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Plasticity in resource allocation and nitrogen use efficiency in riparian vegetation:
implications for nitrogen retention

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ABSTRACT

In this work, we summarize current understanding of the function of riparian zones, and describe an investigation of changes in nitrogen use efficiency (NUE, production per unit N taken up) and resource allocation of a riparian shrub in response to changes in N availability. Empirical work included measuring leaf %N and root to shoot ratios (R:S) of individual riparian shrubs (*Baccharis salicifolia*, or seepwillow) growing at a range of N availabilities in the field, and growing in fertilized and unfertilized plots in a field fertilization experiment. In both observational and experimental work, %N of plant tissues was positively related to N availability, and R:S was negatively related to N availability. We used a simulation model to investigate feedbacks between seepwillow responses to, and effects on, N availability. In the model, plasticity in resource allocation and NUE in response to changes in N lead to lower productivity at low N supply and higher productivity and lower retention at high N supply than plants constrained to a constant %N and R:S. Furthermore, uptake became relatively more important as a retention mechanism when plants responded to high N supply. These feedbacks could have significant effects on N retention by riparian zones in watersheds experiencing large fertilizer inputs of N, or on ecosystems experiencing high rates of atmospheric N deposition.

Keywords: Riparian vegetation, nitrogen retention, denitrification, resource allocation, nitrogen use efficiency, plasticity

INTRODUCTION

Riparian zones are known to retain nitrogen from groundwater flowing through riparian soils (Lowrance 1998). Over the last 20 years, this phenomenon has led to extensive use of riparian buffer strips to reduce nitrogen inputs to streams draining agricultural watersheds. Retention (here defined as the difference between hydrologic input and output) tends to be particularly strong when geologic or hydrologic factors force water to move through the rooting zone in upper soil horizons (Hill 1996, Schade et al. 2001), emphasizing the importance of plant activities for N retention. The mechanism by which riparian plants cause N retention has been difficult to determine in many systems (but see Schade et al. 2001), but is generally considered to be some combination of a direct effect through plant uptake and an indirect effect through stimulation of denitrification (Lowrance et al. 1984, Peterjohn and Correll 1984, Groffman et al. 1992, Hill et al. 1998, Gold et al. 1998, Ettema et al. 1999, Hill 2000). The ultimate fate of retained nitrogen, and therefore, the long term effectiveness of riparian zones as buffer strips, depends largely on the relative importance of these mechanisms. Nitrogen retained in plant biomass via uptake will eventually be made available to the stream, or transported to downstream ecosystems when all or part of the plant dies. Nitrogen lost to denitrification is returned to the atmosphere as N_2 , and is permanently lost from the pool of N available to most organisms. The goal of this work is to explore some of the factors that may influence the relative importance of these processes, and implications for N retention.

The response of plants to changes in N availability has received little attention

from riparian ecologists although these responses have great potential to influence both the magnitude of retention and the relative importance of direct and indirect mechanisms. These responses include changes in the amount of production per unit of N taken up, or nitrogen use efficiency (NUE; Vitousek 1982, Chapin 1980), and patterns of resource allocation (Reynolds and D'Antonio 1996), manifested as changes in tissue N concentration and root to shoot ratios (R:S), respectively. In general, increases in N supply lead to higher tissue N concentrations and lower R:S in plants (Hobbie 1992), while decreases in N supply have the opposite effect. Since indirect effects of plants are generally the result of interactions with soil microbes, through production of belowground organic matter, (Clarholm 1985, Whipps and Lynch 1985, Van Veen et al. 1989) a decrease in R:S, if it resulted in a reduction in belowground organic matter production, would lead to reduced rates of denitrification. Furthermore, an increase in tissue N indicates increased uptake and storage of N in plant biomass. The combination of these responses could increase the relative importance of uptake over denitrification as N supply increases (Nadelhoffer et al. 1999), significantly altering the long-term effectiveness of riparian buffer strips in reducing N loading to streams and downstream reservoirs in agricultural watersheds, or in more natural watersheds under enhanced N deposition.

In Sycamore Creek, a Sonoran Desert stream in central Arizona, we have shown that root production by plants stimulates denitrification, which is the main mechanism causing retention of nitrate, particularly in shrub-dominated gravel bars (Fig. 1, Schade et al. 2001). An increase in R:S due to decline of nitrate may further stimulate

denitrification, lowering nitrate still further, causing a greater increase in R:S. The resulting positive feedback loop could lead to potentially severe effects on the growth of the plant. Unfortunately, we do not know very much about the responses of riparian vegetation to changes in nutrient availability, nor the influence of those changes on nutrient retention. Our objectives were 1) to determine how NUE and resource allocation change in a riparian shrub in response to changes in N availability; and 2) to develop a simple model to explore the influence of these responses on nitrogen retention and the relative importance of uptake and denitrification.

SITE DESCRIPTION

The study site was a 300-m reach in the middle section of Sycamore Creek, and consisted of several gravel bars, delineated by surface water on one side and the riparian zone on the other. Previous work has shown that in the absence of plants, nitrate dominates the inorganic nitrogen pool in subsurface water flowing through gravel bars due to high rates of mineralization of particulate and dissolved organic N, coupled with high rates of nitrification in sediments, leading to generally low ammonium concentrations (Holmes et al. 1994). During the study period, these gravel bars each supported several riparian shrubs (*Baccharis salicifolia*, or seepwillow) in dense patches surrounded by bare sediments. Alluvial sediments in the reach were approximately 1.5 m deep on average, and active channel width was ~25 m. Water table elevation was variable, but was generally within 25 cm of the surface of gravel bars during the study period. Vegetation on gravel bars consisted almost entirely of seepwillow. Other minor species included Bermuda grass (*Cynodon dactylon*), and occasional seedlings of

common riparian species, particularly mesquite (*Prosopis glandulosa*) and Gooding's willow (*Salix goodingii*). Due to severe flooding, gravel bars were relatively free of vegetation in the early 1990's. In 1995, flood magnitude and frequency declined, allowing vegetation heavily dominated by seepwillow to regrow. Establishment of seepwillow began in saturated sediments, with successful establishment dependent on the depth of the water table (Stromberg et al. 1996). In the summer of 1998, seedling recruitment was high on several gravel bars, forming large patches of dense vegetation consisting entirely of seepwillow.

METHODS

Response of seepwillow to changes in N availability

Both observational and experimental methods were used to determine the response of seepwillow to changes in N availability. For both methods, changes in tissue %N and root to shoot ratio (R:S) were used as indices for changes in NUE and resource allocation, respectively. Observational work was performed in the spring of 1995. Seventeen sites were selected at various points along five randomly-selected seepwillow colonized gravel bars. At each site, three 25-50 cm tall plants were collected, returned to the laboratory and dried for 48 hours at 60°C. Plants were excavated by digging below the rooting zone (roughly 30-40 cm deep), using a shovel to lift the complete root mass and sediments from the ground. Sediments were gently shaken off of the root mass in the field, and roots were cleaned of sediments more completely by hand in the laboratory. Plants were divided into root, stem and leaf samples, which were weighed separately. Leaf samples were milled and analyzed for

%N. Dry weights were used to calculate R:S. Nitrogen availability was measured in two ways. First, one well was installed to 20 cm below the water table at each of the 17 sites from which plants were collected. Triplicate water samples were collected and analyzed for DIN ($\text{NO}_3 + \text{NH}_4$). Second, a 100 ml sample of unsaturated sediment was collected 10-15 cm below the sediment surface adjacent to each well. Water-extractable N was measured by shaking sediments in 200 ml of distilled water for one minute in the field. Extractant solution was returned to the lab on ice, filtered and analyzed for DIN. NO_3 analyses were run on a Bran and Luebbe TRAACS 800 autoanalyzer using the cadmium reduction method, NH_4 was measured using the phenol-hypochlorite method (Solorzano 1969), and %N in plants was measured on a Perkin-Elmer 2400 CHN analyzer.

A field fertilization experiment was performed in the summer of 1998 using patches of seepwillow seedlings on four gravel bars within the study site. On each gravel bar, two 1-m² plots were established which were similar in density and size distribution of seepwillow plants. The downstream member of each pair of plots was fertilized once a week with 58 g of NH_4NO_3 , roughly doubling the supply of inorganic N available to plants, for 6 weeks. Each week, fertilizer powder was spread evenly across plots, which were subsequently watered with approximately 8 L of stream water. An equal volume of stream water was added to the unfertilized member of each pair each week. Five randomly-selected plants were collected from each plot before the experiment for measurement of biomass and N content. Heights of 10 randomly-selected plants from each plot were measured weekly throughout the experiment. The

80 focal plants were collected after six weeks for measurement of biomass and N content. All plants were divided into leaf, stem and root samples, which were dried and weighed separately. Leaf samples from plants sampled before the experiment and all tissue samples from plants sampled at the end of the experiment were analyzed for %N. The experiment was terminated after six weeks to avoid the confounding effects of mortality of focal plants due to drying of the stream channel. Since each gravel bar was divided into paired control and experimental plots, paired t-tests were used to determine treatment effects.

Influence of seepwillow response on N retention

To meet our second objective, we developed an ordinary differential equation model to explore changes in N retention due to changes in plant characteristics under different N inputs to a seepwillow-colonized gravel bar site. The model consists of two linked submodels (Fig. 2). The first submodel (the N submodel) is simply a mass balance of N and simulates changes in the inorganic nitrogen pool in the seepwillow site over time. We assume that the only inputs of N are from the movement of subsurface water and its N load into the site, and recycling of N from root-derived organic matter. We also assume that a portion of these N inputs are first lost to denitrification as N inputs enter the colonized site (Schade et al. 2001), with nitrogen left in the water after denitrification becoming plant-available N. The plant takes up a portion of this N and the rest is exported. All N inputs are either used or exported at each time step, and due to the dominance of nitrate in subsurface water here, inorganic N is assumed to be mostly nitrate, and therefore potentially denitrified. The second submodel (the root

submodel) simulates changes in root and root-derived detritus biomass over time. In both versions of the model, the root submodel is linked to the N submodel through the effects of root biomass and root detritus on denitrification rates and input of recycled N, and through the effects of nitrogen pool size on root production, mediated through the effects of the N pool on productivity of the plant and by proportional allocation of productivity to roots ($R/R+S$). Here we assume that productivity is limited by nitrogen throughout the simulation, and is not affected by the amount of plant material present.

The equations used in both versions of the model are as follows:

$$\begin{aligned} \frac{\partial R}{\partial t} &= \left(\frac{R}{R+S} \right) \left(\frac{P_{\max} * N_{av}}{k_p + N_{av}} \right) - m_r R \\ \frac{\partial D}{\partial t} &= m_r R - k_d D \\ \frac{\partial N}{\partial t} &= (N_c * Q) + \left(k_d D * \frac{N_d}{D} \right) - \left(\frac{P_{\max} * N_{av}}{k_p + N_{av}} * \%N \right) - \delta - N_{ex} \\ P &= \frac{P_{\max} * N_{av}}{k_p + N_{av}} \\ N_u &= \frac{P_{\max} * N_{av}}{k_p + N_{av}} * \%N \\ N_{av} &= (N_c * Q) + \left(k_d D * \frac{N_d}{D} \right) - \delta \\ \delta &= 0.762 * \ln(R + D) - 4.06 \end{aligned}$$

Both versions used identical equations, the only difference being values used for %N and R/R:S. Discharge through the seepwillow site (Q) was set at $3.8 \text{ m}^3 \text{ d}^{-1}$ (calculated using data from Holmes et al. 1994 and Schade et al. 2001). Plant-available N (N_{av}) was calculated by subtracting denitrification (*) from N input (hydrologic input of N ($N_c *$

Q) plus N recycling from root detritus $\left(k_d D * \frac{N_d}{D}\right)$. In the term for recycled N $\left(\frac{N_d}{D}\right)$

represents the proportion of N in root detritus. Nitrogen uptake is the product of plant productivity (P) and plant tissue %N. Nitrogen export (N_{ex}) is calculated by assuming that all available N not denitrified or taken up by the plant is transported out of the patch in each time step, a reasonable assumption for this system. The change in root biomass (R) is calculated as the difference between root production (first term in root equation) and the loss of root mass to mortality ($m_r R$). Model results shown here used a per capita root decomposition rate (m_r) set at 0.001 d^{-1} . Root production is the product of plant productivity and the proportion of biomass allocated to roots (R/R+S). Root detritus (D) is the difference between root mass lost to mortality and the rate of loss of D to decomposition ($k_d D$). In this context k_d is analogous to root turnover and was set at 0.002 d^{-1} for simulations reported here. The relationship between R, root detritus (D) and * is empirical, derived from data from Schade et al. (2001). Productivity was modeled as a function of plant-available N using a Michaelis-Menton curve, with P_{max} set at 10 g d^{-1} from data used in Schade et al. (2001), and k_p set at 0.42, which gave reasonable results for steady-state plant mass and root mass.

Since our objective was to explore how plant responses influenced N retention, we used two versions of the model, the constant model (Fig. 2a), in which R/R+S (0.44) and tissue %N (2%) were set at average values calculated using all measurements from plants collected in the observational study described above, and the response model (Fig. 2b), in which both R:S and tissue %N were functions of N_{av} . Plant tissue %N was

modeled as a Michaelis-Menton curve, using the equation below, where %N_{max} was set

$$\% N = \frac{\% N_{\max} * N_{av}}{k_n + N_{av}}$$

at 4% and k_n was set at 0.25 for model runs shown here. Changes in R/R+S was modeled using an exponential decay model, using the equation

$$(R / R + S) = 0.1 + (c * e^{k_{rs}N_{av}})$$

in which 0.1 represented the minimum R/R+S (estimated from data collected in this study) and c (maximum R/R+S) was set at 0.69 using data from this study. The rate of decrease of R/R+S (k_{rs}) was set at -1.74. Since the two models differ only in the constraint on these plant characteristics, we can consider alterations in N retention and the relative importance of uptake and denitrification as a result of plasticity in plant characteristics by comparing output of the two models.

Most of the parameters in these models were based on direct measurements of those parameters, however k_p, k_n, k_{rs}, k_d and m_r were arbitrarily set at values which gave results for plant and root production and biomass that matched empirical data. We examined the effects of changes in these variables in a sensitivity analysis that focused on their influence on the relationship between constant and response models. We varied all four parameters across a range from 25% - 400% of the value used in the model results presented here, and ran simulations at each value across the range of N input values presented here. We also compared model output from the response model

at $N = 0.1$ to field data for four variables for which reliable data were available from Schade et al. 2001. This level of N was chosen because it is similar to N concentrations reported for Sycamore Creek (Holmes et al. 1994, Schade et al. 2001).

Both dynamic and steady state behavior of the two models was compared under a range of N input values. We defined steady-state to be the time at which the rate of change in the change in plant productivity was $< 0.0001 \text{ g d}^{-2}$. Values of N input were calculated by multiplying inorganic N concentration in water flowing through gravel bar sediments by an estimate of discharge of water through a seepwillow-colonized site. Discharge (Q) was calculated using an estimated velocity of water through gravel bar sediments of 1 m/h (Holmes et al. 1994), and an estimate of the cross-sectional area of the zone of influence of the plant (Schade et al. 2001). Nitrogen concentrations in subsurface water in gravel bars are typically in the range of $0.1\text{-}0.3 \text{ mg L}^{-1}$ (Holmes et al. 1994, Schade et al. 2001). In this analysis, we used concentrations ranging from $0.02 - 1 \text{ mg L}^{-1}$, which resulted in N input rates from $0.08 - 3.8 \text{ g d}^{-1}$.

We ran simulations of both constant and response models, focusing on plant and root production, N retention, and the relative importance of plant uptake and denitrification as retention mechanisms. We examined process rates and plant and root biomass at steady-state, as well as cumulative plant and root mass and N retention. We calculated cumulative effects by running all simulations for 5 years (1825 days), which was the approximate age of the oldest plant (Schade personal observation). All simulations were run using Matlab, version 6.

RESULTS

Response of seepwillow to changes in N availability

In the observational work, NO_3 was the dominant form of DIN in both sediments and subsurface water collected from wells (Fig. 3 a,d). Water-extractable DIN in sediments was positively related to leaf %N (Fig 3b) and this relationship was linear. Root to shoot ratio of plants was negatively related to N in sediments (Fig. 3c), and this relationship was curvilinear, with the best fit between R:S and the natural logarithm of water-extractable DIN. Neither tissue %N nor R:S was significantly related to DIN in water from wells (Fig. 3e,f). In the fertilization experiment (Table 1), fertilized and unfertilized plots were not significantly different in any variables before the beginning of the experiment. After six weeks of fertilization, fertilized plots were significantly higher in tissue %N of roots, stems and leaves, and significantly lower in R:S. Change in height of focal plants was significantly higher in fertilized plots. In contrast, biomass changes were not significantly different.

Influence of seepwillow response on N retention

Steady-state values for rates of productivity, export, uptake and denitrification from model simulations increased with increasing rates of N input (Fig. 4a-d), with the exception of denitrification rates from the response model (Fig. 4d). Steady-state denitrification rates in the response model decreased at high N input ($> \sim 2.2 \text{ g d}^{-1}$), and were lower in the response model than the constant model (Fig. 4d). Conversely, rates of uptake and productivity were lower in the response model at low N input, and uptake, productivity and export were all higher in the response model at high N input (Fig. 4a-c). The ratio of denitrification to uptake (Fig. 4e) was higher in the response model at low N

input and lower at high N input, while % retention was similar between the two models at low N input, and lower in the response model at high N input (Fig. 4f). Denitrification was the dominant mechanism of retention in all simulations of both models, generally responsible for > 70% of N retained (Fig. 4g,h).

The transient behavior of the two models was also very different. At all N input levels, root biomass and detritus accrued more rapidly in the constant model, with the difference in the two models increasing with increases in N input (Fig. 5). Furthermore, both root biomass and detritus reached a lower steady-state in the response model than in the constant model at high N input (Fig. 5c,f). In both models, the onset of denitrification was delayed until a threshold level of root biomass was reached, with longer delays at low N input (Fig. 6a-c). At high N input, denitrification was delayed longer in the response model, and had a lower steady state, while at low N input the delay was the same, but the constant model had a lower denitrification rate at steady state (Fig. 6a-c). Uptake started out higher, and was higher at steady state in the response model at high N input. At low N input uptake was lower in the response model at steady state (Fig. 6d-f). Productivity and export behaved very similarly to each other (Fig. 7), with much of the difference reflected in the rate of change, which was higher in the response model at low N, and in the constant model at high N. This resulted in higher productivity at steady-state in the constant model at low N, and in the response model at high N.

Cumulative values after 5 years for all variables were very similar to patterns of steady state rates (Fig. 8). When we consider total mass of N retained, both %

retention and the ratio of denitrification to uptake were lower than when only steady-state rates were considered (Fig. 8f,g compared to 4e,f). Output from the response model at $N = 0.1$ mg/L compared relatively well with the four variables for which reliable field data were available (Table 2), suggesting that the response model is a reasonable approximation of what is happening in the field at N input rates observed at Sycamore Creek. We do not claim, however, that this represents a rigorous validation of the model.

DISCUSSION

Results from both observational and experimental work suggest that seepwillow plants respond to variation in nitrogen availability with changes in both NUE and resource allocation. Both %N and R:S of plants collected in the observational study were significantly related to water-extractable N in sediments (Fig. 3). In addition, results from the fertilization experiment showed that plants from fertilized plots had higher tissue %N, and lower R:S than plants from unfertilized plots (Table 1). Coupled with a larger change in height of plants from fertilized plots (Table 1), these results suggest N-limitation of seepwillow growth. However, since biomass was not different between fertilizer treatments, height differences could be due solely to change in resource allocation and not to increases in production. In general, N limits in-stream production in Sycamore Creek (Grimm 1987), as well as terrestrial production in deserts in general (Lajtha and Whitford 1989), leading us to suspect that N limitation is more likely than limitation by other nutrients.

The change in resource allocation by seepwillow in response to changes in N

availability may have large implications for N retention due to the importance of denitrification, fueled by belowground organic matter production by the plant, as a mechanism of NO_3 retention (Schade et al. 2001). The response of seepwillow to lower N availability (increased allocation to roots), coupled with loss of NO_3 due to increased root production, may lead to a positive feedback leading to low N, with severe consequences for the plant if N availability limits seepwillow production. Furthermore, the increase in %N of tissues with increases in N availability should increase the relative importance of uptake in N retention, particularly if seepwillow production also increases with N availability, as we would expect if N is limiting. The model described above (Fig. 2) was designed to investigate the interaction between response and effect of seepwillow, and the implications of this interaction for plant production, N retention and the relative importance of denitrification and uptake as retention mechanisms.

The results of simulations at a range of N input rates indicate that positive feedbacks could result from plasticity in resource allocation and NUE in seepwillow and its effects on N supply. Comparing the two models, we see that at low N input the response model gives lower uptake and productivity than the constant model (Fig. 4), which is consistent with the action of a positive feedback leading to lower N availability. The relationship between constant and response models was reversed at high N input. Productivity differences are small, and it is difficult to estimate error around these values in this model, however, the other changes we are observing are in part a function of these differences in productivity, suggesting they are in fact important differences. The response model showed lower denitrification, higher uptake, and higher productivity

than the constant model, which is consistent with the action of a positive feedback leading to higher N availability. In fact, denitrification rate at steady-state decreased at high N input in the response model. The relative importance of denitrification, and both total and % retention, were lower in the response model at high N input than the constant model. Interestingly, the relationship between the two models changed at approximately $N = 0.6 \text{ mg/L}$ for steady-state rates of all variables (Fig. 4). This abrupt change suggests a threshold at which the response model shifts from a low N positive feedback to a high N positive feedback. Positive feedbacks imply that the system should continue to change in the direction of the positive feedback, however, all simulations eventually reached steady-state for all variables. This is most likely the result of constraints on both %N and R:S built into the model.

The main purpose for comparing these two models was to determine the influence of plasticity in %N and R:S on N retention. Overall, these models show that changes in these variables in response to changes in N availability may lead to lower retention when N supply is high. Moreover, the mechanism of retention becomes less mediated by microbes and more a direct effect of uptake under high N input when plants can respond. Furthermore, steady-state values from the response model at low N input compared favorably with values from field data (Table 2), suggesting that this model is a reasonable approximation of what is happening in the field at this site. Clearly, changes in resource allocation and NUE due to plant responses modeled here may have a significant influence on retention at high N inputs, resulting not only in lower retention rates, but also in increased importance of retention by plant uptake, a

temporary mechanism. We lack, however, reliable information to assess the performance of the model at N inputs higher than those we typically observe in Sycamore Creek, so these results must be viewed with caution.

Our model also does not consider the potential effects of floods, both in terms of effects on the establishment of plants, but also as a source of N and organic matter that may fuel belowground processes. Indeed, floods do have an overriding influence on a number of structural and functional characteristics of desert streams (Grimm 1987). In terms of N dynamics in gravel bars, however, previous work suggests that belowground processes are much more tightly linked to instream production between floods than to import of organic matter by floods (Holmes et al. 1994, Jones 1995). We believe that the major effect of floods on the processes described here is the removal and transport of plant biomass from these gravel bars to downstream ecosystems. This effect reduces the importance of plants in N retention by reducing plant biomass. It also highlights the effects of changes in the relative importance of uptake vs. denitrification. If uptake is the dominant mechanism, than retained N will be returned to the ecosystem when the plant dies, either through flood removal or normal patterns of senescence. As a management tool this transient storage may not be as effective in achieving long-term removal of N as gaseous loss via denitrification, particularly in a flood-dominated ecosystem.

The link between denitrification and root biomass upon which our model is based is an empirical relationship that does not take into account the effects of changes in root turnover on microbial processes. Our assumption is that this empirical relationship

holds over a range of N supply rates, consequently we are also assuming fine root turnover rates are constant over the complete range of N inputs modeled here, and that changes in root biomass are entirely the result of changes in carbon allocation to roots. An extensive literature exists on N deposition and fine root dynamics, however the results have been mixed and little consensus has developed on the generality of root responses (Nadelhoffer 2000). Hendricks et al. (1993) outline two hypotheses regarding the effects of increased N on root carbon allocation. The first hypothesis suggests that carbon allocation to roots is reduced at high N supply, and root turnover is not affected, resulting in lower root biomass at High N. Second, carbon allocation to roots may not change significantly when N supply increases, but root turnover rates increase, also leading to lower root biomass. Our model assumes the first hypothesis is the correct one. If this is not the case, the consequences for our model are quite significant. If root turnover rates increase under high N supply, then the empirical relationship between root biomass and denitrification would change and we would not observe a decrease in denitrification at high N as in figs. 4 and 8. Unfortunately, we do not have the data to test these hypotheses in our system, and this represents an important direction for future research on riparian systems in general.

Support exists in the literature for both increased (Aber et al. 1985, Nadelhoffer et al. 1985, Pregitzer et al. 1995) and decreased root turnover rates (Vogt et al. 1986, Pregitzer et al. 1993) with increases in N deposition. Some have suggested that this discrepancy can be explained by methodological differences (Nadelhoffer 2000, King et al. 2001). However, even when these differences are taken into account, studies still

exist which support both hypotheses (Burton et al. 2000, Ostertag 2001). Burton et al. (2000) suggest that these differences may be the result of a difference between the effects of species shifts within a plant community and the response of an individual species to N deposition gradients. They further suggest that within a species, decreases in root turnover (increases in root longevity) under increased N availability may be energetically favorable. In essence, plants maintain roots as long as they are providing a large benefit in terms of nutrient uptake, and under high nutrient availability roots provide this benefit for a longer period of time. Their results suggest that our model actually may provide a conservative estimate of changes in denitrification, for if root turnover rates decrease under high N supply, denitrification would decrease faster than shown in figs 4 and 8.

Our results have important implications for our understanding of the influence of riparian vegetation on N retention, and how that will change with changes in N loading. If these plant responses are, in fact, a general phenomenon, riparian zones subject to increased rates of N supply, such as riparian buffer strips in agricultural watersheds, will become less effective at retaining nitrogen, and a higher proportion of N retained will be stored in plant biomass. Direct application of our model to well-established riparian zones in more temperate locations, however, may be problematic due to substantial differences in soil structure and stature of vegetation. Temperate riparian zones generally have more well-developed, organic-rich soils than gravel bars in Sycamore Creek, and denitrification rates may be less influenced by changes in root dynamics described by our model. Hanson et al. (1994), in fact, do show higher rates of

denitrification in response to N enrichment in surface soils of a temperate riparian zone subject to groundwater N inputs from residential septic systems. They attribute this observation to increased growth of plants, and increased litter inputs to surface soils. In contrast, however, substantial evidence exists from similar riparian zones that root dynamics in deeper soil layers control denitrification rates over relatively short time scales (Jacinthe et al. 1998, Gold et al. 1998), suggesting changes in root production may lead to changes in N retention over the course of a few months. In general, root exudation and root turnover are commonly considered to be important sources of carbon inputs to soil and have a strong influence on denitrification (Smith and Tiedje 1979, Haycock and Pinay 1993, O'Neill and Gordon 1994, Hill 1996). Combined with our results, these studies certainly suggest the possibility that the plant responses we describe have the potential to significantly influence N retention in many types of ecosystems, and are certainly worthy of further study.

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Figure 1. Conceptual model of the influence of seepwillow (*Baccharis salicifolia*), a riparian shrub, on NO_3 concentrations in water flowing through gravel bar sediments. Based on results presented in Schade et al. (2001). The main effect of the plant is the production of organic matter, which stimulates denitrification rates. NO_3 is converted into N_2 and lost to the atmosphere.

Figure 2. Conceptual diagram of models used to investigate interaction between response and effect of seepwillow. Both models consist of two submodels, simulating changes in N pools and the production of roots and root detritus. In both models, the two submodels are linked through the effects of N on productivity, and the effects of roots and root detritus on denitrification. A) In the constant model, %N in plant tissue and root to shoot ratio (R:R+S) are constants. B) In the response model, %N in plant tissue and (R:R+S) are functions of nitrogen availability, simulating the response of plants as seen in empirical work.

Figure 3. Inorganic N concentrations in water from A) sediment water extractions and D) wells. Stars indicate differences between forms of inorganic N. Also shown here are relationships between leaf %N and root to shoot ratio (R:S) of seepwillow plants and dissolved inorganic nitrogen (DIN) concentrations in sediment water extractions (B,C) and in wells (E,F).

Figure 4. Daily rates at steady state for response (dotted lines) and constant models (solid lines) for A) plant production, B) plant N uptake, C) N export, D) denitrification, E) denitrification:uptake, F) daily %N retention, G) %retention as denitrification, and H) %retention as uptake. Steady state values are plotted for

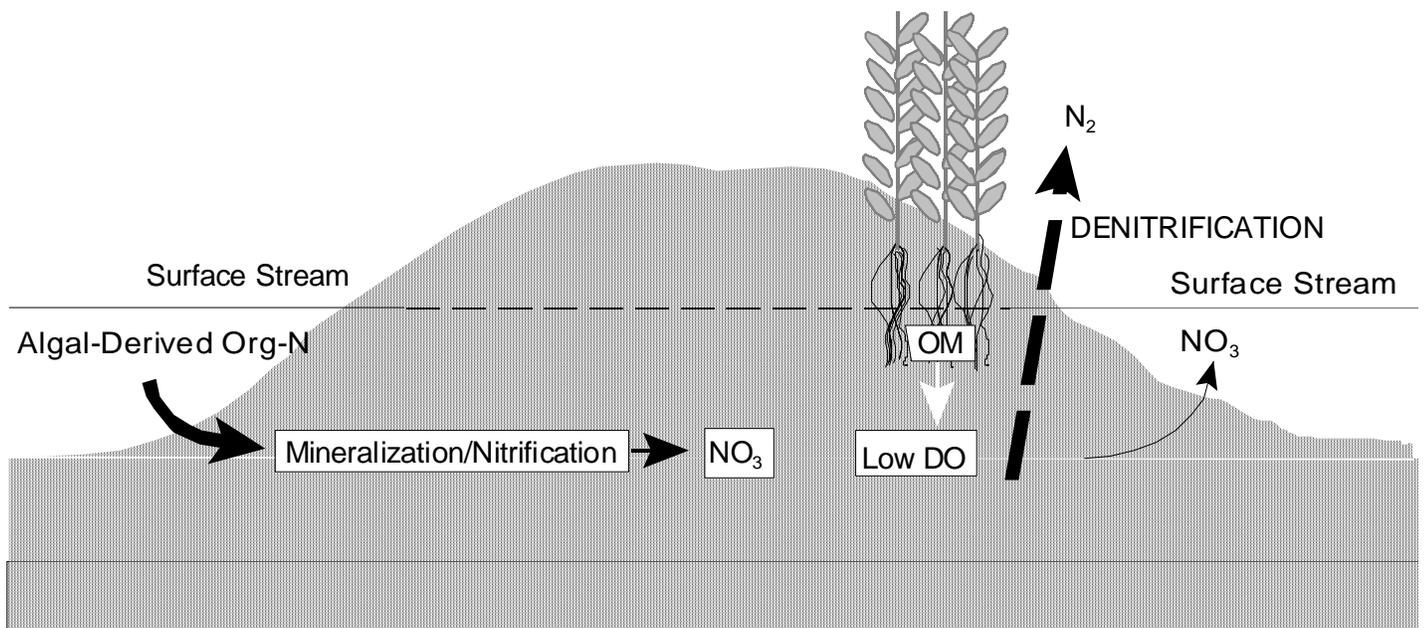
each variable across a range of N concentrations.

Figure 5. Time series for root mass (A-C) and root detritus (D-F) from simulations of constant (solid lines) and response (dotted lines) models run to steady-state (defined in terms of productivity changes as described in methods) for three representative N concentrations. Note differences in time scales for different N concentrations.

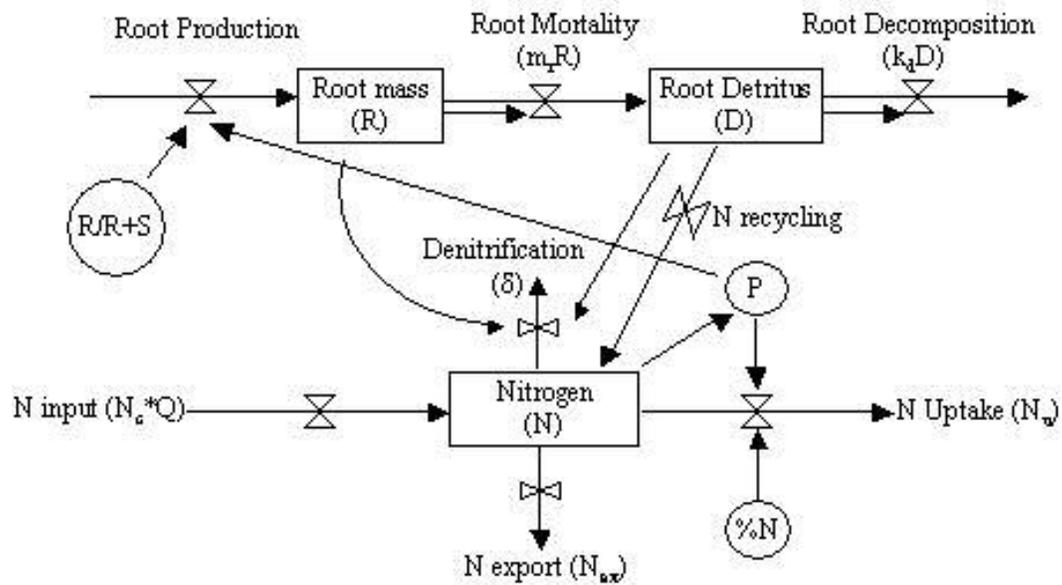
Figure 6. Time series of denitrification (A-C) and plant uptake (D-F) from simulations of constant (solid lines) and response (dotted lines) models run to steady-state (defined in terms of productivity changes as described in methods) for three representative N concentrations. Note differences in time scales for different N concentrations.

Figure 7. Time series of productivity (A-C) and N export (D-F) from simulations of constant (solid lines) and response (dotted lines) models run to steady-state (defined in terms of productivity changes as described in methods) for three representative N concentrations. Note differences in time scales for different N concentrations.

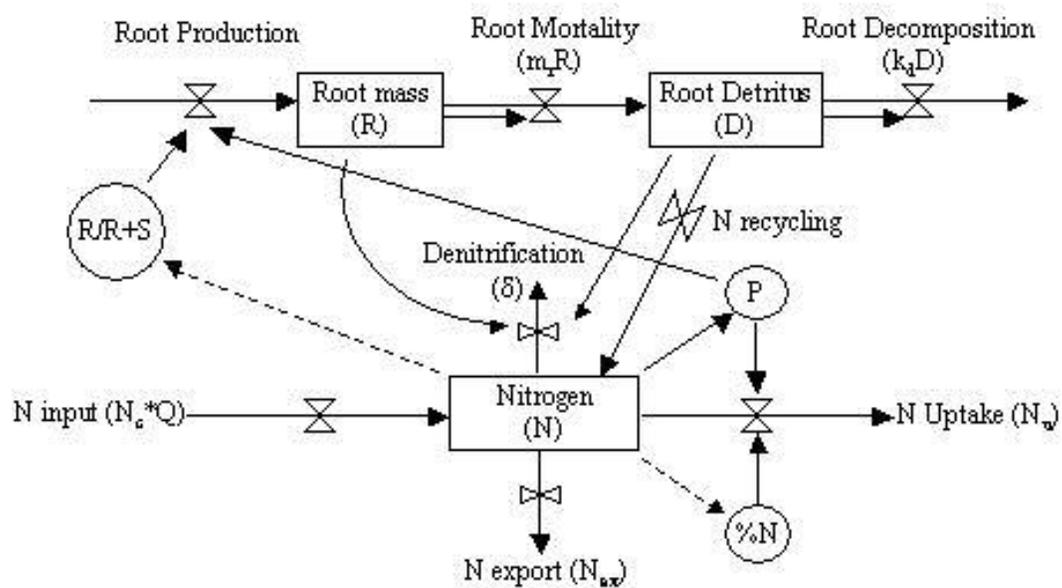
Figure 8. Cumulative values for 5 year simulations for response (dotted lines) and constant (solid lines) models for A) plant production, B) plant N uptake, C) N export, D) denitrification, E) denitrification:uptake, F) cumulative N export, G) % of cumulative N input retained, and H) %retention as denitrification. Steady state values are plotted for each variable across a range of N concentrations.

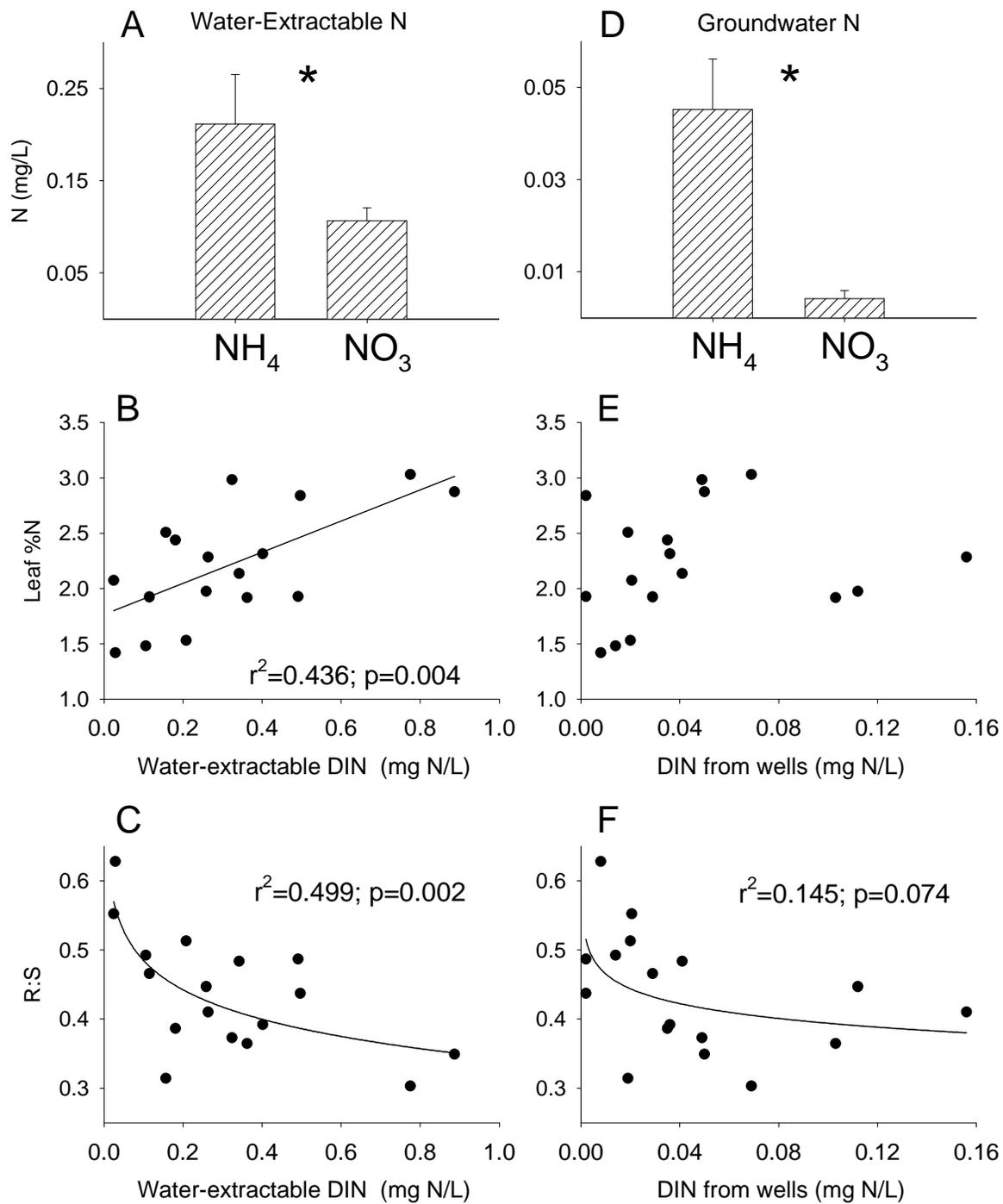


A) Constant Model

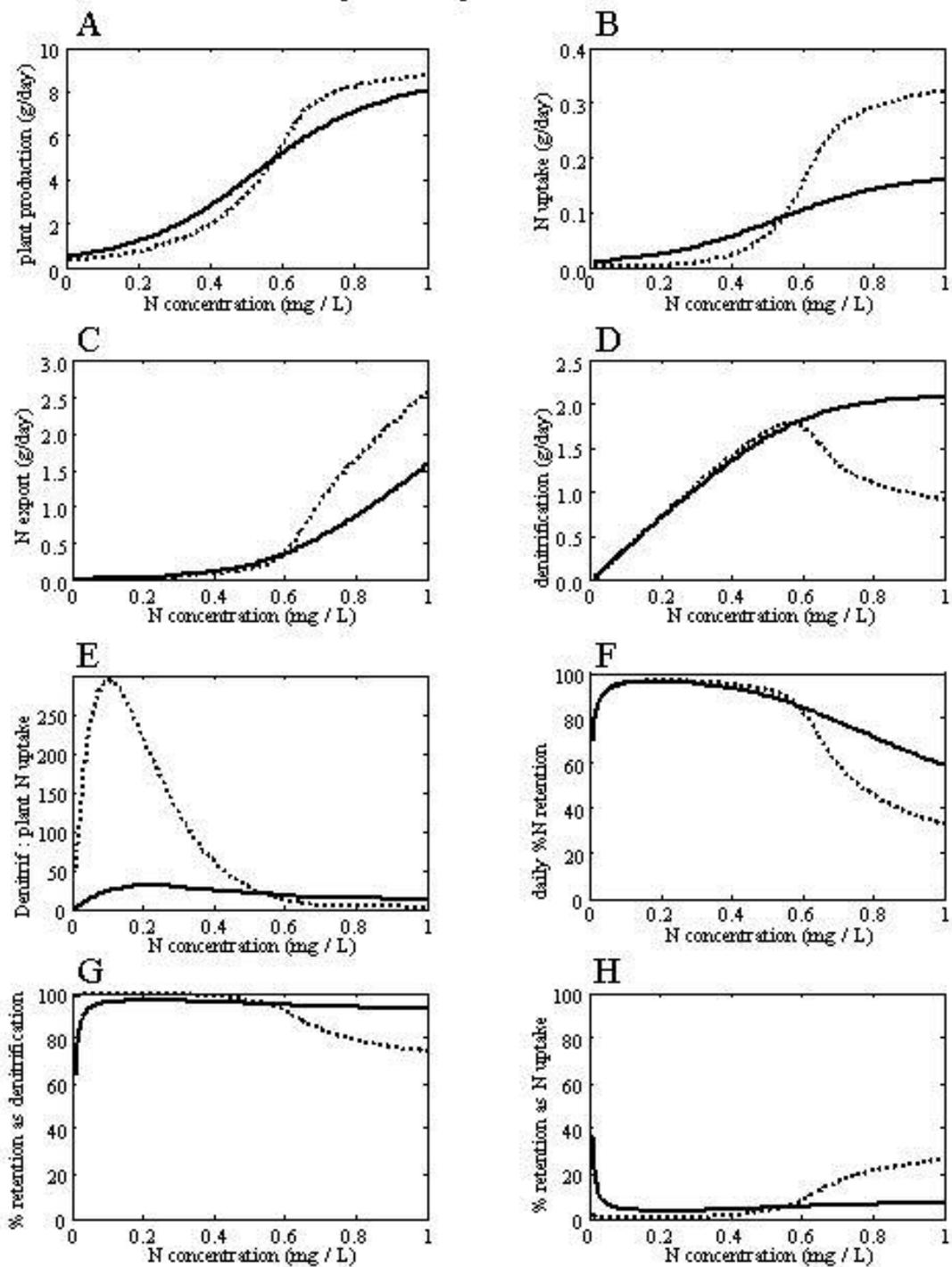


B) Response Model

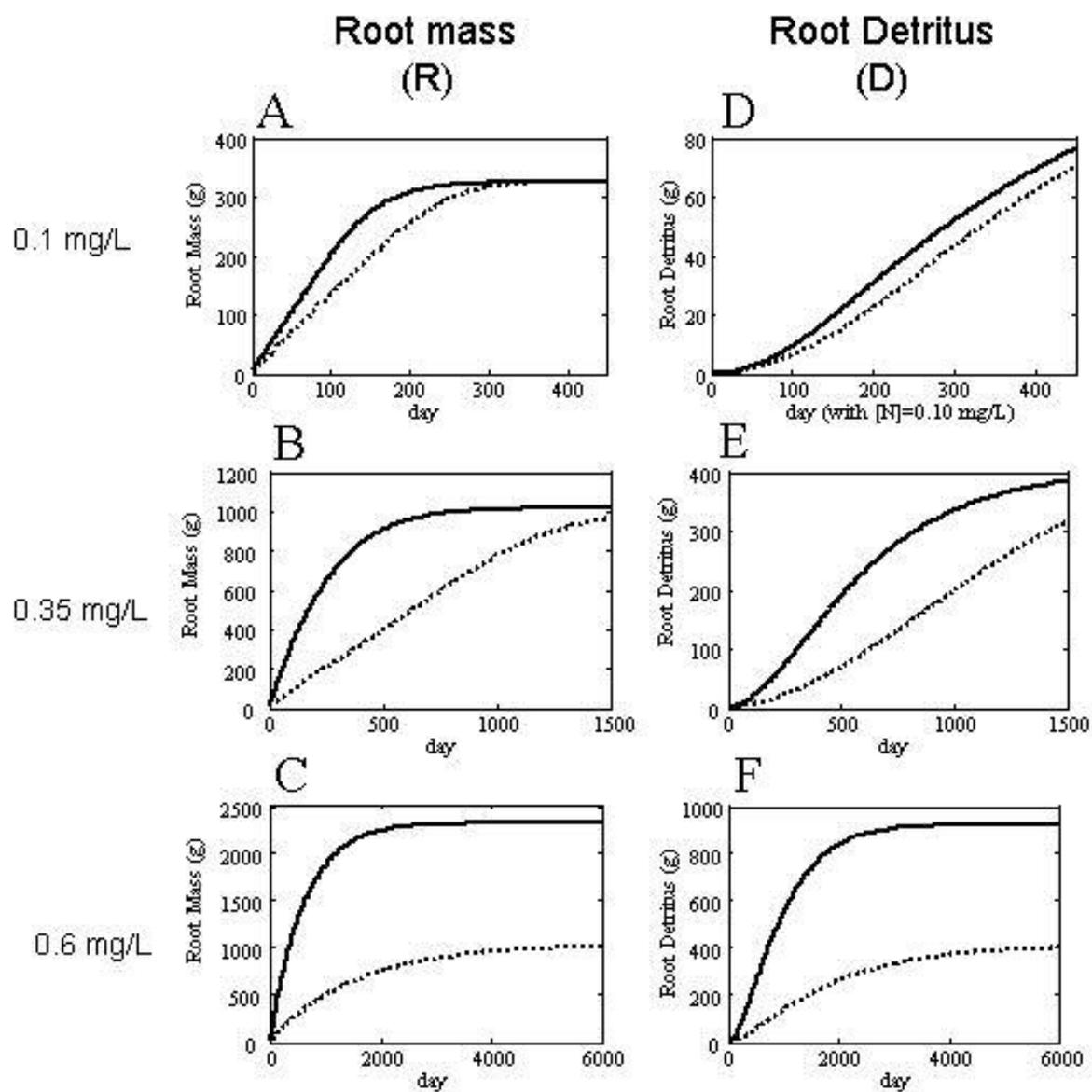


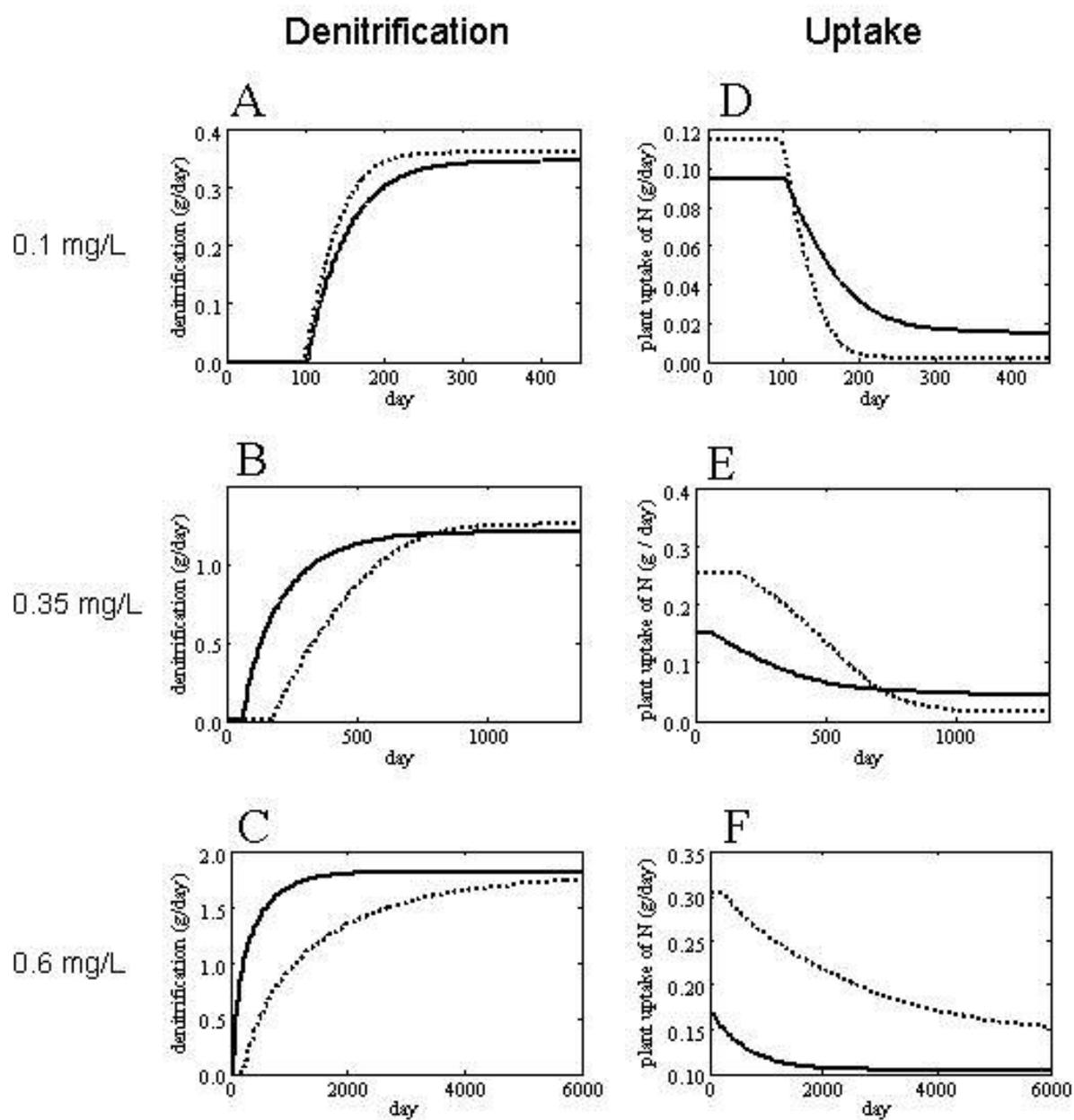


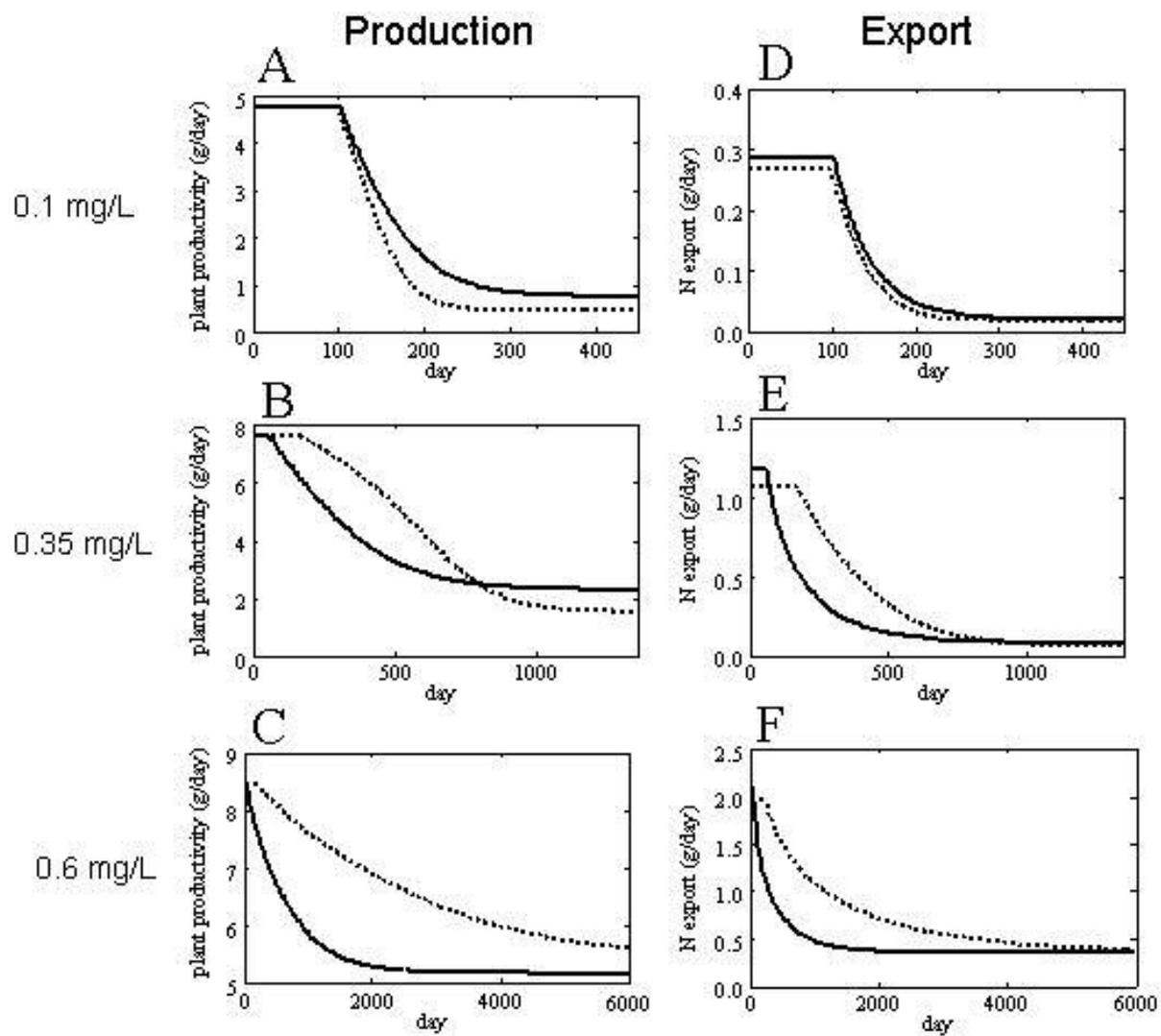
Daily steady state rates



solid constant model; dotted response model







5-year (1825-day) model runs

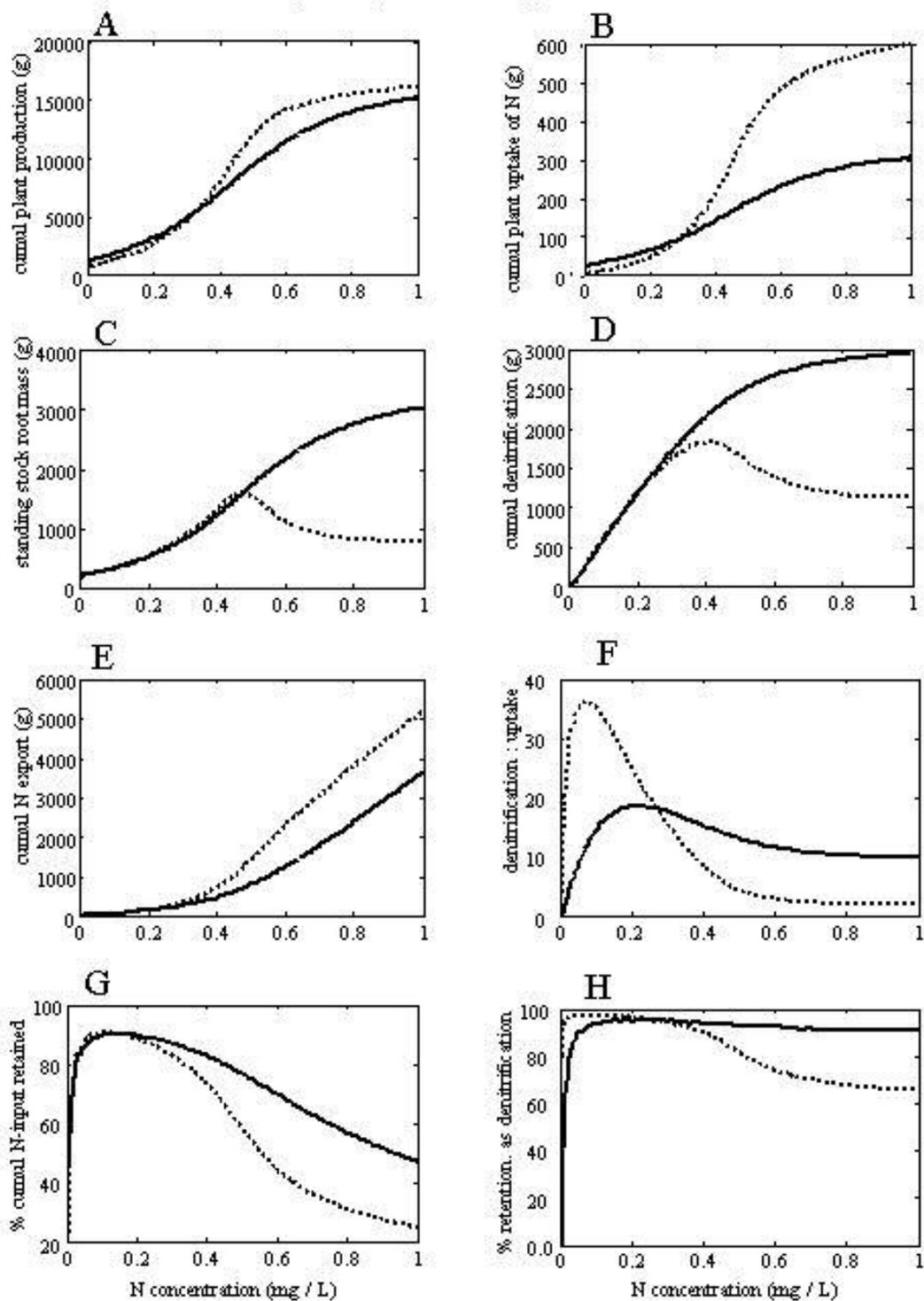


Table Legends:

Table 1. Tissue N concentration, biomass, height and R:S of plants from fertilization experiment. Stars indicate significant differences between fertilized and unfertilized plots, for both absolute levels after fertilization and for changes in these variables in response to fertilizer treatment (paired t-test; $p < 0.05$; $n = 4$ per treatment). Means are reported, with standard errors in parentheses.

Table 2. Comparison of steady-state values for N uptake, plant production and % retention, and cumulative root mass after 5 years from simulation of the response model at $N = 0.1$ to values estimated using field data from Schade et al. (2001). This value of N is used because it is similar to measured N concentrations reported in Schade et al. 2001.

Table 1 - Results from fertilization experiment.

		Unfertilized		fertilized		change	
		before	after	before	after	unfert	fert
Leaf	%N	1.99 (0.16)	1.80 (0.06)	1.90 (0.14)	3.48* (0.37)	-0.19 (0.36)	1.58* (0.70)
	Biomass (g)	0.14 (0.018)	0.62 (0.29)	0.18 (0.016)	1.20 (0.53)	0.48 (0.28)	1.02 (0.54)
Root	%N		0.66 (0.08)		1.66* (0.52)		
	Biomass (g)	0.09 (0.02)	0.86 (0.49)	0.11 (0.013)	0.97 (0.54)	0.77 (0.47)	0.86 (0.54)
Stem	%N		0.57 (0.11)		1.45* (0.54)		
	Biomass (g)	0.08 (0.01)	0.71 (0.34)	0.09 (0.02)	1.01 (0.52)	0.63 (0.34)	0.92 (0.52)
Total	%N		0.99 (0.11)		2.30* (0.66)		
	Biomass (g)	0.31 (0.052)	2.19 (1.12)	0.38 (0.03)	3.18 (1.58)	1.88 (1.09)	2.80 (1.59)
Height (cm)		21.63 (3.68)	30.10 (5.83)	20.80 (3.32)	34.01* (5.87)	8.47 (1.90)	12.72* (1.96)
root/shoot		0.42 (0.05)	0.63 (0.05)	0.46 (0.06)	0.38 (0.04)	0.21 (0.06)	-0.08* (0.06)

Table 2 - Comparison of model with empirical data.

		Schade et al. (2001)
Variable	N = 0.1 mg/L	Field data
Uptake (g/d)	0.005	0.006
production (g/d)	0.51	0.73
% retention	95	91
Root biomass (g)	296	254