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Modelling nutrient-periphyton dynamics in streams with surface–subsurface exchange

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Abstract

Stream ecosystems include both surface and subsurface components that are connected by the flow of water. Processes occurring in subsurface sediments affect those in the surface, and vice versa. A model was developed to investigate the effects of nutrient transformations occurring in subsurface sediments on the growth of surface-dwelling periphyton. In the model the stream is divided into three zones: free-flowing surface water, a surface storage zone where flow is minimal and where periphyton growth occurs, and a subsurface zone. Parameters were based on information from Sycamore Creek, Arizona, a nitrogen-limited desert stream that has been extensively studied. The behavior of the model was examined both at steady state and as it approached steady state after periphyton biomass was reduced to low values, simulating the effects of a scouring flood. Previous work has shown that subsurface sediments are a source of inorganic nutrients, mainly nitrogen, to surface water and to periphyton communities in Sycamore Creek. Thus it was expected that in this model, periphyton biomass would increase when exchange between surface and subsurface zones was increased, and biomass would also increase when the rate of nutrient transformation in subsurface sediments was increased. Model results confirmed the expectations and highlighted the important role of organic nitrogen in mediating the periphyton-nutrient feedback. Post-flood recovery of periphyton biomass was particularly sensitive to elevated concentrations of inorganic nitrogen in flood water. The model shows that processes in the subsurface zone can have a large effect on surface organisms, and illustrates how surface periphyton communities interact with subsurface microorganisms through the recycling of nutrients. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Stream; Hyporheic zone; Subsurface; Nutrients; Periphyton

1. Introduction

Early studies of stream metabolism and nutrient dynamics focused on processes occurring in surface water, but recent work has found that processing rates in subsurface sediments are also substantial (Grimm and Fisher, 1984; Duff and

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Triska, 1990; Jones et al., 1995b; Mulholland et al., 1997). As water flows downstream, it moves vertically and horizontally between the wetted channel and subsurface sediments beneath and beside it. The region of subsurface sediments where water is actively exchanged with the surface (i.e. water in sediments is $>10\%$ surface water in origin) is known as the hyporheic zone (Triska et al., 1989). Thus the flow of water links biological and biogeochemical processes occurring in the surface stream with those occurring in hyporheic sediments.

Biogeochemical processes and processing rates in surface water differ from those in the hyporheic zone. Surface water is in direct contact with the atmosphere, leading to high oxygen levels and primarily aerobic metabolism. Where streams are open to sunlight, periphyton (the algal-bacterial community that colonizes the streambed) and macrophytes are often abundant and can deplete stream water nutrients. In contrast, metabolism in the hyporheic zone is supported by import of organic material and may become anaerobic, depending on the balance between supply of oxygen from the surface and demand by subsurface microbial processes. Oxygen availability plays a key role in determining whether the hyporheic zone is a source or a sink of inorganic nutrients, particularly inorganic nitrogen, to surface waters (Jones and Holmes, 1996; Hedin et al., 1998). In systems where subsurface sediments are well oxygenated, nitrification tends to be high, making the hyporheic zone a source of nitrate to surface water. In systems where subsurface sediments are anoxic, denitrification prevails and the hyporheic zone may be a nitrogen sink.

In this paper a mathematical model is used to explore how processes occurring in subsurface sediments might affect the growth of periphyton in surface water and vice versa. The model is based on empirical studies of Sycamore Creek, AZ, a desert stream with an extensive hyporheic zone. In all streams, the importance of hyporheic zone processes to surface biology depends on: (1) hydrologic exchange between the surface and subsurface; and (2) rates of biogeochemical processes within subsurface sediments (Vervier et al., 1992; Findlay, 1995; Jones and Holmes, 1996; Dent et al., 2000). First the empirical work on hydrologic exchange and on hyporheic processes that forms the basis for the structure of the model is summarized, and then the model and the results of the simulations are described.

1.1. Hydrologic exchange

Hydrologic exchange between free-flowing surface water and slower moving zones, such as hyporheic sediments, is often estimated by injecting a conservative tracer (such as chloride or bromide) at a constant rate into the surface water and measuring changes in tracer concentration over time at downstream sites until a plateau is reached. The injection is then stopped, tracer concentrations drop back to original levels, and the resulting empirical data are fit to a stream transport model to obtain hydrodynamic parameters. Tracer concentrations at downstream sites usually decline slowly after the injection ends. The resulting tracer tail can be modelled by adding a 'transient storage zone' to a one-dimensional standard advection/dispersion model (Bencala and Walters, 1983). This approach provides estimates of the rate of exchange between free-flowing surface water and transient storage, as well as the relative volumes of the surface and transient storage zone. The transient storage zone is a conceptual construct representing an amalgamation of temporary storage of stream water within turbulent eddies, pools, algal mats, backwaters, and subsurface sediments. Tracer additions indicate that the volume of water in transient storage may vary from $\ll 1$ to 18 times the volume of surface water, and exchange rates between the two zones may vary from <1 to 180/day (Broshears et al., 1993; D'Angelo et al., 1993; Harvey et al., 1996; Marti et al., 1997; Morrice et al., 1997). It is difficult, however, to use this measure of general transient storage to separate the volume of the hyporheic zone from other storage areas in the stream. Many tracer injections are relatively short in duration (less than a day), and therefore do not follow the tracer long enough for it to pass completely through large hyporheic zones. Harvey et al. (1996) found that tracer methods were relatively insensitive to exchange with deep alluvial

sediments, particularly at high surface discharges. Castro and Hornberger (1991) distinguish between short-term and long-term storage, where short-term storage results from exchange between faster and slower moving surface water and rapid mixing with the gravel bed (timescale of hours), and long-term storage results from exchange between surface water and deeper hyporheic sediments (timescale of tens of hours). Exchange with deeper hyporheic sediments may be more accurately estimated using direct measurements of subsurface velocity and hydraulic head than with tracer injections (Harvey et al., 1996), though such measurements do not have the advantage of integrating over an entire stream reach. In addition, surface storage zones differ from subsurface zones in residence time and in biogeochemical processes. Therefore it is useful to separate surface storage from subsurface storage, particularly in systems with extensive hyporheic zones. In this model, free-flowing surface water, fast (surface) storage and slow (subsurface) storage are distinguished (Figs. 1 and 3). Data from short-term tracer injections were used to estimate surface storage parameters, and direct measurements of velocity and exchange areas were used to estimate subsurface storage parameters.

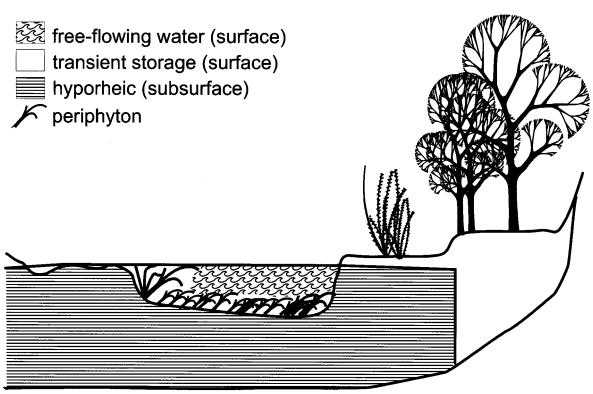

Fig. 1. A stream cross-section, showing the 3 model compartments: (1) free-flowing water, (2) surface transient storage zone, where water moves more slowly and periphyton communities grow (depicted here as vascular plants, for illustrative purposes), and (3) hyporheic zone, including sediments both lateral to and underneath the surface water, but not riparian sediments.

1.2. Hyporheic processes

In Sycamore Creek, concentrations of inorganic nutrients are generally higher in the hyporheic zone than in surface water, making the hyporheic zone a source of inorganic nutrients to surface waters (Valett et al., 1990). Nitrogen is the focus of this study because it limits primary production in this stream (Grimm and Fisher, 1986). Because the hyporheic zone is a source of inorganic nitrogen, nitrogen limitation is alleviated at locations where water moves from the hyporheic zone to the surface (upwelling zones), causing faster growth of periphyton communities (Valett et al., 1994). What causes concentrations of inorganic nitrogen in subsurface sediments to be elevated? This question led to the development of a conceptual model of nitrogen processing in the hyporheic zone (Fig. 2), based on empirical studies (Holmes et al., 1994; Jones et al., 1995a). As water flows through the hyporheic zone, dissolved oxygen concentrations decrease and nitrate concentrations increase. Elevated nitrate concentrations are the result of nitrification of ammonium, which in turn is the product of mineralization of organic nitrogen that enters the hyporheic zone at downwelling zones (where surface water infiltrates subsurface sediments) (Jones et al., 1995a). This creates a positive feedback loop in which nitrogen-limited periphyton communities supply organic nitrogen (in the form of algal leachate or decomposition products) to bacteria in the hyporheic zone, and the bacteria then convert the organic nitrogen back to inorganic nitrogen, thereby increasing concentrations of inorganic (available) nitrogen and alleviating nitrogen limitation in surface water. Note that there is no inflow of groundwater in this scenario; this is typical of streams in arid regions where most stream reaches continually lose water to groundwater aquifers (Fetter, 1988).

The objective was to explore how hyporheic zones might affect nutrient-periphyton interactions, by creating a quantitative model based on hydrologic exchange and the conceptual model of hyporheic nutrient processing just described. The quantitative model enabled one to test the consistency of the conceptual model by making relation-

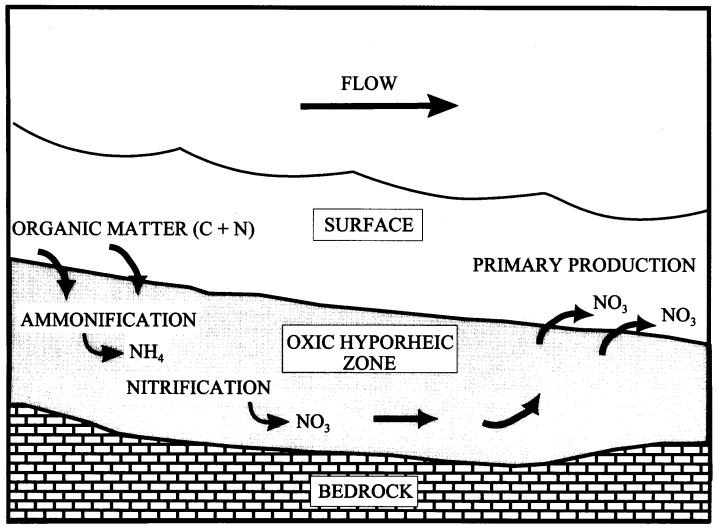

Fig. 2. Conceptual model of nitrogen processing in hyporheic sediments. Labile organic matter from surface-dwelling periphyton is transported advectively into the hyporheic zone, where it serves as a source of organic carbon and nitrogen. Through ammonification, organic nitrogen is mineralized to ammonium and then further oxidized to nitrate. Nitrogen is transported back to the surface as nitrate, where it is available for uptake by primary producers. Stimulation of algal production generates more organic matter that is potentially transported into hyporheic sediments (modified from Jones et al., 1995a).

ships explicit and specific to parameter values measured in Sycamore Creek. Using the model, exchange rates between free-flowing surface water and surface storage (short-term storage) and between surface and hyporheic zones (long-term storage) were manipulated to examine the effect on periphyton growth and nitrogen concentration in each zone. Rates of microbial processes in each zone were also altered. If the conceptual model is reasonable and the quantitative model an accurate representation, the model should produce results that reflect observations of Sycamore Creek. Specifically, it was expected that in the quantitative model, steady state concentrations of inorganic nitrogen in the hyporheic zone would be higher than in surface water, making the hyporheic zone a source of inorganic nitrogen. Furthermore, steady state concentrations of nitrogen would resemble concentrations measured in Sycamore Creek during late succession (when conditions are relatively stable). It was also expected that increases in exchange between surface water and hyporheic sediments would increase steady state periphyton biomass via recycled organic nitrogen released by periphyton. Finally, rates of exchange and microbial processes should affect the rate at which periphyton biomass recovered from a disturbance such as flooding.

2. Site description

Sycamore Creek is a tributary of the Verde River, 32 km northeast of Phoenix, AZ. The modelled stream segment is typical of reaches along a 10-km stretch from 600 to 700 m elevation, where stream substrata consist primarily of coarse sand and gravel that can be several meters deep. Surface water and subsurface water in stream sediments are in close connection, and water moves rapidly through subsurface sediments (>1 m/h on average during baseflow; Valett et al., 1990; Holmes et al., 1994). Subsurface sediments are generally oxic and support high rates of respiration (11.9 g O_2/m^2 per day; Jones et al., 1995b) and nitrification (0.2 g NO_3–N/m^2 per day; Jones et al., 1995a). Riparian vegetation in this lower Sonoran Desert scrub life zone is sparsely distributed along a stream channel that is generally >20m wide, leaving the stream un-

shaded during much of the day. Periphyton communities are abundant, especially in summer, and primary productivity is high (≥ 10 g O_2/m^2 per day; Grimm, 1987). Nitrogen limits primary production during baseflow when hydrologic conditions allow periphyton growth (Grimm and Fisher, 1986). Intense flash floods remove periphyton from the stream channel several times a year. When flood waters recede, periphyton return to pre-disturbance levels in a predictable successional pattern, often within a few weeks (Fisher et al., 1982; Grimm and Fisher, 1989).

3. Model description

DeAngelis et al. (1995) developed a model that examined nutrient-periphyton interactions in flowing surface water and surface transient storage. The model described here is similar, with the addition of a third zone to simulate subsurface processes. The model represents a homogeneous, longitudinal stream section of unit length. Water flows downstream through a free-flowing surface zone and exchanges materials with a stationary surface storage and hyporheic (subsurface) zone. Each of the three zones (free-flowing surface water, surface transient storage, and hyporheic sediments) has a soluble inorganic nitrogen (N) compartment and an organic N compartment (Fig. 3). The organic N compartments represent labile N in non-living, transportable form, either dissolved or particulate. Only labile organic N was modelled because algal-derived organic matter is generally quite labile. The surface storage zone also has a compartment for N in periphyton biomass. The model assumes that all zones are perfectly mixed; there are no diffusion gradients of N concentration within the zones.

Dissolved inorganic and organic N enter and leave the free-flowing water zone at a rate determined by stream discharge. N moves between the three zones according to the flux of water between the zones, which is represented by a first-order mass transfer relationship. The volume of water in each zone remains constant throughout the simulation. Therefore, exchange of solute between zones is proportional to differences in N concentration. Movement is bi-directional with the exception of labile organic N moving into hyporheic sediments; both organic and inorganic N move into hyporheic sediments, but only inorganic N comes out. This is consistent with the conceptual model, in which all labile N is mineralized and nitrified before exiting the hyporheic zone. Nitrogen uptake by biomass follows Monod-type kinetics, with the addition of a term for self-limitation due to a decline in the rate at which nutrients diffuse into the algal mat as biomass increases. Release of N from biomass to transportable organic form follows first-order, donor-controlled

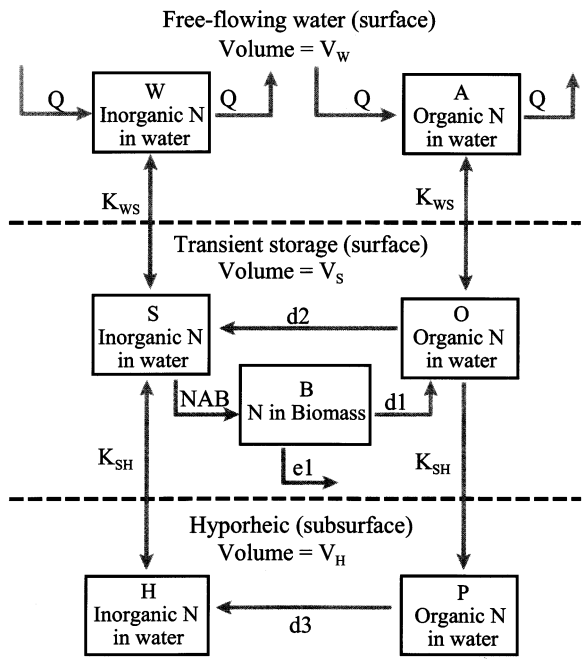

Fig. 3. Model structure. The model consists of three zones: free-flowing water, surface storage, and hyporheic storage, each with a constant volume. Pools of nitrogen in each zone are represented by boxes. Each box or compartment represents a mass of nitrogen (g), and is expressed in the model equations as a concentration (g m^{-3}) times the zone volume (m^3). Thus W represents the mass of inorganic N in free-flowing water and is equal to $N_W V_W$; A is the mass of organic N in free-flowing water ($= N_A V_W$), etc. Fluxes are represented by arrows labeled with the parameter that controls them (see Table 1; NAB = operator nutrient uptake by biomass, see model equations). Each zone contains inorganic and organic N, and N in periphyton biomass is in the surface storage zone. Parameter descriptions are given in Table 1.

kinetics. There is also a permanent loss of N from biomass representing downstream export, denitrification, or both. Organic N is transformed to inorganic form in the surface storage zone and in hyporheic sediments through a first-order mineralization process.

The equations for each state variable in the model are as follows:

$$\frac{d(V_W N_W)}{dt} = Q(iN_{upstream} - N_W) + K_{WS} V_W (N_S - N_W) \quad (1)$$

$$\frac{d(V_W N_A)}{dt} = Q(oN_{upstream} - N_A) + K_{WS} V_W (N_O - N_A) \quad (2)$$

$$\frac{d(V_S N_S)}{dt} = K_{WS} V_W (N_W - N_S) + K_{SH} V_S (N_H - N_S) + d_2 (V_S N_O) - [NAB] \quad (3)$$

$$\frac{d(V_S N_O)}{dt} = K_{WS} V_W (N_A - N_O) + K_{SH} V_S (-N_O) + d_1 (V_S N_B) - d_2 (V_S N_O) \quad (4)$$

$$\frac{d(V_S N_B)}{dt} = [NAB] - d_1 (V_S N_B) - e_1 (V_S N_B) \quad (5)$$

$$\frac{d(V_H N_H)}{dt} = K_{SH} V_S (N_S - N_H) + d_3 (V_H N_P) \quad (6)$$

$$\frac{d(V_H N_H)}{dt} = K_{SH} V_S (N_O) - d_3 (V_H N_P) \quad (7)$$

$$NAB = \frac{r(V_S N_B) N_S}{b_1 + N_S + c(N_B)} \quad (8)$$

where V_W, V_S, and V_H are volumes (m^3) for the free-flowing water, surface storage, and hyporheic sediments, respectively; N_W, N_S, and N_H are concentrations of inorganic N (g/m^3) in free-flowing water, surface storage, and hyporheic sediments; N_A, N_O, and N_P are concentrations of transportable organic N (g/m^3) in free-flowing water, surface storage, and hyporheic sediments, and N_B is the concentration of organic N (g/m^3) in living biomass. Thus each equation describes change over time in the mass of N (g/day) for one compartment.

Import of N from upstream is determined by the flux of water (Q, in m^3/day), and the concentration of inorganic N ($iN_{upstream}$) or organic N ($oN_{upstream}$) arriving at the stream segment (g/m^3). Downstream export of N is determined by Q and the concentration of N in the free-flowing zone. K_{WS} and K_{SH} are transfer coefficients (per day) between free-flowing water and surface storage, and between surface storage and hyporheic sediments, respectively. Release of N from biomass to transportable organic form is controlled by the rate coefficient d_1 (per day); d_2 and d_3 are rate coefficients (per day) for transformation of organic to inorganic N in surface storage and hyporheic zones, respectively, and e_1 controls the rate of permanent loss of N from biomass (per day). Nitrogen assimilation by biomass (NAB) is represented by a Monod-type growth function where the growth rate per unit of periphyton biomass approaches the constant r when the concentration of N in surface storage (N_S) is large. The term $c(N_B)$ in the denominator represents a form of self-limitation caused by a decrease in N availability due to decreased diffusion of nutrients through the algal mat as biomass increases. This form of nutrient uptake was found by DeAngelis et al. (1995) to match experimental data more closely than the standard Monod form, and work on periphyton uptake dynamics in Sycamore Creek has also found evidence of self-limitation (Grimm, 1992).

Both the steady state behavior and the transient dynamics of the system were examined. Transient dynamics were examined after setting periphyton biomass to low levels, simulating a flash flood. Because the model deals with a 'stiff system', where the rate of change of some components (e.g. N in free-flowing water) is much faster than others (e.g. N in biomass), a stiff equation algorithm was used in the simulations.

3.1. Parameterization

Where possible, model parameters were based on observations of Sycamore Creek during the month of June, when disturbance by drought or flooding is rare and periphyton assemblages are generally abundant (Table 1). Discharge and in

Table 1
Model parameters[a]

Parameter	Description	Value	Source
Inputs:			
Q	Stream discharge	1000 m^3/day	Unpublished data
$iN_{upstream}$	Inorganic N concentration	0.03 g/m^3	Unpublished data
$oN_{upstream}$	Organic N concentration	0.05 g/m^3	Iterative model runs
Compartment volumes (per unit length):			
V_W	Free-flowing surface water	0.1 m^3	Marti et al., 1997
V_S	Surface transient storage zone	0.2 m^3	Marti et al., 1997
V_H	Subsurface (hyporheic) zone	0.6 m^3	Calculations (see Fig. 4)
Hydrologic exchange coefficients:			
K_{WS}	Surface water-transient storage	40/day	Marti et al., 1997
K_{SH}	Transient storage-hyporheic	240/day	Calculations (see Fig. 4)
Nutrient cycling rate coefficients:			
d_1	Release of biomass to organic form	0.1/day	Grimm, 1985, 1987
d_2	Mineralization in surface transient storage	0.1/day	Busch and Fisher, 1981; Grimm and Fisher, 1984
d_3	Mineralization in hyporheic sediments	1.0/day	Grimm and Fisher, 1984; Jones, 1995
r	Maximum N uptake rate	10/day	Mulholland and DeAngelis, 2000
b_1	Half-saturation constant for uptake	0.01 g/m^3	Mulholland and DeAngelis, 2000
c	Self-limitation coefficient	0.02	Mulholland and DeAngelis, 2000
e_1	Permanent loss of biomass	0.01/day	DeAngelis et al., 1995

[a] Values are based on late succession measurements from given sources, rounded to whole numbers.

stream inorganic N concentrations have been monitored for over a decade. Upstream organic N concentrations were difficult to estimate because the value in the model represents only *labile* organic N (in dissolved or particulate form). Organic N quality (degree to which it is labile or recalcitrant) is difficult to measure and has not been determined for Sycamore Creek water. The model was run under two scenarios: one in which upstream inputs of organic N were zero, so that all organic N was generated within the modelled reach, and a second in which upstream inputs of organic N were set such that import and export of organic N (including losses from oN in free-flowing water and from oN in biomass) were approximately equal. In the second scenario, the removal of organic N by the reach was balanced by import of organic N from the reach, so that it was in steady state with respect to organic N.

Hydrologic exchange rates between the different zones were based on tracer experiments and calculations from direct measurement (Fig. 4). Short-term tracer injections (<2 h for a 240 m reach; Marti et al., 1997) were used to estimate the relative size of the flowing water and surface storage zones and the exchange of water between them. Direct measurements of subsurface velocity and estimated exchange area were used to calculate the relative size of surface storage and hyporheic zones, and their exchange rates. An average subsurface velocity of 24 m/day, exchange area of 2 m^2, surface water depth of 15 cm, hyporheic sediment depth of 150 cm, and pore space of 20% were used, all based on observations in Sycamore Creek during June (Fig. 4).

Nutrient cycling rates were based on empirical work from Sycamore Creek or from literature values. Release of organic N from biomass (d_1) was based on leaching and algal drift measurements (Grimm, 1985, 1987). Mineralization rate in surface storage (d_2) and in the hyporheic zone (d_3) were based on measurements of respiration in benthic and hyporheic sediments (Busch and Fisher, 1981; Grimm and Fisher, 1984; Grimm, 1987; Jones, 1995). Permanent loss of biomass (e_1) and nutrient uptake coefficients (r, b_1, c) were based on values used by DeAngelis et al. (1995)

and Mulholland and DeAngelis (2000) in their models, since little information was available from Sycamore Creek.

Sensitivity analysis showed that no parameter had a disproportionately large effect on steady state concentration of N in periphyton biomass or on concentration of inorganic N in the different zones (hyporheic N is shown as an example, Table 2). Those parameters that were most influential were examined further (see Section 4).

4. Results

4.1. Steady state

4.1.1. Comparisons with concentrations measured in Sycamore Creek

The steady state concentrations of N in the model were compared with average Sycamore Creek concentrations for two different scenarios: one in which upstream concentration of (labile) organic N was set to zero, and one in which

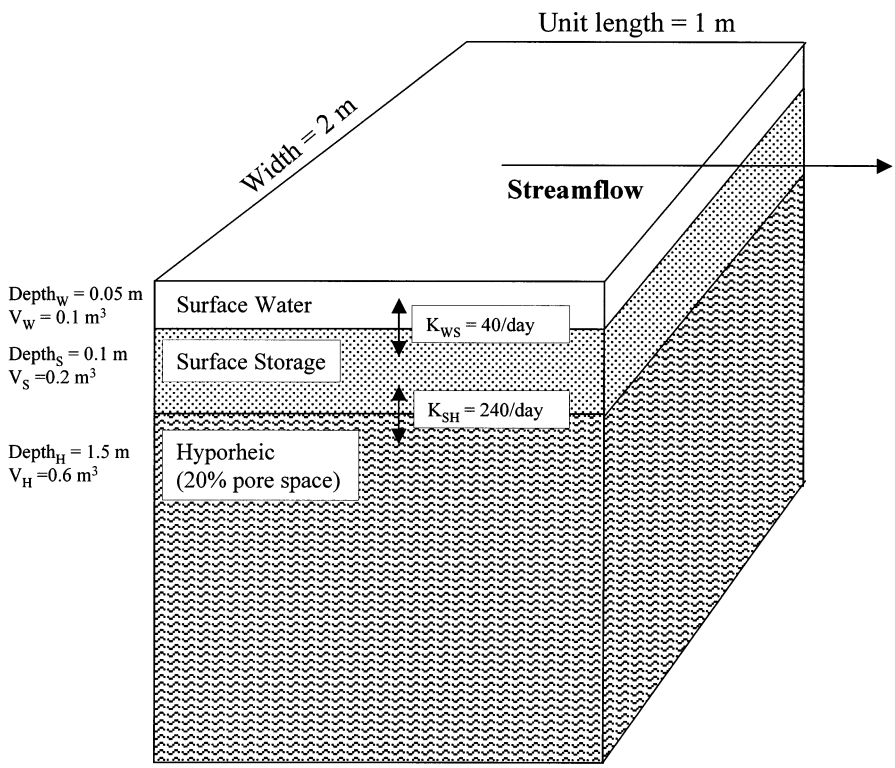

Fig. 4. Calculation of hydrologic exchange parameters from field measurements. The modelled stream section is of unit length and 2 m width, with flowing water of 0.05 m depth (based on field measurements). It is assumed that the different zones are arrayed vertically as shown. K_{WS} comes from short-term injections fit to a hydrodynamics model (Marti et al., 1997). The same injections estimate the volume of surface storage as twice the volume of free-flowing water, giving it a depth of 0.1 m. Depth of hyporheic sediments is 1.5 m (based on field measurements), but only 20% of the sediments are pore space, so volume of water in the hyporheic zone is 0.6 m^3. K_{SH} is estimated from subsurface velocity measurements of 24 m day^{-1} times the exchange area of 2 m^2 divided by the storage zone volume of 0.2 m^3, giving units of day^{-1}. A complete list of parameter values and sources is given in Table 1.

Table 2
Sensitivity analysis for model parameters[a]

Parameter	Percentage change	
	Concentration of N in Biomass (N_B)	Concentration of inorganic N in Hyporheic (N_H)
Inputs:		
Q	–	–
$iN_{upstream}$	4	4
$oN_{upstream}$	6	6
Compartment volumes:		
V_W	5	5
V_S	2	2
V_H	–	–
Hydrologic exchange coefficients:		
K_{WS}	5	4
K_{SH}	4	3
Nutrient cycling rate coefficients:		
d_1	6	4
d_2	–	–
d_3	–	–
r	2	2
b_1	–	–
c	2	2
e_1	5	4

[a] Maximum percentage change in steady state concentration of N in periphyton biomass and iN in the hyporheic, when parameters are changed by $\pm 10\%$ from the values used in the model (Table 1). Dash indicates that the change is $<1\%$.

upstream concentration of organic N was set to 0.05 g/m^3, such that import and export of organic N were approximately equal at steady state. In all cases, modelled steady state values were closer to observed Sycamore Creek values when upstream organic N concentrations were 0.05 g/m^3.

Steady state concentration of inorganic N (iN) and organic N (oN) in the flowing water compartment was controlled by upstream concentration, because upstream–downstream flow through the compartment far exceeded the amount of material exchanged with storage zones. Thus the close match between steady state iN concentration (0.03 g/m^3) and June Sycamore Creek concentration (0.03 g/m^3) was not surprising (Table 3). Similarly, steady state concentration of oN depended on upstream oN concentration (Table 3). Direct comparison with measured concentration of organic N in Sycamore Creek was not possible, because no measurements of the labile portion of the total organic N pool were available. However, when upstream concentration of oN was zero, steady state concentration of labile organic N was only 0.3% of total organic N as measured in Sycamore Creek (Table 3). In other streams, bioassays have shown that labile organic matter makes up a substantial percentage of total organic matter (Claret et al., 1997, 44–76%). When upstream concentration of oN was set to 0.05 g/m^3, steady state concentration of labile organic N in stream water was more reasonable, at 29% of measured total organic N (Table 3).

Steady state concentrations of iN and oN in surface storage were also substantially higher with oN input from upstream (Table 3). Based on N in algal biomass, steady state concentrations in surface storage were closer to those observed in Sycamore Creek when upstream concentrations of oN were set to 0.05 g/m^3 than when they were set to zero (Table 3).

According to the conceptual model of nutrient processing in subsurface sediments, concentration of iN should be higher in the hyporheic zone than in flowing water, making the hyporheic zone a source of iN. In the quantitative model, it was not possible to reproduce this scenario when upstream input of oN was zero (Table 3). With no upstream input of oN, the ultimate source of all N was upstream iN, and recycling within the system could not cause steady state concentration in the hyporheic zone to surpass upstream concentration. However, when upstream input of oN was added, recycling within the system increased hyporheic concentration of iN beyond concentrations in surface storage and in flowing water. Hyporheic oN is again difficult to compare to field values. Dissolved organic nitrogen (DON) in the hyporheic zone of Sycamore Creek is quite low, suggesting that particulate N may be an important source for hyporheic processes (Table 3), but concentrations of labile DON and labile particulate organic N (PON) have not been measured.

4.1.2. Effects of upstream inputs of inorganic and organic N

The effects of upstream concentrations of iN and

oN on steady state concentration of iN in all three compartments and in periphyton biomass are shown in Fig. 5. Steady state iN in flowing water tracked upstream iN closely (Fig. 5a). Concentration of iN in surface storage and hyporheic storage increased linearly with upstream inputs of iN, though the slope was reduced by algal uptake. N in algal biomass increased with increasing upstream input but did not completely deplete iN in surface storage water due to the effect of self-lim itation (decreased diffusion of nutrients as periphyton biomass increases). Steady state concentration of iN in surface storage, hyporheic, and algal biomass also increased with increasing upstream input of oN (Fig. 5b).

4.1.3. Effects of exchange rates K_{WS} and K_{HS}

The flux of water between the free-flowing zone and surface storage (K_{WS}) affected steady state surface storage and hyporheic iN concentration and N in biomass (Fig. 6a). As exchange increased, steady state concentrations in hyporheic iN and N in biomass increased, particularly for low exchange rates ($K_{WS} < 60$/day). At higher exchange rates, changes in steady state concentration leveled off. Exchange of water between surface storage and the hyporheic zone (K_{HS}) also affected steady state concentration (Fig. 6b). As more water was exchanged with the hyporheic zone, steady state N in biomass increased. The increase was greater at lower exchange rates, but the effect decreased more slowly than that of flowing water–surface storage exchange, so that increases in exchange with the hyporheic zone continued to substantially increase N in biomass for rates as high as 100/day (K_{HS}, Fig. 6b). Inorganic N concentration in surface storage increased with storage-hyporheic exchange, but iN concentration in the hyporheic zone decreased (Fig. 6b).

4.1.4. Effects of nutrient cycling rates

Of the nutrient cycling parameters, release from biomass (d_1) and export from biomass (e_1) had the largest effects on steady state concentration of N

Table 3
Steady state values for two model runs (upstream concentration of organic $N = 0$ and 0.05 g/m^3) compared to average concentrations in Sycamore Creek, $\pm$S.E.[a]

Compartment	Model steady state values (g N/m^3)		Sycamore Creek (g N/m^3)
	o$N_0 = 0$	o$N_0 = 0.05$	
Flowing water:			
iN in water (N_W)	0.030	0.030	0.03 ± 0.006[b]
oN in water (N_A)	0.00004	0.050	0.14 ± 0.01[c] (DON)
0.02 ± 0.002[d] (PON)			
Transient storage:			
iN in water (N_S)	0.006	0.015	?
oN in biomass (N_B)	27	69	57 ± 11[c]
oN in water (N_O)	0.010	0.030	?
Hyporheic:			
iN in water (N_H)	0.016	0.046	0.09 ± 0.01[e]
oN in water (N_P)	0.829	2.42	0.12 ± 0.01[e] (DON)
			5.76 ± 0.61[f] (PON)

[a] All organic nitrogen (oN) values from the model refer to the labile fraction of the organic N pool, whereas values from Sycamore Creek are total organic N. DON, dissolved organic nitrogen; PON, particulate organic nitrogen; FPOM; fine particulate organic matter.
[b] Sampled in June from 1978 to 1995 ($n = 38$); unpublished data.
[c] Sampled in June from 1992 to 1995 ($n = 9$); unpublished data.
[d] Sampled in summer from 1981 to 1983 ($n = 7$); Grimm (1987), assuming PON is 5% of FPOM.
[e] Sampled in June from four wells from 1992 to 1995 ($n = 35$); unpublished data.
[f] Sampled in three locations from 1992 to 1993 ($n = 135$); Jones et al. (1995b), assuming PON is 10% of POC.

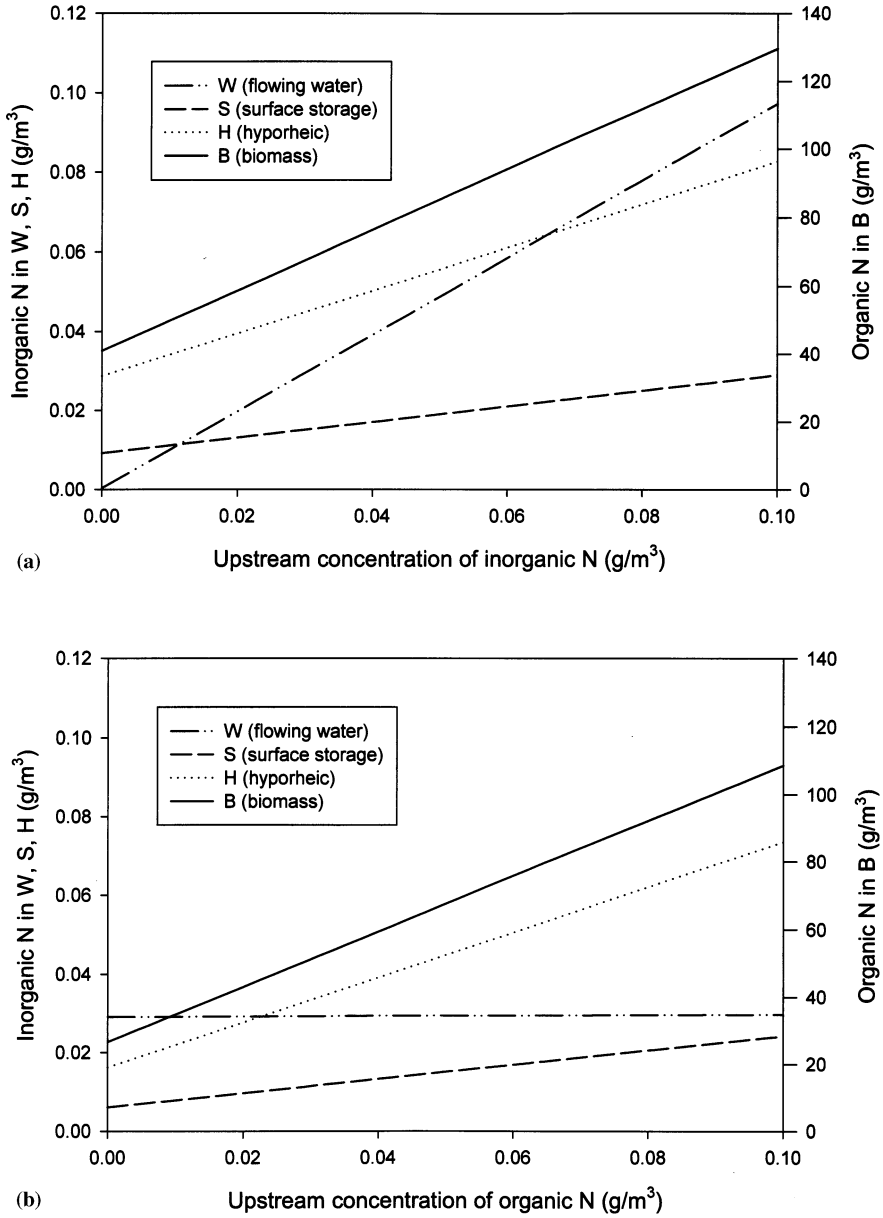

Fig. 5. Effect of upstream concentration of inorganic (a) and organic (b) nitrogen on steady state concentration of N in W (free-flowing water), S (surface storage), H (hyporheic), and B (periphyton biomass).

in biomass (Table 2). The rate of release of N from biomass (d_1) was inversely related to N in biomass (Fig. 7a). Change in the rate of permanent export from biomass (e_1) had similar effects. How would N in biomass be affected by changes in the allocation of N loss between release, which is available for recycling, and export, which is not? When the rate of release from biomass (d_1) was linked to the rate of permanent export from biomass (e_1), increases in release (at the expense ofexport) increased steady state biomass N (Fig. 7b). Rates of mineralization in the surface (d_2)

and hyporheic zone (d_3) did not significantly affect steady state concentration of N in biomass or iN in any compartment.

4.2. Transient dynamics

System recovery from a disturbance was examined by initializing all compartments to low N values to simulate the effects of a scouring flood. When upstream input of inorganic and organic nitrogen were kept at constant values, the system took over 150 days to return to N concentrations close to steady state values, particularly in periphyton biomass (Fig. 8a). However, this is not a

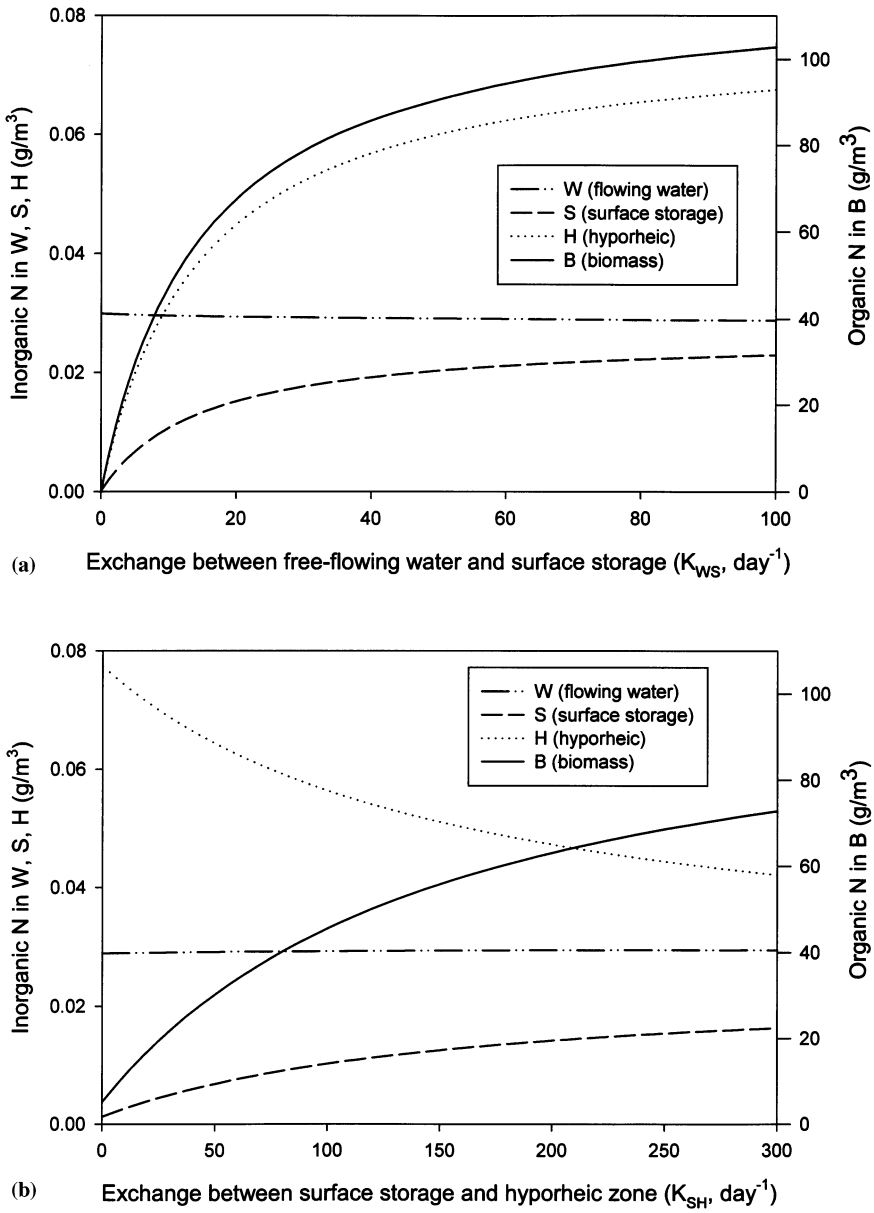

Fig. 6. Effect of exchange between free-flowing water and transient storage (a) and between transient storage and hyporheic zone (b) on steady state concentrations of N in W (free-flowing water), S (surface storage), H (hyporheic), and B (periphyton biomass).

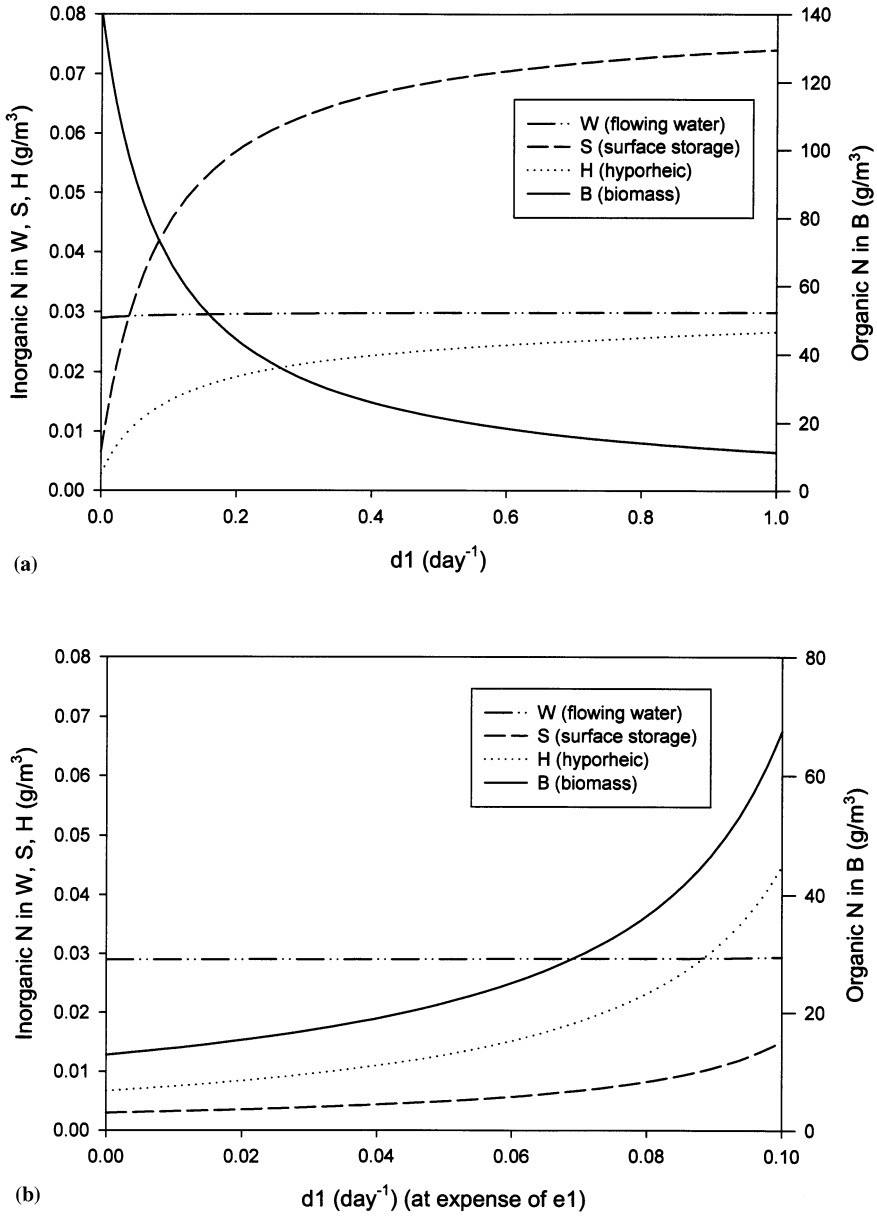

Fig. 7. Effect of release rate of organic N from periphyton biomass (d_1) on steady state concentrations of N in W (free-flowing water), S (surface storage), H (hyporheic), and B (periphyton biomass). (a) The effect of changing d_1 independently. (b) While d_1 is increased, e_1 is reduced by an equivalent amount, such that the overall release rate of N remains constant, while an increasing proportion of N released is available for recycling instead of being lost from the system.

realistic simulation of post-flood conditions, since flood waters are generally high in inorganic N concentration, and remain high for some time after the flood recedes (Grimm, 1992). Therefore concentrations observed during and after a spring flood were also used as upstream concentrations of inorganic N. In this case, the system recovered much more quickly, within about 30 days (Fig. 8b).

As expected, recovery of periphyton biomass was dependent on the rate of mineralization in the hyporheic zone (d_3) (Fig. 9). N in biomass accumulated more quickly when mineralization in the hyporheic zone was faster, both when upstream input of inorganic N was constant and when it was elevated by flood water. The effect was most pronounced for mineralization rates less than

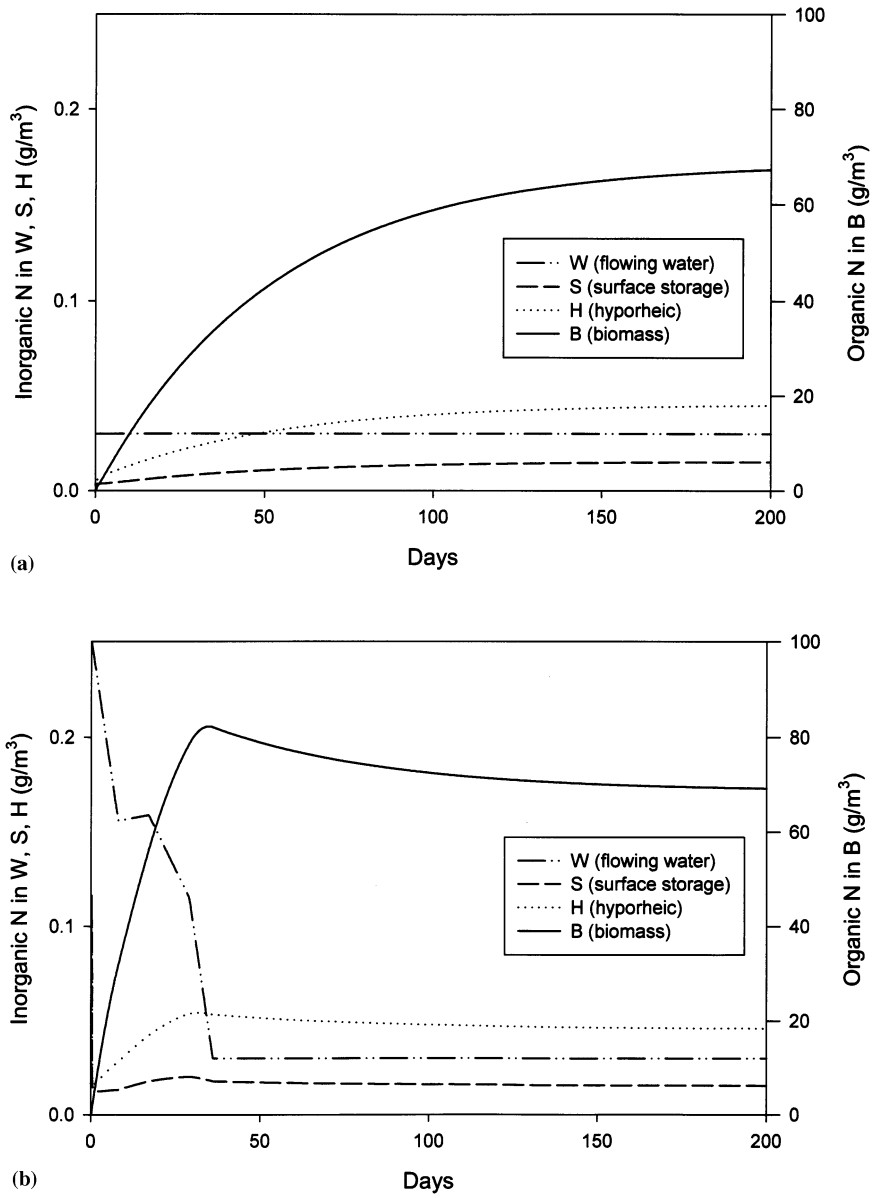

Fig. 8. Changes in concentrations of N in W (free-flowing water), S (surface storage), H (hyporheic), and B (periphyton biomass) over time. Initial values of all pools were set to 0.1 g m^{-3}. (a) Upstream concentration of inorganic N was maintained at the steady state value of 0.03 g m^{-3}. (b) Upstream concentration of inorganic N followed the decline measured during a March 1993 flood, eventually reaching the same steady state concentration. Upstream inputs of inorganic N are not shown on the graph because steady state N in W (flowing water) follows the identical pattern.

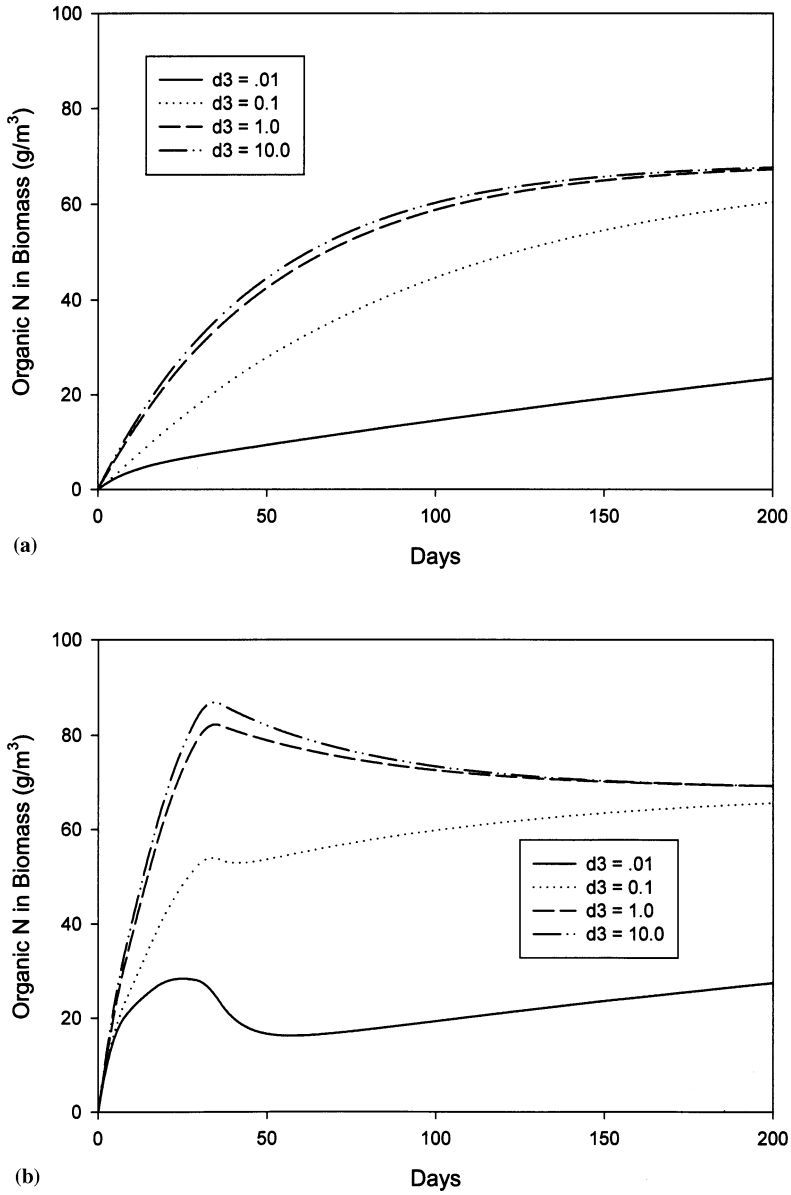

Fig. 9. The effect of changes in mineralization rate in the hyporheic zone (d_3) on recovery of N in B (periphyton biomass) over time. Initial values of all pools were set to 0.1 g m^{-3}. (a) Upstream concentration of inorganic N was maintained at the steady state value of 0.03 g m^{-3}. (b) Upstream concentration of inorganic N followed the decline measured during a March 1993 flood, eventually reaching the same steady state concentration.

1/day; rates higher than this did not cause N in biomass to accumulate much faster. When upstream input of inorganic N followed flood concentrations, N in biomass sometimes overshot its steady state value, causing a decrease in N in biomass after about 40 days (Fig. 9b). A high rate of mineralization in the hyporheic zone exaggerated this phenomenon. In all cases, rate of miner alization in the hyporheic zone affected the rate of recovery of algal biomass but not the final, steady

state concentration of N in biomass. Other nutrient cycling parameters and exchange rate parameters did not have noticeable effects on the post-flood recovery of the system.

5. Discussion

5.1. Steady state

The mathematical model was based on a conceptual model of nutrient-periphyton interactions in streams with aerobic hyporheic zones (Fig. 2). The quantitative model enabled us to test the consistency of the conceptual model by making relationships explicit and giving parameter values specific, realistic values. As predicted by the conceptual model, modelled concentration of inorganic N in hyporheic sediments exceeded concentration in surface water at steady state when upstream–downstream linkage of organic N was included. Steady state values from the mathematical model were also fairly consistent with values observed in Sycamore Creek where appropriate comparisons were available, such as high concentration of organic N in periphyton biomass and low concentration of inorganic N in surface water.

The model highlights the importance of the dynamics of organic N, which are poorly understood at present. Variation in composition and quality of organic N and organic carbon (C) make these compounds difficult to follow using standard analytical methods. Concentrations of total dissolved organic carbon (DOC), for example, may remain fairly constant along subsurface flowpaths where considerable metabolism occurs (Jones et al., 1995b), perhaps because the fast turnover of labile organic matter is masked by a large amount of recalcitrant organic matter. Further work on identifying patterns in labile constituents of organic matter (McKnight et al., 1997; Findlay et al., 1998) would enable improvements in the parameterization and testing of the model. In addition, the supply and quality of organic carbon may affect processing of nitrogen. For example, hyporheic respiration in Sycamore Creek is limited by C, causing N to be released rather than retained during mineralization (Jones, 1995). If C was not limiting, the hyporheic zone might be a sink rather than a source of inorganic N. With more information on organic C and N, the model could be extended to include interactions between carbon, nutrients, and periphyton in the stream.

In the model, increase in exchange between flowing water, surface storage, and hyporheic sediments increased the steady state concentration of N in periphyton (Fig. 6). This is consistent with the framework proposed by Findlay (1995), in which the importance of hyporheic sediments to stream systems depends in part on the proportion of discharge that passes through the hyporheic zone. As more water passes through hyporheic sediments, the effect of hyporheic processes on the stream ecosystem increases. Studies of nutrient retention have found that whole stream nutrient retention, as measured by uptake length, increases with the relative size of the subsurface zone and with the amount of exchange between surface and subsurface (Vervier et al., 1992; Valett et al., 1996; Mulholland et al., 1997). Similar results were found in a model of surface–subsurface interactions in which subsurface processes retained N (Mulholland and DeAngelis, 2000).

The specific rate of exchange between surface storage and hyporheic sediments in the model (K_{SH}) is based on the assumption that exchange occurs uniformly across the entire stream bottom (Fig. 4). In reality, exchange is localized in certain areas, called upwelling and downwelling zones (Valett et al., 1990). This spatial separation increases residence time of water in the hyporheic zone, compared to the model. Due to this discrepancy, the transfer of organic N from the hyporheic zone back to the surface was eliminated from the model, to ensure that all labile oN was transformed into iN in the hyporheic zone (as specified by the conceptual model). A promising area of future work is to model the impact of the hyporheic zone in a spatially explicit manner. It is likely that in such a model, surface–subsurface interactions would increase periphyton biomass at upwelling zones and decrease it at downwelling zones. If surface water patches of very low nutrient concentration occur, nitrogen-fixing cyanobacteria may colonize these patches and increase the overall nitrogen load in the stream via nitrogen fixation (Fisher et al., 1998a). A spatially-explicit model of

surface–subsurface interactions could address many interesting questions relating to system heterogeneity and its effects on nutrient retention.

The other factor in the framework of Findlay (1995) that determines the importance of hyporheic processes to whole system behavior is the rate of biogeochemical processes within hyporheic sediments. In the model presented here, the hyporheic zone is a source, rather than a sink, of organic N. The rate of processing did affect the rate at which the system recovered from disturbance (Fig. 9). Microbially-mediated nutrient processing rates in the hyporheic zone are likely to be higher than in surface waters ($d_3 > d_2$) due to the higher surface area to volume ratio of subsurface sediments. Variation in processing rates within sediments could result from variation in organic matter quality and in availability of nutrients. Empirical work has yet to examine the effects of these factors on the contribution of hyporheic zones to whole system measures. The model suggests that variation in hyporheic processing rate might have particularly strong effects on system recovery.

In systems where subsurface sediments are sinks for inorganic nutrients, increased exchange with the subsurface results in higher retention rates (shorter uptake lengths) (Valett et al., 1996; Mulholland et al., 1997; Mulholland and DeAngelis, 2000). In the model, the hyporheic zone is a source, rather than a sink, of inorganic N. How does increasing exchange with subsurface sediments affect whole system N retention in this case? Since the hyporheic zone is an inorganic N source, an increase in exchange between surface and subsurface water enriches surface water with inorganic N. If this inorganic N were exported (by downstream transport), system N retention would decrease. However, if the added inorganic N were used within the system by periphyton, as it is in the model, neither export of inorganic N nor system N retention would be affected by increasing exchange. In fact, since the hyporheic zone in the model transforms organic N from the surface water into inorganic N, it is a sink for organic N, causing organic N export to decrease. Thus the system becomes more retentive of total N (organic + inorganic) as exchange with subsurface sediments increases. This is evident from the fact that in the model, steady state N in algal biomass increases with exchange; that is, the total amount of N stored in the reach increases. Thus interaction between hyporheic processes and surface stream processes may significantly increase whole system nutrient retention, even when the hyporheic zone is a source of inorganic nutrients (Fisher et al., 1998b). On a longer time scale, nutrients stored in the reach as algal biomass will eventually be exported during floods. However, temporary retardation of downstream movement of N (in any form) may also enhance conditions for denitrification (conversion of inorganic N to gaseous N_2), the only mechanism for permanent N removal.

5.2. Transient dynamics

The existence of steady state, or equilibrium, is suspect in any ecosystem, and desert streams are no exception, being particularly prone to disturbance by flooding and drought. Sycamore Creek experiences an average of 6 floods per year (Fisher and Grimm, 1988), most of which decimate the periphyton community through scour or burial by sediment deposition. Post-flood recovery is rapid. Periphyton biomass often returns to pre-flood levels within 30 days after spring or summer floods (Grimm and Fisher, 1989). In the model, the recovery of periphyton biomass to pre-disturbance levels took over 150 days when all parameters were unchanged by disturbance (i.e. they remained at steady-state values). Time to recover was reduced dramatically when upstream inputs of inorganic N were temporarily elevated by flooding (Fig. 8), suggesting that enhanced nutrient availability is an important factor in rapid post-flood recovery. This hypothesis was tested experimentally by Peterson et al. (1994) and was not supported, in that algae exposed to high nutrient concentration after manual scouring did not grow faster than algae exposed to low nutrient concentrations. The duration of exposure to elevated nutrient concentrations was very short, however (4 h). Further experimental work is needed to resolve the contradiction between the model and this result.

As was expected, processes occurring in the hyporheic zone affected the rate at which periphyton biomass recovered from disturbance. Changes

in the rate of exchange between surface and subsurface zones affected steady state N in periphyton biomass more dramatically than rate of recovery, whereas changes in the rates of biogeochemical processing in the hyporheic zone affected rate of recovery only, and not steady state N in biomass. For this model, all parameters were kept constant during post-flood recovery except upstream inputs of inorganic N. In reality, many parameters change over time after flooding, including stream discharge, rates of exchange between surface and subsurface zones (Valett et al., 1994; Jones et al., 1995b; Marti et al., 1997), and rates of mineralization and nitrification in subsurface sediments (Jones et al., 1995a). In late succession, increased mineralization may cause hyporheic sediments to become anaerobic, which would have large effects on nitrogen-transforming processes. In addition, although total dissolved organic N concentrations remain fairly constant over successional time (unpublished data), the amount of labile organic N should also increase as the periphyton community grows. Finally, the periphyton assemblage itself undergoes successional changes, moving from a community dominated by fast-growing diatoms, to filamentous green algae, to nitrogen-fixing cyanobacteria (Fisher and Grimm, 1991). Understanding of post-flood recovery would improve if future models could incorporate these temporal changes as well.

Another limitation of the model relates to the hydrologic connection between hyporheic zones and algal mats. In the model, nutrients from free-flowing water and from hyporheic sediments move into surface transient storage before being utilized by periphyton. As periphyton communities grow, self-limitation reduces the rate of nutrient uptake, regardless of the source of the nutrients. It seems likely that water moving out of sediments through algal mats might actually reduce the effects of self-limitation by diffusion in two ways: (1) by providing a source of nutrients to cells close to the sediment, as opposed to cells at the top of the mat; and (2) by increasing water movement through the mat. This would increase the importance of the subsurface zone as a source of nutrients for surface periphyton. On the other hand, growth of periphyton mats could also reduce the amount of exchange between surface transient storage and hyporheic sediments (K_{SH}) (Katznelson, 1989). More detailed modelling of the interactions between water flow, algal growth and nutrient uptake would be useful, particularly coupled with a spatially explicit approach.

6. Conclusion

A quantitative model simulating the effect of surface–subsurface interactions on periphyton growth and nitrogen dynamics in an arid land stream was developed. The model builds on an earlier model with two vertical components by including a third, subsurface component and shows that this component may be important to periphyton growth and to whole system nutrient retention. Results of model simulations were consistent with field observations, supporting a conceptual model of how surface periphyton communities interact with subsurface microorganisms through the recycling of nutrients. Results also support the suggestion that the importance of subsurface processes to whole system dynamics depends on the proportion of discharge passing through subsurface sediments and on rates of subsurface biogeochemical transformations.

Model simulations suggest that more empirical data are needed on organic matter quality, specifically on concentrations and transformations of labile organic pools. More empirical information on hydrologic connections and on effects of elevated N on algal recovery would also increase the understanding of the system. Future modelling work could benefit from taking a spatially explicit approach that incorporates localized exchange between different components of the stream ecosystem.

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