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A review

The biogeochemistry of nitrogen in freshwater wetlands

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Abstract. The biogeochemistry of N in freshwater wetlands is complicated by vegetation characteristics that range from annual herbs to perennial woodlands; by hydrologic characteristics that range from closed, precipitation-driven to tidal, riverine wetlands; and by the diversity of the nitrogen cycle itself. It is clear that sediments are the single largest pool of nitrogen in wetland ecosystems (100's to 1000's g N m^{-2}) followed in rough order-of-magnitude decreases by plants and available inorganic nitrogen. Precipitation inputs (< 1–2 g N m^{-2} yr^{-1}) are well known but other atmospheric inputs, e.g. dry deposition, are essentially unknown and could be as large or larger than wet deposition. Nitrogen fixation (acetylene reduction) is an important supplementary input in some wetlands ($< < 1$–3 g N m^{-2} yr^{-1}) but is probably limited by the excess of fixed nitrogen usually present in wetland sediments.

Plant uptake normally ranges from a few g N m^{-2} yr^{-1} to $\sim$ 35 g N m^{-2} yr^{-1} with extreme values of up to $\sim$ 100 g N m^{-2} yr^{-1}. Results of translocation experiments done to date may be misleading and may call for a reassessment of the magnitude of both plant uptake and leaching rates. Interactions between plant litter and decomposer microorganisms tend, over the short-term, to conserve nitrogen within the system in immobile forms. Later, decomposers release this nitrogen in forms and at rates that plants can efficiently reassimilate.

The NO_3 formed by nitrification (< 0.1 to 10 g N m^{-2} yr^{-1}) has several fates which may tend to either conserve nitrogen (uptake and dissimilatory reduction to ammonium) or lead to its loss (denitrification). Both nitrification and denitrification operate at rates far below their potential and under proper conditions (e.g. draining or fluctuating water levels) may accelerate. However, virtually all estimates of denitrification rates in freshwater wetlands are based on measurements of potential denitrification, not actual denitrification and, as a consequence, the importance of denitrification in these ecosystems may have been greatly over estimated.

In general, larger amounts of nitrogen cycle within freshwater wetlands than flow in or out. Except for closed, ombrotrophic systems this might seem an unusual characteristic for ecosystems that are dominated by the flux of water, however, two factors limit the opportunity for N loss. At any given time the fraction of nitrogen in wetlands that could be lost by hydrologic export is probably a small fraction of the potentially mineralizable nitrogen and is certainly a negligible fraction of the total nitrogen in the system. Second, in some cases freshwater wetlands may be hydrologically isolated so that the bulk of upland water flow may pass under (in the case of floating mats) or by (in the case of riparian systems) the biotically active components of the wetland. This may explain the rather limited range of N loading rates real wetlands can accept in comparison to, for example, percolation columns or engineered marshes.

Introduction

Recent quantification of both extensive and intensive loss of freshwater wetland habitats (Craig et al. 1980; Larson et al. 1980; Frayer et al. 1984) has focused attention on the structure, function, and values of this diverse group of ecosystems. The values attributed to these wetlands are as diverse as the ecosystems themselves. For example, wetlands provide critically important habitat, continually and seasonally, for many species of birds and mammals (Tiner 1984). In addition, the promise of using the natural "assimilative capacity" of wetlands to treat waste water and improve river water quality has been a subject of active research for decades (van der Valk et al. 1979; Nichols 1983; Howard-Williams 1985). Finally, in areas where peat-forming wetlands are extensive, peat-mining has been an economically important industry for centuries. This commercial interest in wetlands has accelerated in recent years due to an increased pressure to exploit the nutritive value of wetland peat for agriculture and plantation forestry.

Of the many elements necessary to sustain biotic production in wetlands, nitrogen presents special research challenges due to its chemical versatility. This versatility is expressed in the various valence states nitrogen can occupy (-3 to $+5$), the intricate array of biotic and abiotic transformations in which nitrogen participates, and by the fact that, like few other elements, nitrogen occurs naturally in soluble and gaseous phases.

The purpose of this paper is to review the state of particulate understanding about the biogeochemistry of N in freshwater wetlands. The general ecology of wetlands has been discussed recently in edited volumes by Moore & Bellamy (1974); Good et al. (1978); Greeson et al. (1979) & Gore (1983a). A variety of wetland types has received special attention by different authors: riparian wetlands (Brinson et al. 1980); pocosins (Richardson 1981); tidal freshwater wetlands (Odum et al. 1984); bogs, fens, and other mires (Heal & Perkins 1978; Soresson 1980; Larsen 1982; Wells 1981); and bottomland hardwoods (Clark & Benforado 1981; Wharton et al. 1982). Reference to these works will quickly show that our understanding of integrated nutrient cycling, especially nitrogen cycling, is rudimentary. In this review, I will point out what I believe we know well and what I believe we most need to address. Other pertinent information may be found in reviews by Whigham & Bayley (1979) and Howard-Williams (1985).

Classification of freshwater wetlands

Classification of freshwater wetlands is a research topic unto itself (see for example Cowardin et al. (1979) & Moore (1984). In the United States, the classification scheme proposed by Cowardin et al. (1979) is widely recognized and I will use it here. According to this classification scheme a wetland must meet two general criteria:

— the water table is at, near, or above the land surface long enough to promote hydric soils
— the dominant vegetation are hydrophytes

Thus wetlands are distinguished from other ecosystems by poorly drained soils, water-loving plants and potentially variable hydrologic conditions. Freshwater wetlands are further delineated from marine and estuarine wetlands by ocean-derived salt contents that remain below 0.5 ppt during low flow periods.

To reasonably limit the scope of this review I will not consider deepwater habitats. Such habitats have substrates that, according to US Soil Conservation Service guidelines are "non-soils" because the low water level is still too high to allow emergent vegetation to grow. Cowardin et al. (1979) place this level at 2 m below low water. The systems I will discuss are classified, for the most part, as Palustrine, although certain Riverine tidal emergent and Lacustrine littoral emergent wetlands are closely related and will be discussed as appropriate. For ease of discussion and consistency with older literature, I will refer to various ecosystems as non-tidal marshes, tidal marshes, bogs, fens, and swamps.

The nitrogen cycle: general comments

The nitrogen cycle in flooded soils has been described by Tusneem & Patrick (1971); Ponnamperuma (1972); and Keeney (1972), among others. Figure 1 shows the fundamental components of the nitrogen cycle, without reference to any particular ecosystem. Superimposed on this simple, symmetrical representation are various trophic transfers (e.g. herbivory and predation) and phase transfers (e.g. litterfall) that give each wetland a site-specific nitrogen "personality."

Nitrogen cycling in wetlands is controlled by the same interdependent variables that control wetland formation; e.g. climate, hydrology, geomorphology and vegetation. The dynamics of wetland formation have been discussed elsewhere (Gorham 1957; Heinselman 1975; Malmer 1975; Gore 1983b) but several observations bear repetition. The effects of climate are expressed through hydrology and temperature. For example, marshes cannot form and the mobility of nitrogen is severely reduced if there is not an excess of precipitation over evapotranspiration to supply surface or subsurface runoff. In addition temperature, through its effect on biochemical kinetics, will control the rates at which microbes and plants process nitrogen.

Hydrology, in concert with geomorphology, is second only to climate as

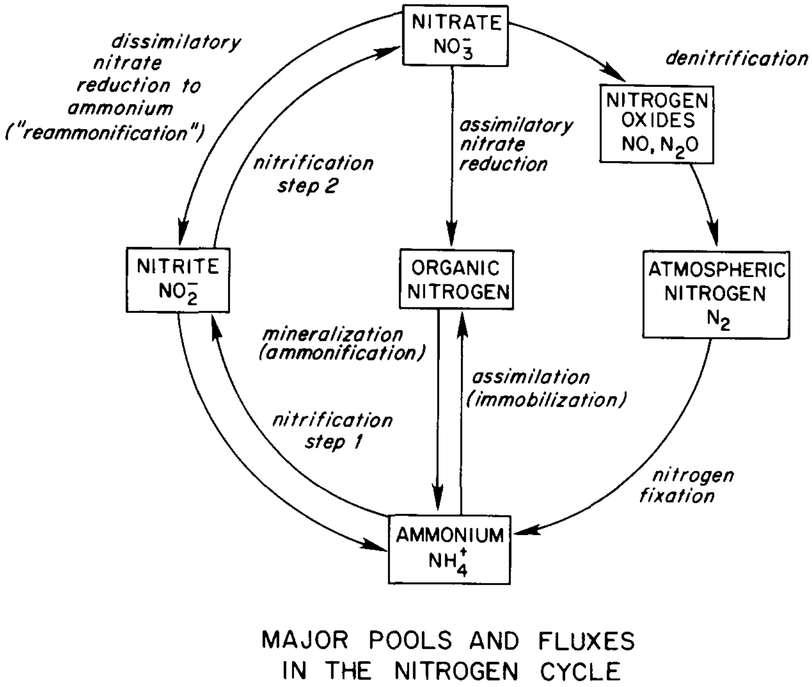

Fig. 1. Basic components of the nitrogen cycle in any ecosystem.

a variable that controls marsh formation and nitrogen cycling. Clearly, the amount of water required to maintain wetland formation will be different if the wetland forms on a slope as opposed to a basin. In addition, the importance of hydrologic export will differ substantially between basin bogs and sloping fens. Verry & Boelter (1979) stress the importance of hydrologic flushing as a direct influence on wetland nutrient availability and Odum et al. (1983) stress its influence on primary productivity.

Finally vegetation, in response to climate, hydrology and geomorphology, can control nitrogen cycling. Plant production obviously depends on a readily available supply of mineralizable nitrogen, which, due to local insufficiencies, often limits primary production. Even after death, plant litter and the microbes growing on it can control the internal dynamics of nitrogen in wetlands, as will be discussed later.

The nitrogen cycle in a particular wetland responds dynamically to the master variables: climate, hydrology, geomorphology, and vegetation. In the sections that follow I will focus on the individual pools, inputs, interconversions, and exports of nitrogen in freshwater wetlands.

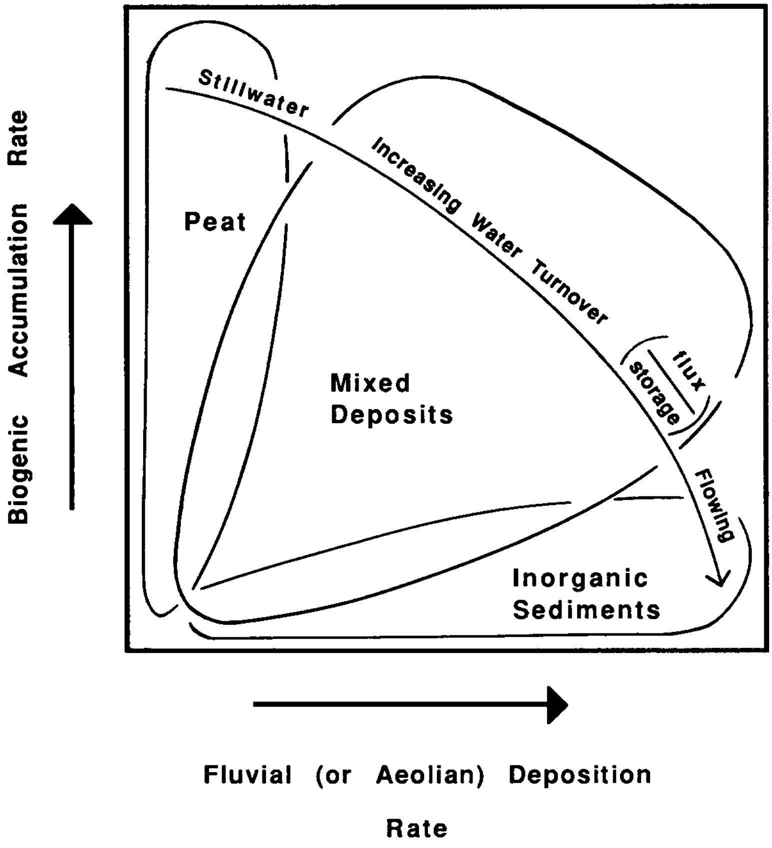

Fig. 2. Organic and inorganic composition of wetland soils and sediments as a function of biogenic deposition rate and fluvial or aeolean deposition rate. Water turnover is shown as increasing from peat deposits (still water) to inorganic alluvial sediments (flowing water). Modified with permission of authors from Brown et al. 1978.

Nitrogen pools

The sediment pool

Sediments are usually the largest pool of nitrogen in wetlands (Bowden 1984a). The actual amount of nitrogen accumulated in a wetland sediment will depend on the balance between plant production and decomposition and on the balance between allochthonous import and particulate export (Fig. 2). These balances in turn are influenced by the master controlling variables discussed above.

Although the total content of nitrogen in sediments is relatively easy to measure by Kjeldahl analysis, two factors limit the usefulness of such data found in the literature (e.g. Richardson et al. 1978). First, relatively few authors have chosen to express their data on an areal basis, which is most useful for budgets. Even where such data are provided, comparisons are difficult due to differences in the depth used to integrate nitrogen concentrations.

More important, total nitrogen does not accurately reflect the amount of nitrogen that is available to the biota for uptake. A majority of the nitrogen in wetland sediments is in forms that are resistant to decomposition (under the prevailing conditions within the sediments) and so are unavailable for plant uptake. As yet there is not a universally accepted method to estimate potentially mineralizable nitrogen in sediments.

The total sediment nitrogen content for a variety of wetland habitats is shown in Table 1. Typical values for the top 20 or 30 cm of sediment, a depth that is generally coincident with the rooting zone of aquatic plants, are roughly a few hundred to a few thousand g N m^{-2}.

Plant biomass N

Due to interest in the productivity of wetland plants, there is more information about the content of nitrogen in plant tissues than for any other wetland component. Two factors introduce variability in these data sets, however. Boyd (1978) has shown convincingly that the nutrient content of wetland plants is inherently variable. Variation exists between plant parts (Gaudet 1975), between stages of maturity (Boyd 1969 & 1970), between individual

Table 1. Selected values for standing stock of total nitrogen in various wetland sediments.

System description	$gN \cdot m^{-1}$	Integrated to depth (cm)	Reference
Theresa Marsh, Wisconsin reed marsh	1696	3–15 cm	Klopatek (1978)
Uganda	96	mat only	Gaudet (1976)
papyrus swamp	1210	peat only	
North River Massachusetts riverine tidal marsh	255	10 cm	Bowden (1982)
Pennine, UK blanket bog	330	30 cm	Martin & Holding (1978)
Houghton Lake, Michigan leatherleaf/birch bog fen	683	20 cm	Richardson et al. (1978)
Stordalen, Sweden subarctic mire	342	30 cm	Rosswall & Granhall (1980)
Okefenokee, Georgia cypress swamp	1693	91.5 cm	Schlesinger (1978)
Coastal Plain, N. Carolina blackwater swamp	163–336	12.5 cm	Qualls (1984)

plants (Boyd & Hess 1970), and between stands (Boyd 1978). For example, Boyd (1978) calculated that the coefficient of variation for nitrogen concentration in five samples from one *Typha latifolia* stand was 8.5% and was 21.8% for 30 different stands *Typha latifolia.* He concludes that it is necessary to carefully measure nutrient contents in plants rather than rely on literature for any study that requires this information.

The second factor that introduces variability in plant nutrient content data, is our poor knowledge of belowground biomass relative to aboveground biomass (Whigham et al. 1978). Quantitative sampling of belowground biomass and separation of live belowground plant parts from belowground litter continue to be fundamentally difficult problems in wetland ecology. A variety of factors, including plant morphology, perennial versus annual life cycle, nutrient loading, and tolerance to flooding influence the aboveground/belowground ratio in plants. More experimental work such as that by Whigman & Simpson (1976) showing biomass allocation patterns in wetland plants, needs to be done.

Table 2 shows typical values for plant nitrogen biomass in a variety of wetlands. Nitrogen in plant biomass is roughly in order of magnitude lower than the N content in sediments. The total standing stock of nitrogen in wooded swamps (e.g. Schlesinger 1978) exceeds that in herbaceous wetlands due to the greater biomass of perennial tissue in wooded swamps. However, on the basis of net primary production, the nitrogen in each years' new growth may not be that different from herbaceous wetlands. Clearly, the *Cyperus papyrus* swamps described by Gaudet (1977) are exceptional. Individual plants may attain heights of 5 m and standing crops of > 5 g dry matter m^{-2}. In addition, enrichment with sewage effluent may elevate nitrogen standing stocks to unusually high levels. The high values for *Glyceria grandis* reported by Murdock & Capobianco (1979) are for a stand just below a sewage treatment outfall.

Inorganic nitrogen

The mass of inorganic nitrogen in wetland sediments is usually at least an order of magnitude lower than plant biomass nitrogen and several orders of magnitude less than sediment total nitrogen. The close balance between nitrogen supply rates by mineralization and uptake rates by wetland biota (see below) insures that the inorganic N pool is small and that it turns over rapidly.

Most of the inorganic nitrogen in wetland sediments is in the form of ammonium (Bowden 1984a; Martin & Holding 1978; Hemond 1983, Qualls 1984). Under the waterlogged conditions characteristic of wetland sediments, oxygen tensions are usually low. This favors denitrification (see below) and as a consequence nitrite and nitrate nitrogen are usually rare.

Table 2. Reported values for the standing stock of plant nitrogen in various wetlands. Values are for total biomass above and belowground.

System description	$gN{\cdot}m^{-2}$	Dominant species	Reference
Eagle Lake, Wisconsin palustrine marsh	32.8	*Typha glauca*	Davis & van der Valk (1983)
Lake Ogletree, Alabama palustrine marsh	1.9–44.3	*Justica americana* *Alternatha philoxeroides*	Boyd (1969)
Theresa Marsh, Wisconsin palustrine marsh	8.8–31.5	*Typha, Carex* *Scirpus* spp.	Klopatek (1978)
Lake Mendota, Wisconsin lacustrine marsh	28	*Typha latifolia*	Prentki et al. (1978)
Michigan Hollow, New York palustrine sedge fen	~4–23	*Carex lacustris*	Bernard & Solsky (1977)
Inlet Valley, New York palustrine sedge fen	~8–~19	*Carex lacustris*	Bernard & Hankison (1979)
Uganda papyrus swamp	61.61	*Cyperus papyrus*	Gaudet (1976)
Cootes Paradise, Ontario palustrine fen	45.9–72	*Glyceria grandis*	Murdoch & Capobianco (1979)
North River, Massachusetts riverine tidal marsh	18	*Typha, Carex* *Calamagrostis*	Bowden (1982)
Pennine, UK blanket bog	12	*Caluneto-Eriophoretum* ± *Sphagnum* spp.	Martin & Holding (1978)
Houghon Lake, Michigan rice fen	10.1	*Chamaedaphne calyculate* *Betula pumila*	Richardson et al. (1978)
Stordalen, Sweden subarctic mire	5.9	*Rubus chamaemerus* *Eriophorum vaginatum*	Rosswall & Granhall (1980)
Okefenokee, Georgia cypress swamp	99.6[a] 5.7[b]	*Taxodium distichum*	Schlesinger (1978)
Dismal Swamp, N. Carolina algae	0.42[c] 1.18[d]	*Chlorophycaea-Cyanophyceae* *Pinnularia/Eunotia* spp.	Atchie et al. (1983)

[a] Above water perennial biomass only
[b] Above water current years' growth only
[c] Periphyton mats on marsh surface
[d] Phytoplankton in water column

Consumers

The biomass and nitrogen standing stock of consumers is not well documented for wetlands but is probably small compared to plant and sediment biomass. Martin & Holding (1978) report that microorganisms contain

2 g N/m^2 in the British blanket bog they studied. Rosswall and Granhall (180) report values for microorganisms of 0.09 to 2.2 g N/m^2 for several subarctic wetlands. Coulson & Whittaker (1978) reviewed animal production dynamics in British moorlands and report a total animal biomass in two peat ecosystems of 3.73 and 10.4 g/m^2. Given any reasonable tissue nitrogen content, these organisms must contribute < 1 g N/m^2.

Consumers may, however, have important impacts on wetland N cycling. Reader (1979) reports that during outbreaks, insects can completely defoliate bog vegetation. Manny et al. (1975) and McColl & Burger (1976) report that nesting Canada geese and Franklin's gulls, respectively, can mobilize large quantities of nitrogen and phosphorus in the water column. Insects, birds, and mammals are probably more important as agents of internal reorganization than they are as net nitrogen transporters.

Nitrogen inputs

Atomospheric deposition

In ombrotrophic (rain-fed) bogs, atmospheric deposition is the only source of nitrogen to the ecosystem. Even in more hydrologically open fens, marshes, and swamps, atmospheric deposition can be an important source of new nitrogen. In addition to numerous citations in the wetland ecology literature, there is a wealth of new information on atmospheric nitrogen inputs due to recent interest in the effects of atmospheric deposition (acid rain) on ecosystem health.

Table 3. Reported values for wet deposition rates of ammonium, nitrate, and organic nitrogen to various wetlands.

System description	$g\ N \cdot m^{-2} \cdot yr^{-1}$			Reference
	NH_4-N	NO_3-N	Org-N	
Rhode River, Chesapeake Bay riverine tidal emergent	0.27	0.43	0.47	Jordan et al. (1983)
Sippewissett Marsh, Massachusetts coastal salt marsh	0.23	0.14	0.39	Valiela & Teal (1979)
Pennine, UK blanket bog	0.60	0.10	—	Martin & Holding (1978)
Thoreau's Bog, Massachusetts basin bog	0.25	0.50	—	Hemond (1983)
Black Spruce bog, Minnesota basin bog	0.17	0.17	0.38	Verry & Timmons (1982)
N. Wales, UK (clean) blanket bog	0.67	0.84	0.89	Press & Lee (1982)
S. Pennine, UK (dirty) blanket bog	1.79	1.43	1.40	Press & Lee (1982)

In general, wet deposition adds roughly 0.5 to 1 g N m^2 yr^{-1} as ammonium and nitrate. There does not appear to be a consistent pattern to the relative importance of ammonium versus nitrate. This is probably a function of the local source areas near the wetlands studied (e.g. Press & Lee 1982).

In addition, both organic −N and dry deposition may be important components of atmospheric deposition yet neither has received much attention. The input of organic-N in rainwater can be as high or higher than the input in inorganic nitrogen. Table 3 lists selected citations for which ammonium, nitrate, and dissolved organic nitrogen in precipitation were all measured. It is apparent from these data that organic nitrogen can make a substantial contribution to atmospheric inputs.

Dry deposition of both particles and gases may be quantitatively important in some areas. Using data published by Delany & Davies (1983) for a grassland, I calculate that the input of NO_X to the grasses they studied could be 0.4–0.8 g N m^{-2} over a 100 d period. Huebert & Robert (1985) measured dry deposition rates of HNO_3 vapor to grasses that were equivalent to 0.08–0.10 g N m^{-2} during a 100 d period. Two values for dry deposition are reported in the wetlands literature. Prentki et al. (1978) report a dry fall of 1.6 g N m^{-2} yr^{-1} to Lake Mendota in the city of Madison, Wisconsin. Rosswall & Granhall (1980) calculated a dry deposition of 0.13 g N m^{-2} yr^{-1} at Stordalen in Sweden based on wash-out ratios of nitrogen in wet deposition. However, I am unaware of any direct measurement of dry deposition to wetland ecosystems.

Input of N to wetlands by organic-N in wet deposition and by dry deposition of NO_X and HNO_3 may exceed the input of nitrogen as NH_4^+ and NO_3^- in wet deposition. The potential importance of these inputs to ombrotrophic bogs is obvious and should be considered in studies of more hydrologically open wetlands, as well.

Nitrogen fixation

Prior to the introduction of the acetylene reduction assay (ARA) by Hardy et al. (1968), field ecologists had to depend on mass balance or ^{15}N studies to determine nitrogen fixation rates. The cost and labor to use ^{15}N prevented its widespread use outside the agronomic research community. The ARA proved to be simple to use, inexpensive, highly sensitive, and perhaps too straightforward. Rice & Paul (1971) and Smith (1980) have warned that the ARA should be calibrated against direct fixation of $^{15}N_2$ to best estimate nitrogen fixation rates. Problems of variable C_2H_2:N_2 reduction ratios, differential solubility and diffusion of C_2H_2 and N_2 and *de novo* ethylene production in soil will all lead to overestimates of nitrogen fixation by the ARA.

Table 4. Reported estimates of nitrogen fixation in various wetlands. Except for the report by Chapman & Hemond (1981), all of these estimates are based on uncalibrated measurements of acetylene reduction activity and are probably overestimates.

System description	Estimated $gN \cdot m^{-2} \cdot yr^{-1}$	References
Ontario *Glyceria-Typha* marsh	12	Bristow (1974)
Harvard Forest, Massachusetts various palustrine marshes	0.2–1.0[a]	Kana & Tjepkema (1978)
Oregon *Juncus balticus*	8[a]	Tjepkema & Evans (1976)
Thoreau's Bog, Massachusetts basin bog	1	Chapman & Hemond (1981)
Pennine, UK blanket bog	0.05–3.2	Martin & Holding (1978)
Survey, European bogs	0.07	Waughman & Bellamy (1980)
poor fens	0.50	
rich fens	2.1	
Stordalen, Sweden, bogs	0.03–0.15	Granhall & Selander (1973)
fens	0.16–11.9	
James Bay, Ontario muskegs	undetectable	Blasco & Jordan (1976)
Harvard Forest, Massachusetts *Myrica gale* fen	3.4	Schwintzer (1979)
Gainesville, Florida cypress domes	0.75–2.81	Dierberg & Brezonik (1983)

[a] Assumes a 100 day active season

These warnings have not been heeded as can be seen in Table 4. There are no freshwater wetland studies that rely on ^{15}N exclusively to determine nitrogen fixation and only Chapman & Hemond (1982) appear to have field-checked their ARA against ^{15}N. Thus we might view the values in Table 4 as potential estimates.

Nitrogen fixation (ARA) rates range from a few hundredths of a g N m^{-2} yr^{-1} to about 10 g N m^{-2} yr^{-1} with most values around 1 g N m^{-2} yr^{-1}. Factors affecting nitrogenase enzyme activity in flooded soils have been discussed by Ogan (1982, 1983) and by Buresh et al. (1980). Granhall & Selander (1973) showed that the spatial variability between sub-sites at the bog-fen complex they studied varied from 0.16 to 11.9 g N m^{-2} yr^{-1} with the highest values due to blue-green algae alone or in association with plants (epiphytic not symbiotic).

The study by Waughman & Bellamy (1980) is notable in that they surveyed 45 subsites in 17 different bogs, fens, and mires in Europe, Great Britain, and Malaysia. In an intensive study at a German site, they found decreasing ARA activity in the order rich-fen > poor-fen > bog. This result is interesting because one might expect higher fixation in ombrotrophic bogs than in minerotrophic fens since the presence of fixed N has been observed to suppress nitrogen fixation (Dierberg & Brezonik 1983; Ogan 1982, 1983, but see Buresh et al. 1980). The observation is consistent, however, with another unexpected observation, i.e. that the inorganic nitrogen content of fen pore water is generally less than that of bog water (Waughman 1980; Schwintzer & Tomberlin 1982). Both of these results may reflect a higher rate of production and consequent higher rate of nutrient turnover in fens than in bogs.

Hydrologic inputs

It is difficult to generalize about the importance of nitrogen inputs to wetlands by either surface or subsurface inputs. Leaching rates to a wetland will be a function of the types of activities on upland areas, not the type of wetland. In addition, the average areal loading rate is a function of wetland size not wetland type, and because there is usually a directional component to the loading, different parts of the wetland will receive different loading rates (Verry & Timmons 1982).

Finally, for hydrologic inputs to have an effect on wetlands they must actually come in substantial contact with biotic components of the wetland. This may seem an obvious statement, but in many wetlands there may not be substantial hydrologic contact with the biota. For example, in floating wetlands the living portion of the mat may be physically isolated from nitrogen contained in water flowing beneath the mat (Gaudet 1977; Verhoven et al. 1983; Sesser & Gosselink 1984). Even in non-floating wetlands there may be little contact between open water flow and the marsh itself. I found, for example, that mineralization of organic matter in a freshwater, tidal, riverine marsh dominated by *Typha latifolia, Carex lacustris,* and *Calamagrostic canadensis* was sufficient to support annual plant growth exclusive of any inputs from the river (Bowden 1982, 1984b). In this and other cases, hydrologic inputs may only restore small losses of nitrogen by, for example, denitrification and burial while the bulk of nitrogen in plants is recycled and the bulk of nitrogen in surface and subsurface flow passes through the wetland unaltered by the biota.

There are of course examples where hydrologic inputs are important. The careful budgets constructed by Valiela & Teal (1979) and Verry & Timmons (1982) show the importance of NO_3^- and NH_4^+ to a salt marsh and a black spruce bog, respectively. Gosselink (1984) discusses the importance of sediment import as a nitrogen source to marshes of the Mississippi delta.

Internal nitrogen dynamics

Translocation

Translocation has various definitions in the literature but here refers to the removal of nitrogen from dying annual tissues to storage in perennial tissues. Thus translocation conserves nitrogen that might otherwise be lost in litterfall. This would seem to be a "rational" strategy for wetland plants that typically live in an environment where nitrogen is in short supply (Small 1972a, b). However, Schlesinger (1978) concluded that a negligible amount of nitrogen is translocated by cypress. Hopkinson & Schubauer (1984) used their own Klopatek's (1978) data to suggest that freshwater marsh plants may recycle nitrogen less efficiently than salt marsh species due to lower translocation rates by freshwater species. Although there is an extensive literature on C and mineral translocation in plants (e.g. Epstein 1972; Gauch 1972) there is surprisingly little quantitative information about N translocation. To my knowledge, ^{15}N has not been used to study translocation of N by typical wetland plants.

Evidence for translocation is usually based on a comparative mass balance between nitrogen in aboveground annual tissues and belowground perennial tissues. The results of Klopatek (1978), Kistritz et al. (1983) and Hopkinson & Schubauer (1984), are typical. Using Kistritz et al. (1983) data as an example (Fig. 3), during the early growing season the mass of aboveground biomass nitrogen increases rapidly at the expense of nitrogen stored in belowground perennial tissues as well as by *de novo* uptake. During senescence, a reverse trend is observed; the mass of the nitrogen aboveground decreases while that below increases. The usual interpretation of these data is that nitrogen has moved from the dying aboveground tissues to the perennial belowground tissues.

An alternative explanation is possible, however. There is no reason to believe that perennial belowground tissues cease to take up nitrogen coincidentally with tissue death aboveground (see Prentki et al. (1978) regarding P uptake). Certainly, if the perennial tissues remain metabolically active, the potential for continued N uptake remains. A lack of photosynthate from leaves to support metabolic activity in roots and rhizomes is not a sufficient explanation for decreased uptake belowground because the translocation process itself must require energy. Consequently the pattern shown in Fig. 3 could be explained by leaching loss from aboveground tissues (see below) and coincident, independent, *de novo* uptake by perennial belowground tissues.

It is likely that both translocation and post-senescent uptake by perennial tissues operate simultaneously. A mass balance of net changes in above- and

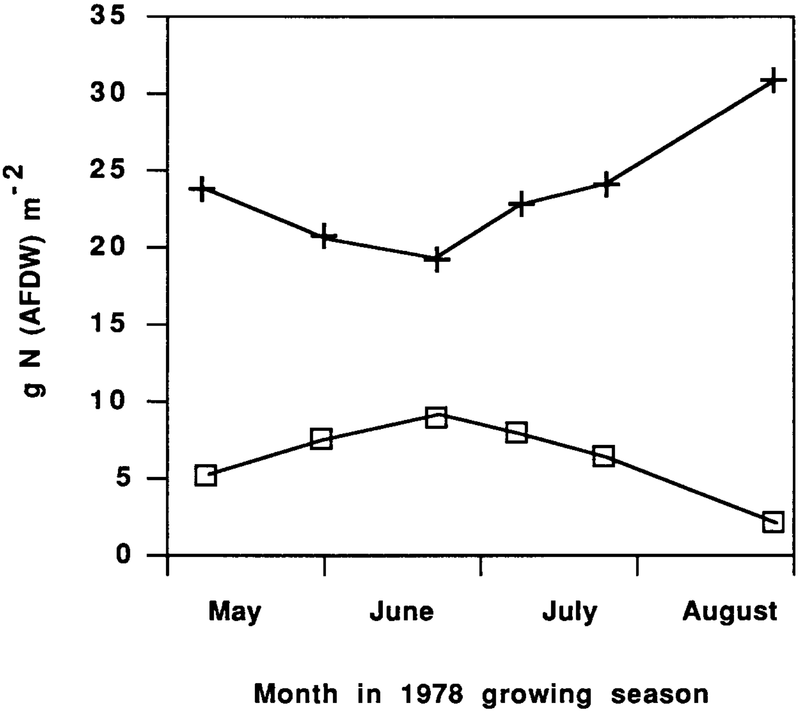

Fig. 3. Aboveground (□) and belowground (+) fluctuations in total N standing stocks, based on ash-free dry weight (AFDW), in a *Carex lyngbyei* marsh, from Kistritz et al. 1983, modified with permission from Est. Res. Fed. Vol. 6 © 1983.

belowground biomass nitrogen cannot, however, distinguish between these two possibilities because the system is, in a modeling sense, underdetermined. The biogeochemical problem this presents is that translocation is a conservative internal recycling mechanism while uptake is ultimately a consumptive throughput mechanism. The no-translocation scenario places greater demands on plant uptake and, because litterfall has been better quantified than leaching, implies that leaching rates must be higher than required by the translocation scenario.

Decomposition and mineralization

Nutrients bound in living tissues are returned by decomposition to forms that plants can assimilate. Broadly defined, the decomposition process for nitrogen includes leaching, net accumulation, and net mineralization. These processes operate in sequence with broad overlap.

There are few quantitative, direct estimates of leaching losses from live or dying tissues. Leaching refers to the rapid loss of water soluble nitrogen compounds. These could range from inorganic forms to amino acids and high molecular weight organic forms such as DNA and plant pigments. These compounds are usually present at higher concentrations inside the plant than out, a condition that must be actively maintained by the plants. When the plant dies, this gradient cannot be maintained and cells begin to rupture, which leads to rapid losses of soluble nitrogen.

Leaching of plant material is usually estimated from the initial rapid phase of weight loss observed during litter bag studies. The observations discussed by Brinson (1977); Odum & Heywood (1978) and Chamie & Richards (1978) are typical. Unlike carbon, however, the mass of nitrogen in litter may not decrease at all and may even increase over time, causing net accumulation. This does not mean that leaching does not occur, rather, microbes that rapidly colonize the dying plant tissues may immobilize a large portion of the nitrogen that leaches from dying plants as well as nitrogen that is external to the plants.

The balance between microbial immobilization and microbial mineralization is the final component of the decomposition process. Mineralization refers specifically to the conversion of organic matter to inorganic constituents by microbial degradation. For nitrogen, the primary product of mineralization is ammonium, hence the synonym "ammonification." Net mineralization is the difference between gross mineralization and gross immobilization or uptake; a positive net mineralization means that gross mineralization to ammonium exceeds gross immobilization of ammonium.

Net mineralization is easy to measure but may seriously underestimate the gross rates of nitrogen turnover by benthic microbes (Bowden 1984b). In freshwater tidal marshes on the North River in Massachusetts, I found that gross mineralization in the marsh sediments could exceed net mineralization by many times (Table 5). Consequently net mineralization is a poor indicator of actual microbial activity in wetland sediments.

Table 5. Estimated gross mineralization, gross immobilization, and net mineralization rates (13 °C) in the top 5 to 10 cm of emergent marsh sediments on the North River, Massachusetts (from Bowden 1984b).

Date	ng NH_4-N (cm^3 fresh sediment)$^{-1}$ h^{-1} (± 1 SD)		
	Gross mineralization	Gross immobilization	Net mineralization
Sep 80	100 ± 26	76 ± 23	24
May 81	424 ± 136	[424]	0
Aug 81	125 ± 6	28 ± 7	97
Sep 81	84 ± 2	20 ± 2	64
Sep 81	109 ± 4	−1 ± 4	110
Nov 81	244 ± 42	73 ± 14	177
Dec 81	56 ± 8	12 ± 3	44
Mean ± 1 SE	163 ± 49	90 ± 56	73 ± 22

The dynamic. balance of gross mineralization and immobilization in flooded soils is described in detail by Tusneem & Patrick (1971). The most important point for this discussion is that for high C:N ratios typical of fresh litter (20 to 70:1, Daubenmire (1974); Gauch (1972); Larcher (1975)), microbes must immobilize or fix (Dierberg & Brezonik 1981) nitrogen to use the C. This explains the observation mentioned above, that the mass of N in the litter-microbe complex within a litter bag may remain the same or even increase as C decays away. At a C:N ratio of roughly 20:1 (Daubenmire 1974) no additional nitrogen is required by the decomposer microbes and positive net mineralization ensues (ammonium production). Melillo et al. (1982) have shown that the point of inflection for terrestrial litter is controlled by lignin/nitrogen ratios in fresh litter, and suggests that this may be generally valid.

The net effect of the decomposition process is to conserve N within the sediment while C is respired away. Plant litter and the microbes that grow on it are crucial because they temporarily sequester nitrogen that might otherwise be flushed out of wetlands hydrologically (Brinson 1977; Qualls 1984). I recently described a tight internal N cycle in tidal freshwater marshes on the North River (Bowden 1984b, 1986a). In these marshes, *Typha, Carex,* and *Calamagrostis* litter persist on the marsh surface all winter. Microbes on the litter immobilize nitrogen under aerobic conditions and mineralize nitrogen under anaerobic conditions (Bowden 1986a). I suggest that fresh, aerobic litter acts like a cap on the marsh that prevents nitrogen loss from high-N sediment pore water to low-N river water and may even extract nitrogen from the river water when the marsh is flooded. Eventually this aerobic litter is compacted, forms anaerobic peat, and becomes a net source of nitrogen that is available to plants for uptake. Morris & Bowden (1986) concluded that this transition occurs within the top few cm of sediment near the roots. It is possible that because of litter immobilization, the marsh as a whole immobilizes nitrogen even when the plants are not actively assimilating nitrogen and that nitrogen thus immobilized is released months or even years later for plant uptake. The advantage to the ecosystem is that the supply rate of nitrogen is buffered against short-term deficiencies in N supply rate that might occur for example during drought periods when the hydrologic supply rate of nitrogen might be insufficient to support growth.

Plant uptake

The dynamic aspects of nitrogen uptake by wetland plants have been described in a series of papers by Boyd (Boyd 1969, 1970, 1971; Boyd & Hess 1970). Briefly, Boyd found that the peak rate of nitrogen uptake precedes the peak rate of net production. The peak rate of net production occurs early in the season and is followed by a period in which the N content of the plants gradually declines. Nitrogen uptake can be characterized by an initial period of luxury uptake followed by a period of dilution due to continued C fixation in excess of N uptake. Although Boyd worked with a limited number of typical wetland plants, it is likely that his observations are valid generally.

Estimates of plant uptake are most often based on measured biomass production and the nutrient content of plant tissues. Several problems inherent in tissue analysis were mentioned earlier. These problems are compounded by problems inherent in production estimates, discussed for example by Whigham et al. (1978) and Brinson et al. (1981). In particular, it is often difficult to account for intraseason turnover of plant biomass by either leaf mortality or herbivory. In addition, as discussed above, the uncertainty about belowground biomass and production is generally high.

For comparative purposes it is probably reasonable to equate plant nitrogen demand with net primary productivity. It is beyond the scope of this paper to review the literature on primary production in freshwater wetland plants; excellent reviews will be found in Keefe (1972), Whigham et al. (1978), Richardson (1979) and Brinson et al. (1981). Figure 4 from Brinson et al. (1981) illustrates several important generalizations, i.e. primary production (and presumably N uptake) are lowest in northern bogs where a combination of low temperature, ombrotrophic conditions, and short growing seasons conspire to keep production low. Tropical minerotrophic reed swamps have the highest production and N demand. There is a suggestion that primary production in hydrologically energetic (e.g. tidal) systems may be higher than in energetically quiescent systems. This agrees substantially with Odum et al. (1983) who observed higher production in a tidal *Zizaniopsis miliacea* (giant cutgrass) marsh than in a similar impounded marsh.

Ignoring the extreme values in Fig. 4, I concluded that primary production in temperate wetlands of all types is remarkably similar, about 0.5 to 2 kg dry weight m^{-2} yr^{-1}. These values are consistent with those reported by Richardson (1979) and Whigham et al. (1978). If the C:N ratio of plant material is on the order of 30 or 40:1 (lower than freshly dead litter) then we might expect annual nitrogen uptake on the order of 5 to 35 g N m^{-2} yr^{-1}. Reference to the existing literature suggests that this expectation is reasonable (Table 6).

Net mineralization within wetland sediments may supply a major portion of the immediate demand for N by plants and in some cases may actually limit plant uptake. For example, I found a good correspondence between measured net mineralization and plant demand in the North River wetlands

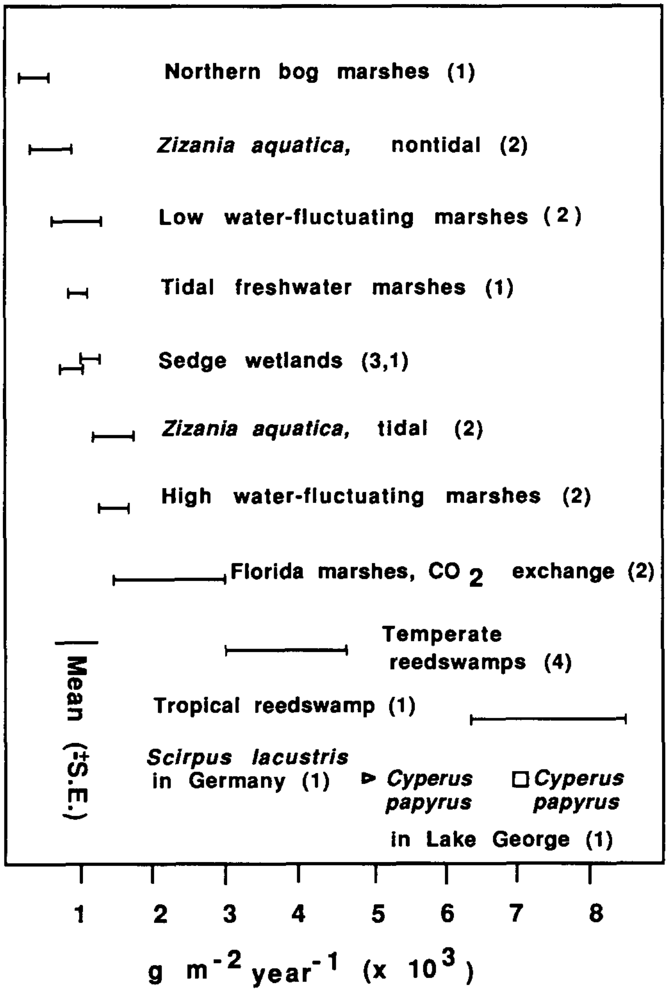

Fig. 4. Net biomass production of nonforested wetlands. Numbers in parentheses following marsh type identify components measured: 1 = aboveground, 2 = mostly aboveground, 3 = above- and belowground, 4 = whole ecosystem. From Brinson et al. (1981) modified with permission from Ann. Rev. Ecol. Syst. Vol. 12 © 1981 by Annual Reviews, Inc.

(Bowden 1984b). Mineralization is probably also the dominant source of N in floating mat bogs and swamps (Verhoven et al. 1983; Gaudet 1977). Ultimately nitrogen must be imported by, for example, N fixation or precipitation to balance inevitable losses (see below), but these imports are probably small relative to the internal mineralization-immobilization cycle. Where additional sources of nitrogen are plentiful (e.g. sedimentation (Gosselink 1984)) production may be higher.

Nitrate is generally scarce or non-existent in wetland soils and as a

Table 6. Plant nitrogen uptake data for selected wetland species.

System description	$gN \cdot m^{-2} \cdot yr^{-1}$	Dominant species	Reference
Theresa Marsh, Wisconsin palustrine reed marsh	17.5	*Scirpus fluvatilis*	Klolpatek (1978)
Michigan Hollow, New York palustrine sedge fen	15.9	*Carex lacustris*	Bernard (1977)
Inlet Valley, New York palustrine sedge fen	10	*Carex rosata*	Bernard & Hankinson (1979)
Uganda papyrus swamp	103.3	*Cyperus papyrus*	Gaudet (1977)
North River, Massachusetts riverine tidal marsh	22.3	*Typha. Carex Calamagrostis*	Bowden (1982)
Pennine, UK blanket bog	6	*Caluneto-Eriophoretum* ± *Sphagnum* spp.	Martin & Holding (1978)
Thoreau's Bog, Massachusetts basin bog	< 3	*Sphagnum* spp.	Hemond (1983)
Houghton Lake, Michigan rich fen	3	*Chamaedaphne calyculata* *Betula pimula*	Richardson et al. (1978)
Stordalen, Sweden subarctic mire	0.67	*Rubus chamaemorus* *Eriophorum vaginatum*	Rosswall & Granhall (1980)
Bog forests and fens	5	unspecified	P'yavchenko (1960) quoted in Waughman & Bellamy (1980)
Okefenokee Swamp, Georgia cypress swamp	5.7	*Taxodium distichum*	Schlesinger (1978)
Florida cypress domes	1.04	*Taxodium distichum* *Nyssa sylvatica*	Dierberg & Brezonik (1983)

consequence wetland plants may have adapted to assimilate ammonium preferentially. Havill et al. (1974) observed that many of the Ericaceae that inhabit bogs do not or cannot use nitrate as a nitrogen source, even when it is added artificially. They attributed this to acid conditions in bog sediments, but it could as well be an adaptation to an environment where ammonium is consistently more plentiful than nitrate. On the other hand, Press & Lee (1982) observed that nitrate reductase activity can be induced in *Sphagnum* spp. when NO_3^- is supplied. Clearly, more research is needed on the form of nitrogen wetland plants prefer and the limitations the wetland environment places on nitrogen uptake.

It is interesting to note that most studies conducted to date indicate that primary productivity in coastal salt marshes is limited largely by N. Fertilizer additions of N stimulate plant growth while additions of P or K do not. (Broome et al. 1973; Sullivan & Daiber 1974; Valiela et al. 1975; Mendelssohn 1979). In contrast, fertilizer addition experiments in freshwater wetlands yield variable results. (See for example Reader 1978; Neeley & Davis 1985; Stewart & Ornes 1975). In different freshwater ecosystems N, P, K, or some other factor entirely may limit primary production.

Nitrification

Ammonium not taken up by plants or tightly bound to sediments may be nitrified. Nitrification may be autotrophic ($NH_4^+ \rightarrow NO_3^-$) or heterotrophic (reduced organic N → oxidized N compounds). Nitrification has been studied extensively and has been reviewed recently by Focht & Verstraete (1977) and Belser (1979). Factors that can limit autotrophic nitrification in wetland environments include a lack of available O_2, acid conditions, competition from plants, allelopaths, and lack of available phosphorus (Bowden 1986a). Heterotrophic nitrification is less well studied and little is known about factors that control it (Schimel et al. 1984; Castignetti & Hollocher 1984).

Although autotrophic nitrification has been one of the most intensively studied nitrogen transformations, it remains perhaps the least well quantified. Research on nitrification has been hindered by the lack of a convenient analytical tool such as acetylene reduction for nitrogen fixation or acetylene block for denitrification. A variety of nitrification inhibitors (principally N-Serve or 2-chloro-6-(trichloromethyl) pyridine) have been used to measure nitrification rates indirectly, but incubations are often done on ammonium-enriched slurries that have little relevance to field conditions.

The wetland literature on nitrification is especially small. Jones & Hood (1980) isolated a *Nitrosomonas* species from a Louisiana freshwater marsh and found that optimum growth in culture occurred at pH 8.5, 35 °C, and ammonium concentrations greater than 0.5 g/l. If this is representative of the conditions required by autotrophic nitrifiers, it is easy to see why their activity in cold, acid, oligotrophic bogs and fens is far below potential activity.

Andersen & Hansen (1982) used a typical enriched (NH_4Cl) slurry approach to study nitrification in a Danish *Phragmites australis* community. Their estimated nitrification rates were at least $50\,mg\ N\ m^{-2}\ d^{-1}$ ($5\,g\ N\ m^{-2}\ yr^{-1}$ for a 100 d season). Martin & Holding (1978) used a percolation column approach to quantify nitrification rates of $0.003\,g\ Nm^{-2}\ yr^{-1}$ in a British blanket bog. Rosswall & Granhall (1980) concluded that nitrification was negligibly small in the bog and fen site they studied at Stordalen, Sweden. I used a hybrid ^{15}N/N-Serve approach to quantify nitrification rates of 11 g N m^{-2} yr^{-1} in the *Typha, Carex* and *Calamagrostis* marshes on the North River (Bowden 1982, 1986a).

Dissimilatory nitrate reduction

Two forms of dissimilatory nitrate reduction occur in wetland sediments. Denitrification, the most familiar form, leads to an export of nitrogen from ecosystems, as discussed below. Dissimilatory reduction to ammonium (reammonification in Fig. 1) conserves nitrogen as ammonium within the system. Buresh & Patrick (1978) originally suggested that reammonification only occured under highly reducing (low redox) conditions such as exist in salt marshes due to the SO_4^{2-} reduction couple and was probably quantitatively unimportant. Later, DeLaune & Patrick (1982) modified this conclusion and suggested that under more realistic conditions of NO_3^- supply rate, reammonification might be important.

Reammonification has been measured in only two freshwater wetlands. Hemond (1983) found that reammonification was about 0.55 g N m^{-2} yr^{-1} in Thoreau's Bog, an ombrotrophic bog in Massachusetts, USA. This may be compared to 0.25 g N m^{-2} yr^{-1} input in precipitation and 2.5 g N m^{-2} yr^{-1} recycled by net mineralizaton. I measured reammonification rates of 0.5 g N m^{-2} yr^{-1} in the North River tidal freshwater marsh sediments, about 120 km south of Hemond's site. This was ~ 2% of net mineralization at my site (Bowden 1984b). The importance of reammonification as a mechanism of nitrogen conservation is essentially unknown for most wetlands.

Nitrogen exports

Hydrologic exchange

Export of nitrogen from wetlands is inextricably connected with the hydrologic characteristics of the wetland. At one extreme there is the ombrotrophic raised bog, where hydrologic export is zero. At the other extreme there is the floating mat swamp or fen where hydrologic throughput might be quite large and yet little affected by the wetland biota (Novitzki 1979). In between, there are the tidal or fluctuating water-level marshes where water may import or export nitrogen depending on local conditions.

Table 7 summarizes information on hydrologic N export from a variety of wetland systems. Note that the studies listed in Table 7 are reports on natural marshes (i.e. not sewage amended or artificial marshes, see below). It is apparent that, in comparison to internal transformations such as uptake

Table 7. Hydrologic export of nitrogen from selected wetland types. A positive sign means that nitrogen was imported by the wetland; a negative sign means that the wetland exports nitrogen.

System description	gN· m^{-2}·yr^{-1}				Reference
	NH_4-N	NO_3-N	DON	PN	
Rhode River, Chesapeake Bay (high)	−0.15	−0.70	−2.60	−2.9	Jordan et al.
riverine tidal marsh (low)	−1.3	−0.35	−1.8	+0.9	(1983)
Patuxent River, Chesapeake Bay riverine tidal marsh	−0.39	−0.92	−2.11	−0.25	Heinle & Flemner (1976)
Thoreau's Bog, Massachusetts basin bog	−0.31	−0.15	−0.1	–	Hemond (1980, 1983)
Black Spruce bog, Minnesota basin bog	−0.07	−0.03	−0.54	—	Verry & Timmons (1982)
Coastal Plain, North Carolina pocosins	−0.03	−0.01	−0.32	—	Richardson (1983)

or mineralization, nitrogen export is small. In tidal systems nitrogen may even be imported. This is consistent with the general conclusion that wetlands are nutrient deficient systems.

It is important to note, however, that nitrogen export measured on the downstream side of a wetland ignores upland additions of N in surface and subsurface runoff. For example, Correl (1981) measured 7 t N/yr exported from intertidal marshes on the Rhode River (Chesapeake Bay), but 10 t N/yr were imported from uplands for a net import of 3 t N/yr. Similarly, Verry & Timmons (1982) measured 0.64 g N m^{-2} yr^{-1} output from a black spruce (*Picea mariana*) bog in Michigan. However the bog received 1.27 g N m^{-2} yr^{-1} from precipitation and hydrologic input from aspen-covered uplands. Some nitrogen will always be exported from wetlands because it is highly unlikely that the concentrations of all forms of nitrogen that could be exported (e.g. NO_3^-, NH_4^+, DON, PN) will ever be zero. On the other hand, it appears that this export is generally small and in many cases wetlands may be net sinks for hydrologically transported N. Other wetlands may be nitrogen sinks only seasonally, taking up nitrogen during the growing season but remobilizing some or all of the fixed N during the off-season (Simpson et al 1978).

Denitrification

Denitrification refers specifically to the respiratory reduction of NO_3^- by microbes to gaseous oxides of nitrogen and ultimately to dinitrogen gas (N_2^0). Prior to the advent of electron capture gas chromatography (EC-GC), denitrification was usually estimated by difference in mass balance studies. This approach is subject to a number of shortcomings as discussed

Table 8. Estimated rates of denitrification in various wetland types. All values greater than 1 $gN \cdot m^{-2} \cdot yr^{-1}$ were determined under conditions that favor vigorous denitrification. As a consequence, most of these values should be viewed as potential rates only.

System description	$gN \cdot m^{-2} \cdot yr^{-1}$	Reference
Lake Arreskov, Denmark palustrine reed swamp	5	Andersen (1981) Andersen & Hansen (1982)
Great Meadows, Massachusetts palustrine wetland	55	Bartlett et al. (1979)
Lake Wingra, Wisconsin palustrine marsh	0.2	Prentki et al. (1978)
Ontario various lacustrine	0.25	Chan & Knowles (1979)
Lake Wingra, Wisconsin palustrine	0.002–0.11	Goodroad & Keeney (1984)
Pennine, UK blanket bog	0.1	Martin & Holding (1978)
European survey bogs	6.3–373	Muller et al. (1980)
Stordalen, Sweden subarctic mire	undetectable	Rosswall & Granhall (1980)
European survey fens	28	Muller et al. (1980)
Florida cypress domes	0.15	Dierberg & Brezonik (1983)
Bayou Sorrel, Louisiana palustrine swamps	35	Engler & Patrick (1974)
European survey hardwood swamps	15–306	Muller et al. (1980)

for example by Focht (1978). More recently, sensitive direct measurements of N_2O evolution (either with or without C_2H_2 to block the reduction of N_2O to N_2) have been made by EC-GC. Direct measurements of denitrification in the field are difficult, however, because the large background of atmospheric N_2 obscures emissions from denitrifiers. More often, rates reported in the literature are for measurements of sediment slurries, under anoxic environments with added NO_3^- and occasionally added glucose (see for example Muller et al. 1980). Such rates must be viewed as potential estimates with questionable relevance to field conditions. Tiedje et al. (1982) suggest that these potential estimates are 40 to 1000 times higher than actual field rates.

Table 8 lists the results from several studies of denitrification in different types of wetlands. Of these, only the study of Goodroad & Keeney (1984) could be considered an *in-situ* estimate (although it may be low because N_2 evolution was not measured). If the other potential estimates are off by 40–1000 ×, as suggested by Tiedje et al. (1982), then denitrification losses from most freshwater wetlands may be < 1 g N m^{-2} yr^{-1}.

Denitrification is not the only mechanism that results in gaseous losses of nitrogen. I reviewed the mechanisms of gaseous nitrogen loss from natural (non-agricultural) ecosystems (Bowden 1986b) and concluded that, at the level of the local N budget, these losses are not important. Again, this is consistent with the supposition that wetlands are generally nutrient deficient systems. However, N gas losses may be quite high in coastal salt marshes where there is a constant input of nitrate in tidal water.

Change as a biogeochemical agent

In recent years there has been an increasing interest in the role and effects of successional and anthropogenic change on the ecosystem functions of wetlands. Wetlands exist at the interface between terrestrial and aquatic ecosystems and might be expected to respond more dramatically than other ecosystem types to hydrologic fluctuations caused by climate or alterations by humans.

Recent surveys confirm that change is an important factor in wetland ecology (Gosselink & Baumann; Frayer et al. 1983; Tiner 1984). However, there are conflicting views on whether this change is predominantly man-induced (Frayer et al. 1983; Hardisky & Klemas; Tiner 1984) or natural (Larson et al. 1980; Golet & Parkhurst 1981). Natural changes that could influence N biogeochemistry include succession (Hofstedder 1983; Tallis 1983), beaver activity (Naiman & Melillo 1984), shoreline subsidence (Craig et al. 1980) and fire (Wilbur & Christansen 1983). Anthropogenic changes that could affect N biogeochemistry include highway and other urban construction (Golet & Parkhurst 1981), canal building (Craig et al. 1980), and especially agriculture (Frayer et al. 1983; Tiner 1984).

Frayer et al. (1983) estimate that in the US 11×10^6 acres of palustrine wetlands were lost between ~ 1950 and ~ 1970, primarily to agricultural activities. The effects of draining for agriculture or forestry on N biogeochemistry have been studied by Grootjans et al. (1985), Tate (1980), and Lee et al. (1975). In general, draining increases loss of inorganic nitrogen which could have an impact on plant growth and downstream water quality.

A potentially large impact on N cycling in wetlands could occur if substantial acreages are used to treat secondary sewage. This idea has been studied intensely over the past ten years and the results, summarized by Kadlec & Kadlec (1979), van der Valk et al. (1979) and Nichols (1983), suggest that if carefully planned, wetlands can effectively assimilate N and P in waste water, at least for several years. Changes that can be expected when sewage is added included increased denitrification, decreased nitrogen fixation, sediment sorption of NH_4^+, increased tissue N concentrations with concomitant changes in litter decomposition dynamics, and increased productivity (Dierberg & Brezonik 1985; Brinson et al. 1984, Neeley & Davis 1985). There is still concern that over a period of many years the capacity of wetlands to remove N and P could be exhausted (Nichols 1983; Simpson et al. 1983). In addition, large additions of N and water are likely to cause alterations in plant community composition and we should anticipate whether these changes are acceptable. Kadlec & Kadlec (1979) summarized existing information on the few long-term field-trials that exist and concluded that the long-term assimilative capacity for N is high but may be limited for P. The high capacity for N is probably a result of the ability of wetlands to purge fixed N from the system by denitrification.

Synthesis

It is clear that sediments are the single largest pool of nitrogen in wetland ecosystems (100's and 1000's g N m^{-2}) followed in rough order-of-magnitude decreases by plants and available inorganic nitrogen (Fig. 5). Turnover times for these pools follow a similar trend with slowest turnover in the sediment pool (hundreds of years) and fastest turnover in inorganic pools (days or hours).

Several flux rates are also well characterized. Precipitation inputs ($<$ 1–2 g N m^{-2} yr^{-1}) are well known, but inputs due to dry deposition are essentially unknown and could be as large or larger than net deposition. Nitrogen fixation (acetylene reduction) is an important supplementary input in some wetlands ($\ll$ 1–3 g N m^{-2} yr^{-1}) but is probably limited by the excess of fixed nitrogen usually present in the sediments of these systems.

Based on the literature on net primary production I conclude that plant uptake normally ranges from a few g N m^{-2} yr^{-1} to $\sim$ 35 g N m^{-2} yr^{-1} with lowest values in cold northern and hydrologically stagnant systems and highest values in warm temperate or tropical and hydrologically active systems. Most of this material falls to the wetland surface where an elegant interaction between plant litter and decomposer microorganisms tends, over the short-term, to conserve nitrogen within the system in immobile forms. Later, decomposers release this nitrogen in forms that plants can reassimilate.

During the internal cycle between available ammonium, live plants and dead litter nitrogen there are "leaks" to nitrification ($<$ 0.1 to 10 g N m^{-2} yr^{-1}). The NO_3^- formed by nitrification has several fates which may tend to either conserve nitrogen (uptake and dissimilatory reduction to ammonium) or lead to its loss (denitrification). Both nitrification and denitrification operate at rates far below their potential and under proper conditions (e.g. draining or fluctuating water levels) may accelerate.

It is important to note that virtually all estimates of denitrification rates

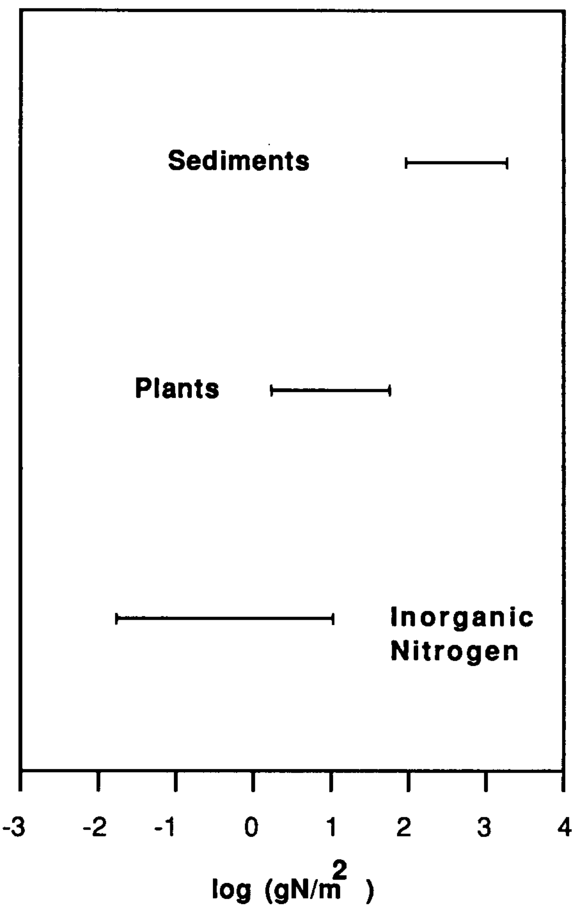

Fig. 5. Primary pools of nitrogen in freshwater wetlands. The values depicted in this Figure are the ranges of values reported in Tables 1 and 2 for sediments and plants plus the range of values reported in the literature for inorganic N (W.B. Bowden unpublished data).

in freshwater wetlands are based on measurements of potential denitrification, not actual denitrification. As a consequence, the importance of denitrification in these ecosystems may have been overestimated. The problem is apparent in Fig. 6, which compares ranges of various nitrogen transformation rates reported in the literature and listed in tables in this report. Figure 6 shows that internal transformations (plant uptake and mineralization) greatly exceed measured inputs (precipitation and nitrogen fixation). In addition, note that mineralization is a larger source of nitrogen for plant uptake than the sum of precipitation plus nitrogen fixation. Most important, however, note that denitrification greatly exceeds hydrologic export and even exceeds plant uptake. Even if other sources of nitrogen are considered (e.g. dry deposition) it is unlikely that wetlands could sustain a N drain as

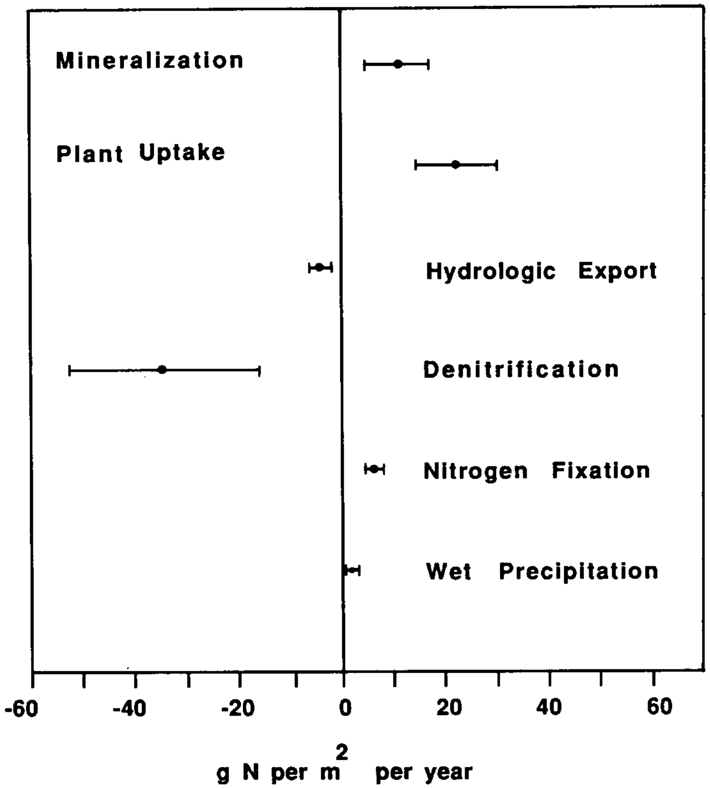

Fig. 6. Comparison of various ecosystem inputs, interconversions, and exports for freshwater wetlands. Values reported in this Figure are the means ± 1 SE of the values reported in Tables in this report plus values for sediment net mineralization in the literature (W.B. Bowden unpublished data).

large as that depicted. If these potential denitrification estimates are reduced by 40–1000 × as suggested by Tiedje et al. (1982) then the denitrification estimates come in line with hydrologic exports and probably balance hydrologic inputs.

The overall picture depicted by Fig. 6, modified by lower denitrification rates, is one of conservative recycling: larger amounts of nitrogen cycle within the system than flow in or out. Except for closed, ombrotrophic systems this might seem an unusual characteristic for ecosystems that are dominated by the flux of water, however, two factors limit the opportunity for N loss.

At any given time the fraction of nitrogen in the system that could be lost by hydrologic export is probably a small fraction of the potentially mineralizable nitrogen and is certainly a negligible fraction of the total nitrogen in the system. Second, freshwater wetlands may be more isolated from the bulk flow of water through them than we usually think. In ombrotrophic bogs hydrologic export is unimportant by definition. In other bogs, fens and swamps the bulk of upland water flow may pass under (in the case of floating mats) or by (in the case of riparian systems) the biotically active components of the wetland. This may explain the rather limited range of N loading rates real wetlands can accept (Nichols 1983) in comparison to percolation columns (Dierberg and Brezonik 1985) or engineered marshes.

Recommendations

There are many areas where knowledge of the biogeochemistry of N in freshwater wetlands is quite limited and additional research would be desirable.

1. Belowground production is still not well known, which introduces substantial uncertainty in estimates of sediment N turnover.
2. Realistic estimates of nitrification and denitrification are virtually nonexistent.
3. Translocation is presumed to play an important role in nitrogen conservation, and yet I know of no direct evidence for N translocation (i.e. ^{15}N studies).
4. Although net mineralization is easy to measure, estimates of gross N turnover in sediments and the consequences of associated microbial activity on C, P, and S dynamics is largely unknown.
5. The importance of dry deposition is unknown but could be large, especially in wetlands close to urban centers.
6. Factors limiting primary productivity are not well defined. How do nutrients, space, water, light and temperature interact? Is N often a limiting factor?
7. As a practical matter, what are the limits to the assimilative capacity of wetlands for nitrogen?
8. How do changing land use patterns affect wetland nitrogen cycles?

Two final recommendations are worth noting. Work by Boyd (1978) on plant nutrient contents and Basilier & Granhall (1978) on nitrogen fixation, for example, suggest that wetlands are inherently variable both temporally and spatially. As a consequence, funding agencies must be willing to support a certain amount of seemingly repetitive ancillary research. Until we better understand the type of information that is transferable between systems we will have to duplicate some information within systems to best understand how they function.

Finally, research in the field of wetland ecology could be characterized as largely autecological. To understand how these systems work (and to conserve increasingly scarce research dollars) we must work towards a synecological understanding of specific ecosystems. In our current state we run the same risk of Kipling's blind men trying to describe an elephant: our knowledge of the parts may obscure our understanding of the whole.

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