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Cycling and retention of nitrogen and phosphorus in wetlands: a theoretical and applied perspective

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SUMMARY. 1. This review considers the internal fluxes and transformations of nitrogen and phosphorus in wetland ecosystems. Emphasis is placed on the dynamic nature of nutrient cycling and the review is slanted towards an applied perspective, namely the possible use of wetlands as sinks for unwanted nutrients.

2. A number of basic concepts pertaining to wetland ecosystems are first explained. These are: successional time scales, exchange equilibria and the concepts of storage and throughflow, resource consumption and supply including the ideas of new and regenerated nutrients and the nutrient spiralling concept. Much of the following review material is referenced back to these concepts.

3. Descriptions of the basic pathways of nutrients through different types of wetland systems are given with the emphasis placed on the movement into and out of the major storage compartments of wetland systems.

4. The problems of conversion of qualitative information (or data in concentration units) on nutrient movements and transformations, into data on mass flows are then discussed. The importance of understanding groundwater, evapotranspiration processes and the effects of floods and seasonality on mass flow calculations can be significant. Unidentified groundwater sources can dilute nutrient concentrations, and evapotranspiration can increase concentrations. The pattern of throughflow can also alter nutrient levels. Increasing residence time has the effect of decreasing nutrients in the wetland outflow.

5. The review then considers the effects of adding nutrients to wetlands. The concept of the loading capacity is discussed in relation to the length of time a wetland can continue to remove nutrients from throughflow. Sediment accumulation and degassing are seen as the major long-term nutrient sinks. Nutrient enrichment results in biological changes to wetlands. These involve both changes in species composition and productivity. Not all are deleterious.

6. The literature indicates that natural wetlands are not particularly

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effective as nutrient sinks when compared with conventional stripping plants but their value lies in removal of diffuse nutrient runoff at low concentrations. Dealing with this type of runoff by conventional means is not generally feasible.

7. Recent studies show that artificially created wetlands can be effective systems for nutrient (particularly N) removal only if their internal removed mechanisms are understood and if these are optimized by management techniques.

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1. Introduction

1.1. The approach

The study of wetlands as ecosystems began only in the 1940s with Lindeman's studies on Cedarbog Lake (Lindeman, 1942), and with the work of Odum (1957) and Teal (1962) in the 1950s and early 1960s, which first quantified the role of detritus in aquatic systems.

Subsequent to those early studies there has been a proliferation of books from all over the world dealing with wetlands (Dykyjova & Kvet, 1978; Good, Whigham & Simpson, 1978; Greeson, Clark & Clark, 1978; Gopal,

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Turner & Wetzel, 1982; Gore, 1983; Denny, 1985). This sudden interest in wetlands is not only because of their intrinsic interest as ecosystems and, indeed, several authors have attempted to quantify their monetary value (Gosselink, Odum & Pope, 1974; Thibodeau & Ostro, 1981; Larsen, 1982). The most obvious financial significance of wetlands (see e.g. Greeson *et al.* 1978) is their apparent ability to assimilate waste products from human activities (Kadlec & Tilton, 1979; Rogers, Rogers & Buzer, 1983) although Whigham (1982) injected a note of caution into the concept that they could be of widespread use for waste-water management. With gathering interest in wetlands there is clearly a need for a more theoretical look at wetlands as ecosystems before considering them merely as 'treatment plants'.

One benefit of the applied interest in wetlands has been that it has allowed for largescale experimentation. By artificially changing nutrient inputs, for instance, a number of important effects at the system level have been described which have enhanced our basic knowledge of nutrient cycling. Wetland research in recent years has demonstrated the mutual interdependence between applied and theoretical approaches to the study of ecosystems. Of particular interest at the ecosystem level is not only the obvious ability of wetlands to filter particulate material, but rather the way in which these systems process and transform dissolved nutrients. Wetlands are areas which share properties of both terrestrial and aquatic systems, and of both lotic and lentic systems. The movements through, and transformations within, wetlands of nutrients such as nitrogen and phosphorus might therefore be expected to show characteristics which differ from their terrestrial and aquatic counterparts.

The aim of this review is to examine the ways in which nutrients, specifically nitrogen and phosphorus, are processed in wetlands, and to use this information to explore the feasibility of using wetlands for nutrient retention. To do so, I have adopted a dynamic and perhaps more fundamental approach than that taken in the existing literature (e.g. Kadlec & Tilton, 1979; Whigham, 1982). Here, a theoretical background is provided with the description of a number of basic models of nutrient cycling. The types and complexity of nutrient pathways and the factors affecting the quantitative movement of nutrients through wetlands are then illustrated. This is followed by a discussion on the consequences of the addition of nutrients to wetlands. The final part of the review is an integration of the applied and theoretical concepts with suggestions for future approaches to this subject.

1.2. Functional types of wetland

For the purposes of this review I define a wetland (after Cowardin *et al.*, 1979) as follows: an area where the water table is at or

above the land surface for long enough each year to promote the formation of hydric soils and to support the growth of aquatic vegetation *much of which is emergent (photosynthetic organs above the water surface)*. The words in italics are my addition, to exclude certain non-vegetated areas or regions of submerged vegetation included in Cowardin *et al.* (1979).

Within this broad definition we can subdivide wetlands in a number of ways according to system function (rather than by morphological, taxonomic or habitat criteria). Useful subdivisions for the purposes of this review are:

(a) Freshwater versus brackish or saline wetlands. The latter, if along the coast, are characterized by having two directions of flow, one of which is often more saline and with different levels of nitrogen and phosphorus than the other.

(b) Permanently inundated versus periodically inundated wetlands. The periodic (e.g. seasonal) drying up of a wetland will have a marked effect on system function as the aquatic component disappears, soil microbial processes become 'terrestrial', and aquatic vegetation is available to consumers from adjacent terrestrial areas.

(c) Periodically snow-covered or frozen wetlands versus continuously non-frozen wetlands. Nutrient cycling in the former is intermittent and affected by low temperatures, physical stresses or freezing, freeze concentration of salts and several other cold-climate effects (Hobbie, 1980).

(d) Rooted versus floating wetlands. This is an often overlooked functional separation of wetland types and is especially important in considerations of nutrient cycling. In rooted wetlands the dominant wetland vegetation is rooted in the sediment, and the sediment thus plays a major role in nutrient cycling (Fig. 1a). This is the common wetland type of temperate regions. Wetland literature generally refers to this type. Examples would be the Phragmites reed swamps of Europe and the Typha and Scirpus marshes of North America. In floating wetlands, vegetation is not rooted in the sediment but forms a floating mass (Fig. 1b). Recycling of nutrients is from plant mat, including detritus, to water and back. In some cases a floating wetland can develop from a rooted wetland as in Plaur (Plav) formation in



FIG. 1. Diagrams of a rooted wetland (A) and a floating wetland (B). Arrows show possible patterns of water flow. Floating wetlands are characteristic of large areas of the tropics.

central European *Phragmites* or *Typha* systems (Hejny, 1971). Examples of floating wetlands are the papyrus (sudd) swamps of Africa (Gaudet, 1977), the floating meadows of South America (Junk, 1970; Howard-Williams & Junk, 1977) or even perched bog (e.g. review by Gorham, 1957).

1.3. Basic concepts

1.3.1. Successional time scales. Wetlands are generally placed as early seral stages in a vegetation succession from aquatic to terrestrial (Odum, 1971) and therefore might be expected to change rapidly with time. However, in the natural situation there is conflicting evidence as to the rate of change of wetlands (see Sculthorpe, 1967; van der Valk, 1981; Tallis, 1983). The rate of progression of wetland vegetation from shallow open water to a dense community of emergent plants can be of the order of weeks (Howard-Williams, 1975; Gaudet, 1977, 1982) to thousands of years. Some of the African papyrus swamps have underlying peat deposits 30 m thick (Thompson & Hamilton, 1983) suggesting thousands of years of accumulation. As they are intermediate stages between truly terrestrial and truly aquatic systems, a change in water level will result in a shift of the wetland towards either of these states. However, although there are documented cases of long-term stability or even a shift to a more aquatic state, the general direction of wetland succession is to a reduction in water level and a change to a drier state.

Natural changes in water level in a wetland can be brought about by autogenic or allogenic processes. The former are those caused by the growth of wetland plants themselves, and the latter by external factors. Raising of the bed of the wetland by litter deposition would be autogenic, and siltation or precipitation of incoming suspended material in throughflow waters would be an allogenic process. However, wetland succession involves a complex interplay of both autogenic and allogenic processes (van der Valk, 1981; Patten, 1984). The latter clearly modify the former and in many cases external factors such as fires, drawdowns or floods can maintain a wetland at an apparently stable state for long periods (e.g. Okefenokee swamp, Hamilton, 1978; Patten, 1984).

Transitions between a wetland and terrestrial states can also occur by anthropogenic disturbances. Drainage, plant cutting and lumbering may all change wetlands considerably, and Tallis (1983) argues that eutrophication is potentially the most important of contemporary anthropogenic disturbances. The maintenance of wetlands as wetlands will therefore require an environment in which water level changes in the long term are minimal.

During periods of relatively constant environmental conditions when we can expect autogenic processes to control the vegetation succession three general ecological principles pertaining to nutrient cycling apply (see Odum, 1971).

(a) Initially, nutrient cycles are 'open' which means high flow-through relative to storage. Nutrient cycles are dominated by inorganic forms of the elements.

(b) As autogenic succession progresses, nutrients become progressively tied up in biomass and dead organic matter.

(c) Nutrient cycling gradually becomes 'closed' with large stores relative to inputs and

outputs. The ability of systems to trap and hold nutrients increases with time.

As wetlands change due to succession, the true importance of these three nutrient cycling principles will change. An appreciation of the time scales in which a wetland maintains itself, or can be maintained, is of fundamental importance in the long-term consideration of wetlands as nutrient traps, and in the maintenance of wetland nutrient cycles. In many cases, particularly where catchment development is occurring, wetlands might be thought of as transitory ecosystems.

1.3.2. Exchange equilibria. Haves & Phillips (1958) formulated a simple model of nutrient exchange which, although presented in the context of an open water system, has some useful basic concepts in a consideration of wetland nutrient cycles. These authors showed the necessity of viewing phosphorus in aquatic systems as being distributed in a state of dynamic equilibrium between the water and the solids (i.e. plants, sediments, detritus). This means that if phosphorus is added to the water phase, the equilibrium is temporarily shifted, and will rapidly return to the steady state as the phosphorus is taken up by the various fractions of the solid phase. Thus, after re-establishment of the equilibrium there will be more phosphorus in the system but not necessarily in the water.

This situation can be represented diagrammatically by Fig. 2(a). Each exchange is governed by a rate coefficient k_1 , k_2 . If we now take a unidirectional flowing system where the nutrient input is x and the output is y, at a steady state (equilibrium state):

$$y = x - (k_2 - k_1)x$$

= (1 - k_2 + k_1)x (1)

that is the output equals input less change in storage, and storage is the sum of the solid material compartments (Fig. 2b).

If we take this concept a step further and examine the change in output with time the situation can be envisaged as shown in Fig. 3. When the input (x) is applied and maintained at a constant rate, and expressed in terms of mass time⁻¹ then the ratio of the output (y) to input with time will follow the curve shown in Fig. 3, phase A.

For a short period after the addition of x, a decrease in y relative to x will occur (phase A in Fig. 3a). The rate at which this takes place will be defined by the composite of k_1 and k_2 values (see Fig. 2). The system will adjust to the input, and the curve will flatten to an equilibrium level in the output (phase B in Fig. 3). At this point the net storage value $((k_2-k_1)x)$ will be constant with time.

Phase B will continue until one or more of the components is limited in its ability to remove x (i.e. by space). At this point k_1 for those species is reduced and the y/x ratio increases as shown in phase C(1) or C(2) in Fig. 3.



FIG. 2. (a) Diagrammatic representation of equilibrium exchanges. Dissolved reactive phosphorus (DRP) in the water is taken up (k_1) and released (k_2) by various solid components of the system. The level of DRP in the water at any time is therefore governed by the composite effect of all the uptake and release rates. (b) Simplified diagram of a system with a throughflow. The output (y) is governed by the exchange equilibria (k_1, k_2) between the various storage compartments and the throughflowing water such that $y=x-(k_2-k_1)x$.



FIG. 3. The output (y)/input (x) ratio of a nutrient added to a hypothetical wetland as a function of time. See text for details.

Phase C(3) will also be demonstrated when the amount of x is increased further until the input is so high that k_1 is reduced to k_2 and from eqn (1), y=x. At this point the system would be overloaded by the input.

The y/x ratio can be changed by altering the rate of throughflow (changing the residence time). If the residence time of the throughflowing water is faster than the turnover times dictated by k_1 and k_2 , then the y/x equilibrium level will rise. The converse will also apply.

However, while such a model can be conceptualized for phosphorus (Fig. 1), nitrogen is a special case because of the biologically mediated interactions with the gas phase (Nfixation and denitrification). Thus in certain conditions favourable for denitrification, for instance, N loss to the gas phase can prevent accumulation irrespective of the state of N in the solid phase (see section 4.3.3).

1.3.3. Resource consumption and supply. Tilman (1982) considered a resource to be any substance or factor which is consumed by an organism and which can lead to increased growth rates as its availability is increased. Inorganic plant nutrients are classed as 'essential resources' in that they are required for growth and one is unable to substitute for another which may be in low availability.

In any habitat, a total pool of nutrient is present in a number of forms, some of which are available for uptake (consumption) and some of which are unavailable.

In a steady state system (e.g. Fig. 2) when

nutrient input = output, and plant growth =mortality, if nutrient inputs from outside the system are less than consumption rates then nutrient regeneration (recycling) must occur from the unavailable pool. The oceanographic literature distinguishes between 'new' nutrients and 'regenerated' nutrients (cf. Dugdale & Goering, 1967). Tilman (1982) argues that under steady state conditions in a given habitat (unit area of wetland) there is an upper limit (T) to the amount of available nutrients which can exist (i.e. a carrying capacity). Nutrient recycling rates are therefore dependent on the proportion of available (A) (new and regenerated nutrients) to the unavailable form (U) (nutrients in storage, cf. Fig. 2).

Recycling rates (production and consumption of regenerated nutrient) can therefore be described in terms of an instantaneous change in the available form:

$$dA/dt = a(T - A) \tag{2}$$

where *a* is a proportionality constant.

The regeneration rate or rate at which A re-enters the system and is re-utilized decreases as the proportional amount of the available form increases. So when A is large relative to the total carrying capacity (T) regeneration or recycling rates will be low.

In a hypothetical wetland system with a flowthrough (Fig. 2) there is continual replenishment of the available pool by new nutrient in addition to the regenerated nutrient. Even in a steady state when input=output an increase in the renewal rate (=decrease in the residence time) of A by new nutrient will have the same effect as increasing the pool size of A and the rate of recycling or re-utilization of regenerated nutrient within the wetland will decrease. The relevance of this to a flowing water system is seen in the next section.

1.3.4. Nutrient spiralling. Webster & Patten (1979) pointed out that nutrients in streams do not 'cycle' in one particular place. Because of the continuous downstream movement of water and particulate materials, a nutrient cycle is displaced and becomes a spiral. Elwood et al. (1983) pointed out that spiralling rather than cycling is a concept that is applicable to all open ecosystems but is a particularly useful concept for describing nutrient dynamics in systems where a continuous unidirectional transport of materials is a major feature of the system. Figure 4 illustrates some of the basic components of a nutrient spiral. The spiral length S represents the average downstream distance travelled by a nutrient atom as it completes a spiral from water, through particulate components and back to the water. The distance a nutrient atom will travel in component $i(S_i)$ is given by the upstream supply rate of the nutrient F_i (mass per unit time) divided by the utilization rate or exchange flux (mass per unit stream length per unit time) R_i . Thus

$$S_i(\mathbf{m}) = F_i(\mathbf{g} \, \mathbf{s}^{-1})/R_i(\mathbf{g} \, \mathbf{s}^{-1} \, \mathbf{m}^{-1})$$
 (3)

 S_i is also equal to the reciprocal of the length constant for disappearance of the nutrient which has units of m⁻¹ (Newbold *et al.*, 1981).

The spiral length index *S*, defined here as the sum of the distance travelled through the water (S_w) and through the particulates (S_p) is an index of utilization of nutrients provided to an aquatic system with a flowthrough. If nutrient utilization in a system is to increase then *S* will decrease (Newbold *et al.*, 1981). However, an increase in water pathlength for a given direct distance downstream (i.e. tortuosity) will have the same effect (see e.g. Rosendahl & Waite, 1978).

We would therefore expect S_w to increase with increasing water flow rates and with decreasing release rates or regeneration rates from particulates. It would decrease with increasing nutrient uptake rates (i.e. increasing biomass and growth rates of stream biota) and decreasing water velocities. Spiral length can thus be a time dependent feature when uptake rates are greater at, say, one part of the year than another.



FIG. 4. Nutrient spiralling in a flowing water ecosystem. (a) A nutrient atom travels an average downstream distance (S_w) in the water before being taken up by particulates in which form it travels distance S_p before returning to the water. Total spiral length= S_w + S_p . (b) Downstream nutrient fluxes (g s⁻¹) in the water (F_w) and particulates (F_p), and exchange fluxes (g m⁻¹ s⁻¹), of nutrients from water to particulates (R_w) and from particulates to water (R_p). Redrawn from Elwood *et al.* (1983).

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Determination of spiral length S, or pathlength (S_i) for a component of an aquatic system or its reciprocal can therefore provide a useful quantitative measure for comparisons between different flowing water systems, a characteristic of many wetlands. Newbold et al. (1981) used ³²P tracer to measure the lengths S_w and S_p and therefore total spiral length. The index S_w which Elwood *et al.* (1983) term the Uptake Length is an index of the effectiveness of the stream biota in removing nutrients from the water column. In a steady state system, a short-term tracer experiment theoretically measures S_w without the complications of nutrient regeneration. However, in many areas such experiments are not feasible but where ambient nutrient depletion with distance downstream is observed we can define an index of Net Uptake Length S'_w derived from the nutrient uptake rate minus the regeneration rate. The reciprocal of S'_w is the Net Uptake Length constant K_w (m⁻¹).

Kadlec (1978) noted that by plotting ammonium and phosphorus concentrations downstream through a wetland, these nutrients disappeared at a rate proportional to their concentrations. That is, nutrient uptake followed first order kinetics. Similarly Fisher (1977) proposed a loading coefficient (k) when the downstream concentrations (C_o) were equal to $C_i \exp(-k \cdot z)$ where C_i is the input concentration and z is the stream length (Fisher, 1977).

when describing nitrate loss from streams but his model included stream width and discharge. His constant (ϱ) is the areal uptake of the nutrients (g m⁻² s⁻¹) divided by the concentration (g m⁻³) and has units of m s⁻¹. It is related to K_w by:

 $K_w = \rho w/Q$

where w is stream width.

Reference back to the previous section (note steady state assumptions) will make the point that for a given regeneration rate of nutrient through a (wetland) system K_w , (and hence S'_w) will be constant. An increase in the regeneration rate of the nutrient (if it is in available form—see section (1.3.2.) will reduce K_w and increase Net uptake length S'_w . Fig. 5(a) shows the expected time course (from eqn 2) of depletion of 'new' nutrient when the available pool A is a large and a small propor-



FIG. 5. (a) Time course of 'new' nutrient in water in a system with no throughflow when the available pool of nutrient is a large (slope 1) and a small (slope 2) proportion of the carrying capacity. First order kinetics are assumed. (b) In a flowing system the slope of the decrease in concentration of an available nutrient (A) downstream will depend on the proportion of that nutrient to carrying capacity (T). When renewal rates are high, or residence times are short, A is a high proportion of T (slope 1), and the slope will be less than when renewal rates are low (long residence times) (slope 2).

tion of the carrying capacity T in a closed nutrient cycling system where uptake is dependent on regeneration.

In an open flowing system we can follow the expected change in the available form with distance downstream (Fig. 5b). Again it is evident that increase in the available form in relation to the carrying capacity, due to high velocity or short residence times for instance, will result in a decrease in slope K_w .

Figure 6(a) shows the relationship between ambient nutrient concentration and downstream distance in a macrophyte dominated stream in New Zealand and Fig. 6(b) shows ³²P tracer depletion when ambient P was constant in an American woodland stream.

Cooper & Cooke's data from the New Zealand stream (Fig. 6a) confirm the predicted course shown in Fig. 5(b) in that the increasing



FIG. 6. (a) The effect of discharge (Q) on the slope of the decrease in concentration of nitrate with downstream distance in a New Zealand stream colonized by *Glyceria fluitans*. The slope of the line for a given Q is equal to $1/S'_w$. Data from Cooper & Cooke (1984). (b) Decrease in ³²P (as PO₄–P) with downstream distance in a North American woodland stream. The slope is equal to $1/S'_w$. Data from Newbold *et al.* (1981).

discharge (replacement rate) results in a decrease in slope (K_w) . Table 1 shows some calculated K_w and S'_w values from various sources.

2. Nutrient pathways in wetlands

2.1. Introduction

It is, of course, possible to draw any number of complex webs showing theoretical pathways of nutrients in a wetland ecosystem, just as it is possible to draw networks of energy pathways. Such webs I seldom find useful beyond impressing the reader with ecosystem complexity. However, when broken down into smaller sections they can be instructive. Figure 2, for instance, is one simple wetland model showing exchanges between throughflowing water and storage compartments. Figure 7 is a more complex version of the same in which eqn (1) (section 1.3.2) can be rewritten as:

$$y = x \left\{ 1 - \sum_{i=1'}^{i=n} (k_{(2i)} + k_{(2i)-1}) \right\}$$
(4)

where 1' ... n are storage compartments.

Note that k_{11} and k_{12} in Fig. 7 refer to nitrogen fixation and denitrification processes involving atmospheric exchange. However, this is a simplification as some intermediate products (e.g. N₂O) can accumulate in waters (Yoh, Terai & Saijo, 1983).

At the next scale of complexity the number of transfers becomes enormous. Figure 8 illustrates the transfers between water and sediment (represented only by k_1 , k_2 in Fig. 7) via one species of aquatic plant in winter and summer only. The figure shows both acropetal and basipetal movement of phosphorus in

TABLE 1. Proportionality constants (ρ and K_w) and Net uptake lengths in the water phase (S'_w) estimated from nutrient removal studies in streams and wetlands. ρ values for the top seven references were calculated by Cooper & Cooke (1984). The bottom line gives the Newbold *et al.* (1981) estimate of true uptake length (S_w) and its reciprocal k_w (see text) estimated from tracer studies. * Insufficient data given for calculation.

Nutrient	$\begin{array}{c} \mathcal{Q} \\ (m \ h^{-1}) \end{array}$	$\frac{K_w}{(\mathrm{m}^{-1})}$	<i>S</i> ' _w (m)	Reference
NO ₃ -N	0.0035-0.0046	*	*	Kaushik et al. (1975)
	0.017	*	*	van Kessel (1977)
	0.0046	*	*	Robinson et al. (1978)
	0.83	0.068	15	Hoare (1979)
	0.054-0.061	0.013-0.034	30-80	Cooper & Cooke (1984)
	0.095	0.4×10^{-3}	2500	Howard-Williams et al. (1982)
	0.0088-0.0225	$2.1 \times 10^{-6} - 5.4 \times 10^{-6}$	$>1 \times 10^{5}$	Hill (1981)
NH ₄ -N	*	0.031	33	Kadlec (1978)
TDP	*	0.044	23	Kadlec (1978)
		k_w	Sw	
DRP	*	0.006	166	Newbold et al. 1981



FIG. 7. Diagram of a wetland system expanded from Fig. 2(b) to show the major storage compartments and the exchanges (k_1-k_{14}) associated with throughflowing water. Output (y) can be calculated from eqn (4). Modified from Sloey *et al.* (1978).

summer but not in winter at the study site (36° 14′ N). In this species (*Nuphar luteum*) both leaves and roots are involved in nutrient absorption, and k_2 on Fig. 8 is greater than k_1 in this case.

At a further stage of complexity in the vegetation component we can consider the complex algal and other microflora of the aufwuchs and mycorhizal associations which develop on the macrophytes themselves, and which can play an important part in nutrient cycling. Although direct transfers of carbon between macrophytes and such attached algae have been demonstrated (Wetzel & Allan, 1971) as far as I am aware similar interactions involving N and P have not been convincingly demonstrated. What is clear, however, is that this attached algal flora may be capable of removing as much or more nutrients from the surrounding water than the macrophyte substrate (Schwoerbel, 1968). Howard-Williams & Allanson (1981) calculated that in a low P environment almost twice as much phosphorus added to the water was taken up by Cladophora epiphytic on Potamogeton pectinatus L. than by the Potamogeton itself although the biomass of the latter was some 30 times greater.

In the next section I will discuss transfers of nutrients into and out of several of the storage compartments shown on Fig. 7.

2.2. Transfer of nutrients into and out of storage compartments

2.2.1. Vegetation $(k_1, k_2 \text{ in Fig. 7})$. As shown above and in Fig. 8, the vegetation compartment is a complex of emergent and submerged shoots, with roots in the water, floating mat or sediment and with underground storage tissues. Epiphytic algae further complicate the compartment.

Uptake rate k_1 (Fig. 7) from wetland water will depend on the importance of root v, shoot absorption. This in turn may be dependent on the relative importance of basal (in the sediment) v, adventitious (in the water) roots. Clearly in floating wetlands (Fig. 1) most uptake will be via roots, whilst in rooted wetlands (Fig. 1) there may be little direct uptake by the foliage from the water.

Denny (1972) proposed a model to assess the importance of root v. shoot uptake by aquatic plants. This is based on the relative proportion of root to shoot biomass, and on the degree of anatomical specialization of the root system. Most emergent macrophytes in rooted wetlands have a high root–shoot ratio and a specialized complex root system. In such cases we might expect a net transfer of nutrients from the sediments to the plants and then, following plant death, to the water (a nutrient 'pump' effect). However, many emer-



FIG. 8. The complexity of phosphorus pathways in the vegetation compartment (*Nuphar luteum* (L.) Sibth, and Smith). The extent of upward and downward daily flux (data as μ g-at.) varies seasonally. From data of Twilley, Brinson & Davis (1977).

gents do have adventitious 'water roots' as well as basal roots in the sediment. Examples are *Phragmites, Vossia, Nasturtium* spp. and *Apium nodiflorum* (L.) Lag. Such roots are the primary organs for nutrient absorption in some cases. Cumbus & Robinson (1977). for instance, found that phosphate, potassium and iron are absorbed primarily by the adventitious roots of *Nasturtium officinale* R.Br. although the basal (in sediment) roots also functioned in this capacity, particularly when nutrients were in low supply in the water. Correll, Faust & Severn (1975) used ${}^{32}P$ tracer to follow the path of phosphorus added to a *Typha* marsh. They found that the sediment surface roots of the *Typha* were responsible for P absorption. There was no evidence of direct absorption from the water or from deeper sediments.

Basipetal translocation of nutrients to the root-rhizome system was suggested to occur in *Phragmites* by Bjork (1967). It has subsequently been shown to occur in several macrophyte species (e.g. Fig. 8). Welsh & Denny

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(1979) and Denny (1980), who reviewed the literature on this, found that the direction of travel of a nutrient in a plant depended on many factors including plant structure, tissue requirements and availability and type of nutrients in surrounding solutions.

Internal translocations, such as shown in Fig. 8, have been suggested as mechanisms for nutrient conservation within wetland plants when external supplies are low. There is evidence that, in some cases, elements in short supply can be translocated out of senescing tissues and into younger plant parts or to over-wintering rhizomes at the end of the growth season in temperate regions (Boyd, 1970, 1971; Mason & Bryant, 1975; Klopatek, 1978). In the latter case these elements would be translocated to the young shoots at the beginning of the next growing season. In



FIG. 9. Seasonal changes in tissue phosphorous content in aboveground and belowground tissues of *Typha glauca* Godr. Data from Bayly & O'Neill (1972).

almost all temperate wetland species, nutrient concentrations are at their highest in the young shoots and in the early stages of growth, nitrogen and phosphorus are accumulated faster than dry matter. The inverse relationship between shoot and rhizome phosphorus is shown in Fig. 9. Such internal recycling may be the reason for the low proportion (<32% and <36%) of the variation in tissue N and P in Typha latifolia L. and Saururus cernuus L. which is explained by external nutrient concentration (Boyd & Hess, 1970; Boyd & Walley, 1972). The extent to which nutrients are recvcled internally in this way in nutrient-rich versus nutrient-poor situations has not been explored, but Klopatek (1978) hypothesizes that phosphorus retentive mechanisms have developed in wetland ecosystems allowing for the conservation of this, often growth-limiting, element and thereby slowing P flux outwards. Davis & van der Valk (1983) found that as much as 45% of the N and P lost from living Typha glauca shoots was translocated to the rhizomes and stored. Van der Linden (1980) estimated that between 25% and 50% of the nitrogen in Phragmites was recycled internally after storage in the rhizomes during the winter. Thus, internal recycling can account for half the annual flux of N and P through these plants. In tropical floating wetlands, where plant growth and nutrient uptake is not seasonally restricted, uptake rates and N and P are similarly higher in young shoots than in older ones (Gaudet, 1977). However, Gaudet's detailed description of nutrient cycling in a Cyperus papyrus mat did not include internal recycling.

Internal recycling of nutrients in plants will clearly influence calculations of downstream nutrient flux when we consider the basic concepts of resource supply and nutrient spiralling discussed earlier in section 1.3. From eqn (3) it is clear that spiral lengths are dependent on the uptake and release rate of nutrients (R_i) . Internal cycling in the vegetation component will reduce R_i thereby increasing S.

Pathway k_2 from live vegetation to water can occur by leaching, herbivores, frost, natural or man-made fires, or by active excretion into the water as has been proposed for *Zostera* by McRoy and co-workers (e.g. McRoy & Barsdate, 1970). Although the first three pathways have been documented for temperate and studied in a tropical floating wetland by Gaudet (1977). He found that in terms of concentration (μ g l⁻¹) and stock (μ g m⁻²) greater quantities of N and P were lost by leaching in rainwater from intermediate aged shoots than from old or young ones. The effects of fire are discussed in the following section.

2.2.2. Detritus $(k_3, k_4$ in Fig. 7). Once wetland vegetation dies, a large and complex series of nutrient transformations occur. These are all associated with leaching of detritus and simultaneous decomposition. I do not intend to review the now extensive literature on macrophyte decomposition processes but will select some limited examples to illustrate some major, and perhaps unrecognized, points in this process. The central role of detritus in nutrient retention by wetlands was illustrated by Davis & van der Valk (1983) who suggest that the most important result of wetland macrophyte production is the annual deposition of litter. Nutrient uptake and release in the litter layer, they suggest, are largely responsible for determining the effectiveness of their studied *Typha* marsh as a nutrient trap. Although this statement is clearly of relevance to rooted wetlands a different type of detrital processing occurs in floating wetlands.

Figure 10, redrawn from Davis & van der Valk (1983), shows the relative magnitude of pathways k_3 and k_4 in a rooted wetland. The data raise an important question in general wetland nutrient dynamics. That is, does decomposition result in nutrient regeneration to the water? Are through-flowing waters enriched by the decomposition process? The extensive experiments by Howarth & Fisher (1976) showed that when nutrients were plentiful, the decomposing tissue acted as a locus for nutrient accumulation by micro-organisms, but when nutrients were in short supply regeneration to the water occurred. The data of Davis & van der Valk (Fig. 10) show that in Eagle lake less N and P were lost by decomposition



FIG. 10. Nutrient (N and P) changes in the litter component of a *Typha glauca* stand over a period of a year. Data as mg m⁻² for N and P and g m⁻²×10⁻¹ for dry mass. After Davis & van der Valk (1983).

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processes than accumulated on the decomposing detritus. Thus decomposition, rather than acting as a recycling mechanism, would further enhance nutrient uptake from throughflow. It seems, therefore, that in some conditions (most likely to be oligotrophic) rate $k_3 > k_4$ but in others (nutrient rich) $k_4 > k_3$. In the basic nutrient cycling concepts described earlier (section 1.3.1., Fig. 5) it was stated that regeneration rates (k_4) are slowed when the available pool of the resource (A) is a large proportion of the system carrying capacity (T). These examples from wetland detrital pathways can therefore adequately be explained by the concept expressed in Fig. 5(b).

Apart from microbial oxidation of the dead material a pathway often overlooked is fire. Large tracts of both tropical and temperate wetlands are regularly burnt (van Rensburg, 1971; Faulkner & de la Cruz, 1983; van der Linden, 1980; Howard-Williams, 1979) and up to 70% of the above-ground standing stock of N can be lost to the atmosphere in this way. Burning similarly increases turnover rates of elements such as P, Ca and Mg and, in terrestrial grasslands, losses to the atmosphere of P and Mg in particulate form (the amount depending on meteorological conditions) occur (Allen, 1964). Bayley & Odum (1976) developed a simulation model of the Everglades marsh system in Florida in which fire was included as a forcing function. The model demonstrated sharp transitory peaks of phosphorus in marsh waters following fires.

When we consider wetland succession (section 1.3.1) we can appreciate that accumulation of detritus results in this component acting as a major long-term nutrient store. Over time periods of years the wetland is not in a steady state and the accumulated nutrients may not be in a form (or location) which would allow regeneration (see sections 1.3.3 and 1.3.4) to take place. Detritus in some cases, therefore, can become a 'sediment' sink for nutrients.

2.2.3. Fauna (k_5 , k_6 in Fig. 7). The role of fauna in wetland nutrient cycling is not well understood. Quantification of processes associated with benthic faunal activity in wetland habitats is to a large extent limited by the spatial heterogeneity described by Moss (1980). In some cases faunal mediated processes may be significant. By adding ³²P tracer to a dense submerged *Potamogeton pectinatus*

canopy and determining the amount of tracer which was accumulated in various biological fractions, Howard-Williams & Allanson (1981) found that 17% of the added ³²P ended up in the invertebrates. However, in that study the benthic fauna consisted of the mussel Musculus virgilae Barnard which has high filtering rates (c. 8 l g⁻¹ (shell free dry wt) h^{-1}) and is probably exceptional in its contribution to nutrient cycling. An examination of the role of benthic fauna in carbon flows in wetlands may give a first approximation of their role in nutrient cycling. Most wetland benthic fauna are detritus feeders and studies on wetland carbon flows such as those of the Phragmites reed swamps of Neusiedlersee (Imhof, 1973) indicate that 6% or less of the primary production is processed by the fauna. In some wetlands, however, grazing animals (normally vertebrates) can play a role. Coypu (Myocastor), swans and herbivorous fish all have been shown to be locally important in grazing. The net effect of such activities is to speed up nutrient regeneration rates (through faeces or physical damage). In some tropical African wetlands Hippopotamus result in nutrient inputs to wetlands as they graze on terrestrial systems at night, and much of this is recycled to the water through faeces during the day (Viner, 1975). These animals, and others such as coypu, also play a role in maintaining or creating channel flow through wetlands. Increasing channel flow will tend to reduce residence times, and increase spiral length with a reduction in nutrient processing rates.

In general, however, the role of fauna in flowing waters would be to decrease spiral length. The regeneration rate of nutrients locked up in litter or live plant material has been shown to increase as a result of faunal activity (Elwood *et al.*, 1983). Quantitative studies on such processes in wetlands are awaited.

2.2.4. *Micro-organisms* $(k_9-k_{12}$ in Fig. 7). Direct nutrient uptake in significant amounts from the water by microflora in wetlands (pathway k_9) is likely to be determined by two processes: decomposition of the detritus, and nitrification/denitrification. Uptake from the water by decomposers is likely to occur when an abundant supply of nutrient is available in the water but, in oligotrophic conditions, there is likely to be a release from detrital tissues to

the water as discussed in sections 1.3.3 and 1.3.4 above. Correll *et al.* (1975) showed that following the addition of phosphorus to an experimental plot in a *Typha* marsh the P was rapidly immobilized by the detrital layer microflora. In this form phosphorus moved both vertically downwards and horizontally. There was no evidence of rapid P release to the through-flowing water.

Microbial pathways associated with the nitrogen cycle can account for large amounts of nitrogen in wetlands. Losses of ammonium-N if not due to uptake by algal or macrophyte vegetation (pathway k_1) can be due to nitrification. In the absence of denitrification such losses would be balanced by subsequent increases in NO₃-N. In other words, as it is possible for apparent NH₄-N losses to be merely a step in nitrogen transformation, calculations of uptake rate constants and spiral lengths for dissolved nitrogen species (e.g. Table 1), can be misleading. Only by careful study of all N components can one distinguish between short-term transformation and uptake (i.e. loss to a storage component for a time greater than, say, 1 day). Nitrification during decomposition of emergent macrophyte detritus has been shown to result in the regeneration of over 50% of the original N as NO₃-N (Fig. 11). The opposite process, that of dissimilatory nitrate reduction, may also occur in reducing wetland soils (Buresh, DeLaune &



FIG. 11. Release of nitrogen compounds from decomposing watercress at two temperatures in aerobic conditions. Dry matter loss (dashed line) was calculated from an exponential fit to the original data, r=0.92 and 0.94 at 10°C and 20°C. Bars: \pm SE. DON=Dissolved organic nitrogen. After Howard-Williams *et al.* (1983).

Patrick, 1978). Loss of nitrogen from wetlands by denitrification can be significant. The recent applicability of the acetylene block technique to measure such loss rates (k_{12}) (e.g. early work by Yoshinari, Hynes & Knowles, 1976) has resulted in a number of measurements of potential and in situ denitrification rates in wetlands (e.g. Viner, 1982; Bartlett et al., 1979: Howard-Williams & Downes, 1984: Hemond, 1983). Denitrifying bacteria require NO₃-N as a substrate when O₂ is too low for aerobic respiration. The process thus occurs at low redox potentials, e.g. below +350 mV (Keeney, 1973). For rapid denitrification, therefore, an anaerobic environment must be juxtaposed to a source of NO₃-N. Complex redox patterns are often associated with wetland soils (Howard-Williams, 1984) which make this habitat ideal for the denitrification reaction. This process is discussed later in section 4.3.3 and see Table 7.

Apart from denitrification to N₂, nitrogen losses can occur by volatilization of ammonia. or by evolution of N₂O as an intermediate in denitrification or under certain conditions during the process of nitrification (Elkins et al., 1978). Losses of N₂O are thought to be small relative to N₂. Seitzinger et al. (1980) report a ratio of 250:1 for N₂ to N₂O being evolved. Smith & DeLaune (1983) studied the evolution of NH₃-N and N₂O-N from Spartina marsh soil cores. Losses were directly related to added NH₄ concentrations (Table 2) and in the case of NH₃, pH was an important determining factor also. However, the losses reported in Table 2 were recorded at pH 7.0-7.5, lower than that reported for other systems with significant NH₃ volatilization.

Nitrogen fixation rates (k_{11}) have been studied in a number of wetlands. Dierberg &

TABLE 2. Ammonia and nitrous oxide evolution from *Spartina* marshes following fertilization with $(NH_4)_2SO_4$. From Smith & DeLaune (1983).

Marsh	NH ₄ -N	NH ₃ -N	N_2O-N
	application	volatilized	evolved
	(mg m ⁻²)	(mg m ⁻²)	(mg m ⁻²)
S. alterniflora	0	6.0	2.2
	57	12	2.2
	1469	34	15
S. patens	0	0.9	0.4
	57	2.8	0.6
	1243	15	29

Brezonik (1981) report rates of 0.39 g N m⁻² vear⁻¹ for N-fixation in the litter of a Florida Cypress dome, and Hanson (1977) estimated 52 g m⁻² year⁻¹ for a Georgia Sparting marsh. Of this about 1% was contributed by microorganisms epiphytic on the Spartina and the remainder was due to sediment microorganisms. In a tropical floating wetland, Viner (1982) reported N-fixation rates of 8.0 g m⁻² vear⁻¹, and in a Sphagnum bog Chapman & Hemond (1981) report rates of 1.0 g N m⁻² vear⁻¹ fixed. Although apparently low in relation to salt marsh fixation, this input was the most significant source of N for the whole bog system. Hanson (1983) summarized daily Nfixation rates for nine saltmarsh species and demonstrated considerable spatial variability in rates. Dicker & Smith (1980) conclude that great spatial heterogeneity (vertical and horizontal) in the N-fixation ability of saltmarsh sediments makes quantitative areal rates of N-fixation a risky calculation.

Close interactions between macrophytes and N-fixers in wetlands have been suggested. Root exudates (carbohydrates) by the macrophytes are suspected to enhance N-fixers (Dicker & Smith, 1980) and Sphagnum has been shown to make immediate use of N fixed by associated Nostoc colonies (Basilier, 1980). The effects of nutrient loading of wetlands on N-fixation is discussed later (section 4.4.1). Hemond (1983) has recently compiled a well integrated budget for nitrogen in a wetland (Sphagnum bog) system in which the central role of micro-organisms is demonstrated. This budget (Fig. 12) again illustrates the crude approximation of the pathways in Fig. 7 and the great complexity of wetland nutrient cycles in nature. Pathways k_{11} and k_{12} can have significant effects on calculations of uptake or regeneration rate constants as nitrogen is not cycling (spiralling). These two pathways are inputs and outputs to the system and many of the equilibrium assumptions discussed in section 1.3 are not applicable when significant amounts of nitrogen are processed by these mechanisms.

2.2.5. Sediment (k_{13} , k_{14} in Fig. 7). These pathways essentially cover the non-biologically mediated exchanges between sediment and through-flowing water. The most important of these processes is that of sedimentation or trapping of particulate materials by wetlands in



FIG. 12. Components of the nitrogen cycle in a Sphagnum bog. Data as g m⁻² year ¹. After Hemond (1983).

some hydrological conditions, and erosion of particulates under other hydrological conditions. In addition NH4⁺ can be involved in cation exchange reactions (Kadlec & Tilton, 1979) and reactive phosphorus can undergo adsorption or desorption onto sediment particles (Dolan et al., 1981; Kadlec & Tilton, 1979). The trapping of incoming particulate material by wetlands takes place due to a reduction in water velocity, but, as pointed out by Kadlec & Tilton (1979), this can change rapidly as water velocities increase. Thus, whilst Hartland-Rowe & Wright (1975) found a 95% reduction in suspended matter passing through a Canadian wetland, Mudroch & Capobianco (1979) found that levels of suspended solids in wetland inflows and outflows varied considerably on a seasonal basis with outflow levels sometimes exceeding those of the inflows.

Wolaver *et al.* (1983) examined the annual phosphorus and nitrogen budgets for a salt marsh and found that 93% of the trapped phosphorus and *c*. 70% of the trapped N was

in the form of particulate matter. Schouten (1976) found that all of the bed load and 50%of the suspended load in runoff in the Puketurua Experimental Basin in New Zealand was deposited in the basin wetlands. This is hardly surprising, as Mulholland (1981) points out that, compared with streams, the lower gradients in swamps may result in a higher retention efficiency for particulate matter, particularly coarse particulate matter. Wetlands are characterized by low water velocities and throughflow with little erosive power. Channels are often poorly defined and pathways of water are tortuous. Thus water retention times for wetlands are likely to be greater per unit length than those of streams. Thus the retention efficiency $[(\Sigma \text{ inputs}-\Sigma \text{ outputs})/\Sigma \text{ in-}$ puts] for organic matter in a swamp stream was calculated as 0.63 compared with 0.04 and 0.34 for two contrasting upland streams (Mulholland, 1981). In streams, the concentration of particulate matter increases exponentially with discharge (e.g. Bormann, Likens & Eaton, 1969) but Mulholland (1981) points out that in swamp stream systems flood water is likely to be routed laterally, overspilling channels and the corresponding lower water velocities would not entrain organic debris even during floods. Thus the effect of floods may, in some cases be to enhance sedimentation (pathway k_{13}) in wetlands. Dawson (1981) points out that the presence of emergent vegetation in a stream radically alters the pattern of suspended matter transport by decreasing water velocities and increasing deposition for a given discharge.

An integral part of any study to calculate nutrient spiral length or processing efficiency is the measurement of F_p , the downstream flux of nutrient in the particulate phase (Newbold et al., 1981; section 1.3.4 above). While the literature on the transport and transformations of particulate material in streams is extensive, this field has not been well studied in wetlands and apart from the differences in sedimentation reported above there may be other significant differences. We might expect that the proportion of N lost by fluvial processes from a wetland would be less than that from a stream because of the greater proportion of gaseous loss processes in a wetland. There is clearly a need to study the dynamics of particulate material in wetlands, especially in relation to the hydrological regime.

The importance of sediments as long term sinks for nutrients in artificially enriched wetlands has been shown by de Jong (1976), Williams (1980), Dierberg & Brezonik (1983a) and others and is discussed more fully in section 4.3.

3. Mass flow of nutrients

3.1. Introduction

All natural wetland functions are a result of, or are closely related to wetland hydrology (Carter *et al.*, 1978). This must be the case as definitions of wetlands are based on hydrological characteristics. An understanding of wetland hydrology is therefore essential to an appreciation of nutrient flows both in terms of velocity, direction and, most importantly, quantities expressed as mass per unit time (mass flow). Mass flow (g s⁻¹) of a nutrient is obtained by the product of the nutrient concentration (g m⁻³) and discharge of water (m³ s⁻¹). While section 2 concentrated on descriptions of pathways and on concentrations of nutrients within wetlands, this section considers mass flows of nutrients into and out of wetlands.

The simplest way of considering flows through a system (i.e. a wetland) is to view it as a 'black box'. Thus an artificial boundary is set up around the wetland and only flows in and flows out are considered. Retention in the box is the difference between the two. Such an approach is taken in Fig. 2(b) and Fig. 3 where y/x ratios were discussed, and internal pathways within the box are not considered. Although simple in concept, the black box approach to viewing wetland nutrient flows has some major problems, not all of which are adequately covered in the literature. An inputoutput nutrient budget for a wetland depends on a hydrological budget which in simple terms can be given as

$$P + SW_i + GW_i = E + SW_o + GW_o + \Delta S \qquad (5)$$

where P=precipitation, E=evapotranspiration, GW=groundwater, SW=surface water, subscripts i and o refer to input and output, and ΔS is a change in storage. Units are as volume per unit time. The product of a nutrient concentration (with units of mass per unit volume) and each of the above elements (volume per unit time) would provide an input-output nutrient budget (mass per unit time).

3.2. Factors affecting mass flows

3.2.1. Groundwaters and dilution. Whigham & Bayley (1978) list eighteen studies dealing with nutrients in wetlands. Only seven contained data for input and output in terms of mass flow. Of these, six considered groundwater outputs and only one groundwater input. Table 3 provides a list of studies in which the inputs and outputs of nutrients to wetlands are considered in mass flow units. Few of them include groundwaters in the budget, the assumptions (presumably) being that groundwater contributions are either negligible or GW_i=GW_o. As wetlands are often groundwater discharge areas, such assumptions could be quite misleading. Several examples are given in the recent literature showing how groundwater inputs may or may not affect

Reference	Element	GW	Notes
Hemond (1983)	Ν	*	Atmospheric exchanges, precipitation, runoff. Com- ponents of N cycle. Recorded as g m ⁻² year ⁻¹ .
Gaudet (1976)	Ν, Ρ		Precipitation and surface flows, kg year ⁻¹ for swamps.
Fetter et al. (1978)	Р		kg year ⁻¹ precipitation and surface flows only.
Steward & Ornes (1975)	Р		kg ha ⁻¹ week ⁻¹ inputs and storage.
Dolan et al. (1981)	Р		mg m ⁻² day ⁻¹ inputs, outputs ΔS and P and E.
Huff & Young (1980)			P, E, GW and SW hydrologic budget.
Boyt et al. (1977)	N, P	*	g m ⁻² year ⁻¹ all components.
Yates & Sheridan (1983)	Ν, Ρ	*	g ha ^{-f} month ⁻¹ rain and surface and subsurface output (whole catchment).
Woodwell et al. (1979)	N, P		kg dav ⁻¹ for flax pond. Inputs, outputs (surface).
Vega & Ewel (1981)	Р		Surface inflow outflow kg. Inputs, ΔS g m ⁻² year ⁻¹ .
Valiela et al. (1978)	N.P	*	Precipitation and groundwater.
Patten & Mathis (1982)			Hydrologic model.
Peverly (1982)	N.P		kg day ¹ surface flows only.
Prentki et al. (1978)	Р		g m ⁻² dav ⁻¹ ΔS only. Lakeshore marsh.
Crisp (1966)	Ν, Ρ	*	Precipitation and surface output for bog kg ha ⁻¹ year ⁻¹ .
Dierberg & Brezonik (1983a, b)	Ν, Ρ	*	Inputs, outputs including percolation to groundwater in <i>Cypress</i> domes. g m ⁻² year ⁻¹ .

TABLE 3. Data on nutrients entering and leaving freshwater wetlands quantified in terms of mass flow

P=precipitation; E=evapotranspiration; SW=surface water; ΔS =storage of water.

GW=groundwater.

* Studies where GW was considered.

surface water outputs from wetlands (Sloey, Spangler & Fetter, 1978; Patten & Mathis, 1982; Valiela *et al.*, 1978). A useful introduction is seen in the four wetland hydrologic classes of Novitski (1978): (1) surface water depressions: (2) surface water slopes; (3) groundwater depressions; (4) groundwater slopes.

In the first two types the wetland does not intersect the groundwater table, the groundwater plays a negligible role in the hydrology. In type 3, groundwater inputs may not be large but in type 4 the groundwater discharges in the wetland as springs or seeps. Such wetlands commonly occur at the bottom of hillsides or on a slope where geological conditions inhibit further downward percolation of water. In such cases, groundwater may represent 50% or more of the water budget. However, it may be that in spite of considerable quantities of groundwater entering a wetland area, this has little effect on surface flows. Patten & Mathis (1982) show that although 25% of the water entering the Okefenokee swamp is groundwater, this remains separate from the surface water and leaves again as a discrete package. In contrast, the major source of nutrient nitrogen to a tidal wetland on the U.S. coast was in the groundwater (Valiela *et al.*, 1978). This entered the wetland primarily as NO_3 -N and DON where it was biologically transformed such that over 50% of the N left in particulate form.

Thus, when two or more inputs to a wetland exist, the outflow nutrient levels reflect not only biological transformations or removal within the wetland (section 1.3 above) but also the effects of the mixing of these inputs. This mixing effect has a number of consequences for sampling at the wetland (black box) output. Inputs of dilute groundwaters can change surface water concentrations by dilution. Steady state assumptions as modelled by Fig. 3 can be markedly altered by pulses of dilute groundwater such that y/x can decrease irrespective of any change in the wetland nutrient processing efficiency, and concepts such as nutrient spiral length assume no input and output within the study section.

Table 4 shows how the concentrations of N and P in water leaving a wetland can be considerably less than those in the measured inflows. These differences can largely be ascribed to dilution, with the wetland organisms playing a lesser part. Thus the reporting of percentage reduction in nutrients passing

Budget	Total dissolved phosphorus $(n=5 \text{ years})$	Dissolved inorganic nitrogen (<i>n</i> =6 years)
Input average (g m ⁻³)	2.87	7.67
Output average (g m ⁻³)	0.20	0.67
Reduction in conc. $(C_c)^*$	93	91
Reduction due to dilution (c) +	66	58

TABLE 4. Mean values from a 6 year study of nutrient removal from added wastewater by a wetland (modified from Kadlee, 1981)

Output average

Input average +100 (based on concentrations above).

⁺ Reduction due to dilution computed by dividing total N or P input (as mass flow) by volume of water leaving to get potential output concentration. This reduction would be observed if the wetland itself did nothing.

through wetlands, which is based on concentration differences, is often somewhat questionable (Tilton & Kadlec, 1979).

3.3.3. Evapotranspiration. Evaporative effects can markedly alter wetland hydrological regimes and thus nutrient budgets as estimated by blackbox input–output studies. Water losses by evaporation can vary widely from a low 60% to well over 100% of those from an equivalent open water surface (Rijks, 1969; Linacre *et al.*, 1970; Smid, 1975). Clearly assumptions on evaporative losses being equivalent to those of an open water surface for budget calculation (e.g. Linsley, Kohler & Paulhus, 1982) can be misleading.

Apart from modifying nutrient mass flows by altering the hydrology, evaporative processes can change the nutrient status of wetlands by a process of concentration and nutrient loss in evapotranspiration. The concentration of nutrients in wetland waters by evaporation was one of the factors assumed responsible for increases in levels of nutrients in several tropical wetlands (Visser, 1962; Howard-Williams, 1973; Gaudet, 1976). Losses of nutrients (specifically ammonia) in the transpiration stream have been shown to occur in several terrestrial situations and in at least one wetland plant, rice (*Oryza sativa* L.) (da Silva & Stutte, 1981).

Finlayson & Chick (1983) clearly demonstrated the concentration effects of evaporative losses on nutrients in the outflow from aquatic plant (*Typha, Phragmites*) beds, where 32– 49% of the added water was lost by evapotranspiration. 3.2.3. Floods and seasonality. With the exception of strongly springfed systems in headwater areas, the hydrology of most wetlands is such that significant changes in flow rates and/or water levels occur during flood (and dry period) events or on a seasonal basis corresponding with wet or dry seasons. Such hydrological changes clearly have a great effect on wetland nutrient cycles and retention ability.

(a) Flood effects. Although the effects of wetland vegetation on floodwaters have been fairly well studied (Carter et al., 1978), the effects of flood events on wetland water quality have not. Single floods can wash out or deposit large quantities of nutrients. Gosselink & Turner (1978) review the evidence demonstrating that in some cases the higher the flooding velocity of wetland throughflow the greater the sediment input. In such cases those parts of the wetland near channels where water velocity is greatest receive greater amounts of nutrient rich sediment than areas further from channels. This is ultimately reflected in greater plant productivity along channel margins. Whilst inorganic sediments are frequently deposited in wetlands by flood events, such events frequently wash out organic matter (Gosselink, Hopkinson & Parrondo, 1977). Odum & de la Cruz (1967) found that the rate of export of particulate organic matter was directly proportional to discharge rates in a Georgia salt marsh. The frequency, intensity and extent of the rainfall prior to sampling was one of the major factors contributing to variability in N and P in Florida swamp Cvp-

ress domes (Dierberg & Brezonik, 1983b). Jones & Lee (1980) stress that the ability of a wetland system to remove phosphorus depends on the number of large storm events. Mulholland et al. (1981) have reported one of the few studies on the effects of flooding on the water quality of freshwater wetlands. They found that dissolved (passing through 0.45 µm membrane filters) N and P generally exceeded particulate forms during non-flood (baseflow) discharges. During floods dissolved N and P increased but fluxes of phosphorus were dominated by the particulate fraction. Peak concentrations occurred before or during peak discharges, a phenomenon well known for headwater streams. They conclude that floods play a major role in the annual phosphorus flux in the wetland.

Glandon *et al.* (1981) found that total N and P released from a Michigan wetland as a result of rain was of approximately the same proportion of total N and P release as the rain induced discharge was to total discharge. Thus over a 95 day period 57% of total discharge was a result of rain. These rain induced discharges accounted for 53% of the total P and 61% of the total N flux over the period.

(b) Seasonal effects. Both the hydrology and the uptake of nutrients by wetland vegetation can vary seasonally. As plant growth plays a significant role in wetland nutrient cycling this is not surprising in temperate latitudes where growth is closely coupled with temperature and day length. In these latitudes nutrient cycles in spring and summer are very different from those in autumn and winter (see section 2.1 and Fig. 8). Gaudet's work in the tropics (Gaudet, 1977, 1978, 1982) and that of Junk (1983) demonstrates that seasonal changes in wetland nutrient flux are associated with rainfall (rainy season v. dry season) rather than temperature.

In temperate wetlands Harrison, Keller & Dimovic (1960) and Howard-Williams, Davies & Pickmere (1982) found that nitrate was removed from throughflow in summer by plant growth, but no removal occurred in winter. Similarly a >50% reduction in phosphorus occurred in Theresa Marsh in summer due to biological uptake but a large export of P from the marsh took place in spring and autumn. These were due to ice melt and decomposition respectively (Klopatek, 1975). In tropical

swamps and wetlands subject to major seasonal changes in water level or throughflow, pulses of nutrients can be released by reflooding of dry soils where nitrification has occurred (Howard-Williams, 1972; McLachlan, 1970) or by covering standing litter (section 2.2). This latter process, and subsequent decomposition, is responsible for the autumn pulse of P found in some temperate marshes. Richardson *et al.* (1978), however, suggest that high NO₃-N levels in spring in temperate wetlands are due to the inhibition of denitrification in the low water temperatures found at this time, rather than a release of NO₃-N *per se.*

3.2.4. Rates of throughflow. Nutrient retention in wetlands is governed not only by the number of floods (i.e. changes in the hydrograph) but also by the rates (velocity) of throughflow and residence time of the water. This was discussed in theoretical terms in section 1.3 (see e.g. Fig. 5). Peverly (1982) found that retention of nutrients by a wetland occurred only when throughflow rates were low. McColl (1979) suggested that the ponding effect of aquatic plants on flowing waters, whilst affecting discharge, reduced current speeds so that particulate P was sedimented and a longer contact time allowed for greater absorption of dissolved P. If water moves through a wetland more rapidly than the ability of the vegetation to remove N and P then there will be appreciable flowthrough of these nutrients (Jones & Lee, 1980). Such findings are not surprising when we consider Fig. 3 (section 1.3.2). If throughflow rates are more rapid than the uptake and release constants (k) then v/x (output/input) ratio will increase. For the same reasons spiral length increases as discharge increases as k is inversely proportional to discharge (section 1.3.4). This effect is demonstrated for NO3-N in a vegetated stream (Fig. 6a). It is also interesting to note that increasing current velocities can alter the nutrient species (i.e. induce nutrient transformations) in wetland throughflow. Gaudet (1979), for instance, found that increasing dissolved oxygen levels were associated with increasing throughflow rates in a tropical floating swamp. This resulted in the reduced forms of N (NH3, DON, NO2) declining, compensated for by an increase in NO₃-N. The importance of the residence time in dictating nutrient uptake in experimental wetlands was stressed by de Jong (1976) and Spangler, Sloey & Fetter (1976). This will be discussed further in section 4.2 of this review.

4. Nutrient enrichment of wetlands

4.1. Introduction

Section 2.2 (e.g. Fig. 7) emphasized the role of the storage compartments in mediating the fluxes of nutrients through wetlands. The storage compartments have finite boundaries or carrying capacity (section 1.3.3) and when the stores are full, the capacity to absorb nutrients breaks down as shown theoretically in Fig. 3, phase C. This, in turn, induces a number of other effects which will be dealt with in this section. These include changes in plant species composition, changes in productivity, and changes to the consumers and detritivores. Before examing these changes, however, it is necessary to examine the concept of loading capacity.

4.2. The loading capacity

The addition of nutrients to wetlands will result in a loading of the storage compartments. As stressed in the discussion on Basic Concepts, the transfer rates of nutrients from compartments to throughflow and to each other, and the boundary size of these stores will determine the ultimate capacity of the whole wetland to retain nutrients. Information on the nutrient loading capacity of wetlands is slowly emerging.

An early reference to this was the work of Stake (1968) in a Swedish stream. Reductions in P down the stream were attributable to uptake by aquatic plants. However, a point was reached where nutrient additions from farmlands were such that no further reductions in P were detected. In other words, the amount in the available pool (A) approached the carrying capacity (T) and $dA/dt \rightarrow 0$ (see eqn (2) in section 1.3.3). Studies in Europe (Crisp, 1970; Robinson & Cumbus, 1977) and New Zealand (Gifford, 1981; Vincent & Downes, 1980) show that watercress (Nasturtium officinale) has a high nutrient uptake rate and watercress beds can significantly reduce dissolved N and P from throughflowing waters. However, McColl (1974) reported a

watercress-dominated stream which showed no reduction in NO₃-N, the reason being that an overflow discharge from a sewage works continually loaded the stream, saturating the system with available nutrient. Steward & Ornes (1975) added sewage effluent at a phosphorus loading rate of 2.6 kg ha⁻¹ week⁻¹ to a *Cladium* marsh in the Florida Everglades. They found that the system was overloaded with nutrients in only 8 weeks. after which there was no further phosphorus removal.

As the atmosphere is a sink for nitrogen in systems where denitrification occurs, we can visualize a wetland with suitable sediment redox conditions which is saturated with phosphorus but with a continued capacity for nitrogen assimilation. An example might be the Kincheloe wetland (Kadlec & Kadlec, 1978) which has removed nitrogen from a wastewater discharge for 20 years, but now exports phosphorus at concentrations of 1–3 mg l^{-1} indicating P but not N saturation.

The loading capacity of wetlands varies seasonally, particularly in temperate regions where biological activity is reduced in winter. Lee, Bentley & Amundson (1975) suggest that over an annual cycle the net absorption of P by a wetland is negligible because P absorbed during summer is released the following spring. Harrison et al. (1960) and Sloev et al. (1978) point out that when plants in wetland systems cease to grow in winter, nutrient overloading occurs. This can be clearly seen in the seasonal changes in the macrophyte dominated Whangamata Stream in New Zealand (Fig. 13). With winter die off of macrophytes nutrient removal from throughflow ceased. Other studies demonstrating the seasonal breakdown in loading capacity are those of Mitsch (1977) and Spangler et al. (1976). Dolan et al. (1981), working in Florida, found no seasonal effects of P uptake in their wetland study sites. They suggest that the warm temperate climate of the area allows for continued operation of the essential biogeochemical processes involved in P assimilation. The major sink for P in their site was the sediment. and continued long-term P uptake was dependent on peat production and soil uptake. However, this lack of seasonality could also be due to the fact that these palustrine wetlands do not undergo the major seasonal changes in hydraulic loading which are characteristic of



FIG. 13. Seasonal changes in NO₃-N concentrations at an upstream (solid circles) and a downstream (open circles) site in a New Zealand stream colonized by watercress (*Nasturtium officinale* R.Br.). Discharge was the same at both sites. Mean biomass of watercress (line with stars) is also given. Variability in biomass data are given in the data source: Howard-Williams *et al.* (1982).

more northern wetlands in the U.S.A. (Richardson *et al.*, 1978).

Cooper & Cooke (1984) found no evidence of seasonality in NO₃-N uptake in headwater streams in New Zealand which were densely colonized by *Glyceria* spp. These streams are spring fed with a relatively constant discharge.

When for a given time period, changes in wetland storage compartments are minimal, and inputs \approx outputs, a steady state with respect to nutrient flows has been reached (Fig. 3, phase B). Within the given time period the wetland system's capacity to remove nutrients may be negligible. Peverly (1982) found a stream system close to equilibrium for N and P in that input loads balanced outputs. Similarly Vega & Ewel (1981) found that P uptake from sewage effluent entering Lake Alice, Florida, was balanced by losses in the outflow. Thus there was no further loading capacity and only macrophyte harvesting could remove P in the long term.

In some cases the natural loading capacity of a wetland system can be altered by addition of nutrients in inappropriate forms. McNabb (1976) suggests, for instance, that the growth of submerged macrophytes requires aerobic conditions. Therefore, the addition of a high BOD loading with nutrients to submerged communities can have a deleterious effect. In terms of the equilibrium exchange model (Fig. 2a) in section 1.3.2 this is equivalent to reducing the size of the storage compartment. If the ability of the storage compartments to effect exchange rates (k) is limited by an unfavourable environment then k for the system will decrease. In the Bellaire wetland wastewater treatment facility, plant canopy damage as well as root exposure resulted from a hydrological overloading, with a consequent reduction in the removal capacity. Pope (1981) found that problems associated with sludge accumulation in artificial wetlands meant that these did not operate as nutrient removal systems. This topic will be discussed later (section 5).

4.3. Long-term nutrient sinks

If wetlands can remove nutrients for time spans of greater than 1 year (i.e. a seasonal cycle) the long-term fate of these is of particular interest. There are a number of possible long-term pathways; degassing (nitrogen), sediment accumulation (N and P), incorporation into longlived plant biomass such as the woody tissue of trees in certain types of wetland, and grazing or harvesting.

4.3.1. Experiments and models. Table 5 lists

Wetland	Length of time of enrichment (years)	Reference
Bellaire	12	Vega & Ewel (1981)
Brillon	56	Spangler et al. (1976)
Cypress domes*	5	Dierberg & Brezonik (1983a, b)
Dundas	62	Mudroch & Capobianco (1979)
Great Meadows	68	Yonika & Lowry (1978)
Houghton Lake	4	Hammer & Kadlec (1983)
Kincheloe	25	Kadlec & Bevis (1979)
Lake Alice	6	Kadlec (1981)
Sippewissett Marsh	3	van Raalte <i>et al.</i> (1974)
Wildwood	20	Boyt <i>et al.</i> (1977)

TABLE 5. Wetlands where deliberate nutrient enrichment has occurred for periods of 3 years or more

*This study also monitored changes following cessation of nutrient enrichment.

a number of wetlands which have received nutrient additions in the form of wastewaters for long periods of time. Although there have been changes in some of these in recent times the older ones in particular were still functioning to some extent as nutrient traps in 1978 (Kadlec & Kadlec, 1978).

In the absence of detailed long-term information on the behaviour of nutrient storage compartments and sinks, short-term nutrient pathways have been included in mathematical models of wetland systems which have been used to assess long-term human impacts on wetlands. A brief review of the number of these models is given in Mitsch *et al.* (1982) but three are particularly relevant here. Gupta (1977) and Dixon & Kadlec (1975) have used simulation models of wetlands to examine the implications of long-term nutrient additions.

Both these models were large-scale simulations which divide the wetland into spatial blocks each with discrete chemical and biological units so that spatial patterns in a wetland can be incorporated. Within each block, nutrients are shown to cycle among biotic and abiotic components and to exchange with surroundings. Each block has the characteristics of an ecosystem model.

Dixon & Kadlec's preliminary model examined the effect of wastewater discharges on the organic matter components of a wetland. Most of the detrital components showed increases in mass with time following nutrient additions, whilst in a 'natural' wetland (no addition of nutrients) there was no apparent detritus accumulation. The model suggested that in the long term a live vascular plant biomass may be stimulated by low level additions of nutrients but it would be retarded by high nutrient additions. Figure 14 shows the 10 year simulations for the litter compartment from this model. Incoming nutrients are accumulated, at least for 10 years, in the detrital components of the wetland.

The authors stress that although the sensitivity analysis on the model suggests it is robust enough to be used as an aid to decision making, the results only give an indication of relative rather than absolute effects of added water and nutrients.

Gupta (1977) took Dixon & Kadlec's model a stage further by aiming to simulate the subdivisions of a real wetland (Houghton Lake wetland) with the blocks in the model. Simulation of long time periods (c. 100 years) indicated that the 100 ha wetland could absorb summer wastewater discharges of up to 6000 $m^{-3} day^{-1}$ containing 0.36, 0.08 and 0.41 g m^{-3} of NO₃-N, NH₄-N and PO₄-P without outflow waters consistently containing as much as 0.2 g m⁻³ of each of these nutrients. One fifth of the wetland (in the vicinity of the discharge) would however become saturated in 20 years. Both these models suggest that long-term accumulation of nutrients occurs in the detrital and sediment compartments.

Hammer & Kadlec (1983) adopted a different modelling approach. They used a mass balance equation to predict the distance and/or time for the removal of a dissolved substance.



FIG. 14. Simulated relative changes in litter biomass in a wetland over a 10 year period at three nutrient loading rates. Data from the model of Dixon & Kadlec (1975).

The central assumption of their model is that from a point source nutrient discharge in a wetland, the compartments become progressively saturated with time from the source in a direction downstream. Thus if the source is in the centre of a wetland there will be a saturated zone around this where none of the nutrients are absorbed. From the edges of this zone outwards, nutrients are removed at a rate proportional to the concentration (see e.g. equ (2) and section 1.3.4). Incorporated in the model are both long-term 'sinks' such as nutrient incorporation into woody tissue and sediment accretion, and temporary storage (nonwoody plant biomass, detritus). Comparison of the model's predictions on the expansion of the saturated zone with observed concentrations from Houghton Lake wetland treatment site over a 3 year period have shown good agreement.

4.3.2. Nutrient accumulation. Accumulation of nutrients in detrital and soil compartments of wetlands has been documented in a number of studies. Some African swamps, for instance, have up to 30 m of accumulated peat beneath them (Thompson & Hamilton, 1983). Richardson *et al.* (1978) record large stores of nutrients in accumulated peat (Table 5).

Whilst N and P are bound in organic form in accumulated peat, the organic sediments of wetlands also adsorb reactive phosphorus and in some cases ammonium. Phosphorus adsorption on to aquatic soils is a well-documented phenomenon (Syers, Harris & Armstrong, 1973; Twinch & Breen, 1982) and Correll *et al.* (1975) showed P movement downwards

TABLE 6. Stocks of tota	IN and P in the top 20 cm o	f peat in three wetland ty	pes. Values as kg ha ⁻¹
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Wetland	Total N	Total P	Reference
 Fen peat. Houghton Lake. Michigan Canadian blanket bog African papyrus swamp. Henya 	6380	242	Richardson <i>et al.</i> (1978)
	370–2240	28–102	Pollett (1972)
(a) Peat	4860	106	Gaudet (1976)
(b) 'Sludge'	5220	84	

through *Typha* marsh soils once added P had been incorporated into the microflora.

However, quantitative information on the relative importance of sediment adsorption processes versus uptake by the various plant and microbial communities of wetlands is not readily available. The information generally consists of studies on isolated components of a wetland. Exceptions to this are the studies on the Cypress domes of Florida and work on artificial wetlands. Dolan et al. (1981) specifically addressed their study to identification of the nutrient sinks in a Cypress dome. The mass balance calculations from this study showed that 69.2% of the inflow P ended up in the sediments, 23.2% in below-ground biomass and 5.2% in above-ground dead plant matter. The remaining 2.5% flowed out of the experimental area. In a related study Dierberg & Brezonik (1983a, b) concluded that the Cypress domes removed <33% of the N and P added in treated sewage effluent. However, when concentrations of these substances in the discharge water of the shallow aquifers below the domes were examined, it appeared that >90% of these elements were removed. The associated sediments and strata in the underlying aquifers were responsible for most of the nutrient removal.

In discussing the large artificial wetland at Vermontville (Michigan, U.S.A.), Williams (1980) stated that seepage through the soil is necessary to account for 90% of the P removed. He stressed that the system operated basically as a flood irrigation facility. Similar conclusions can be drawn from the other studies (de Jong, 1976; Fetter, Sloey & Spangler, 1978).

Two experiments have maintained suitable controls (rare in this type of study) which included unvegetated basins similar to those planted with macrophytes. Fetter, Sloey & Spangler (1976) found that the unplanted control basin performed almost as well as those with *Scirpus* beds. The physical and chemical properties of the soils and their microbial populations were clearly the principal compartments for nutrient cycling. In a more recent study Gersberg, Elkins & Goldman (1983) examined the nitrate removal capacity of fourteen small artificial 'wetland' plots planted with three genera of macrophytes (*Typha*, *Scirpus* and *Phragmites*). For the whole year, removal efficiency for total nitrogen was 27% for the vegetated beds and 25% for the unvegetated beds. Denitrification in the soil was the main N removal process (see sections 2.2.4 and 4.3). The addition of an endogenous carbon supply in the form of methanol or plant mulch improved total nitrogen removal to 95% and 60% respectively.

4.3.3. Degassing. Microbial transformations in the nitrogen cycle are important processes in N loss from wetland waters. Nitrogen can be lost as N₂ or N₂O during denitrification, or N₂O can be lost by nitrification under certain conditions. In addition to these processes, NH₃ volatilization (Table 2) has been shown to occur from salt marsh soils (Smith & DeLaune, 1983), and direct NH₃ losses can occur to the atmosphere from rice plants themselves growing in aquatic soils (da Silva & Stutte, 1981). These processes were described in section 2.2.4. The importance of these losses relative to other sinks is not well documented though. Often, the proportion of nitrogen lost by denitrification is calculated by a mass balance difference (e.g. Hill, 1979; Tilton & Kadlec, 1979; Fetter et al., 1978).

Table 7 gives data on wetland denitrification where the process has been measured. Comparative studies of denitrification versus aquatic plant uptake have been examined in New Zealand streams dominated by macrophytes. Howard-Williams & Downes (1984) found denitrification rates of 1-80 mg N m⁻² day⁻¹ which, when compared with macrophyte uptake of 900-1500 mg m⁻² dav⁻¹ during maximum growth, was a small proportion of total N loss from the stream. Cooper & Cooke (1984) found denitrification accounted for 25% of the N uptake from two headwater streams. Viner's (1982) data on papyrus mats and sediments for Lake Naivasha (Kenya) showed potential denitrification rates of 1.5-12.9 mg N m⁻² day⁻¹. In comparison with plant uptake of N from the floating swamps here of 350 mg m² day⁻¹ (Gaudet, 1977), denitrification may also appear to be a small component of N uptake.

In a controlled field study, Gersberg *et al.* (1983) found that wetland plants played little role in N loss, the most important process being denitrification. Unvegetated plots removed almost as much N as plots covered with *Scirpus, Typha* or *Phragmites.*

Site	Reference	Method	Denitrification rate*
Lake Naivasha, Kenya (F)	Viner (1982)	Potential (added NO ₃) rates, acetylene block method	1.5-12.9
Great Meadows, Mass., U.S.A. (F)	Bartlett et al. (1979)	Potential (added NO ₃) rates, Warburg respirometry	550+
Phragmites swamp, Arreskov Sø, Denmark (F)	Andersen (1981)	Laboratory rate, sediment NO ₃ uptake	55
Bayou Sorrel, Louisiana, U.S.A. (F)	Engler & Patrick (1974)	Laboratory rate, sediment NO ₃ ⁻ uptake	350
Whangamata Stream, New Zealand (F)	Howard-Williams & Downes (1984)	<i>In situ</i> rates, acetylene block method	1-84
Barataria Bay, Louisiana, U.S.A. (S)	Engler & Patrick (1974)	Laboratory rates, sediment NO ₃ uptake	740
Barataria Bay, Louisiana, U.S.A. (S)	Smith & DeLaune (1983)	In situ based on N ₂ O emissions and a 250:1 N ₂ : N ₂ O ratio	<7000
Barrow tundra pond, Alaska (F)	Prentki et al. (1980)	Potential (added NO ₃) rate; field study with ¹⁵ N	0.03
White Cedar swamp, U.S.A. (F)	Tiedje et al. (1982)	Potential (added NO ₃) rates, acetylene block method	110

TABLE 7. Denitrification rates in wetlands or streams dominated by emergent macrophytes. Rates as mg N m⁻² day⁻¹, *Hourly rate $\times 24$, \pm Assume 10 cm deep dry wt of sediment= 2.5×10^4 g m⁻². F=freshwater; S=saline.

However, although the New Zealand studies and those from the tropics indicate a much larger relative loss of N by macrophytes, some of this is merely in temporary storage, to be returned to the throughflow water in a transformed (i.e. particulate) state. Denitrification, on the other hand, is a permanent loss. Conditions for denitrification to occur at maximal rates are unusual, requiring low redox potentials combined with a source of oxidized nitrogen. Changes to wetland soil environments resulting from nutrient additions are likely to affect sites for denitrification, as well as other processes. Such changes are documented in the next few sections.

4.4. Effects of nutrient enrichment

4.4.1. Changes in biota. (a) Primary producers. Changes to the flora of wetlands following the addition of nutrients are to be expected. An excellent long-term record of such changes has been documented for the wetlands of Norfolk in England (Moss, Leah & Clough, 1979). Increasing eutrophication in the nineteenth century resulted in the development of filamentous epiphytes on the aquatic plants. The disappearance of the *Chara*dominated flora of the broads in about 1912 was probably associated with the building of the first sewage treatment works for Norwich city in 1908, which discharged into these wetlands, and resulted in the development of further filamentous algal and phytoplankton growth. Both Characeae and submerged vascular macrophytes ultimately disappeared from a number of the broads.

Similarly, filamentous algal growth in fertilized Cladium plots in Florida suppressed the natural Chara and Utricularia growth (Steward & Ornes, 1975). Whigham & Simpson (1976) recorded an increase in the amount of coverage of benthic algae in a freshwater tidal marsh following nutrient additions as sewage effluent. They also found that significant changes occurred to the species composition of annual herbs, whilst the perennial plants were relatively unaffected. Artificial enrichment of dense Potamogeton pectinatus beds with N and P resulted in the rapid development of a cover of filamentous algae over the macrophytes. This occurred at fairly low levels of enrichment of 25 mg m⁻³ week⁻¹ of dissolved reactive P and 250 mg m⁻³ week⁻¹ of dissolved inorganic N (Howard-Williams, 1981).

Ewel (1976) and Dierberg & Brezonik (1983a) found that the most conspicuous effect of the application of sewage effluent to *Cypress* domes in Florida was the development of small free-floating macrophytes. These were

Spirodela oligorhiza (Kurz) Hegelm. in summer and Lemna perpusilla Torr. in winter. They appear to have the same effect as filamentous algae in adversely affecting submerged macrophytes, in this case Utricularia. This was probably due to the prevention of re-aeration and the resulting near anoxic conditions which developed under a cover of the free-floating species (Dierberg & Brezonik, 1983a) as well as restricting light penetration. Blue-green algal development following enrichment has been shown to inhibit the growth of water chestnut, *Trapa natans* L. (Tsuchiya & Iwaki, 1979).

Considerable site to site variability in the effects of nutrient additions on the larger emergent perennials of wetlands occurs. Although Whigham & Simpson (1976) found little change to the perennials, the complete replacement of Typha by Glyceria in a Canadian wetland followed nutrient inputs in sewage effluent (Mudroch & Capobianco, 1979). In the Bellaire treatment system, the wetland trees, mostly birch, spruce and cedar, had died out in a 100 m zone downstream of the input (treated sewage effluent) point. However, other perennials (e.g. Typha) had invaded (Kadlec, 1981). The significance of such changes to system processing efficiency will be discussed in section 5.

In tropical Waigani swamp in Papua New Guinea, nutrient enrichment apparently resulted in a reversal of the hydrosere with the replacement of an emergent and nymphaeid flora by open water (Osborne & Leach, 1983). Similar variability in response occurs in salt marshes. Whilst Salicornia was replaced by Spartina following nutrient additions (Valiela, Vince & Teal, 1976), Jeffries & Perkins (1977) found salt marsh communities changed little over a 4-5 year period of enrichment. They recorded greater year to year variation within a treatment than between treatments of different nutrient additions. These authors concluded that factors limiting plant growth and performance in the salt marsh were low water potentials and high salinities in summer. Therefore nutrients were not limiting growth in any of the species present.

(b) *Microflora*. Changes in wetland microflora following nutrient additions are inevitable but have only been recorded in a few studies with contrasting results. Unfortunately the effects of the nutrients have usually not been discriminated from the effects of the medium (usually sewage effluent or sludge) in which the nutrients occur.

Sherr & Payne (1981) found that after 9 months of sewage sludge addition to the *Spartina alterniflora* Loisel. marsh, significant decreases in potential denitrification rates occurred in the top 15 cm of soil. They suggested that the inhibitory effect was one of direct toxicity on the denitrifying bacteria, but did not identify the inhibitory compound. These results contrast with those of Valiela, Teal & Sass (1975) who found elevated seasonal rates of denitrification in parts of a Massachusetts salt marsh which had received sewage sludge.

It is interesting to note that nitrogen fixation in wetlands has also been found to be inhibited by the addition of sewage sludge or other nitrogen rich compounds such as urea (Fig. 15). van Raalte et al. (1974) found that N-fixing bacteria used alternative N compounds in preference to fixation if the former were in plentiful supply. They suggest that this shift in the nitrogen cycle may remove substantial amounts of N from throughflowing water. Dierberg & Brezonik (1981) found that Nfixation contributed 14% of the N increment found on decomposing Pond Cypress leaves in a natural Cypress dome. In a dome enriched with sewage effluent, this amount was reduced to 1%. Presumably the swamp water provided this difference as described in section 1.3. However, in contrast to these studies, Hanson (1977) found that the addition of N to a wetland stimulated N-fixation. This was due to its effect in enhancing Spartina production and the subsequent production of root exudates which were important for the maintenance of N-fixing microbial populations.

(c) *Secondary producers*. Kadlec & Tilton (1979) have reviewed the literature on the effects of sewage effluent on secondary producers in wetlands, the main points being that invertebrate densities and diversity are reduced as a result usually of lowered dissolved oxygen concentrations. However, of the wetland vertebrates, bird life responded positively to nutrient additions.

In the studies of Moss (1976) and Hall, Cooper & Werner (1970) nutrients were added in salt form to replicated macrophyte dominated ponds. Moss concluded from these experi-



FIG. 15. N_2 fixation rates in wetlands are reduced in the presence of high concentrations of alternative N compounds. After van Raalte *et al.* (1974).

ments that the addition of high levels of nutrients (0.09 g m⁻² P week⁻¹ and 0.91 g m⁻² N week⁻¹) had no significant effect on total benthic invertebrate biomass.

It would appear from the available data that the carrier medium (e.g. sewage effluent) has a greater effect than the nutrients themselves on wetland secondary producers.

4.4.2. *Changes in productivity.* If nutrients are limiting plant growth we might anticipate that, in spite of species shifts, increasing productivity would result from nutrient additions. This is certainly substantiated from the available evidence. However, of greater signifi-

cance to a wetland in the long term is not the increase in production rate, but the attendant increase in organic matter accumulation and possible acceleration of the hydrosere (Waigani swamp being one documented exception; Osborne & Leach, 1983).

Figure 16 shows the effects of nutrient additions in the form of sewage sludge fertilizer on salt marsh biomass (the production to maximum biomass ratio (P/B) in this marsh was between 1 and 2). Increases in biomass were detected after 1 year of treatment and remained for 3 years of treatment. The authors believed that the factor responsible for these



FIG. 16. Aboveground biomass (mean \pm SE) of salt marsh vegetation during 4 years of study under three treatments of added fertilizer (sewage sludge). Solid circles=heavy application; triangles=light application; open circles=control. After Valiela *et al.* (1975).

E. C.	Dry weight production (kg m 2 yr 1)			
treatment	Low marsh	High marsh		
High *	1.32 ± 0.12	1.26 ± 0.11		
Lowt	0.86 ± 0.04	1.38 ± 0.23		
Control (no additions)	0.51 ± 0.01	0.63 ± 0.05		

TABLE 8. The effects of three fertilizer regimes on production rates of two saltmarsh communities. Values are means of 3 year study periods (\pm SE). Data from Valiela *et al.* (1975).

 $\{25.2 \text{ gm}^2 \text{ week}\}$ with $10^{\ell} \epsilon \text{ N}$ and $2.6^{\ell} \epsilon \text{ P in the fertilizer.}$

increases was the nitrogen component of the fertilizer. Table 8 shows the means (±SE) from the study period in two salt marsh types. Production in the high treatment was 3 times that of the control. Similarly in a Florida freshwater marsh significant increases in plant biomass occurred with nutrient (sewage effluent) loading (Dolan et al., 1981) and confirmatory data of this effect has been reported from other wetlands (Gallagher, 1975; Hartland-Rowe & Wright, 1975; Mudroch & Capobianco, 1979). A differential response to N and P additions to a salt marsh was recorded by Patrick & DeLaune (1976) who found that nitrogen additions significantly increased production, but P additions did not.

When factors other than nutrients limit plant growth in wetlands, nutrient additions will be unlikely to affect plant production. The reasons for this can be clearly appreciated when we refer back to the basic concepts (section 1.3). Phase B on Fig. 3 continues until one or more components of the system show a reduced ability to process the inflow nutrient. Such a reduction can occur due to saturation, or due to some growth-limiting effect such as decreasing space, increasing toxicity from NH4, heavy metals or increasing salinity. An example of this has been referred to in section 4.4.1 (Jefferies & Perkins, 1977). Solander (1983) found that in fertilized subarctic Carex and Equisetum marshes phosphorus uptake by these plants increased but production did not. In these conditions, growth was regulated by summer temperatures rather than nutrient supply. A negative feedback mechanism acting on plant growth in fertilized salt marshes was recorded by Chalmers (1979). She found that nutrient additions increased plant growth but at the same time this caused greater transpiration rates. Higher salinities resulted which then restricted further growth.

5. Concluding perspective

5.1. Unique features of wetland nutrient cycles

Exchange equilibria (Fig. 2) dictate that a biological system such as a wetland will have a certain capacity to 'buffer' concentrations of incoming nutrients dissolved in the water phase. The ability of wetlands to act as a buffer may be higher per unit area than that of other aquatic systems such as open streams, ponds, lakes because: the storage compartments are large in relation to throughflow volume (Figs. 2 and 7); the system is complex with many storage compartments which have different uptake and release mechanisms (section 2); retention times of water are long relative to open channel streams (section 3.2.4); and surface areas for nutrient exchange per unit volume of water are high.

Where nutrient levels in the inflows to a wetland are increased, organisms with the most rapid uptake rates will respond first. These are likely to have a high absorbing surface area to total volume ratio (Odum, Kuenzler & Blunt, 1958). Such organisms will be small in size and form a relatively small storage compartment. For instance, the addition of ³²P tracer to a dense macrophyte community showed that the filamentous epiphyte algae, a small fraction of the total plant biomass, had a P uptake rate 10 times that of the macrophytes (Howard-Williams & Allanson, 1981). These would absorb twice as much of an added pulse of P as would the

macrophytes on a per unit area basis. Correll *et al.* (1975) found that added ³²P to a *Typha* marsh was rapidly incorporated by the microflora. The *Typha* roots utilized this later, presumably from the interstitial water (see Fig. 7).

It is not surprising, therefore, to find from the literature that when wetlands are enriched with nutrients the microflora and the small free floating macrophytes (e.g. Lemnaceae) increase (section 4.4). As the flux of nutrients from one compartment to another is a function, not only of uptake rates (k) but of compartment size (section 2), this increase in the size of the storage compartment has a positive feedback effect on the ability of the system to buffer the concentrations of dissolved nutrients.

While considerations of exchange equilibria provide a useful framework for viewing nutrient transfers about a point in space over relatively short time periods, a basic feature of wetland nutrient cycles are the longitudinal (upstream to downstream) characteristics. Thus nutrients are continually moving downstream at different speeds depending on their distribution in the different storage compartments and throughflow. In longitudinal movement through a wetland, nutrients will tend to spiral through various fractions (as described in section 1.3.4). An integral part of the nutrient spiralling concept states that the spiral length is inversely proportional to the metabolic activity of the system through which the water flows. Wetlands are generally considered to be very productive systems so we might envisage on this basis alone that spiral lengths would be shorter than the 200 m estimated for a woodland stream (Newbold et al., 1981). However, abiotic factors will also affect spiral length, perhaps the most important being stream flow regime (section 3.2). The importance of parameters associated with the flow regime can be illustrated by reference to the equation of Hoare (1979).

$$C_0 = C_1 \exp\{w\varrho z/Q\}$$
(6)

where C_0 and C_1 are output and input concentrations of a nutrient, z is the distance between C_0 and C_1 , w is stream width, Q is discharge and ϱ is a proportionality constant inversely related to spiral length (see section 1.3.4). Q is

calculated from velocity times cross section area.

In a wetland, the actual path length a parcel of water travels per unit distance (z) downstream from an input will be greatly increased due to physical barriers set up by the macrophytes. In addition, wetland flow will incorporate a large 'dead zone' component. Dead zones are regions of stagnant water which occur along the line of flow, such as holes in the streambed, backwaters, etc. (Valentine, 1982). These have the effect of increasing dispersion and reducing velocity. Increased pathlength and decreased velocity will both facilitate biological uptake mechanism and hence tend to shorten spiral length.

The above discussion suggests that in natural wetlands we can expect short spiral lengths and efficient nutrient utilization. However, when wetlands are enriched this may not be the case because nutrient regeneration rates decrease as the amount of available nutrient increases (sections 1.3.3 and 1.3.4). Wetland storage compartments have a finite capacity (loading capacity) so when these are full the available nutrient concentration in the water will rise, resupply will be reduced and nutrients will no longer be retained. In practise, this means that the zone of the wetland closest to a point of nutrient inflow will become a less efficient buffer with time until saturated (i.e. o becomes very small). The saturated zone will gradually extend downstream (Hammer & Kadlec, 1983). The loading capacity of a wetland will be exceeded when the saturated zone extends the distance z in eqn (6). The literature in section 4.2 demonstrates the loading capacity for a number of wetlands. This concept of loading capacity is readily seen in terms of spiral length. From section 1.3.4 we see that total spiral length is the sum of S_w and S_p . S_w is defined as the length of stream a nutrient molecule remains in the water phase and is calculated as F_w/R_w where F_w is the downstream mass flow (g s⁻¹) and R_w is the uptake rate per length of stream (g m⁻² s⁻¹). As the storage sites in the wetland become saturated, R_w will decrease and S_w will increase. Similarly $S_p = F_p/R_p$ where F_p is the downstream flux in particulate phase and R_p is the release flux from the particulates. In a steady state system, $R_w = R_p$ (Newbold *et al.*, 1981) but when nutrients are accumulating in stores $R_n > R_p$. In

wetlands, velocity of water is low and F_p may be negligible in all but storm events (section 3.2.2). According to the concepts of resource consumption and supply, and nutrient spiralling, the increasing enrichment of wetlands will result in a decrease in R_p . R_w will exceed R_p and storage will increase. This is shown to be the case in the long-term numerical models of wetland enrichment (section 4.3.1) and from measurements where phosphorus has been considered (section 4.3.2). Nitrogen, however, does not behave as simply as will now be discussed.

The gaseous phase in the nitrogen cycle (N-fixation, denitrification) has a number of repercussions on the concepts of wetland loading capacity, equilibrium exchanges and nutrient spiralling. The first point to be made is that inputs of nitrogen from the atmosphere (N-fixation) and outputs to the atmosphere (denitrification, volatilization, etc.) involve different organisms, and occur at different rates. Therefore steady state equilibrium assumptions involving the gas phase cannot be made. In conditions of low nitrogen supply, N-fixation can increase the N content of the particulate pool without influencing $R_{\rm m}$ or N uptake from the water. However, when additional N-nutrients are available (i.e. F_w increases) wetland microbial communities tend to use this source rather than N-fixation (section 4.4.1). Thus R_w will increase.

Denitrification has an opposite effect. As the NO₃-N taken up by denitrifiers is evolved as N₂ gas it takes no further part in downstream metabolism. This will tend to increase the ratio F_P/R_p and therefore spiral length. Wetland systems appear to have high denitrification rates (sections 2.2.4 and 4.3.3) which can be significantly higher than nitrogen uptake by wetland plants (Gersberg et al., 1983). In such systems spiral length is likely to be very long and will not really reflect metabolic activity as theory predicts (Elwood et al., 1983). The relative importance of different wetland components in nutrient cycling thus clearly varies with the type of nutrient under consideration.

The literature indicates that the larger aquatic plants, which characterize wetland systems, play a relatively minor role in nutrient uptake (sections 2.2 and 4.3). The bulk of short-term nutrient transfers and long-term storage is carried out by the microflora and the sediments of wetlands. Removal of nutrients by a wet soil has been shown to be just as efficient as removal by a vegetated wet soil (e.g. Gersberg *et al.*, 1983). The function of wetland macrophytes, however, can be listed as follows:

(a) In some areas they play a role in providing suitable redox (i.e. habitat) conditions for denitrifying bacteria as well as a supplementary source of carbon.

(b) Nitrification of macrophyte detritus (Howard-Williams, Pickmere & Davies, 1983) can provide a NO_3 -N source from particulate material for denitrification.

(c) By creating barriers to flow, macrophytes cause an increase in dispersion, a decrease in water velocity and an increase in 'dead spaces' (section 3.2 and above). Retention times of water through wetlands are increased and possible nutrient spiral lengths decreased. This is closely coupled with increasing nutrient metabolism by sediments and microflora.

(d) Emergent plants in artificial wetlands have a role primarily for aesthetic reasons and odour control (Gersberg *et al.*, 1983).

(e) Wetland vegetation can greatly enhance wildlife values (e.g. Weller, 1981) and the establishment of artificial wetlands for nutrient removal has improved local wildlife values in at least one documented case (Williams, 1980).

5.2. Wetlands for nutrient removal

If a wetland is acting as a nutrient sink, in any pathway other than denitrification, it is not in a 'steady state'. Changes with time are therefore expected (section 1.3.1) and have been recorded (section 4.4). These changes take place as a response to three factors: (a) increased production, (b) species changes, and (c) the problems of the 'carrier',

(a) Nutrient enrichment results in increasing primary production in wetlands where abiotic factors (drought, salinity) do not limit growth (section 4.4.1). Successional rates are therefore increased by rising rates of litter deposition (section 4.3.1).

(b) Nutrient enrichment causes species changes resulting in a proliferation of fastgrowing plants with high surface absorption area to volume ratios such as filamentous algae, and Lemnaceae (section 4.4.1). These can have deleterious effects, particularly on redox conditions.

(c) Nutrients are usually applied to wetlands with a 'carrier' such as treated sewage effluent or in the form of sewage sludge. Often this carrier has a greater effect than the nutrients. Sludge, for instance, can contain high levels of heavy metals, and this type of carrier will almost certainly affect the oxygen regime and microbial activity of some wetland areas (Valiela *et al.*, 1977; McNabb, 1976; Sherr & Payne, 1981; Kadlec & Tilton, 1979).

Even when nutrient enrichment is stopped, wetland sediments and vegetation will continue to release stored nutrients for long periods. In the case of the Florida *Cypress* domes release was still continuing after 20 months of sampling (Dierberg & Brezonik, 1983b). It is inevitable, therefore, that in spite of the ability of many wetlands to reduce nutrient loads over extended time periods (section 4.3) long-term nutrient loading will have a deleterious effect on natural wetland systems.

Kadlec & Tilton (1979) point to the controversy between preservationist groups in the U.S.A., who wish to see the remaining wetlands completely protected, and those involved in navigation or agriculture who push for substantial modification or destruction of wetlands. Kadlec & Tilton point out that the use of wetlands for wastewater purification is between these two camps as it will partly alter a wetland but not destroy it.

The preservationist argument in many countries is powerful and is clearly gaining ground as further emphasis is placed on national agencies to examine scarce wetland resources (Wetlands Task Group, 1983; Reilly, 1978; Goodrick, 1970). On the other hand, pressures for agricultural land have not diminished either. Gilman (1982) points out that in view of the increasing demand for marginal lands for agriculture in Great Britain, wetland management and agriculture can no longer be viewed separately.

As substantial areas of wetland are required for large-scale nutrient removal I suspect that their use for this purpose may be increasingly difficult to justify. For instance, Moss *et al.* (1979) suggest that the only way to restore the nationally valuable recreational resource of the Norfolk Broads in England is to reduce the nutrient loads entering this wetland area.

5.3. The use of artificial or created wetlands

As arguments for the conservation of natural wetlands increase, the creation of artificial wetlands must be considered. Two types of artificial wetland are available; constructed wetlands to remove point source discharges, and created wetlands along natural waterways to remove diffuse sources of enrichment at low loading rates.

The use of artificial wetlands (shallow ponds specially constructed and planted with wetland species) for wastewater purification was pioneered by Dr Kathe Seidel in the 1950s (Seidel, 1976). Since then the use of these systems has grown and the technology developed to the stage where her system has been patented (U.S. Patent 3,770,623; Nov. 6, 1973) by the Max-Planck Institute in West Germany. Pope (1981) reported on an evaluation of this process for waste water treatment. An 11 month study showed that raw screened wastewater could be treated to the standard of secondarily treated water by the artificial wetland. However, a 2 month study to test the efficiency of the system as a tertiary treatment method showed that although NH4-N was reduced to 50%, NO3-N increased considerably with passage though the system giving a total dissolved inorganic N removal of only 5%. Total phosphorus inputs were only reduced by 13%.

de Jong (1976) described the use of a 1 ha pond planted with *Scirpus lacustris* for purification of camping ground effluent. He found that the ability to remove N and P compounds increased with the residence time of water through the system (see sections 1.3.4, 3.2.4 and 5.1). At the optimum residence time for BOD and COD treatment (10 days), the artificial wetland removed 35% of the inflowing P and 50% of the Kjeldahl-N. However, as Kjeldahl-N does not include NO₃-N the value of 50% for N may be an over-estimation of the total-N lost, particularly in view of the increases reported by Pope (see above).

Spangler *et al.* (1976) similarly demonstrated the positive relationship between the retention time of the throughflow and phosphorus removal in an artificial wetland. Reduction in total P varied between 5% and 25% whilst dissolved inorganic N (90% of which was NO₃-N) was highly variable ranging from an increase in NO₃-N of 47% on one occasion to a 60% reduction in another.

Finlayson & Chick (1983) found reductions of 42–75% of total nitrogen and 68–79% total phosphorus (as mass flow) in effluent passing through trenches planted with *Typha*, *Phragmites* and *Scirpus*. However, as dissolved inorganic forms of N and P make up less than half the total N and P in their analyses, it appeared that much of the reduction was due to the filtering of particulate forms rather than nutrient transformation or recycling.

It seems from these studies that most wetlands which have been constructed artifically are not particularly effective at removal of dissolved nutrients. Furthermore, where appropriate studies have been done, the major sink for nutrients in artificial wetlands is the soil, and soil percolation may be an important part of wetland design (section 4.3). However, in a recent controlled experiment Gersberg et al. (1983) found over 90% reduction in NO3-N entering an artificial wetland following attempts to optimize the performance of the denitrifying bacteria with supplementary carbon (section 4.3.3). These authors conclude that, to date, most studies of this kind have not attempted to maximize the efficiency of the primary nutrient removal process, or the loading application rates, and that if this is done the performance of artificial wetlands in the retention of dissolved nutrients could be greatly improved. Clearly this should be the next stage in experimentation rather than merely recording input-output flows from the wetland 'black box'. Rate processes and factors controlling these need to be quantified within the black box, and the black box approach eliminated

The concept of created wetlands along natural waterways to remove diffuse sources of enrichment such as agricultural runoff needs further consideration. Such 'wetlands' develop or can be assisted to develop in protected riparian strips along stream margins where shading is not severe. This vegetation type with associated microflora can remove significant quantities of N and P at low loading rates (Crisp, 1970; McColl, 1974, 1979; Vincent & Downes, 1980; Cooper & Cooke, 1984;

Howard-Williams et al., 1982). Stream vegetation is often considered undesirable as it affects the stream flow regime and may hinder recreational activities and fish migrations (Westlake & Dawson, 1982: Dawson, Kern-Hansen & Westlake, 1982; Kouwe, 1983). However, in some areas these may not be important values, and in others this vegetation could be managed to allow for adequate stream flow while still maintaining some uptake. In areas where diffuse runoff is seen as a longterm problem (e.g. in catchments above oligotrophic lakes) such wetland systems, although not as effective as chemical stripping plants, may be the only feasible method of nutrient reduction

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Note added in proof

Several papers on wetland nutrient dynamics have been published since acceptance of this review. Of particular relevance to the content of this review is that by Shaver & Melillo (1984) as it provides the first experimental evidence for concepts discussed in section 1.3.3. They found that as N and P availability increased, the efficiency of uptake, recovery and use of these elements by wetland plant decreased.

Shaver G.R. & Melillo J.M. (1984) Nutrient budgets of marsh plants: efficiency concepts and relation to availability. *Ecology*, **65**, 1491–1510.

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Appendix 1. List of symbols

Order of appearance as in text. Units of mass, length and time are shown here using gram (g), metres (m) and seconds (s) for convenience.

Symbol	Description	Unit
k	Rate constant for nutrient exchange or uptake	5-1
X	Nutrient input to a system	0 s ⁻¹
V	Nutrient output from a system	0 5 1
T	Carrying capacity of nutrient in a defined system	0
A	Available form of nutrient in a defined system	5
U	Unavailable form of nutrient in a defined system	5
S	Total spiral length	5
S_i	Downstream distance a nutrient atom travels in component <i>i</i>	m
Sw	Distance travelled in water or Uptake Length	m
Sp	Distance travelled in particulates or turnover length	m
F_i	Nutrient supply rate (flux) in component <i>i</i> (e.g. F_w =flux in water phase, F_w =flux in particulate phase)	g s ⁻¹
R _r	Nutrient utilization (exchange) rate by component <i>i</i> (e.g. R_w =exchange flux from water to particulates and R_p =exchange flux from particulates to water)	$g s^{-1} m$
S'_w	Net Uptake Length	m
K_w	Net Uptake Length constant for disappearance of nutrient from the water in a flowing system	m^{-1}
C_{o}	Nutrient concentration in water at output from a system	9 m ⁻³
C_i	Nutrient concentration in water at input to a system	g m -3
z	Defined stream length	m
0	Specific uptake proportionality constant	m s ⁻¹
W	Stream width	m
Q	Stream discharge	$m^{3} s^{-1}$

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