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**Plant nitrogen budget under elevated carbon dioxide level: regulation by
nitrogen absorption and assimilation**

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Objective: The overall objective is to assess root physiological and morphological characteristics that may alter plant N acquisition capacity in response to rising atmospheric CO₂ concentration. There is increasing evidence that plant and ecosystem responses to elevated levels of CO₂ will ultimately depend on availability and acquisition rate of other resources such as N (Bazzaz 1990, Eamus and Jarvis 1989). Therefore knowledge of any changes in root capacity to acquire N is crucial in predicting plant and ecosystem responses to high CO₂. Here we are testing two major hypotheses ; 1) elevated CO₂ will enhance root N uptake kinetics and 2) CO₂ enrichment will increase root preference for NO₃⁻ as opposed to NH₄⁺. High CO₂ enhances root energy status (BassiriRad *et al.* 1996a) which should in turn favor energy-intensive processes such as NO₃⁻ uptake and assimilation. The above hypotheses are being tested on a range of species from native and agricultural ecosystems using a combination of field, lab and growth chamber studies. We have demonstrated a considerable interspecies variation in root N uptake responses to CO₂ enrichment (BassiriRad *et al.* 1996a, b and c, and in current work) and attempts are now underway to evaluate if such variations are correlated with different functional groups (e.g., C₃ Vs C₄ or grasses vs. shrubs).

a comprehensive growth model, using physiological and allocation parameters, has been largely completed and will be used to analyze the completed experimental data. The goal of the modeling effort is to test relations among all the changes that (a) are predicted from physiological principles and (b) promise to reduce radically the number of "free parameters" needed to predict performance at high CO₂. A major physiological prediction for item (b) is that the fraction of N taken up as nitrate increases at high CO₂, based on the alleviation of energetic limitations on nitrate reduction. More deeply, we are using a model of functional balance of root and shoot (Gutschick, 1993; Gutschick and Kay, 1995) that strongly relates diurnally-averaged uptake rate, v (or the detailed kinetic parameters, V_{max} and K_m), to root:shoot ratio, r , and which predicts tissue N content from both v and r . The model uses the photosynthetic utility of N in leaves, p^* , to make the prediction.

Approaches: Effects of elevated atmospheric CO₂ concentration on root N uptake capacity and preference was tested in both growth chamber and field-grown plants. Dr. Goyal of the Agronomy Department at UC Davis provided the host lab for the N uptake kinetics. Plants were grown at CO₂ partial pressures of either 35 or 70 Pa at the Controlled Environmental facility of UC Davis. Both NH₄⁺ and NO₃⁻ were present at an equimolar concentration in a circulating hydroponic system. The first set of kinetic experiments examined the CO₂ effects on soybean, sunflower and sorghum at various stages of development. We used a novel approach involving a fully automated computer-based system to determine NO₃⁻ and NH₄⁺ uptake kinetics simultaneously by intact root systems. Other growth and physiological parameters such as biomass allocation, tissue N concentration and leaf photosynthesis were also measured in order to address the mechanisms by which CO₂ may alter N uptake kinetics. We have also completed a set of experiments at two open-top field sites in Oak Ridge National Laboratories (with Rich Norby) and National Soils Dynamics Lab in Auburn, AL (with Hugo Rogers). Both of these experiments involved a novel *in situ* technique to determine uptake kinetics of NH₄⁺ and NO₃⁻ in intact root systems of red and sugar maple (in ORNL) and sorghum and soybean (in SNDL).

The data on uptake kinetics, root:shoot allocation, photosynthetic performance, and growth are being incorporated into a model of CO₂-induced changes in plant performance.

The model of physiology and growth that we seek is an analytic model, that is, with explicit equations in closed form and preferably algebraic solutions. In contrast to common numerical simulations, the closed formula allows predictions of performance upon inspection.

Results to date: Root N uptake property is highly responsive to the growth CO_2 partial pressure, however, this response is highly dependent on the species, inorganic N form and growth stages (Fig. 1). The important implication is that information obtained from one species at one stage of development using only one form of inorganic N can not adequately predict plant and stand-level N uptake responses to CO_2 enrichment. Contrary to our hypothesis 1, elevated CO_2 did not enhance root absorption rate of N in either species (Fig. 2) when rates were estimated from the kinetics parameters at an external NH_4NO_3 concentration of $100 \mu\text{M}$. Obviously the biomass data (Fig. 3) indicate a greater demand for N in response to CO_2 enrichment particularly at the end of the experimental period. However, CO_2 may in fact, reduce N demand via increased Photosynthetic N Use Efficiency (PNUE is currently being processed for these two species). In addition, the apparent downregulation of photosynthesis observed here (fig. 4) may form another basis for a lower plant demand for N. Alternatively, a higher N demand in response to high CO_2 can be met by a greater allocation of biomass to roots. In fact, root:shoot ratio increased significantly in soybean, but remained virtually unchanged in sunflower in response to high CO_2 (Fig. 3) indicating that soybean may be better able to acquire N than sunflower as the CO_2 partial pressure increases.

The increased preference for NO_3^- Vs NH_4^+ in sunflower (Fig. 2) at high CO_2 is consistent with hypothesis 2 and our previous findings (BassiriRad *et al.* 1996a, b) though greater preference for NO_3^- was only apparent at the later ontogenic stages. In fact, rates of NO_3^- absorption changed very little with time (Fig. 1) indicating that the apparent shift in preference is most likely caused by a decrease in NH_4^+ uptake capacity of the older roots than an increase NO_3^- uptake capacity per se. In contrast to sunflower, soybean roots took considerably more NH_4^+ than NO_3^- in response to CO_2 enrichment at all except one date (Fig. 2). It is unclear how CO_2 may increase root and plant preference for NH_4^+ . Uptake and assimilation of NH_4^+ is considerably less energy requiring than NO_3^- . However, elevated CO_2 may enhance the supply of C skeleton as substrates required for NH_4^+ assimilation. The better ability to assimilate NH_4^+ may in turn, act as a feedforward for NH_4^+ uptake.

Our combined model, to date, is analytic in describing uptake kinetics (Michaelis-Menten), functional balance, and shifts in photosynthetic utility. Thus far, modeling has been used to enhance analysis of uptake data for kinetic parameters.

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Figure legends:

- Fig. 1** Kinetic parameters ($V_{\max}$ and K_m) for root NH_4^+ and NO_3^- uptake in soybean (top 4 graphs) and sunflower (bottom 4 graphs) plants at various stages of growth at different CO_2 concentrations.
- Fig. 2** Estimated total N absorption rate (left) and percent N taken as NO_3^- for soybean and sunflower at various stages of growth at different CO_2 concentration.
- Fig. 3** Total biomass, relative growth rate and root:shoot ratio responses of soybean and sunflower to ambient and double the ambient CO_2 concentration at various stages of growth.
- Fig. 4** Photosynthetic and leaf area responses of soybean and sunflower to ambient and double the ambient CO_2 concentration at various stages of growth.

Fig. 2

Fig. 3

Fig. 2