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A modelling study of discontinuous biological irrigation

by **Bernard P. Boudreau¹** and **Roberta L. Marinelli^{1,2}**

ABSTRACT

Irrigation of infaunal dwellings can lead to significant alteration of solute distributions in sediments. As a result, sediment-seawater fluxes of nutrients and dissolved carbon are greatly enhanced, and the biology of benthic communities is affected. The most realistic mathematical representation of irrigation and its effect on sediment geochemistry is Aller's (1980) cylinder model. One critical assumption of this model is that burrows are irrigated continually, and that burrow water solute concentrations are identical to overlying water concentrations at all times. However, the vast majority of infaunal tube- and burrow-dwelling organisms irrigate periodically, i.e. in an on/off cycle. During periodic irrigation, the solute concentration at the tube wall may vary between the limits imposed by the flux from the porewater and the concentration in the overlying water. We introduce modifications to the cylinder model which allow for periodic irrigation. We assess how periodic irrigation affects solute profiles and fluxes of two chemical constituents, silica and ammonium, for different population densities (distance between burrows) and organism sizes (burrow radii). Silica and ammonium follow first and zeroth order reaction kinetics, respectively, and illustrate the behavior of two general reaction classes.

Model results show that the effects of periodic irrigation vary with the class of reaction considered. For silica, radially-averaged profiles during discontinuous irrigation varied less than 15% from those with continuous irrigation for nearly all burrow sizes, burrow distances and reaction rate constants considered. However, we observed large temporal changes (as much as a factor of 6) in the areally-averaged silica flux over the irrigation cycle. Despite this time-dependence, the time-averaged silica flux was similar to that calculated for the continuous case. For ammonia, radially-averaged solute profiles were extremely sensitive to the duration of irrigation. In this case, the differences between discontinuous and continuous irrigation were greatest when the duration of irrigation was short (e.g. 5 min), and when the inter-burrow distance was small. As with silica, there was a strong time-dependence in areally-averaged ammonia flux when irrigation was periodic. However, the time-averaged ammonia flux is identical to the flux calculated for continuous irrigation. Our results suggest that irrigation behavior can affect the local burrow environment and this imposes a time dependence on solute fluxes.

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1. Introduction

Irrigation of infaunal dwellings by their residents is accomplished by the exchange of tube or burrow water with overlying water. Irrigation, also known as ventilation, is conducted primarily for respiratory exchange or food collection. This process can lead to significant alteration of oxidation-reduction conditions and interstitial solute profiles and can enhance greatly sediment-seawater fluxes of nutrients and dissolved carbon (e.g. Aller, 1977, 1980, 1982; Christensen *et al.*, 1984; Emerson *et al.*, 1984; Hines and Jones, 1985). As a result, irrigation also affects the ecology of sedimentary habitats and the magnitude of benthic-pelagic coupling. Higher abundances of microbes and meiofaunal-sized organisms are found in close association (millimeters) with irrigated burrows or tubes (Reise, 1981; Meyers *et al.*, 1987, 1988; Dobbs and Guckert, 1988). Macrofaunal aggregations may be driven by irrigation-induced alteration of sediment chemistry (Marinelli, 1994). The contribution of benthic remineralization to water column productivity is intimately related to the presence and activity of the benthic fauna (Zeitschel, 1980; Doering, 1989). Irrigation is most important in coastal and shelf environments where macroinfaunal abundances are relatively high, and benthic carbon cycling is most important (Berner, 1992). An examination of irrigation is, therefore, essential in understanding the biology and geochemistry of nearshore benthic environments.

The need to account quantitatively for irrigation effects has resulted in the development of different types of models to characterize the geochemistry of ventilated sediments (e.g. Aller, 1977; Goldhaber *et al.*, 1977; Smethie, 1981; Boudreau, 1984; Emerson *et al.*, 1984). To date the most realistic model is Aller's (1980, 1988) cylinder model. In this model, irrigated sediment is represented as a collection of packed, regular, hollow cylinders. The "center hollow" portion represents the tube or burrow and contains continuously irrigated water. The annular region surrounding this cylinder is the lateral sediment region whose chemistry is affected by irrigation of the burrow (Fig. 1). Solutes move through the porewaters only by molecular diffusion, but they can enter or leave the sediment both at the actual sediment-water interface and along the burrow wall. Thus, irrigation acts to increase the surface area available for exchange. Predicted profiles of solute concentrations using the cylinder model generally agree well with measured profiles from nearshore sediments (Aller, 1980; Aller and Yingst, 1985).

Below, we introduce and justify a modification to the cylinder model, one which addresses a potentially important behavior of infauna, i.e. temporally discontinuous irrigation. We assess how discontinuous irrigation affects solute gradients and sediment seawater fluxes of two porewater constituents, silica and ammonium. Silica dissolution and ammonium production represent two general classes of reactions, first and zeroth order respectively, and give insight into the behavior of other solutes with similar attributes. Finally, we examine how discontinuous irrigation affects both geochemical and ecological processes in nearshore sedimentary environments.

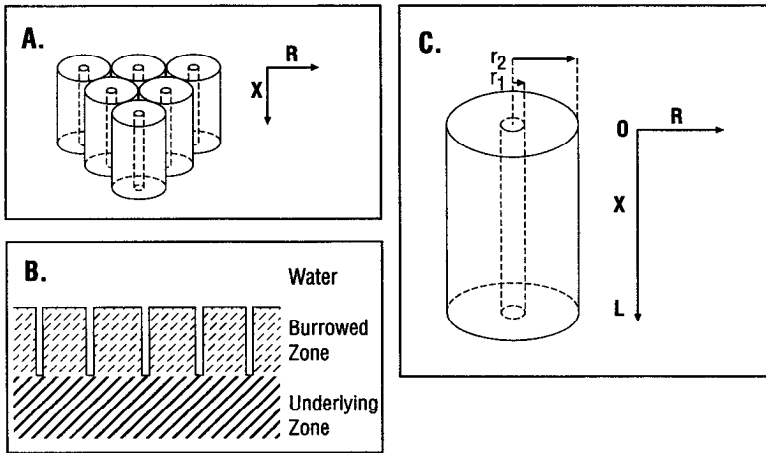


Figure 1. Schematic representation of Aller's packed-cylinder model for irrigated sediment. (A) Upper region of the sediment is idealized as a collection of packed annuli. (B) Vertical cut through the sediment showing the relationship between the irrigated and non-irrigated zone below. (C) Relationship between a typical burrow annulus and the cylindrical coordinate system used to describe it in Aller (1980). (Reproduced with permission of the author, the Geochemical Society and Pergamon Press.)

a. Mathematical description of the cylinder model with continuous irrigation. The cylinder model assumes that the burrow is radially symmetric, and uses a diffusion-reaction model in the cylindrical coordinate system to describe solute distributions in the annular sediment region as a function of time and space. For constant porosity, no adsorption or advection, and simple kinetics, the equation for a dissolved solute reads (Aller, 1980):

$$\frac{\partial C}{\partial t} = D'_s \frac{\partial^2 C}{\partial x^2} + \frac{D'_s}{r} \frac{\partial}{\partial r} \left(r \frac{\partial C}{\partial r} \right) + k_s (C_s - C) - R_o e^{-ax} + R_1 \quad (1)$$

where $C \equiv$ concentration of the dissolved solute, $x \equiv$ depth in sediment relative to the sediment-water interface, $r \equiv$ radial distance from the center of the tube/burrow, $t \equiv$ time, $D'_s \equiv$ molecular diffusion coefficient of the solute corrected for the effects of tortuosity, $k_s \equiv$ first-order dissolution rate constant, $C_s \equiv$ equilibrium concentration, R_o and $R_1 \equiv$ rates of consumption/production by reactions with spatial dependence only, and $a \equiv$ depth-attenuation coefficient.

The term on the left side of Eq. (1) accounts for net accumulation (or disappearance) of the solute with time. The first two terms on the right-hand side describe molecular diffusion in the porewaters, in the vertical and radial directions respectively. The next three terms allow for various reactions affecting the solute, i.e. $k_s(C_s - C)$ for first order reaction, $R_o e^{-ax}$ for attenuated zeroth-order reaction, and R_1 for un-attenuated zeroth-order reaction.

The first-order reaction indicates that a solute is produced (or consumed) when its local concentration, C , is different than some equilibrium value, C_s , that is usually dictated by thermodynamic and kinetic considerations. Consequently, this form of reaction is well suited to describe silica production by the dissolution of siliceous tests (Hurd, 1972). The zeroth-order reaction indicates a reaction rate independent of the concentration of the solute. The solute is simply the by-product of an irreversible reaction in which it does not participate as a reactant. Zeroth-order reactions are well suited to describe the production of the by-products of organic matter decomposition. Berner (1980) and Westrich and Berner (1984), amongst many others, have forcefully argued that microbial decomposition is well described by a first-order reaction in the organic matter concentration only. The by-products can affect this reaction indirectly (e.g. by promoting exclusion zones in the sediments for O_2 and SO_4^{2+} utilizers), but there is no direct involvement in the kinetics (Aller, 1980). Therefore, zeroth-order kinetics are reasonable descriptors of the production of ammonium and similar solutes.

A key element to the statement and solution of this model is the introduction of boundary and initial conditions. The boundary conditions employed by Aller (1980) are:

$$C = C_o \quad x = 0 \quad (2a)$$

$$C = C_o \quad r = r_1 \quad (2b)$$

$$\partial C / \partial r = 0 \quad r = r_2 \quad (2c)$$

$$\partial C / \partial x = B \quad x = L \quad (2d)$$

with an initial condition:

$$C = C_i \quad t = 0 \quad (3)$$

where $r_1 \equiv$ radius of the tube, $r_2 \equiv$ the outer radius of the sediment annulus, $L \equiv$ axial length of the tube, C_o and C_i are known constant concentrations and B is a prescribed gradient at $x = L$.

Just as each term in Eq. (1) has a physical or chemical interpretation, each boundary condition, Eqs. (2a) through (2d), has a meaning related to the biogeochemical behavior of the system being modelled. Specifically, Eq. (2a) states that the concentration at the sediment-water interface is held constant at all times. If C_o is set equal to the solute concentration in the overlying waters, then there is perfect, instantaneous exchange between porewater and overlying water, i.e. that the overlying waters are an infinite pool for the solute and that boundary layer effects (Boudreau and Guinasso, 1982; Dade, 1993) are ignored. Eq. (2b) implies that irrigation must be continuous, such that the concentration at the tube wall is always the same constant, C_o , again usually the overlying water value. Eq. (2c) says that

there is no diffusive flux of the solute across the outer surface of the sediment annulus, $r = r_2$, in the radial direction. Another identical annulus is assumed to exist on the other side of this surface so that the concentration field is a mirror image on the other side. Consequently, there is no net radial flux, and chemical modifications produced by an adjacent irrigated burrow do not interfere with the gradients established by the sediment annulus under consideration (Aller, 1988; Marinelli, 1994). Finally, Eq. (2d) allows for the existence of a flux of solute created by reactions below $x = L$.

We have reconsidered the boundary condition imposed by Eq. (2b), that of continuous irrigation, because it has broad biological significance and potentially important geochemical implications. The vast majority of infaunal tube- or burrow-dwelling polychaetes (e.g. members of the families Arenicolidae, Terebellidae, Onuphidae, Maldanidae, Nereidae) exhibit discontinuous irrigation (Wells, 1949; Dales, 1961; Mangum, 1964; Mangum and Sassaman, 1969; Kristensen, 1988), often as a result of internal timing (e.g. Wells, 1949) or external stimulation (e.g. Wells, 1951). As a result, during an irrigation cycle the solute concentration at the tube wall is likely to vary between the limits imposed by the flux from the porewater and the overlying water value. This observation is supported by previous studies, which have shown that the composition of tube water and sedimentary solutes adjacent to the tube wall, and fluxes from irrigated burrows, can vary measurably through an irrigation cycle (Kristensen, 1983; Meyers *et al.*, 1987, 1988; Kristensen *et al.*, 1991b; Forster and Graf, 1992). Unfortunately, the irrigation effects documented in these empirical studies may be species-, solute- or location-specific. There is no general model for assessing the effects of intermittent irrigation on solute profiles or fluxes for a variety of chemical reactions.

b. Description and solution of the discontinuous irrigation model. To extend the Aller model so that it describes periods of non-irrigation, it is necessary to account for the behavior of solutes in the tube ($0 \leq r \leq r_1$), as well as in the sediment porewaters. This necessitates some degree of approximation. As we are interested in the maximum effect(s) of periodic irrigation, we assume that during intervals of non-irrigation that the tube waters are stagnant, i.e. that free molecular diffusion is the only transport process acting in the tube waters. This ignores any mixing due to the movement of the tube dweller. In fact, we ignore altogether the presence of the organisms and assume that only water is present in the tube. We are fully aware of the shortcomings of this arrangement, but it allows calculation of maximal effects. During irrigation all tube water is replaced continuously with overlying water so that the solute concentration at every point in the tube is always the overlying value, C_o . The method of irrigation or direction of the irrigation current is unimportant.

Technically, we also treat periodic irrigation as if it were in phase for all burrows, i.e. each worm irrigates or rests at the same time. This assumption allows us to retain

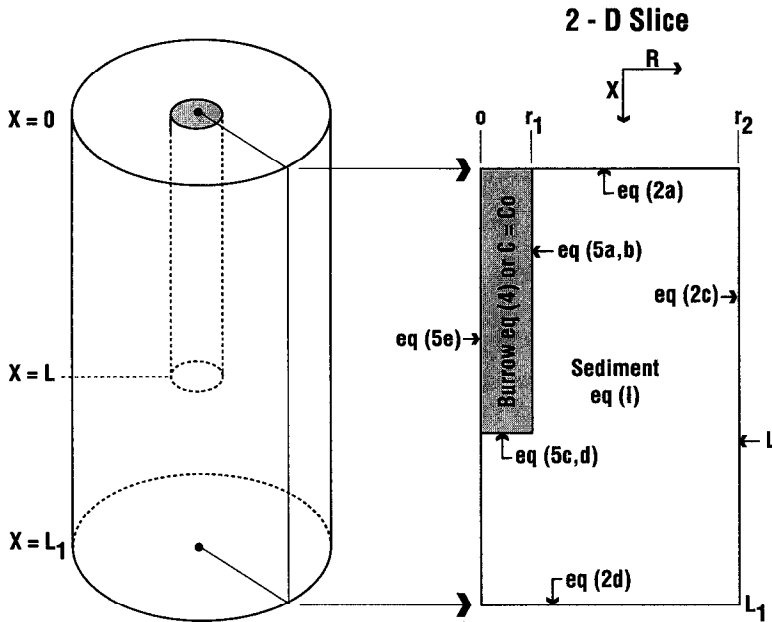


Figure 2. Schematic illustration of the modified cylindrical burrow-sediment region modelled in this study. The lower portion of the cylinder is extended to include 5 cm of underlying sediment. Eq. (1) governs solute conservation in the sediment region. Eq. (4) applies in the tube during non-irrigation periods. During irrigation, $C = C_o$. The surfaces on which the boundary conditions apply (Eqs. 2a–2d, 5a–5e) are also indicated.

boundary condition (2c). However, later calculations show that the effects of periodic irrigation decay rapidly from the burrow wall, so that Eq. (2c) is valid for all cases considered here, even if the irrigation is not in phase. On the other hand, the phasing of irrigation does have some consequences to the interpretation of the flux results.

In addition to the above, the vertical extent of the model domain, L_s , was extended 5 cm below the tube floor in order to capture the flux across the tube floor, i.e. $L_s = L + 5$ cm. All calculations were done with a tube 15 cm in length, so that $L_s = 20$ cm. Boundary condition (2d) is applied consequently at $x = L_s$.

Eq. (1) then describes solute behavior at all times in the sediment region: $r_1 \leq r \leq r_2$ for $0 \leq x \leq L$ and $0 \leq r \leq r_2$ for $L \leq x \leq L_s$ (Fig. 2). During non-irrigation, the solute concentration in the tube water ($0 \leq r \leq r_1$ and $0 \leq x \leq L$) is governed by the simplified equation:

$$\frac{\partial C}{\partial t} = D_s \frac{\partial^2 C}{\partial x^2} + \frac{D_s}{r} \frac{\partial}{\partial r} \left(r \frac{\partial C}{\partial r} \right) \tag{4}$$

where D_s is the free molecular diffusion coefficient of the solute. During irrigation

$C = C_o$ at all points in the tube. Along the tube-sediment interface (see Fig. 2), we assume that concentration and flux are continuous during non-irrigation periods:

$$(C(x \leq L, r_1, t))^+ = (C(x \leq L, r_1, t))^- \quad (5a)$$

with

$$\left(\varphi \theta^{-2} \frac{\partial C}{\partial r} \Big|_{r_1} \right)^+ = \left(\frac{\partial C}{\partial r} \Big|_{r_1} \right)^- \quad (x \leq L) \quad (5b)$$

and

$$(C(x = L, 0 \leq r \leq r_1, t))^+ = (C(x = L, 0 \leq r \leq r_1, t))^- \quad (5c)$$

with

$$\left(\varphi \theta^{-2} \frac{\partial C}{\partial x} \Big|_L \right)^+ = \left(\frac{\partial C}{\partial x} \Big|_L \right)^- \quad (0 \leq r \leq r_1) \quad (5d)$$

where θ is the tortuosity, φ is the porosity of the sediment (assumed constant), and the superscripts + and - indicate that a boundary is approached from larger or smaller values of x or r . Crossing the center line $r = 0$, the concentration is symmetrical in any radial direction, so:

$$\frac{\partial C}{\partial r} \Big|_{r=0} = 0 \quad (5e)$$

Otherwise, Eqs. (2a,b,c) are employed at the remaining boundaries. In writing Eqs. (5a-5d) we have ignored any specific effects on diffusive exchange due to the reduced/enhanced permeability of the burrow lining (see Aller, 1983), and any changes in reaction rates as a function of tube characteristics (Kristensen *et al.*, 1991a). While the latter may be important in simulating real data, the presence or absence of a tube lining of different geochemical characteristics is a secondary consideration in our comparative study.

The resulting model was solved by implicit operator-splitting finite-differences (Mitchell and Griffiths, 1980). The model was run for 10 days of model time, after which the initial transient had decayed and a simple periodic system cycling between irrigation and non-irrigation conditions had been established for each case, i.e. the concentration distributions at each step in an irrigation/non-irrigation cycle were identical regardless of which cycle we examined.

c. Parameter values. Aller (1980) has shown that solutes like silica that evolve from a first-order reaction, i.e. $R_o = R_1 = 0$ in Eq. (1), have a different response to irrigation than ammonium-like solutes that are produced/consumed by zeroth-order reactions,

i.e. $k_s = 0$. Therefore, we have examined the behavior of both types of solutes with respect to discontinuous irrigation.

Some aspects of our calculations were common to both types of solutes. In particular, irrigation was allowed to last for periods of 5, 15, 20, 30, 45 and 60 (continuous) minutes out of each hour. We believe these irrigation frequencies reflect reasonably natural frequencies (Wells, 1949; Dales, 1961; Kristensen, 1988). Various combinations of the tube radius, r_1 (i.e. 2 mm to 1 cm), and domain radius, r_2 (2 to 4 cm), were employed, and the tube floor, $x = L$, was set to 15 cm.

For examination of silica (first order reaction kinetics), we used parameter values consistent with those in Aller and Yingst (1985), i.e. $D_s = 8.33 \times 10^{-4} \text{ cm}^2 \text{ min}^{-1}$, $C_o = 0.12 \text{ mM}$, $C_s = 0.47 \text{ mM}$, $r_2 = 2\text{--}4 \text{ cm}$, $r_1 = 0.2\text{--}1.0 \text{ cm}$, and $R_0 = R_1 = 0$. The rate constant for dissolution, k_s , was permitted to vary between 0.14×10^{-1} and $0.14 \times 10^{-5} \text{ min}^{-1}$, a range which brackets the value in Aller and Yingst (1985). For examination of ammonium production (zeroth order reaction kinetics), we carried out calculations similar to those for silica, but with $R_o = k_s = 0$, $R_1 = 0.694 \text{ mM min}^{-1}$, $C_o = 0$, $C_i = 0.2 \text{ mM}$, and $B = 1.0 \times 10^{-2} \text{ mM cm}^{-1}$. This ammonium production rate is consistent with that measured by Aller and Yingst (1985) in their experiments.

2. Model results and discussion

Silica ($R_0 = R_1 = 0$). Aller's (1980) initial study of continuous irrigation determined that this process had little influence on the radially-averaged concentration profile of silica-like solutes. The radially-averaged concentration is the average concentration in a slice of sediment perpendicular to the axis of the tube or burrow, or mathematically,

$$\bar{C} = \frac{\int_{r_1}^{r_2} Cr dr}{r_2^2 - r_1^2} \quad (6)$$

(Aller also integrates over a finite sampling thickness in the x -direction, but this additional averaging is not needed for our study.) Our analysis shows that the radially-averaged silica distributions in periodically irrigated sediments are similar, although not identical, to those seen in the continuous irrigation case (Fig. 3). Of all parameters that were tested (r_1, r_2, k_s), a change in the radius of the sediment annulus (r_2), akin to high population abundances of organisms (*sensu* Aller, 1980), produced the largest difference between radially averaged silica profiles during continuous versus discontinuous irrigation (Figs. 3a–3d). When r_2 (cylinder size) was held constant and r_1 (burrow radius) was varied, there was little change in the predicted silica profiles for constant versus intermittent ventilation (Figs. 3c–3f). This effect may seem contradictory because, in the absolute sense, the effects of irrigation on solute exchange should be greatest where the surface area for exchange relative to the sediment volume is high. Thus, a change in r_1 might result in larger differences

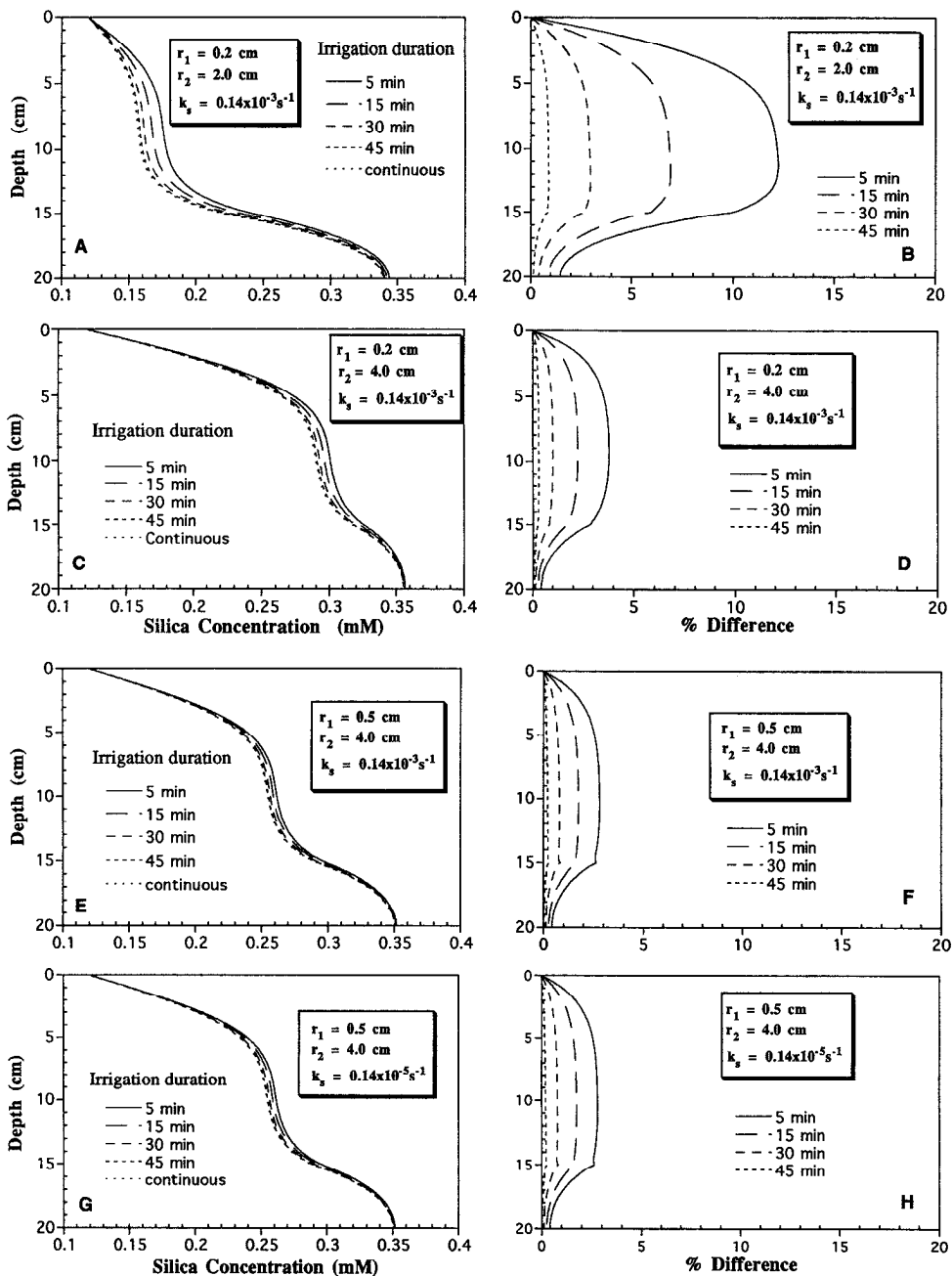


Figure 3. The left diagrams are plots of the radially-averaged concentration of silica versus depth for various combinations of r_1 , r_2 and k_s , with $L = 15$ cm, 55 minutes into an irrigation cycle. The plotted curves correspond to different durations of irrigation in the cycle, i.e. 5, 15, 30, 45 minutes in the cycle, as well as continuous irrigation. The right diagrams display the difference between the continuous and each discontinuous case in the corresponding diagram on the left. Other conditions used in these calculations were set to match those of Aller and Yingst (1985), i.e. $C_o = 0.12$ mM, $C_i = 0.361$ mM, $C_s = 0.47$ mM, and $B = 0$.

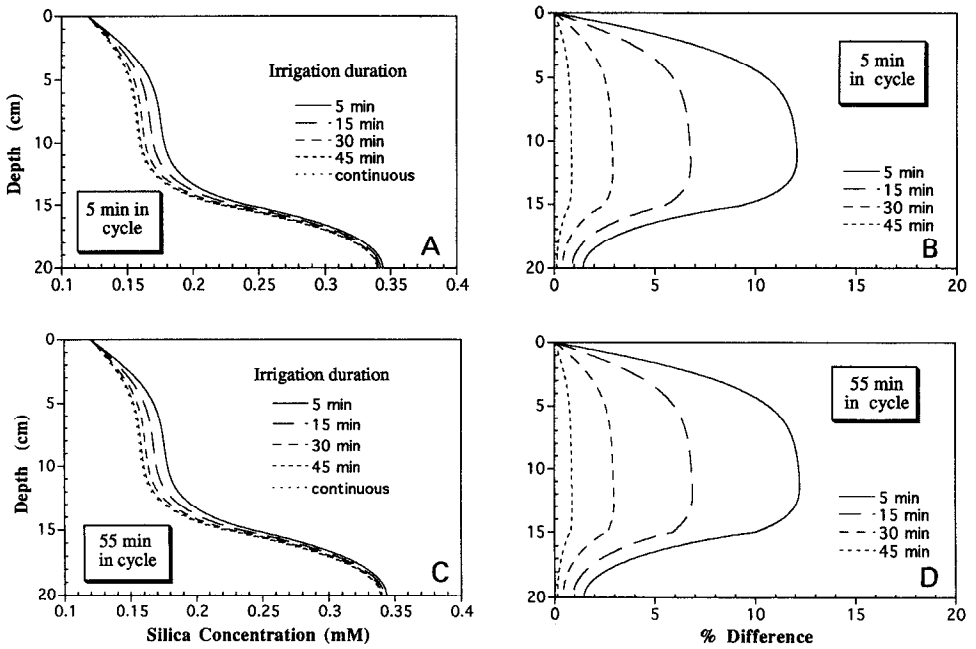


Figure 4. Diagrams similar to those of Figure 3 for silica, with $r_1 = 0.2$, $r_2 = 2.0$, $k_s = 0.14 \times 10^{-3} \text{ min}^{-1}$, and $L = 15 \text{ cm}$. The upper plots illustrate solute profiles and differences between continuous and discontinuous irrigation cases 5 minutes into an irrigation cycle. The lower plots illustrate solute profiles and differences between continuous and discontinuous irrigation cases 55 minutes into an irrigation cycle.

between discontinuous versus continuous irrigation if r_1 was large relative to r_2 . However, such combinations rarely occur in nature, i.e. we have never observed or read of large organisms with population densities high enough to warrant a test of these parameter combinations. Thus, for practical purposes, the silica gradients produced by intermittent irrigation vary most from the continuous irrigation case when the effective population abundance (*sensu* Aller, 1980) is high. Finally, model runs with different reaction rate constants showed slight differences in the absolute porewater silica concentrations, but little sensitivity to different irrigation frequencies (Figs. 3e–3h).

Our results also show that radially-averaged silica gradients arising from intermittent irrigation do not change markedly over the irrigation cycle. Model runs for different irrigation frequencies were examined at different times during an irrigation cycle. Silica profiles for all irrigation frequencies were nearly identical whether observed early (5 min) or late (55 min) into the hour-long irrigation cycle (Fig. 4).

This damped sensitivity to irrigation frequency is attributable, in part, to the restricted distance, δ , over which concentration fluctuations occur in the sediment during the irrigation cycle. This distance is approximately given by the Einstein

relationship:

$$\delta = (2D_s\tau)^{1/2} \quad (7)$$

where τ is the duration of the irrigation cycle, i.e. 60 min. Using the D_s value given above, δ is 0.3 cm. This represents a small fraction of even our smallest sediment thickness, i.e. $r_2 - r_1 = 1.8$ cm; thus, temporal variations affect only a small portion of the sediment, and the porewaters outside this zone reflect the time-averaged concentration along the burrow wall. For the irrigation frequencies we used, the differences between continuous and discontinuous cases are never more than 15%.

Additional insight can be gained from analysis of the first order reaction term $k_s(C_s - C_o)$ using the parameter values assigned to model runs. For silica dissolution to be sensitive to irrigation frequency, silica concentrations in tube water would have to approach the apparent saturation concentration C_s relatively soon after irrigation ceased. For $k_s = 0.14 \times 10^{-1}$ (the highest reaction rate constant used in model runs), $C_s = 0.47$ mM, $C_o = 0.12$, and a non-irrigation period of 55 min, the maximum amount of silica dissolution would be 0.27 mM. This value is well below the apparent saturation value of 0.47 mM. These calculations show that intermittent irrigation significantly affects radially-averaged silica profiles only if (1) the dissolution rate constant is large and if C_s and C_o are close in value or (2) the duration of non-irrigation is much longer than those tested here. We consider both of those tenets unrealistic in light of reported values for silica concentrations and dissolution rates (Aller and Benninger, 1981; Emerson *et al.*, 1984; Helder and Anderson, 1987), and irrigation behaviors for organisms in nearshore environments (Wells, 1949; Dales, 1961; Mangum, 1964; Mangum and Sassaman, 1969; Kristensen, 1988).

Aller (1980) established that the effects of continuous irrigation on silica are most noticeable in the flux across the sediment-water interface. Here, we define the interfacial flux for a single annulus (burrow) as the amount of dissolved solute crossing the sediment-water interface and the burrow wall and floor per unit time per unit area. To determine nature of the modifications due to discontinuous irrigation, we also calculated the total flux of silica, J_T , across the sediment-water and burrow-water interfaces (modified from Aller, 1980):

$$J_T = J_L + J_r + J_0 \quad (8)$$

where

$$J_L = \frac{2A_L}{A_T r_1^2} \varphi D_s \int_0^{r_1} \frac{\partial C}{\partial x} \Big|_{x=L} r dr \quad (9a)$$

$$J_r = \frac{A_r}{A_T L} \varphi D_s \int_0^L \frac{\partial C}{\partial r} \Big|_{r=r_1} dx \quad (9b)$$

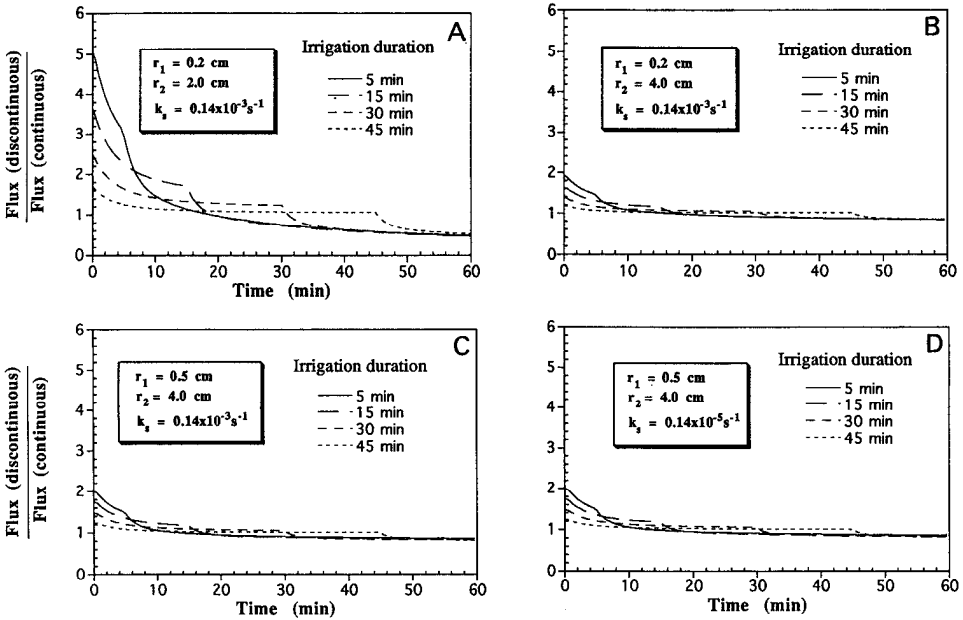


Figure 5. A plot of the ratio of the instantaneous total flux of silica from an annulus, J_T , with discontinuous irrigation to that with continuous irrigation versus the time elapsed from the beginning of an irrigation cycle. Plots are for various combinations of r_1 , r_2 and k_s , with $L = 15$ cm. The irrigation occurs at the beginning of the cycle, and lasts for the times indicated in the key for the plotted curves.

and

$$J_0 = \frac{A_0}{A_T \left(\frac{r_2^2}{2} - \frac{r_1^2}{2} \right)} \varphi D_s \int_{r_1}^{r_2} \frac{\partial C}{\partial x} \Big|_{x=0} r dr \tag{9c}$$

with $A_L \equiv$ area of the tube floor, $A_r \equiv$ area of the tube wall, $A_0 \equiv$ area of the annular region at the sediment-water interface ($x = 0$ and $r_1 \leq r \leq r_2$), and $A_T \equiv A_L + A_r + A_0$.

The results of our calculations point toward two seemingly contradictory conclusions. First, the magnitude of the flux can change appreciably during the course of an irrigation cycle. Figure 5 illustrates the ratio of the J_T with various periods of non-irrigation to the J_T with continuous irrigation through an irrigation cycle. With long quiescent periods and small annular regions (r_2), fluxes can vary by as much as a factor of 6 through the cycle (e.g. Fig. 5a and 5b). However, neither burrow radius (r_1) nor the reaction rate constant (k_s) significantly affected the relative fluxes in discontinuous versus continuous irrigation (Fig. 5b–5d). For most cases we studied, the mean variation in fluxes through the cycle was between a factor of 2 to 3.

These large temporal changes in fluxes are due to silica build up in the porewaters and the burrow during long periods of non-irrigation; consequently, the flux at the burrow wall falls. When irrigation begins, the concentration in the tube water is immediately changed to that of the overlying waters. However, the porewater concentrations adjacent to the tube reflect the previous non-irrigated conditions, which results in a strong gradient across the tube wall and, therefore, a large flux. The flux is set by the local gradient on the sediment-side of the burrow wall, i.e. within the distance δ calculated above. The changes in concentration within δ of the burrow wall do change appreciably with the irrigation cycle, even if the radially averaged concentration is nearly constant (e.g. Fig. 3).

In contrast to the large changes that can occur in silica fluxes at a given time over an irrigation cycle, we have found that the time-averaged flux over the irrigation cycle, \bar{J}_T , i.e.

$$\bar{J}_T = \frac{1}{\tau} \int_t^{t+\tau} J_T dt' \quad (10)$$

is essentially equal to the flux predicted by the continuous-irrigation model, irrespective of the duration of the non-irrigation period tested. In Eq. (10), t in the integration limit is an arbitrary time and t' is a dummy variable. The mean flux \bar{J}_T represents the area under each curve in Figure 5, and these areas are within 15% of one another. This is true for all r_1 , r_2 and k_s values tested in our calculations. The extra flux at the beginning of periodic irrigation nearly balances out the lower than average flux during the quiescent period to produce virtually the same average flux as in the continuous irrigation case.

Ammonium ($R_o = k_s = 0$). Aller (1980) concluded that the behavior of ammonium and other solutes (e.g. phosphate) produced by zeroth-order reactions (i.e. independent of their own concentration) is different from that of silica for continuous irrigation. Specifically, the radially-averaged concentrations of ammonium-like solutes are quite sensitive to the spacing and sizes of burrows. Conversely, the interfacial fluxes of such species are not dependent on the irrigation process.

Our model results suggest that the duration of irrigation has an appreciable impact on the \bar{C} changes with depth (Figs. 6–8). The magnitude of the effect varies with the parameter values. In each of Figures 6–8, the two left diagrams plot \bar{C} with depth for irrigation that lasts 5 min each hour in the top diagram, and 20 min each hour in the bottom diagram. The four plotted curves in each of these two diagrams represent \bar{C} depth profiles at 5, 30 and 55 minutes into the irrigation/non-irrigation cycle, as well as when irrigation is continuous in time. (The curves are superimposed in some of the diagrams.) The right diagrams in each of these figures are plots of the percent difference between the continuous profile and each of the three \bar{C} profiles for discontinuous irrigation from the diagram to their immediate left. These figures

$$r_1 = 0.1 \text{ cm } r_2 = 1.0 \text{ cm}$$

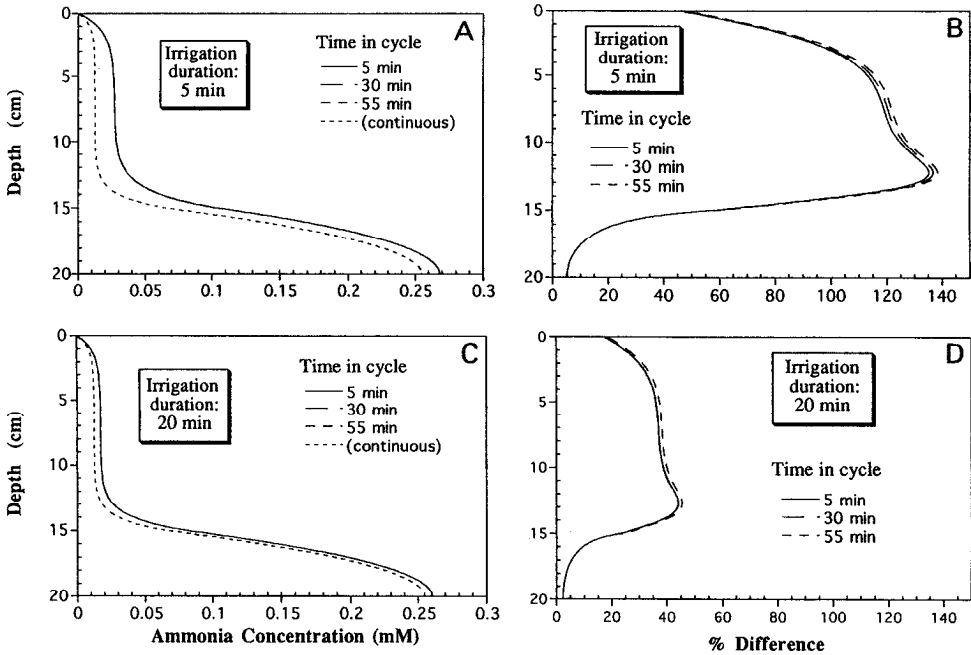


Figure 6. The two left diagrams are plots of the radially-averaged concentration of ammonium versus depth with $r_1 = 0.1 \text{ cm}$, $r_2 = 1.0 \text{ cm}$, $L = 15 \text{ cm}$, $R_o = 0.694 \text{ mM min}^{-1}$ and $R_1 = k_s = 0$. The right diagrams display the difference between the continuous and each discontinuous case in the corresponding diagram on the left. The two upper plots illustrate the conditions when irrigation lasts 5 minutes of every 60 min irrigation cycle, while the bottom plots represent conditions with 20 minute irrigation in the same cycle. The plotted curves correspond to different times in the irrigation cycle, i.e. 5, 15, 30, 55 minutes into the cycle, as well as the curve with continuous irrigation. Other conditions used in these calculations were set to match those of Aller and Yingst (1985), i.e. $C_o = 0.0 \text{ mM}$, and $C_i = 0.2 \text{ mM}$.

illustrate the effects of changing the burrow radius, r_1 , the average domain size, r_2 , and the duration of irrigation, within an irrigation cycle. They represent only a fraction of the cases we ran, but illustrate salient trends. Some specific findings include:

1) Radially-averaged concentrations are higher at any depth with shorter duration of irrigation, an expected result (Fig. 6). More solute is trapped in the sediment with less irrigation. As the duration of irrigation increases, the radially-averaged profiles approach those of the continuous irrigation case.

2) The percent difference in \bar{C} between continuous irrigation and discontinuous irrigation cases increases with increasing values of the burrow radius, r_1 (Fig. 7 vs.

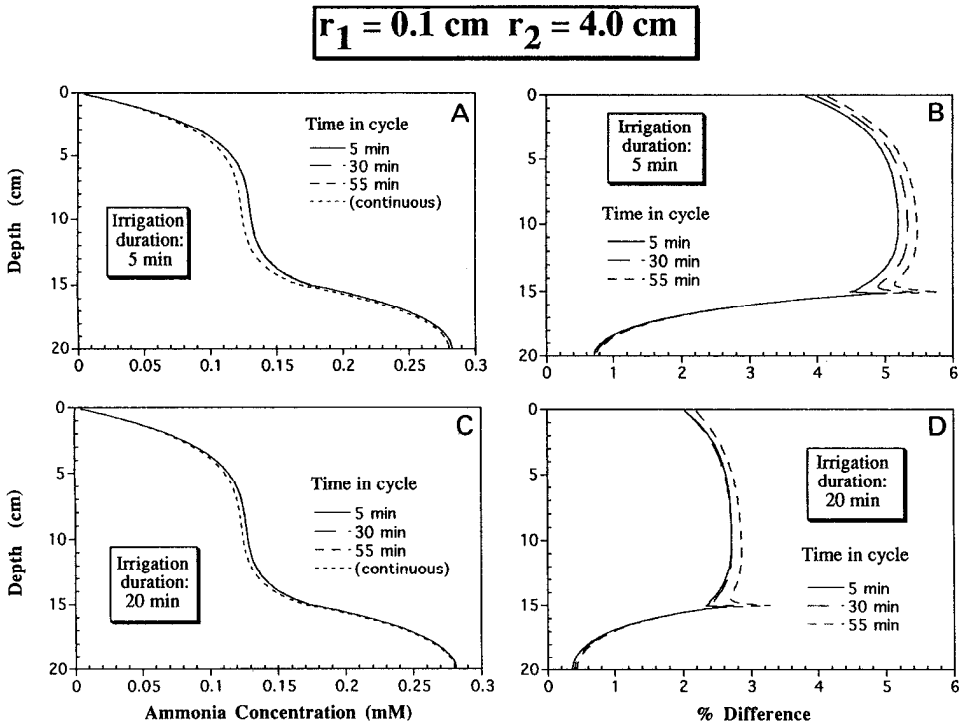


Figure 7. As in Figure 6, but with $r_1 = 0.1 \text{ cm}$, and $r_2 = 4.0 \text{ cm}$. All other parameter values are the same.

Fig. 8), and decreasing values of the sediment annulus size, r_2 (Fig. 6 vs. Fig. 7). The effect is most pronounced for changes in r_2 . As the sediment domain decreases, exchange at the burrow/tube wall plays a proportionately larger role in controlling exchange to the overlying waters. If irrigation removes materials only part of the time, solute will accumulate. As with silica, a change in r_1 might result in larger differences between discontinuous versus continuous irrigation if r_1 was large relative to r_2 . However, as we argued previously, it is more common to observe closely spaced small individuals, rather than densely packed large organisms. Thus, in nature, the effects of discontinuous irrigation on ammonium gradients are most noticeable when the spacings between organisms is small.

3) There are only small differences in the radially-averaged concentrations at each depth through an irrigation cycle for a given set of parameter values. This is a reflection of the small diffusion distances involved in responding to periodic irrigation.

The reason for the difference in the response of radially-averaged concentration profiles of silica and ammonium to continuous irrigation has been briefly addressed

$$r_1 = 0.2 \text{ cm} \quad r_2 = 4.0 \text{ cm}$$

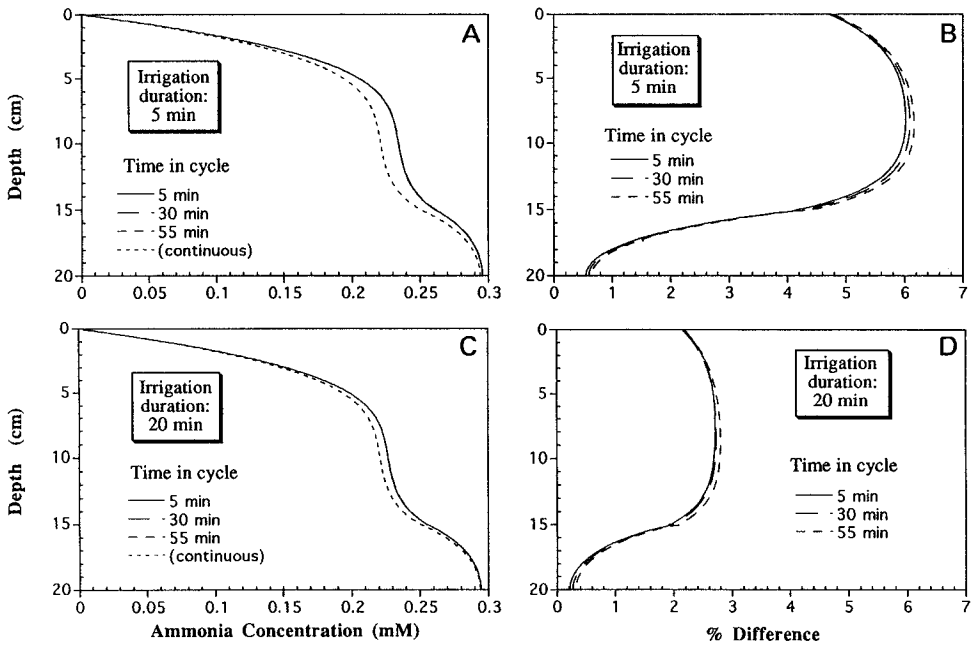


Figure 8. As in Figures 6 and 7, but with $r_1 = 0.2 \text{ cm}$, and $r_2 = 4.0 \text{ cm}$. All other parameter values are the same.

by Aller (1980). He points out that the total flux of each species is related to the total (integrated) production of these solutes. For ammonium, the total production is a fixed quantity, i.e. it is proportional to $\varphi(R_o/a + R_1L)$. This means that the flux is a fixed quantity; thus the concentration distribution in space must adjust itself to give this same flux if the number and spacing of the burrows is altered. Conversely, the total production of silica is not prescribed but feeds back dynamically to the gradient. Higher intensities of irrigation mean higher rates of removal, but that results in higher rates of dissolution (silica production occurring via a first-order reaction). The two effects balance out in terms of concentration profiles. Consequently, irrigation appears to have a smaller effect on the silica distributions but seriously affects silica fluxes.

A similar mechanism also explains the differences when the irrigation is periodic. With zeroth-order ammonium production, the total flux, Eq. (8) above, is again a set constant. Regardless of the irrigation frequency, the total flux over the irrigation cycle, \bar{J}_7 , through the top boundary and the tube wall and floor is a prescribed constant. This can be proved mathematically by integrating Eq. (1) with $k_s = 0$ over the sediment area of interest (i.e. $r_1 \leq r \leq r_2$ and $0 \leq x \leq L$, and $0 \leq r \leq r_2$ and

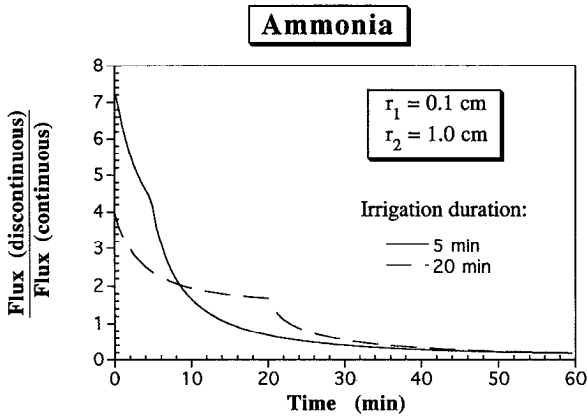


Figure 9. A plot of the ratio of the instantaneous total flux of ammonia from an annulus, J_T , with discontinuous irrigation to that with continuous irrigation versus the time elapsed from the beginning of an irrigation cycle. The irrigation occurs at the beginning of the cycle, and lasts for the times indicated in the key for the plotted curves. Conditions are those of Figure 6 (i.e. $r_1 = 0.1$ cm and $r_2 = 1$ cm).

$L \leq x \leq L_s$) and over an arbitrary irrigation cycle. The result is:

$$D'_s \int_t^{t+\tau} \left(\int_0^L r_1 \frac{\partial C}{\partial r} \Big|_{r_1} dx + \int_0^{r_1} r \frac{\partial C}{\partial x} \Big|_L dr + \left| \int_{r_1}^{r_2} r \frac{\partial C}{\partial x} \Big|_0 dr \right) dt \tag{11}$$

$$= \left(\frac{R_o}{a} (1 - e^{-aL_1}) + R_1 L \right) \left(\frac{r_2^2 - r_1^2}{2} \right) \tau + \left(\frac{R_o}{a} (e^{-aL_1} - e^{-aL}) + R_1 (L_1 - L) \right) \frac{\tau r_2^2}{2} .$$

The left side of Eq. (11) contains the components of total flux that must balance the total production on the right side of this equation. The total flux is then related to the local gradients along the top boundary, the tube wall and the tube floor. If the flux is prescribed, then gradients during non-irrigation must steepen (relative to gradients during continuous irrigation) in order to remove the required amount of ammonium during the shorter period of irrigation. Steeper gradients will result in higher sediment ammonium concentrations, as seen in our model results (Figs. 6–8). Similar behavior is not seen for silica because silica dissolution is dynamically determined. Thus, the frequency of irrigation has only modest effect on their distributions.

Finally, the relative change in the fluxes of ammonium-like solutes through the cycle are illustrated in Figure 9 for the parameter values used to calculate Figure 6. As in the case of silica, there is a large change in the magnitude of the flux with time, but the integrated flux (the area under each curve) is the same as in the continuous irrigation case.

3. Summary and conclusions

Aller's (1980) work shows elegantly that irrigation effects on porewater gradients and fluxes depend greatly on the sizes and spacings of organisms, and the behavior of porewater solutes. Our modelling study indicates an additional dependence on the irrigation behavior of tube-dwelling organisms. As with continuous irrigation, the effects of periodic irrigation vary with the type of solute in question and the property of the solute that is being considered, i.e. depth distribution versus interfacial flux. The depth distributions of solutes like ammonium, that are produced by zeroth-order reactions, can be quite sensitive to the duration of irrigation. Conversely, distributions of solutes like silica, that are produced by first-order reactions, are little influenced by any periodic character to the irrigation. For silica, the difference between continuous and discontinuous irrigation on radially averaged depth profiles was never more than 15%. For ammonium, differences could be >100%. In both cases, radially-averaged profiles produced by intermittent irrigation differ most from those produced by continuous irrigation when the sediment domain (r_2) is small. This situation arises in nature when population densities of irrigating organisms are high.

Our analyses also reveal the nature of temporal changes in radially-averaged profiles and fluxes through an irrigation cycle. In general, there is little variation in radially-averaged profiles of silica or ammonium through the irrigation cycle, due largely to the restricted distance over which concentration fluctuations occur in the sediment during the irrigation cycle. Conversely, there is strong temporal variation in the *instantaneous* flux of both types of solutes within an irrigation/nonirrigation cycle. Despite this variation, the *integrated* flux through the periodic irrigation cycle is always within 15% of the continuous irrigation case. Thus, intermittent irrigation has a strong temporal signature, but the average signal differs little from that produced by continuous irrigation.

These findings have important implications for solute measurement, transport and modelling. First, sampling duration becomes an important consideration in flux measurements. The results in Figures 5 and 9 require that sampling of inphase burrows be done over a period of many irrigation cycles. Sampling of natural burrows with out-of-phase irrigation depends on the number of tubes sampled. Specifically, if the density of burrows is such that no more than a few burrows are sampled, then the device should be deployed over many irrigation cycles. Given the range of irrigation/nonirrigation cycles reported in the literature (1–2 hours), the average duration of flux chamber deployments should exceed this value by at least fivefold. This is particularly relevant when the duration of irrigation is small relative to the non-irrigation period. Conversely, sampling a large number of out-of-phase burrows will allow spatial integration to replace partially temporal integration. Shorter sampling times would be needed. The caveat is that it is not always easy to know the number of active tubes being sampled and if they are out-of-phase; as a result, it is much safer to measure fluxes over many irrigation cycles.

Second, if total, time-averaged fluxes are virtually insensitive to irrigation frequency, as our model suggests, then solute exchange across the sediment-water interface, and the magnitude of benthic-pelagic coupling, is independent of irrigation behavior. However, other attributes of the benthic fauna, e.g. their feeding behavior (Marinelli, 1992), exhibit strong controls on benthic-pelagic exchange. Thus, the composition of the fauna is still an important component in the assessment of material exchange between the sediments and water column. Finally, the continuous irrigation model (Aller, 1980) provides accurate predictions of time-averaged flux, regardless of irrigation frequency. The continuous irrigation model has one major advantage over the discontinuous irrigation formulation. The former has a relatively simple analytical solution and provides reasonably rapid results.

Our model results have additional implications regarding the behavior and distribution of benthic microbes and meiofauna. A number of small (< 1 mm) organisms live in close association with irrigated burrows and tubes (e.g. Reise, 1981; Meyers *et al.*, 1987; 1988). The discontinuous irrigation model suggests that gradients within a small distance of the burrow or tube wall experience the greatest concentration fluctuations and are most affected by changes in irrigation frequency. Thus, the local sedimentary environment around the tube of a frequent irrigator is likely to differ greatly from that of an infrequent irrigator, particularly for solutes following zeroth order kinetics. Given this difference, we suspect that microbial and meiofaunal communities near irrigated burrows may in part reflect differences in macrofaunal irrigation behavior. Thus, irrigation frequency of the infauna, as well as tube composition and exudates, may impact the character of the microbial and meiofaunal assemblage associated with irrigated burrows or tubes.

Finally, our results point to a number of strategies that macrofauna may adopt to cope with porewater conditions common in nearshore environments. Aller (1980) has suggested that organisms might space themselves more closely (reduce r_2 , see Marinelli, 1994) or build larger burrows (increase r_1) to reduce the buildup of noxious solutes like ammonium in their environment. While our results support these conclusions, they suggest additional opportunities provided, or constraints imposed, by irrigation behavior. For example, model results show that porewater ammonium concentrations are lower when the irrigation duration is long. Thus, infauna may benefit not only by reducing the interburrow distance, but also, by increasing the amount of time spent irrigating. For some organisms, this may not be an option, i.e. irrigation is controlled by an internal rhythm, or longer irrigation is too costly. In such cases, it may be most beneficial for these organisms to live near frequent irrigators. While these musings are speculative, they highlight the potential role of irrigation behavior in structuring the composition of benthic environments. Future studies should include geochemical processes, in addition to more traditional biological processes, in assessing the ecology of sedimentary environments.

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