ionic gradient to absorb N in ionic form at a rate higher than N supplied via mass flow of water (De Willigen 1986). Active (diffusive) uptake of N is important because roots cannot always effectively intercept sufficient N when relying on mass flow alone. At limiting soil-N contents, diffusion becomes an increasingly important component of total N uptake (Plhak 2003). It has been shown that N uptake in the grass, tall fescue, does not follow transpiration, but is linked to the C-assimilation rate of the plant (Gastal and Saugier 1989). These studies suggest that the diffusive process of active N uptake is likely to be regulated by the plant.

Recently, more has been learned about the mechanisms that control uptake of NO_3^- and NH_4^+ from the soil. The active and passive components of NO_3^-–N uptake appear to be distributed over four different transport systems (Acco Lea and Azevedo, 2006):

1. Constitutive high-affinity (cHATS)
2. Nitrate-inducible high-affinity (iHATS)
3. Constitutive low-affinity (cLATS)
4. Nitrate-inducible low-affinity (iLATS)

In the case of NH_4^+, only the constitutive transport mechanisms are found. There are no ammonium-induced forms of N uptake (Acco Lea and Azevedo 2006). The high-affinity systems take up N when the concentration in the soil is low and vice versa for the low-affinity systems. Constitutive means that the

mechanism for diffusive uptake is not affected by nitrate concentration in the soil. The nitrate-inducible systems, on the other hand, are affected by nitrate concentration in the soil, meaning that changes in nitrate concentration will cause changes in gene activity and production of enzymes involved in N uptake. These systems allow the rate of N movement into the roots to be regulated by the plant according to the plant's need for N. An N-uptake model for oilseed rape that explicitly accounts for these mechanisms has been developed (Malagoli et al. 2004). This model is presented in chapter 3 of this book.

Uptake of nutrients, especially N, has been an important research topic from a soil fertility management standpoint and was an early topic to be addressed in simulation models of soil processes (Bouldin 1961). Early simulation models accounted for both diffusive and mass-flow components of nutrient movement to roots (Nye and Marriott 1969). The plant component of N uptake was accounted for by two empirical parameters, the root absorbing power (demand) and water flux at the root surface (via transpiration rate). Later efforts employed a Mitscherlich-type equation to model diffusive movement of N to the roots. Much of this work has been summarized in Barber (1995).

The simulation of passive components of N uptake is straightforward, so this method is common in most crop models. The model keeps track of the amount of water taken up through transpiration and the concentration of nitrate in the soil water, and from this calculates total N uptake. Generally, when passive uptake is the main component of N uptake, there is no mechanism for the plant to regulate its N content. Since water uptake is usually dependent on soil water content, if the wettest areas of the soil have low N concentrations, the plant might not be able to take up enough N to prevent limitation of growth. On the other hand, in dry areas, lower transpiration may limit the ability of the plant to take advantage of the larger amounts of soil N that may be present.

Simulation of active uptake provides a mechanism to allow the plant to regulate N uptake. This method is more involved and requires additional parameters. The nitrate-uptake rate is typically simulated using an absorption isotherm in the form of a Michaelis–Menten (MM) equation (Claassen and Barber 1976). The use of Michaelis–Menten kinetics requires information on the maximum rate of nitrate uptake per unit of root length, root radius, root surface, and concentration of nitrate in the soil solution. Usually, average values of these parameters are used. In actuality they may vary over temperature, root age, and mechanism of nitrate uptake. For further information, see Buysse et al. (1996) and Barber (1995). The maximum rate of N uptake per unit root depends on N demand (Schenk, 1996).

There are few studies that have quantified N-uptake and C-assimilation rates under sunlit conditions using controlled temperatures and different CO_2 concentrations and soil media. Many of the studies were carried out in greenhouses or using artificial light. There is qualitative evidence, however, that the proportion of active uptake in total nitrate uptake decreases as the N in soil solution increases (Plhak 2003). Furthermore, potato plants grown under elevated CO_2 (twice ambient) have been shown to have lower N contents and transpire less water than those grown at ambient CO_2 levels (Conn and Cochran 2006; Bunce 2001). This would impact the relative rates of passive and active N uptake.

10.2 A MODEL OF ACTIVE AND PASSIVE N UPTAKE BASED ON CARBON ASSIMILATION RATE

10.2.1 Objective and Approach

Here we describe one approach to simulate active and passive N uptake based on rates of carbon assimilation, transpiration, and diffusion of N in soil using a Michaelis–Menten approach. Experimental data on relative amounts of active and passive N uptake in potatoes grown in pots in outdoor, sunlit growth chambers are used to determine patterns of passive and active N uptake and carbon assimilation rates under two levels of CO_2 and six N levels. The processes of N uptake were abstracted in a model of diffusive and active N uptake and compared qualitatively with measured data.

10.2.2 Materials and Methods

10.2.2.1 Growth Chambers

The outdoor, sunlit controlled environment chambers used for this study were constructed of clear acrylic and were 2.3 m tall and 1.5 m^2 in cross-sectional area with a total chamber volume of 3360 L. The space available for growing plants in the chambers is 1.0 m^2, excluding the internal ducting. The Soil Plant Atmosphere Research (SPAR) chambers are very similar in design to those in use at Mississippi State University (Reddy et al. 2001). The chambers and the control mechanisms were fully described by Baker et al. (2004). The air handler, mounted at the base of the chamber, contains a squirrel-cage fan that draws air and forces it past resistive heaters and a liquid-cooled heat exchanger on the return path back to the chamber. These heating and cooling elements were used to control air temperature and humidity. Constant relative humidity was maintained at 60%–70% by operating solenoid valves that inject chilled water through the cooling coils located in the air handler of each chamber. These cooling coils condensed excess water vapor from the chamber air stream in order to regulate relative humidity. The temperatures in the growth chambers were maintained to within ±0.2°C of the set points.

A feed-forward, feedback proportional–integral–differential (PID) control algorithm similar to the one described by Pickering et al. (1994) was used to control injection of CO_2. Gas flow was measured and controlled by mass-flow controllers (Omega Engineering, Stanford, CT). The amount of CO_2 injected, the air chamber volume, chamber temperature, and chamber leakage were used to calculate canopy photosynthetic and respiratory rates over 300-s intervals. Carbon dioxide was injected only during the daytime hours when there was sunlight (0600 to 2000 hours, eastern standard time). The photosynthetically active radiation (PAR, measured as photosynthetic photon flux density, PPFD, μmol photons $m^{-2} s^{-1}$) was integrated over the same 300-s intervals. Transpiration was calculated from measurements of water drained from the cooling coils. Some water would have come from direct evaporation from the soil, but this amount is small, since the plants were grown in pots and there was little soil surface exposed to radiation.

The facility includes a dedicated Sun SPARC 5 workstation (Sun Microsystems, Mountainview, CA) used to control chamber atmospheric [CO_2] and record C-assim-

ilation and chamber environmental data (air and soil temperatures, humidity, CO_2 concentration, and solar radiation) every 300 s. Air temperature and relative humidity were also monitored and controlled with TC2 controllers (Environmental Growth Chambers, Chagrin Falls, OH). Incident photosynthetically active solar radiation (PAR) was monitored with a single LI 191 SB radiation sensor (LI-COR, Lincoln, NE) located outside the chambers. The acrylic plastic allows approximately 95% of the PAR to pass through (Kim et al. 2004).

Leakage rates were calculated daily (Baker et al. 2004) as

$$L = \frac{1}{r}\left(\Delta CO_2\right) \tag{10.1}$$

Here L is the leakage rate (μmol CO_2 m^{-2} s^{-1}), e.g., the CER (C exchange rate) without plant uptake, and ΔCO_2 is the gradient of internal-chamber to external-air CO_2 concentrations (μmol CO_2 mol air^{-1}). The value of the resistance, r, was obtained daily by injecting a pulse of nitrous oxide and measuring the decay (Baker et al. 2004). The gradients in equation (10.1) were calculated using ambient CO_2 measurements taken on the same temporal scale as the CO_2 measurements in the chambers. Ambient CO_2 levels varied diurnally from 350 to 550 μmol mol air^{-1} (higher values at night) and have a strong effect on leakage calculations (Baker et al. 2004).

When there were plants in the chamber, the CER represented net photosynthesis. Dark respiration, R_D (μmol CO_2 m^{-2} s^{-1}), was calculated daily as the mean CER between the hours of 0100 and 0400. Although R_D does not account for photorespiration and may be affected by [CO_2], this method has successfully been used to relate carbon assimilation to dry matter (van Iersel and Kang 2002; Timlin et al. 2006) from growth-chamber data. Therefore, R_D was used to adjust for photorespiration during daylight hours. Since this value was obtained for a temperature of 18°C, it was multiplied by 1.5 when applied to daytime C-assimilation rates (23°C). An equation (Constable and Rawson 1980; Milroy and Bange 2003) was used to model gross photosynthesis (P_G) as a function of PPFD (photosynthetic photon flux density). This equation was used to interpolate measurements of P_G for periods when gas-exchange data were missing or out of range (as when the chambers were opened for plant measurements), smooth the data, and obtain P_G values for specific light levels:

$$P_G = P_{max}\left(1 - \exp\left[1 - a \times PAR\right]\right) \tag{10.2}$$

Here P_{max} is the asymptotic rate of gross C assimilation (μmol CO_2 m^{-2} s^{-1}), PAR is photosynthetically active radiation (μmol photons m^{-2} s^{-1}), and a is a coefficient with units of μmol $photons^{-1}$ m^2 s. P_G, gross C-assimilation rate, is calculated as net C-assimilation rate measured in the chambers with respiration added back as a positive number. Unless otherwise noted in this chapter, P_G is reported as gross C assimilation per unit surface area of the growth chamber and is not adjusted for light interception or leaf area. The two coefficients were fitted using Proc NLIN of SAS (SAS Institute 2004).

10.2.2.2 Plant Cultivation and Environment

Three certified potato (*Solanum tuberosum* cv. Kennebec) seed tubers (5 ± 10 g mean fresh weight) were planted at a depth of approximately 5 cm into 3.8-L pots. The soil type was 75% sand and 25% vermiculite by volume (Grace Construction Products, Cambridge, MA). The plants for the two CO_2 treatments were planted at different times using the same six chambers for the two experiments. The elevated CO_2 treatment was the first planting on 13 May 2005, with 50% emergence recorded on 27 May 2005. The ambient CO_2 treatment was the second planting on 22 July 2005, with 50% emergence recorded on 5 August 2005. Since total light and day length were different between the two periods, we did not compare elevated and ambient CO_2 treatments results. The tubers were germinated in pots in the outdoor chambers for the first planting, and the temperature was held constant at 23°C until full emergence. Nitrogen and CO_2 treatments were applied at planting. The pots for the second planting were initially placed in indoor lamp-lit chambers also held at 23°C to allow us to place the pots with emerged plants in the sunlit chambers immediately after harvesting the first planting. These plants were transferred to the outdoor chambers on 8 August 2005. There was about 50% emergence, and all emerged plants had four to six leaves at this time. Two days after all the plants had emerged from a pot, two of the tubers with plants were removed from the pot with as much root mass as possible, and the shoots on the remaining tuber were thinned to a single shoot.

Twelve pots were placed in each of the six chambers. The temperatures in the chambers were maintained at a constant 23/18°C ± 0.1°C day/night 16-h thermal period. Carbon dioxide concentration for the elevated treatment was 700 μmol mol air^{-1}, and 370 μmol mol air^{-1} for the ambient treatment. The value of CO_2 for the ambient treatment was close to the mean daily value measured at Beltsville, Maryland. After planting, six N levels were randomly assigned to the chambers for the elevated CO_2 treatment. The same treatment allocation was used for the ambient CO_2 treatment. This was done to minimize variation due to chamber on CO_2 comparisons within a N level. The N levels were 2, 4, 6, 8, 11, and 14 mM N. Nitrogen was manually applied as a solution three to four times a week to maintain a constant concentration of N in the soil water. Solution was applied in large enough amounts to completely saturate the pot. The N was applied as 50% NO_3 and 50% NH_4 Hoagland's solution.

Additional newly emerged shoots from the tuber were removed by pinching to maintain one main stem shoot per pot. This should not affect photosynthesis rates via source/sink effects. Oparka and Davies (1985) did not find that there was sharing of assimilates among different stems emerging from the same seed-piece.

Nighttime CO_2 was not controlled and varied around the ambient level (350–550 μmol mol air^{-1}). Graded shade cloths were adjusted around the cabinet edges to plant height to simulate shading effects found in a field crop. The plants were not staked.

10.2.2.3 Plant Data Collection

The potato plants were harvested prior to senescence to evaluate plant growth at the time of maximum canopy green leaf area. The harvest dates were 27 July 2005 for

the elevated CO_2 experiment and 27 October 2005 for the ambient CO_2 experiment. The lengths of the growing seasons were 60 and 73 days, respectively. At harvest, plants were separated according to stem, green leaf, and tubers. Leaves and stems were segregated based on position as main stem, i.e., main-stem leaves, second- and third-order main-stem leaves, first- and second-order basal-stem leaves, and first- and second-order apical-stem leaves. Leaf area was measured on all components using a Li-Cor 3100 (Li-Cor, Lincoln, NB) area meter. Nitrogen and C contents were determined on main-stem stem and leaves, second-order stems, and leaves and tubers on three randomly chosen plants from each treatment. Leaves on second-order stems were younger than main-stem leaves and still actively growing at harvest, hence they provided an estimate of N in young tissue. A Perkin-Elmer 2400 CHN analyzer (PerkinElmer Life and Analytical Sciences, Wellesley, MA) was used to determine N content.

10.2.2.4 Calculations for Passive and Active N-Uptake Rates

Daily total N-uptake rates were estimated from measured C/N ratios and daily C assimilation. Here we assumed a constant C/N ratio throughout the growing period. It has been shown that the C/N ratio in potato does not vary greatly until senescence begins (Karley et al. 2002). Passive uptake of N was estimated from daily transpiration rates and the known concentration of N in the soil water. Active uptake was estimated from the difference between total and passive N-uptake rates. Note that calculation of transpiration (passive) uptake was independent of assimilation rates and C/N ratio.

There are a number of assumptions inherent in the analysis of the measured data. To correctly estimate N uptake in transpired water, we must assume that the plant does not filter N from the water and that the ammonium and nitrate forms of N were equally available. Cao and Tibbits (1998) showed that potato makes best use of N in the soil when it is partially in the form of ammonia and nitrate. Although N can be lost in nonsterile media through microbial activities (Smart et al. 1998), we did not believe this was an important mechanism of N loss in our study. Since the plant media had no organic matter, the low C substrate (only from root exudates) would have likely been insufficient to support much microbial growth.

The C/N ratio was only measured at the end of the season, and we calculated N uptake during the early growth period based on (a) current C-assimilation and transpiration rates, and (b) end-of-season N measurement. The N content of secondary-stem leaves was assumed to apply to the new leaf growth in the early season growth period. It is known that stem biomass increases over leaf biomass as N content increases, and this affects distribution of N in the canopy (Gastal and Lemaire 2002). We did scale the total N in the plant for plant component to adjust for stem and leaf differences in N content, but the exact ratio during the active growth phase may have been slightly different than that at the end of the season. We do not expect the differences to be large enough to greatly affect the results, especially the relative differences among treatments, since the ratios of stem to leaf did not change greatly over the growth period. Active uptake was calculated as the difference between two estimated values, and thus contains much of the error in the assumptions.

10.2.3 Simulation Model Description

10.2.3.1 Soil Model

The soil model, 2DSOIL (Timlin et al. 1996), is a two-dimensional modular finite element model of water and solute movement that was developed from SWMS-2D (Simunek et al. 1994). Additional components to simulate atmospheric processes and root and canopy growth have been taken from the model GLYCIM (Acock et al. 1985). Only the ambient CO_2 treatments were simulated, since the plant model does not account for the effects of CO_2 on stomatal conductance to water vapor.

Nitrogen may be taken up by plants by an active process or by a passive process. If the process is active, it is assumed that the plant regulates the concentration at the root surface of the considered chemical, and that both mass flow and diffusion may contribute to the movement of solutes to the root surfaces. Mathematically, however, the two cannot be differentiated. During passive uptake, the movement of solutes to the root surfaces is simulated as pure mass flow with water.

The approach to simulate advective and diffusive movement of N is to combine two equations for the N-uptake rate (I_{in}) by the plant. An absorption isotherm for N as nitrate to move to the root from the bulk soil solution can be described by a Michaelis–Menten-type equation:

$$I_{in} = \frac{I_{max}(C_R - C_{min})}{K_M + (C_R - C_{min})} \tag{10.3}$$

where

I_{in} = NO_3^--uptake rate (mg d^{-1} cm $root^{-1}$)
I_{max} = maximum (asymptotic) rate of NO_3^- uptake at the highest soil N concentration (mg d^{-1} cm $root^{-1}$)
C_R = concentration of NO_3^- at the root surface (mg cm^{-3})
K_M = concentration of NO_3^- in the soil where I_{in} is one-half I_{max} (mg cm^{-3})
C_{min} = minimum concentration of NO_3^- in the soil where plants can still take up N (mg cm^{-3})

The model assumes that solute movement takes place only in the radial soil volume surrounding the root. Furthermore, it is assumed that the concentration–distance profile around a root develops in time in a stepwise manner, and that at each time step it approximates to a steady-state profile (Baldwin et al. 1973). Each root may exploit an average effective volume of soil, which is assumed to be a cylinder corresponding to the average half-distance between the roots. Daily maximum rate of inflow of N as NO_3^- to the roots (I_{max}) depends on root age and is not considered to be regulated by the plant in this study (i.e., it is held constant throughout the simulations).

Equation (10.3) provides an estimate of N-uptake rate as a function of N concentration at the root surface (C_R) and minimum N concentration in the soil solution (C_{min}). Solute flux to the roots, however, also depends on

1. Diffusion rate of NO_3^- in the soil
2. Rate of water flow to the roots
3. Total root length and mean radius of the root
4. Concentration of NO_3^- in the soil water (C_S)

Based on these assumptions, the solute-flux toward the root surface (I_{in}) is also calculated as

$$I_{in} = \begin{cases} 4\pi D(C_S - C_R)\left[\dfrac{\beta^2 \ln \beta^2}{\beta^2 - 1} - 1\right] & a = 0 \\ q_r \dfrac{\left(\beta^2 - 1\right)C_S - \ln(\beta^2)C_R}{\left(\beta^2 - 1\right) - \ln(\beta^2)} & a = 2 \\ q_r \dfrac{\left(\beta^2 - 1\right)\left(1 - a/2\right)C_S - (\beta^{2-a} - 1)C_R}{\left(\beta^2 - 1\right)\left(1 - a/2\right) - (\beta^{2-a} - 1)} & \text{else} \end{cases} \quad (10.4)$$

where

$a = q_r/2\pi D$
$\beta = (r_r^2 \pi L)^{-1/2}$
I_{in} = solute uptake per unit length of the root (as defined in equation 10.3)
D = diffusion coefficient in the soil ($cm^2\ d^{-1}$)
C_S = bulk concentration in solution (mg cm^{-3}), which is obtained from the solution of the convection dispersion equation,
C_R = concentration at root surface (mg cm^{-3})
r_r = root radius (cm)
L = root density (cm root cm^{-3})
q_r = water flow toward the root surface per unit length of the root (cm cm^{-1} d^{-1})

The flow rate for mature, q_{r_m}, and young, q_{r_y}, roots is calculated as

$$q_{r_m} = \frac{u_m}{2\pi l_m} \text{ and } q_{r_y} = \frac{u_y}{2\pi l_y}$$

where u_m and u_y are, respectively, water uptake from soil cells by mature and young root ($cm^3\ cm^{-2}\ d^{-1}$), and l_m and l_y are, respectively, length of mature and young roots in soil cell (cm).

In the soil, diffusion is influenced by the water content of the soil both in terms of the diffusion cross-section and the tortuous pathway followed by the solute through pores. The bulk soil diffusion coefficient is calculated as

$$D = \lambda q_r + \theta D f$$

where

q_r = flow rate to the root (cm cm^{-1} d^{-1})
θ = volumetric soil water content (cm^3 cm^{-3})
D = diffusion coefficient in free solution (cm^2 d^{-1})
λ = soil dispersivity (cm)

f is a "tortuosity" factor that can be estimated as shown by Millington and Quirk (1960):

$$f = \frac{\theta^{7/3}}{\theta_S^2}$$

where θ_S is the soil water content at saturation.

Finally, the unknown concentration, C_R, can be found by simultaneously solving equations (10.3) and (10.4) for C_R. In this case, C_R is determined by the N concentration in soil and the parameters of the MM equation (equation 10.3). Any plant regulation would be achieved by varying the parameters of equation (10.3). If the uptake is limited by the availability of the solute ($C_S < C_R$), then C_R is assumed equal to zero and hence the root acts as a zero sink. The total uptake of the solute is calculated by integrating I_{in} over the entire root system. In the case of ample solute supply, the total solute uptake is determined by the soil supply of N.

An alternative method to simulate active uptake is to determine a value of N uptake, U_d (mg d^{-1}), for the time period based on plant need and distribute it over the entire root zone as follows:

$$\sum_{i=1}^{N} (I_{im}(C_R) \cdot l_{im} + I_{iy}(C_R) \cdot l_{iy}) = U_d \qquad (10.5)$$

I_{in} in equation (10.4) can be considered to be the sum of two components when $a = 2$. The first component is $I_{in}(C_S)$, and the second is $I_{in}(C_R)$ (considering that the two components are additive). Since the component for N uptake in equation (10.4) due to C_R determines plant demand, U_d (equation 10.5), we can set U_d to equal $I_{in}(C_R)$ and then solve for C_R and I_{in}. In equation (10.5), N is the number of soil cells with roots, I_{im} and I_{iy} represent N uptake by mature and young roots from cell i, and l_{im} and l_{iy} are the lengths of mature and young roots in cell i. We assume a common value of C_R to exist along the root surfaces of the entire root system. Soil cells in which $C_S < C_R$ are assumed not to contribute to the solute uptake (except in the transpiration flow). This method, however, is left for a later exercise and is not implemented in this paper.

I_{max} and K_M were determined from the measured data. I_{max} was set to the N-uptake rate for the 14-mM treatment. K_M was set to the concentration of NO_3^- in the soil for the 6-mM treatment, because the inflection point in yield and uptake occurred at about this point.

10.2.3.2 Plant Model

A simple, generic, single-leaf plant model was used to calculate N demand and uptake. Carbon assimilation was a function of sunlight and leaf area. A rectangular hyperbola (Acock et al. 1971) was used to calculate C assimilation as a function of light using parameters from the experiment.

$$P_G = \frac{\alpha I \tau C}{\alpha I + \tau C} \tag{10.6}$$

where

P_G = gross photosynthesis (g CO_2 m^{-2} h^{-1})
I = light integral (mol photons m^{-2} h^{-1})
C = external CO_2 concentration (370 μL L^{-1} [μmol mol^{-1}] air)
τ = canopy conductance to CO_2 transfer (m hr^{-1})
α = canopy light utilization efficiency (g CO_2 mol^{-1} photons)

Vegetative mass is calculated from assimilated C assuming that the vegetative dry matter is, on average, 40% C (Timlin et al. 2006). Respiration rate, R (μmol CO_2 m^{-2} s^{-1}), is a function of vegetative biomass and is calculated from assimilated C as (Timlin et al. 2006)

$$R = -0.03 + 0.008973\ V_M$$

where V_M is vegetative mass (g) and R is in units of g C m^2 h^{-1}.

The daily rates of increase of leaf area and plant height were calculated as a function of C-assimilation rate, time, and a growth coefficient. The growth coefficient was roughly calculated from a relationship between leaf area and biomass determined from the data (some of the C assimilation will produce stem as well during early growth). The purpose of the coefficient was to translate C assimilation into leaf area (units of cm^2 g^{-1}). Since constant temperatures were used in the growth chamber, no temperature dependency was used. To calculate a N deficiency index to adjust C-assimilation rates, we assumed that the plant attempts to maintain an optimum C/N ratio (derived from the experimental data). An actual C/N ratio is calculated from cumulative N uptake and cumulative C-assimilation rates. If the actual C/N ratio falls below the optimum, C assimilation is reduced by an index related to the ratio of actual C/N divided by the optimum. Carbon for root growth was partitioned from total C assimilation, as is done in the soybean model GLYCIM (Acock et al. 1985). Root growth algorithms, also taken from GLYCIM, were used to simulate root growth. These algorithms are appropriate for potato, as they can simulate a fibrous root system without a taproot. Carbon for root growth is partitioned from C assimilation. Relative root growth into a particular soil region is not affected by N content. Since we were simulating a potted experiment, the correct simulation of root dynamics was not critical.

The optimal N/C ratio was set at 0.15 (C/N = 6) at the beginning of the simulation and allowed to linearly decrease to 0.07 (C/N = 14) at the end. This was based on the experimental results for comparison of new and mature leaves.

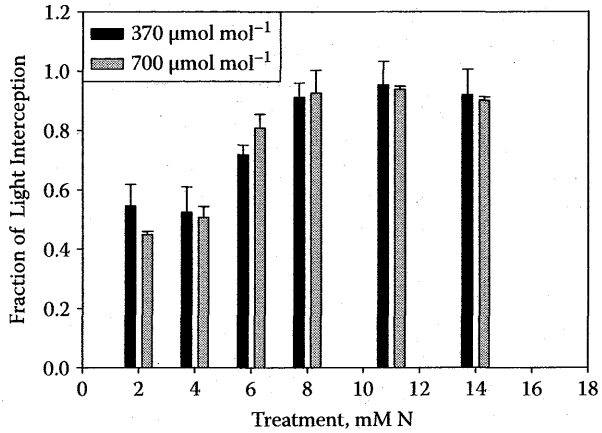

FIGURE 10.1 Maximum mean light interception at end of the season as a function of six N treatments at two levels of CO_2. The data are an average of 5 days.

10.2.4 Results

10.2.4.1 Measured Data

Figure 10.1 shows maximum light interception near the end of the growing season for the six N treatments within each of the two CO_2 treatments. The trends with N are similar for the two CO_2 treatments. Note that there is a transition between 6 and 8 mM N, indicating that, below 8 mM N, a deficiency in N resulted in reduced canopy growth. There was no discernible CO_2 effect on light interception. Figure 10.2 shows mean daily C-assimilation rate as a function of N treatment during the exponential growth phase. The rates at ambient CO_2 levels reached an asymptote at about the 8-mM treatment, consistent with the light-interception data, but assimilation rates

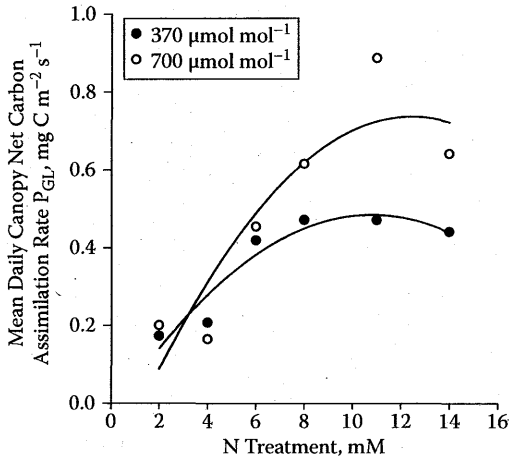

FIGURE 10.2 Mean canopy net C-assimilation rate as a function of six N treatments at two levels of CO_2.

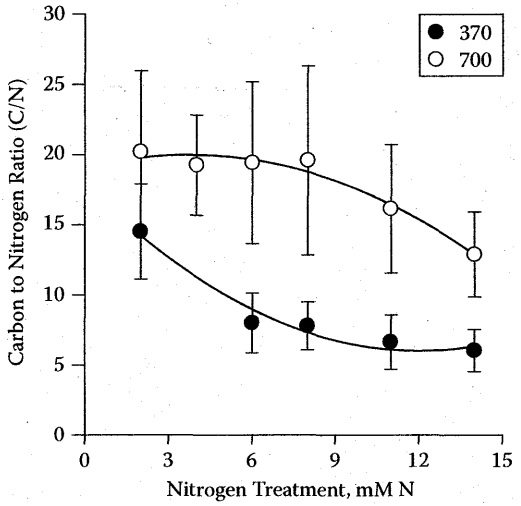

FIGURE 10.3 Mean C/N ratio of aboveground biomass as a function of six N treatments at two levels of CO_2. The error bars indicate variability among plants and plant components (stems and leaves).

were higher for the elevated CO_2 treatment and reached an asymptote at a higher level of N. This is partially due to the slightly longer day length for the first experiment (elevated), as well as CO_2 fertilization. There was little difference between C-assimilation rates for the two CO_2 treatments at the lower N levels. This suggests that there was not enough N or leaf area for the plants to take advantage of the CO_2 fertilization or extra day length.

Measured C/N ratios for the two CO_2 levels as a function of N treatment is shown in Figure 10.3. In both cases, the C/N ratio decreases with increasing N application, a result of the increasing proportion of N in the plant tissue. The C/N ratios are higher for the elevated CO_2 treatments because of relatively reduced N contents. This is consistent with other elevated CO_2 studies with potato (Conn and Cochran 2006).

The mean daily N-uptake rate during the exponential growth phase calculated from the C/N ratio and net C-assimilation rate increases with concentration of N in the soil water (Figure 10.4). The trend reaches an asymptote at higher N application rates. The asymptote appears to occur at a lower N rate for the ambient CO_2 treatment than for the elevated CO_2 treatment. Nitrogen-uptake rates estimated from C-assimilation rates and C/N ratios were higher over all N treatments for the ambient CO_2 treatment. This is primarily due to the measured low C/N ratios at the end of the season in the plants grown under ambient CO_2. Even though the C-assimilation rates (Figure 10.2) were higher for the elevated CO_2 treatment, this was not enough to offset the differences in leaf and stem N contents.

The amount of N taken up in the transpiration stream was not greatly different between the two CO_2 treatments (Figure 10.5). The amount was slightly higher in the elevated CO_2 treatment than in the ambient. This difference is likely due to longer day length and slightly higher light levels for the early summer period during which the elevated CO_2 plants were grown. Studies have reported lower water use in C_3 plants

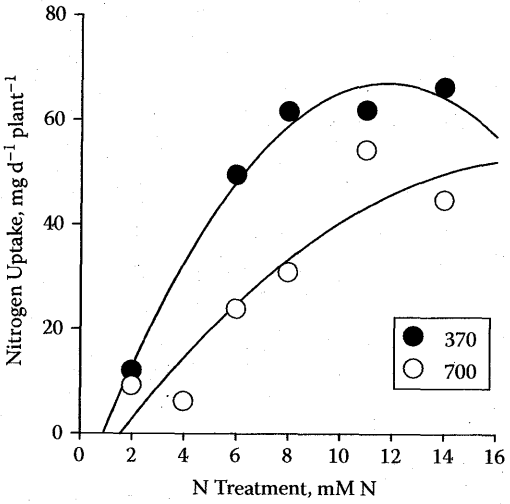

FIGURE 10.4 Total measured N uptake calculated from C/N ratio and net C-assimilation rate as a function of six N treatments at two levels of CO_2.

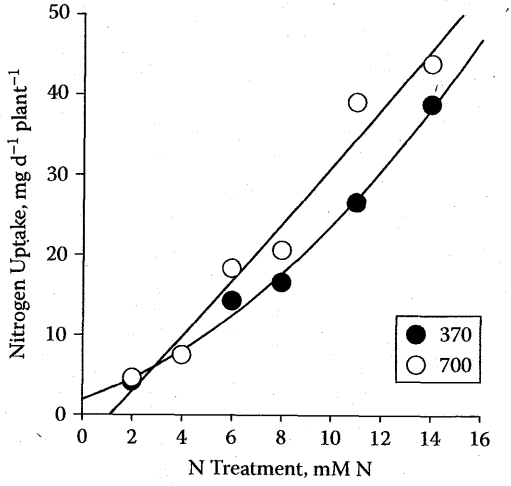

FIGURE 10.5 Mean measured passive N uptake in water (mass flow) as a function of six N treatments at two levels of CO_2.

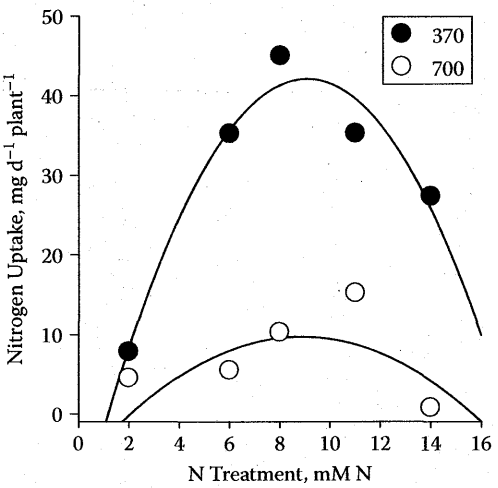

FIGURE 10.6 Mean measured active N uptake (diffusion) as a function of six N treatments at two levels of CO_2.

such as potato under elevated CO_2 (Bunce 2001). Since the plants were grown in pots, there was little exposed soil, so it is not likely there was significant contribution of soil evaporation to the condensate collected from the cooling coils. Nitrogen uptake via transpiration increased linearly with N application rate, with no asymptote at higher application rates. This is mainly a reflection of the size of the canopies and light interception as affected by N application rate. The linear increase with no asymptote results from the way passive uptake of N is calculated. Since the N content of the treatment increases more than the transpiration rate, the trend is largely a function of concentration of N in the soil water. Note that, since transpiration per unit ground area is affected by leaf cover, one would not expect a leaf area effect on transpiration at N applications greater than 8 mM when leaf area was maximal (Figure 10.1).

The rate of N uptake by diffusion calculated as the difference between N uptake in transpiration and total N uptake shows larger differences between CO_2 treatments (Figure 10.6) than for passive uptake. The trend is quadratic for both treatments, with a maximum uptake at about the medium concentration of N in soil water (6–10 mM N). The uptake decreases at the highest N levels. The ratio of N uptake in transpiration relative to total uptake increases as soil water N concentration increases (Figure 10.7). The slope is slightly steeper for the ambient CO_2 treatments than for the elevated ones, but the difference is small. In general, almost twice as much N uptake came from transpiration with elevated CO_2 than with ambient CO_2.

10.2.4.2 Simulations

Simulations were carried out using conditions and N treatments from the ambient CO_2 level. Simulated daily total N-uptake rates are similar to measured results, although the simulated total uptake continues to increase slightly with N rate, while the measured rates reach a distinct asymptote (Figure 10.8). Simulated and measured N as mass flow (passive) are similar, and both show the same increasing trend with

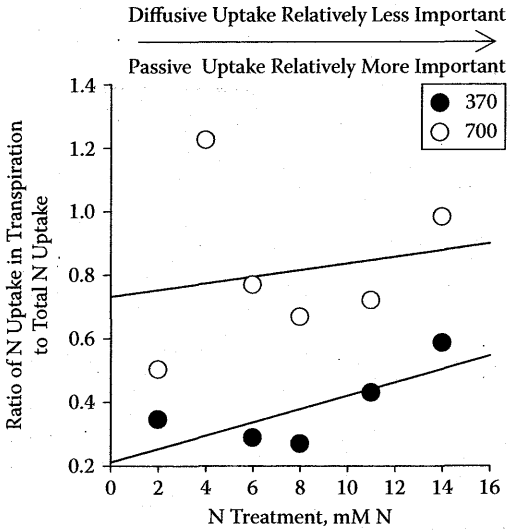

FIGURE 10.7 Ratio of measured N uptake in transpiration to total uptake for six N treatments at two levels of CO_2.

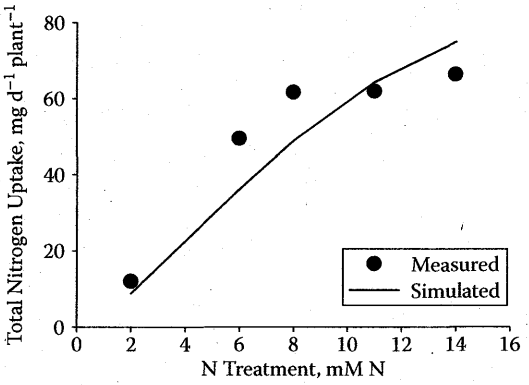

FIGURE 10.8 Simulated and measured total N uptake for the ambient CO_2 treatment.

no asymptote (Figure 10.9). The results for daily diffusive N-uptake rates show the largest differences, especially at the midrange of the treatment amount (6–10 mM). The measured diffusive uptake is about 10–15 mg d^{-1} higher than simulated. This contributes to the differences seen in total N uptake in Figure 10.8. The simulated daily diffusive N-uptake rate does begin to decrease at the higher concentrations of applied N, as seen in the measured data, but the decrease is not as marked (Figure 10.10) and begins at a higher applied N concentration. The trend in simulated total C assimilation is also similar to the measured results, where both exhibit a quadratic trend and reach a maximum at about 8–10 mM (Figure 10.11). The simulated values are higher, however, at the higher N applications.

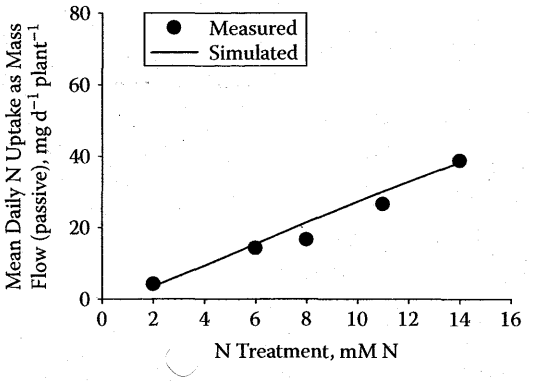

FIGURE 10.9 Simulated and measured N uptake as mass flow (passive uptake) for the ambient CO_2 treatment.

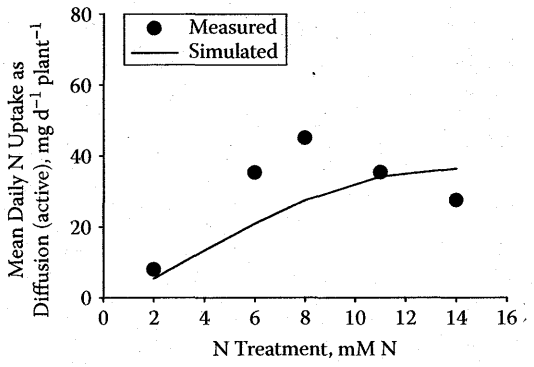

FIGURE 10.10 Simulated and measured N uptake as diffusive (active) uptake for the ambient CO_2 treatment.

10.2.5 Discussion

The measured relationship between C-assimilation rate and soil water N concentration in this study is largely related to the effect of N on canopy growth and light interception (Figures 10.1 and 10.2). Previous research has demonstrated that the effect of N is to increase leaf size and area, leading to increased light interception and canopy-level C assimilation (Lawlor 2002). This is consistent with research showing that N uptake is proportional to relative growth rates (Schenk 1996) (growth rate adjusted for cumulative growth). Hence, the relationship between C assimilation and soil water N concentration is mainly related to the effects of N availability on leaf growth and resultant light interception. At lower levels of soil water N concentration (<8 mM), there was less leaf area and less light interception, resulting in lower C-assimilation rates per square meter of chamber surface. The asymptote for light interception in Figure 10.1 is due to the fact that the plants have reached maximum light interception at 8 mM N, and additional N above 8 mM increased biomass without appreciably increasing light interception. Since respiration is roughly a function

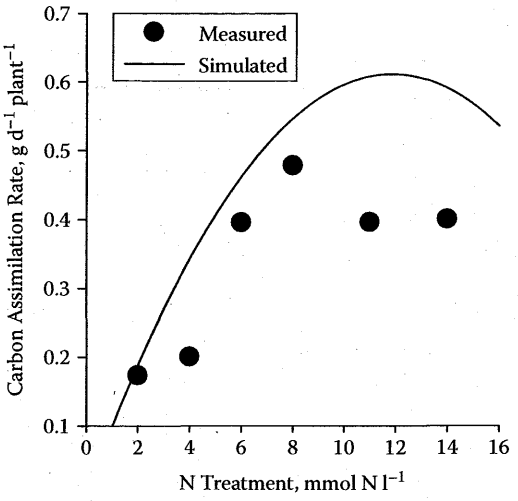

FIGURE 10.11 Simulated and measured C-assimilation rate as a function of six N treatments for the ambient CO_2 treatment.

of the amount of biomass (Amthor 2000; Timlin et al. 2006), the proportion of C lost to respiration will be higher at N levels greater than 8 mM, where N apparently increased biomass without increasing light interception.

The measured results suggest a decreasing rate of N uptake via diffusion (active uptake) as soil water N concentration increases. The differences between the ambient and elevated CO_2 results further suggest that the rate of active uptake is strongly dependent on the N demand of the plant (as defined by an optimum C/N ratio). Where N demand was low (elevated CO_2), active uptake was a smaller component of N uptake. This is in agreement with the observation that plant uptake of N is subject to down-regulation when N demand decreases (Glass et al. 2002). On a whole-plant scale, the regulation of N uptake appears to be related to the C-assimilation rate and light interception. The ability to control N uptake to match C availability would enable the plant to maximize its leaf area in the shortest time possible. Nitrogen is important in leaf growth and, in this study, was the limiting factor in obtaining full light interception for low N concentrations in soil water. Nitrogen limitation will reduce leaf growth and, in turn, reduce C assimilation. This, in fact, is the basis of modeling N in many crop models (Jeuffroy et al. 2002).

Nitrogen uptake in the transpiration stream, by calculation, was related to N concentration of the soil solution and transpiration rate. The increasing uptake rate with N level was largely related to the N concentration in solution, since transpiration rates were not greatly different, especially for treatments at full light interception. Uptake of N via the LATS system (mass-flow uptake) is more responsive to fertilization than the HATS (active uptake) system because it operates at higher concentrations of N in soil water (Malagoli et al. 2004). The response of increasing relative contributions from diffusive uptake as N level decreases, as seen in Figure 10.7 in both the measured and simulated data, has been shown to occur in the experiments as well. At low N levels or at low transpiration rates, diffusive uptake

increases and can offset insufficient N uptake via transpiration (Plhak 2003). Mass-flow rates in a field study (Strebel and Duynisveld 1989) were 15%–33% of total N supply, and the ratio was highest in the surface soils (probably because that was where the water was coming from and N concentrations thus were higher). The diffusive component became more important deeper in the profile, where N contents were lower. In our simulations, the mass-flow component was about 40% at the mid N level (8 mM). Calculations given by Barber (1995, Table 4.4) suggest that the proportion of N taken up in corn as mass flow is about 80% of total uptake. In our study, the total proportion was closer to 60% at the highest N rate (Figure 10.7). Barber's (1995) analysis was based on data from regional values of N availability, water-uptake rate, and N recovery in plant tissue. It was assumed that the available N was primarily found in the upper 20 cm of soil. This would tend to bias values toward mass flow, since the analysis does not differentiate between water uptake from different parts of the soil profile and differences in N availability. There may also be crop differences as Barber's study (1995) used corn. In a study by Strebel and Duynisveld (1989), the diffusive component became more important at N rates lower than 8 mM. Mass flow and diffusive uptake calculated from the measured data, and shown in Figures 10.5 and 10.6, are approximations based on the assumptions outlined earlier. The simulation results (Figures 10.9 and 10.10), however, support these assumptions and demonstrate that the methods and approximations used here enable us to simulate total N uptake and to partition the uptake in a realistic manner to active and passive components.

There was one difference where the simulated diffusive component did not trend to lower rates at higher N levels, but instead reached an asymptote (Figure 10.10) at N levels greater than 6 mM. This may be related to the values for I_{max} and K_M and how they were derived. Only a single value of I_{max} was used to simulate diffusive movement, and the values for I_{max} or K_M may have been too high. Research suggests that they vary in potato, depending on crop growth stage and N demand (Sharifi and Zebarth 2006). The authors attributed this variance to changes in N demand per unit root length. In our model, N demand was mainly determined by how fast the crop could grow, N availability in the soil, and values of the parameters in the MM equation (equation 10.3). If the concentration of N in the soil was low, the gradient for N was high, resulting in increased diffusive uptake over mass flow. The higher gradients that controlled diffusive uptake at low N were a function of the high demand created by the I_{max} and K_M parameters and the low soil N content. Canopy growth rate was determined by the availability of N and the requirement of a specific C/N ratio to maintain C-assimilation rates. It may be worthwhile to investigate alternative measures of simulating plant demand, such as determining C_R in equations 10.3 and 10.4 as a function of plant N requirement.

Uptake of N in our model was controlled indirectly by the C-assimilation rate via the C/N ratio. If there was ample N and C to support the given C/N ratio, the canopy continued to expand and intercept light, resulting in increasing C-assimilation rates until full light interception was achieved. Sufficiency of N was determined by I_{max}, K_M, water uptake, and C-assimilation rates and soil water N concentration. Malagoli et al. (2004) found that HATS uptake (a diffusive component) of nitrate was highest at midday when C-assimilation rates were highest. Since root sugar lev-

els (a product of photosynthesis) are responsible for expression of genes related to nitrate uptake (Matt et al. 2001), it seems reasonable to consider that photosynthetic activity is a regulator of nitrate uptake (Malagoli et al. 2004). Nitrogen uptake via diffusive processes, however, has been observed to drop off after flowering in oilseed rape, even though C-assimilation rates do not change greatly. Malagoli et al. (2004) hypothesized that this may be due to a change in partitioning of C from the roots to the shoots. We did not consider this in our model.

As shown by Malagoli et al. (2004), this research provides additional evidence that N uptake can be modeled using factors such as light interception and C-assimilation and transpiration rates to control N uptake, in addition to an N dilution curve (critical N content) as is used in many current models. There are other factors that we did not consider that may also be important in N uptake; these include root distribution, temperature, senescence, and N recycling, among others. We parameterized values for calculations of N uptake using an N response curve and assumed these parameters were valid over the entire growth period. This may need to be investigated further.

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