# THE EFFECTS OF DRYING AND RE-FLOODING ON THE SEDIMENT AND SOIL NUTRIENT DYNAMICS OF LOWLAND RIVER–FLOODPLAIN SYSTEMS: A SYNTHESIS

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## ABSTRACT

Lowland river–floodplain systems are characterized by a high degree of variability in both the frequency and period of inundation of various parts of the floodplain. Such variation should profoundly affect the processes underlying nutrient transformations in these systems. This paper explores the effect of various hydrologic regimes on nutrient cycles. Partial drying of wet (previously inundated) sediments will result in an increased sediment affinity for phosphorus and will produce a zone for nitrification coupled with denitrification. Hence, partial drying may reduce the availability of nitrogen (N) and phosphorus (P). Conversely, complete desiccation of sediments may lead to the death of bacteria (and subsequent mineralization of N and P), a decrease in the affinity of P for iron minerals, a decrease in microbial activity and a cessation of all anaerobic bacterial processes (e.g. denitrification). Colonization of exposed sediments by terrestrial plants may lead to N and P moving from the sediments to plant biomass. Re-wetting of desiccated soils and sediments will result in an initial flush of available N and P (which can be incorporated into bacterial or macrophyte biomass), coupled with an increase in bacterial activity, particularly nitrification. Inundation of floodplain soils will result in the liberation of C, N and P from leaf litter and floodplain soils. This will result in an increase in productivity, which ultimately may lead to the onset of anoxia in floodplain soils and, consequently, an increase in anoxic bacterial processes such as P release and denitrification. Copyright © 2000 John Wiley & Sons, Ltd.

KEY WORDS: drought; flood; floodplain; nitrogen; nutrients; phosphorus; sediment; soil

## INTRODUCTION

Lowland river–floodplain systems are characterized by a high degree of variability in both the frequency and period of inundation of the various morphological elements of the system. Some elements of the system (e.g. the main channel and deeper parts of some floodplain lakes) may remain inundated under all but the most extreme drought conditions. Conversely, some of the higher parts of the floodplain may be inundated for only a few days or weeks over a period of many decades. The flooding and drying patterns for many lowland systems have changed as a consequence of river regulation. Furthermore, climate change caused by global warming is expected to further alter the flow regimes, of both regulated and unregulated rivers (Thomas and Brandt, 1994; Pierce, 1996; Gregory *et al.*, 1997).

Variations in hydrology may have a profound effect on the processes responsible for nutrient cycling in lowland river–floodplain systems. In this paper an overview is presented of the potential effects that varying the hydrological regime has on the cycling of nitrogen (N) and phosphorus (P) in these systems. In particular, the potential effects of four different hydrological regimes on N and P cycling are examined, viz. (i) N and P cycling in sediments which usually remain inundated (i.e. the river channel or floodplain lakes); (ii) the effects of exposure to air and desiccation on nutrient dynamics in sediment and floodplain soils; (iii) the consequences of re-wetting dried sediment and soils by rain events; and (iv) the effects of inundation of soil as a consequence of flooding.

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This paper is not intended to be a comprehensive review of the effects of wetting and drying on nutrient dynamics. Rather, the intention is to stimulate research interest in this under-represented aspect of floodplain ecology. It is imperative to understand the effects of wetting and drying on nutrient cycling in floodplain ecosystems if we are to have the capacity to make effective management decisions.

There are surprisingly few data on nutrient dynamics in floodplain–river systems (Pinay et al., 1992; Spink et al., 1998). Therefore, in developing this synthesis, the authors have relied heavily on the soil literature (particularly studies on nutrient dynamics in flooded soils such as rice paddies, and studies on the effects of soil drying on nutrient analysis) and, to a lesser extent, on recent research on sediment–nutrient dynamics in wetlands and reservoirs.

In this paper soils and sediments are arbitrarily differentiated by the period of submergence. For the purposes of this paper sediments are inundated for the most part and are rarely exposed to the air, while soils are exposed to the air for longer periods than they are inundated. It is recognized that this definition is not ideal. For example, sediments on the edges of (particularly ephemeral) floodplain lakes may be exposed to the air for significant periods of time while some subsoils may lie permanently beneath the watertable.

## NUTRIENT DYNAMICS IN SUBMERGED SEDIMENTS

### Phosphorus cycle

In non-calcareous sediments, P dynamics are closely related to the cycling of iron (Fe). A stylized representation of the Fe–P cycle in freshwater ecosystems is presented in Figure 1 which shows that orthophosphate (i.e. phosphate, $PO_4^{3-}$) is liberated predominantly from the anoxic part of the sediments. Once released, the P can either be sequestered by biota or by amorphous Fe particles in either the overlying oxic sediments (if present) or the oxic part of the water column.

There is still some conjecture about the mechanisms responsible for P release from the anaerobic part of the sediments; however, it is becoming increasingly obvious that the microbiota are responsible for a significant proportion of this release (e.g. Baldwin et al., 1997; Roden and Edmonds, 1997). A number of mechanisms have been postulated for this P release, including iron reduction, sulphate reduction, polyphosphate hydrolysis and other processes.

During iron reduction, iron-reducing bacteria use Fe(III) oxides and oxyhydroxides as the terminal electron acceptors for anaerobic respiration. In other words these bacteria catalyse the reduction of solid ferric minerals to dissolved ferrous ions. Any phosphate ions that are associated with the solid mineral surface will be released when the surface is reduced (see Figure 1). It has been shown by Lovley et al. (1991) that Fe(III) reduction in sediments is almost entirely mediated by bacteria. However, recent work by Roden and Edmonds (1997) suggests that much of the P released by the reduction of Fe(III) phases may form insoluble complexes with Fe(II) (e.g. vivianite). Roden and Edmonds (1997) contend that P can



Figure 1. The interaction of Fe and P in aquatic sediments (modified after Baldwin et al., 1997); subscript 's' indicates a solid phase

be displaced from these insoluble ferrous phosphates by sulphide ($S^{2-}$) produced as a consequence of sulphate reduction (see below).

Sulphate has been linked with the release of P from many aquatic systems (e.g. Boström *et al.*, 1988; Caraco *et al.*, 1989). Sulphate reducing bacteria use the sulphate ion ($SO_4^{2-}$) as the terminal electron acceptor for anaerobic respiration. The respiratory end product of this reaction is hydrogen sulphide. Sulphide is a strong enough reducing agent to facilitate the reduction of solid ferric minerals to dissolved ferrous ions with concurrent P release (Boström *et al.*, 1988). This reaction is favoured by the insolubility of one of the reaction products, iron sulphide (FeS). As noted above, it has been suggested that $S^{2-}$ can also displace P from insoluble Fe(II) phases (Roden and Edmonds, 1997)—again, the reaction being favoured by the insolubility of the reaction product, FeS.

A number of authors have suggested that bacteria containing polyphosphates (poly-P) as P storage products can hydrolyse these compounds to phosphate under anaerobic conditions, releasing P (Gächter *et al.*, 1988; Davelaar, 1993; Gächter and Meyer, 1993). It has been postulated that under anaerobic conditions these bacteria take up low molecular weight fatty acids, particularly acetate which is first protonated outside the bacterial cell (Wentzel *et al.*, 1986). This acetic acid is taken up by the cell; the acetate is metabolized in the synthesis of poly-$\beta$-hydroxybutyrate (PHB); the excess proton associated with acetic acid is then excluded from the cell as a protonated phosphate ion.

A number of other processes may lead to P mobilization from sediments. Some sediment and soil bacteria are known to produce compounds which have an extremely high affinity for Fe—siderophores (Fett *et al.*, 1998). The siderophores can mobilize Fe from Fe-containing mineral phases (e.g. Hersman *et al.*, 1995), with concurrent release of any P associated with the Fe. Phosphate can also be released from the hydrolysis of organic P compounds. Organic P hydrolysis can be facilitated either by exo-enzymes such as phosphatase (Cembella *et al.*, 1984) and nucleotidases (Azam and Hodson, 1977) which are produced by microorganisms, or, conversely, abiotically by Al, Fe and Mn mineral phases (Baldwin *et al.*, 1995).

*Nitrogen cycle*

A stylized version of the aquatic N cycle is presented in Figure 2. Like the P cycle, the cycling of N is predominantly mediated by bacteria, although there is some evidence that mineral phases such as Mn may play some role (Luther *et al.*, 1997). Furthermore, as in the P cycle, different reactions occur in the oxic and anoxic phases of the sediment. In the oxic part of the sediment, ammonia, produced through the mineralization of organic matter, can be converted to nitrate (via nitrite) by bacterial action, i.e. nitrification. The ammonia also can be either taken up by algae, or, if the pH is sufficiently high, lost to the atmosphere through volatilization (Reddy and Patrick, 1986). In the anoxic part of the sediment, nitrate can either be reduced back to ammonia (dissimilatory nitrate reduction to ammonia) or converted to N gas (denitrification). Dissimilatory nitrate reduction to ammonia (DNRA) preserves N in the system.
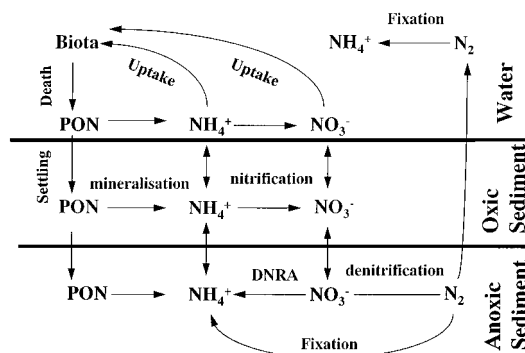


Figure 2. The nitrogen cycle in aquatic systems (modified after Rysgaard *et al.*, 1993) (PON, particulate organic nitrogen)

However, because $N_2$ gas has a low solubility in water, denitrification is a pathway for the removal of N from aquatic systems. This is particularly important if nitrification and denitrification are coupled (i.e. the two processes occur spatially close to each other) because the nitrate produced in nitrification can be quickly converted to N gas rather than being assimilated into biomass. Coupled nitrification–denitrification has to occur at the boundary of oxic and anoxic environments. Such boundaries can be found in microsites within the oxic part of the sediment (Gottschal, 1986), or in the rhizosphere of plants (Reddy et al., 1989; Boon and Sorrell, 1991).

## EFFECTS OF EXPOSURE TO AIR AND DESICCATION ON NUTRIENT DYNAMICS

From the previous section it is obvious that nutrient cycling in aquatic systems is dependent on three interrelated factors: (i) the oxygen status of the environment; (ii) the nature of the inorganic matrix (mineralogy of the environment); and (iii) the microbial consortium present. Desiccation has been reported to alter the chemistry (e.g. De Groot and Van Wijck, 1993) and mineralogy (e.g. Baldwin, 1996) of the sediment or soil and kills up to three-quarters of the microbes (e.g. Qiu and McComb, 1995). Clearly, each of these factors will be affected if sediments that were previously inundated are first exposed to air and then desiccated. However, surprisingly little research has been conducted on the effect of *in situ* drying on N and P cycles in either sediments or soils. With some exceptions (see later), almost all of our knowledge of the effects of drying is derived from the soil literature and most of that is concerned with the effects of laboratory drying on determining analyte concentrations.

When sediments are exposed to the atmosphere, two different effects can be expected. First, the oxygen content of the sediment will increase. The amount of oxygen present in inundated sediments is dependent on the rate of supply of oxygen from the overlying water. This rate is limited by factors such as the rather low solubility of oxygen in water, temperature, presence of metabolizable carbon, bioturbation, and sediment or soil structure (Gottschal, 1986). When sediments are exposed, they are placed in immediate contact with the air. Hence, what may once have been anaerobic zones are now oxygenated. The supply of oxygen to deeper parts of the sediment is further facilitated by the formation of deep cracks in the sediment surface. Second, the moisture content of the sediment will be substantially reduced. During extended periods of drought the sediment water levels may approach zero percent of field capacity.

Exposure to air and desiccation are two separate (but obviously interrelated) processes and each will have a different effect on both the mineralogy and the microbial ecology of the sediment.

### Mineralogy

Because of the amorphous natures of many sediments, it is very difficult to directly identify changes in mineralogy as a function of drying (e.g. by X-ray diffraction). Rather, changes in mineralogy as a function of drying have been inferred from changes in sediment properties, most notably changes in phosphate adsorption isotherms (e.g. Baldwin, 1996).

The principal effect of increasing oxygen on sediment mineralogy will be an oxidation of previously reduced mineral phases. For example, De Groot and Van Wijck (1993) showed that when anoxic sediments from a wetland were initially exposed to air, ferrous sulphides present in previously anoxic zones were rapidly oxidized to amorphous ferric oxyhydroxides. These ferric (oxy) hydroxides have both a large surface area and a very high affinity for P. Therefore, it has been suggested that oxidation of reduced mineral phases is the mechanism responsible for the initially high P binding capacity of recently aerated sediments (De Groot and Fabre, 1993; Baldwin, 1996). It is of note that the oxidation of these minerals, particularly the ferrous sulphides, may lead to a lowering of sediment pH (Howell et al., 1998). Such a lowering of pH may lead to some mineral dissolution (see Boström et al., 1988). Extended sediment exposure has the opposite effect. Over time, as oxidized sediments are allowed to dry, their affinity for P has been shown to be substantially reduced (Sah et al., 1989; Qiu and McComb, 1994; Baldwin, 1996). It has been suggested that this phenomenon is a consequence of mineral aging. As the oxyhydroxides age, they become more crystalline (Lijklema, 1980), the number of P binding sites decreases and hence their affinity for P decreases (Sah et al., 1989; Baldwin, 1996).

*Microbial ecology*

Oxidation and desiccation have a profound effect on the microbial consortium present in previously reduced sediments (e.g. De Groot and Van Wijck, 1993; Qiu and McComb, 1995). In the initial stages of oxidation–desiccation, aerobic and anaerobic nutrient cycling processes continue concurrently, i.e. an oxic sediment zone can overlie a zone of anoxia. This may result in enhancement of microbial activity and consequently the nutrient cycling processes. Reduced substances will be rapidly reoxidized as they move to the aerobic zone, only to be reduced once more as they move back into the anaerobic zone. As an example, decreases in mineral N have been reported for soils and sediments on drying and oxidation (McCarty and Bremner, 1993; Stanley and Boulton, 1995) resulting in a N sink environment. Coupled nitrification–denitrification is at an advantage in the early stages of desiccation; therefore a loss of N to the system may be anticipated.

In the initial stages of desiccation, colonization by terrestrial plants may commence (Junk and Weber, 1995). The macrophytes will be in competition with the microbes for sediment bound nutrients. For example, nitrifying organisms must compete for ammonium with the macrophytes, and for oxygen with aerobic respiring heterotrophic bacteria (Bodelier *et al*., 1998). Thus, ammonium or oxygen may become a limiting factor for nitrification, which, in turn, may limit denitrification activity and losses of N to the system.

As desiccation–oxidation of the sediments proceeds an expanded habitat for aerobic microbiota (including fungi and protozoa) will be created. Conventionally, aerobic heterotrophs are believed to use certain organic substrates (such as lignin) more efficiently than anaerobic microbes; therefore an increase in the mineralization rate of carbon would be expected. This may, at least partially, explain the reported loss of bioavailable carbon (as $CO_2$) during sediment and soil desiccation (Van Schreven, 1967; De Groot and Van Wijck, 1993; McCarty and Bremner, 1993; Mitchell and Baldwin, 1998, 1999). However, it is becoming increasingly obvious that the efficiency of organic substrate utilization is greatest with combined or alternating oxic–anoxic conditions (Hulthe *et al*., 1998).

As sediment oxidation continues, obligate anaerobic bacteria in previously anoxic zones of the sediment will either be killed or form resting stages (Lynch and Hobbie, 1988). Therefore, nutrient processes which rely on anoxic conditions (e.g. denitrification, Fe(III) and sulphate reduction) will be substantially reduced—limited to microsites within the (now) oxic sediment (Gottschal, 1986). Therefore losses of N as a result of denitrification will decrease and the system may become potentially fertile with respect to mineral N. Conversely, P may be predominantly sequestered by the now mostly oxidized mineral phases (De Groot and Fabre, 1993; Baldwin, 1996).

As sediments dry out, a decrease in bacterial biomass and activity may be expected (Van Gestel *et al*., 1991, 1992; De Groot and Van Wijck, 1993). It has been shown that bacterial activity declines linearly with soil water content (Orchard *et al*., 1992; West *et al*., 1992). At the extreme end of sediment and soil desiccation ('baking'), a high bacterial mortality and release of N and P caused by cell lysis has been reported (Birch, 1960; West *et al*., 1988; De Groot and Van Wijck, 1993; Qiu and McComb, 1995) resulting in a flush of N and P upon re-wetting of sediments and soils.

## RE-WETTING

*Initial re-wetting*

Large flushes of mineral N and P have been reported for re-wetted soils and sediments (Birch, 1960; Sparling and Ross, 1988; West *et al*., 1988; Haynes and Swift, 1989; Qiu and McComb, 1995) as a consequence of drying-induced microbial-cell lysis. This nutrient pulse may facilitate bacterial activity. Increases in both microbial numbers and activities have been reported for re-wetted soils and sediments (McLaughlin *et al*., 1988; Van Gestel *et al*., 1992; West *et al*., 1992; Lebuhn *et al*., 1994; Qiu and McComb, 1996; Panikov *et al*., 1997), e.g. increased nitrification activity has been reported for re-wetted sediments (Stanley and Boulton, 1995) and soils (Cui and Caldwell, 1997; Scholes *et al*., 1997). However,

this increased activity may be apparent only for a few days (Qiu and McComb, 1996; Cui and Caldwell, 1997; Scholes *et al.*, 1997).

Increased denitrification activity has also been shown to occur following soil re-wetting (Groffman and Tiedje, 1988). Yet, desiccation does not appear to affect the potential for denitrification in floodplain soils or reservoir sediments (Kern *et al.*, 1996; Mitchell and Baldwin, 1999). Denitrifying bacteria are predominantly facultative anaerobes (Knowles, 1982), hence desiccation–oxidation should be less toxic to these organisms than to the obligate anaerobes such as most sulphate reducing bacteria (Holland *et al.*, 1987).

Macrophytes will compete with bacteria for the nutrients flushed from the soil on re-wetting (Bodelier *et al.*, 1998). Increased plant productivity and uptake of the nutrient pulse following the re-wetting of desiccated soils has been reported for emergent macrophytes (e.g. Cui and Caldwell, 1997). In contrast, the response of submerged aquatic macrophytes will vary depending on the severity of the drought (Hough *et al.*, 1991) and the plant species present (Brock and Casanova, 1997). In general, the nutrient flush is most likely to be used by the microbial consortia in wetland sediments and by terrestrial plants on floodplains (Vegasvilarrubia and Herrera, 1993).

### Repeated wetting–drying cycles

Repeated wetting–drying cycles (as opposed to lengthy periods of inundation or desiccation) affect nutrient cycling in largely unknown ways. Given the above information, possible responses of the microbial nutrient cycling processes to relatively rapid wet–dry perturbations may be hypothesized. The initial and obvious observation is the immediate and potentially long-term change to the microbial community. Alternate oxic–anoxic conditions will select for facultative anaerobic bacteria; obligate bacteria are at a distinct disadvantage. Furthermore, repeated drying of sediments will favour bacteria that can produce drought resistant resting stages, e.g. spores. Lebuhn *et al.* (1994) report a proliferation of 'r-strategist' microbes following re-wetting of dried soils. Obligate anaerobic bacteria such as the sulphate reducers, even if they survive the elevated oxygen levels, will certainly become inactive (Gottschal, 1986) because periods of anaerobiosis will be severely limited in a wet–dry system. Without the action of the anaerobic bacterial nutrient cycling processes (e.g. Fe(III) and sulphate reduction), the release of P from the sediments and soils will decline. At the same time, the potential for aged minerals to sequester P will also decline (Baldwin, 1996). Release of P from these aged minerals will be reduced even if anaerobic conditions return intermittently (Lovley and Phillips, 1986; Mitchell and Baldwin, 1998). Whether this combination of effects leads to an increase or decrease in P concentrations is difficult to predict, but there is no doubt that wetting and drying cycles are a key control for P cycling in soils and sediments (McLaughlin *et al.*, 1995; Mitchell and Baldwin, 1998).

The impact of repeated wetting and drying perturbations on N cycling processes is similarly difficult to predict. As noted earlier, denitrifiers are facultative anaerobic organisms so they should survive this perturbation relatively well. However, growth and activity of nitrifiers in soil have been reported to be severely inhibited by wetting–drying cycles (Franzluebbers *et al.*, 1994). Thus, coupled nitrification–denitrification may be severely limited as a result of this type of perturbation, and consequently the denitrifiers will have to rely on external sources of nitrate. Repeated wetting–drying cycles have also been reported to increase the resistance of certain plant N compounds to microbial attack (Franzluebbers *et al.*, 1994) which may result in long-term N fertility, a decrease in the soil C:N ratio and P, limitation to organic matter mineralization and photosynthesis. The combination of these factors will result in a N sink environment.

Rovira and Vallejo (1997) have reported decreased mineralization of C and N over a 2-year period of wetting and drying cycles in the upper horizon of soils. They noted that the wetting–drying cycles were more inhibitive to C and N mineralization than were low oxic–anoxic conditions in the subsoils. Uptake of nutrients by rice subjected to flush irrigation (wetting–drying cycles) was shown to be reduced compared to the normal flooding regime (Beyrouty *et al.*, 1994). These researchers suggested the decreased uptake resulted from a reduced release of nutrients as an effect of the wet–dry perturbation.

There is no doubt that anaerobic bacteria play a key role in nutrient cycling in floodplain ecosystems. Thus, the efficiency of organic matter mineralization and nutrient cycling in these systems will depend on a fine balance between aerobic and anaerobic processes. Oxygenation is assured in desiccated sediments; however, anaerobiosis depends on a number of factors. These include the structure of the sediment or soil, the temperature (correlated with organic matter mineralization; Schimel *et al.*, 1994) and the presence of bioavailable carbon to support metabolic activity (Gottschal, 1986). If carbon is lost as a result of desiccation (see above), the end result of repeated wetting and drying cycles may be a severe carbon limitation and consequently a decrease in the rate of nutrient cycling. The carbon limitation hypothesis is emphasized by results of a study that subjected soils to wetting and drying cycles. This study reported no lag phase in the mineralization of added carbon, and that microbial mineralization was only slightly lower in wet–dry cycle soils than in continuously-moist soil conditions (Ladd *et al.*, 1995). Thus, the *potential* for organic matter mineralization remains in wet–dry perturbed sediments and soils. Therefore, it is possible that observed reductions in sediment-nutrient processes following episodic wetting–drying cycles is a consequence of mineralization of native carbon, i.e. they are carbon limited.

## INUNDATION OF SOILS

The most significant result of the flooding of soils is isolation of the soil from atmospheric oxygen, and hence the potential onset of anoxia (Faulkner and Richardson, 1989). Consequently, strong similarities exist between the chemistry (Ponnamperuma, 1972) and microbiology (Hutchinson, 1957) of submerged soils and sediments. Thus, the nutrient cycling processes described for submerged sediments will extend to inundated soils. Inundation of soils will lead to a decrease in oxygen and onset of anaerobic conditions (Ponnamperuma, 1972). The rate and extent of oxygen decrease will depend on a number of factors such as the soil structure, the temperature (correlated with organic matter mineralization; Schimel *et al.*, 1994) and the presence of bioavailable carbon to support metabolic activity (Gottschal, 1986). Thus, the way the the timing of a flood affects temperature will also have an effect on the outcome of the nutrient cycling processes as a result of inundation of floodplain soils.

One of the main differences between inundated sediments and submerged soils is the presence of dry leaf litter on the floodplain soils. Rapid leaching of nutrients from this leaf litter can result in an initial pulse of C, N, and P following inundation (Baldwin, 1999). This pulse of nutrients and readily bioavailable carbon can cause a rapid increase of microbial activity and nutrient cycling processes resulting in a highly fertile and productive system. However, this increase in production can quickly lead to the onset of anoxia in the floodwater and underlying soils (Glazebrook, 1995).

Therefore, the outcome of floodplain soil inundation is expected to involve an initial increase in aerobic heterotrophy and nitrification activity. As the duration of the flood extends, the potential for anaerobiosis increases and thus the potential for anaerobic nutrient cycling processes increases. Losses of N as a result of coupled nitrification–denitrification may be expected, with release of P as a result of Fe(III) and sulphate reducing bacterial activity. As is the case with rice paddies, any ammonium and $NO_x$ initially liberated either from leaf leachate or from soil mineralization processes may be lost from the system either through volatilization of $NH_3$ or denitrification (Reddy and Patrick, 1986). The biota may then become N-limited and organisms capable of N fixation may be at an advantage in this environment (Bennett and Albrecht, 1984).

## CONCLUSIONS

From the preceding discussion it is clear that altering the wetting–drying regime will have important effects on nutrient cycles in floodplain systems.

1. Partial drying of wet (previously inundated) sediments will result in an increased sediment affinity for P and will produce a zone for coupled nitrification–denitrification. Hence partial drying may result in reduction in the availability of N and P.

2. Complete desiccation of sediments may lead to a decrease in the affinity of P by Fe minerals, the death of bacteria (and subsequent release of N and P), a concurrent decrease in microbial activity and a cessation of all anaerobic bacterial processes (e.g. denitrification). Colonization of exposed sediments by terrestrial plants may lead to N and P moving from the sediments to plant biomass.
3. Re-wetting of desiccated soils and sediments will result in an initial flush of available N and P (which can be incorporated into bacterial or macrophyte biomass), coupled with an increase in aerobic bacterial activity, particularly nitrification.
4. Inundation of floodplain soils will result in the liberation of C, N and P from leaf litter and floodplain soils. This will result in an increase in productivity, which ultimately may lead to the onset of anoxia in floodplain soils and, consequently, an increase in anoxic bacterial processes such as P release and denitrification.

Clearly the timing of flooding and drying events is critical. Most of the nutrient cycling processes are the result (either directly or indirectly) of microbial activity. Microbial activity in turn is highly dependent on temperature, generally increasing with increasing temperature until a maximum is reached. Therefore, it will be expected that, for example, summer and winter floods will have different impacts on floodplain nutrient dynamics.

## FUTURE DIRECTIONS

The knowledge of the underlying processes is still far from complete, but nevertheless it can be seen that modifying flooding–drying regimes has the potential to be used as a tool for managing nutrient dynamics in floodplain–river systems.

However, there are a number of key questions that need to be explored before we can reliably use wetting–drying cycles as a management tool. For example, while we can speculate on the effects of drying–wetting cycles on the chemistry and microbial ecology of sediments and soils we do not have a good understanding of the detailed mechanisms underlying these effects. In particular, if we are to predict the outcomes of a particular wetting–drying regime we need to know the rates of the key processes, and whether or not the processes are reversible. If they are reversible, are the forward and back trajectories the same or do they exhibit hysteresis?

From our current knowledge base we do not know what effects repeated wetting–drying cycles will have on either the chemistry or the microbial ecology of sediments and soils. For example, do repeated wetting–drying cycles result in a microbial community that can rapidly respond to changes in the hydrologic cycle? If so, this may limit the effectiveness of hydrologic manipulations on nutrient cycling. As a corollary to this question, we do not know how the frequency of perturbations affects microbial community structure. For example, is the microbial community structure of a sediment or soil which is exposed to only very infrequent perturbations the same as that of sediment or soil which has not been perturbed, or does a single perturbation select for microbiota which are resilient to such perturbations?

What are the effects of long-term perturbations on the nutrient cycles? For example, does inundating a soil for a period of years have the same effect as inundating a soil for a period of days or weeks?

It is hoped that this synthesis can stimulate on-going research into the effects of drying and flooding on nutrient dynamics in floodplain sediments and soils.

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