
The Influence of Nutrients on the Coastal Wetlands of the Mississippi Delta

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Abstract

Among the solutions being proposed for reversing wetland loss in the Mississippi River Delta are the creation of diversions to reintroduce suspended sediment carried in the river. In areas of rapid relative sea-level rise, as in the Mississippi Delta, it is generally accepted that a supply of sediment in flood water and mineral sedimentation are critical to sustaining wetlands. But plans to create diversions have raised questions about the collateral effects of nutrients carried in the Mississippi River, effects that may contravene the benefits of sediment. This review finds the balance of empirical and theoretical evidence supports that nutrients benefit above- and belowground plant production and that fresh water and sediment diversions can be effective and beneficial for restoring wetlands in the Delta, especially if designed to maximize sediment inputs. The input of sediment, nutrients, and fresh water will change the community composition of some wetlands and their biogeochemical processes. Most of the nitrogen input should be assimilated or denitrified. Labile organic matter is likely to degrade more quickly, but labile organic matter does not add 'new' soil volume and its speed of decay is of little consequence. Additional research is needed before we fully understand the consequences of nutrients on the preservation of organic matter in sediment, but building on what is known of the activities of lignin-degrading fungi and their enzymes, it is likely that refractory organic matter should increase and contribute positively to sediment accretion.

Keywords

Nitrogen · Nutrient · Plant development · Mississippi river delta · Sediment organic matter · Decomposition · Diversion · Sedimentation · Marsh restoration · Primary production · Model

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Introduction

During the twentieth century a loss was observed of about 25% of coastal wetlands in Louisiana or about 4,800 km² (Britsch and Dunbar 1993; Couvillion et al. 2011). A variety of factors led to this including reduction of sediment input from the basin, pervasive alteration of the hydrology of the deltaic plain, enhanced subsidence due to petroleum extraction, and barrier island deterioration. Perhaps most important was the almost complete elimination of river input to the deltaic plain due to flood control levee construction and closure of distributaries which connected the river to the wetlands

(Day et al. 2007). The overall trend reveals wetland loss is highest in older delta lobes (e.g., Terrebonne basin) and lowest in areas with active river input (e.g., Atchafalaya). Human-induced changes such as these have had important consequences for delta deterioration worldwide (Day et al. 1995, 1997; Syvitski et al. 2009).

The proposed solutions for restoration and stabilization of wetlands in the Mississippi River Delta include the reintroduction of sediment carried in the river by means of a series of river diversions. Diversions from the Mississippi River should generally: (1) affect sediment availability in a relatively small wetland area nearest the inflow site; (2) increase nutrient availability over a larger area; and (3) decrease salinity over an even larger area. Diversions designed to lower salinity over large areas of existing emergent wetlands are called freshwater diversions and are most common from just upstream of New Orleans to Point a la Hache (Boyer et al. 1997; Grossman 2009). The Atchafalaya delta complex can also be considered as a very large diversion. It is not possible to achieve wetland expansion or stabilization through sediment diversions without also introducing fresh water and nutrients, and therein lies the controversy.

One of the concerns is that high nutrient loadings from the Mississippi River, particularly of dissolved nitrogen, will reduce the capacity of highly organic marshes to respond to sea-level rise by increasing the rate of belowground decomposition (Swarzenski et al. 2008). Darby and Turner (2008a) reported that additions of inorganic nutrients reduced belowground biomass in *Spartina alterniflora* marshes in the Mississippi Delta and along the Atlantic coast of the U.S. and Canada. They suggested that this might decrease soil elevation and accelerate the conversion of emergent wetlands to open water. Morris and Bradley (1999) reported that fertilization of a marsh in North Inlet, SC led to an increase in soil respiration rates and a decline in soil organic matter content in the top 5 cm of sediment. Similarly, Wigand et al. (2009) reported a positive relationship between soil respiration rate and nitrogen loading at the watershed scale and an inverse relationship between respiration and soil organic carbon. Deegan et al. (2012) reported that nitrate enrichment of a highly organic New England salt marsh in Plum Island Estuary decreased the biomass of bank-stabilizing roots and increased microbial decomposition of organic matter, leading to a collapse of marsh edges into the creeks. These studies indicate that reduction in belowground biomass and increased soil organic matter mineralization following increased nutrient availability may reduce the capacity of wetlands to keep pace with sea-level rise.

However, other results differ. There are numerous examples in the literature of nutrients increasing root growth and belowground biomass. Anisfeld and Hill (2011) presented results of a 5-year fertilization experiment on a Long Island

Sound salt marsh (with phosphorus and ammonium nitrate) that, like earlier studies, showed that fertilization increased aboveground primary production and CO₂ fluxes from the soil. However, fertilization with neither nitrogen nor phosphorus affected marsh elevation (relative to controls), reduced soil carbon, or decreased belowground primary production. Subsequent work by Morris et al. (2002) showed that the decline in surficial soil organic matter reported earlier (Morris and Bradley 1999) was most likely the result of an increase in sedimentation rate and dilution of soil organic matter by an increased mineral input in the fertilized plots.

This review is part of a broader study by an interdisciplinary group, the Science and Engineering Special Team, tasked with synthesizing the complex issues relating to the efficacy of creating sediment and water diversions along the Mississippi River to stabilize its delta. Our goal was to summarize what is known of nutrient effects, especially of nitrogen, on the production and decomposition of soil organic matter, vegetation, and sediment accretion; and, where possible, to resolve some of the inconsistencies in interpretation of data.

The Fate of Nitrogen

Ammonium is the dominant form of nitrogen available to wetland plants, but there are studies that show nitrate also is assimilated by marsh vegetation when available (Stewart et al. 1973; Mendelsohn 1979; Morris 1982). Indeed, nutrients introduced in river water generally are rapidly assimilated or denitrified by the receiving wetlands, especially nitrate (Lane et al. 1999; Mitsch et al. 2001; DeLaune et al. 2005a; Hyfield et al. 2008; Gardner and White 2010; Lane et al. 2010). Nitrogen fixation provides a major source of nitrogen to natural wetlands (Piehler et al. 1998; Nielsen et al. 2001; Tyler et al. 2003), probably in excess of what is derived from flood water (Abd. Aziz and Nedwell 1986; White and Howes 1994; Tyler et al. 2003), and typically there is more ammonium available in marsh pore water than there is nitrate and ammonium in flood water (e.g., Morris 2000).

The biogeochemistry and distribution of inorganic nitrogen in marsh sediments varies with salinity. This is in part due to the cation exchange properties of soil, which change dramatically with salinity (Rysgaard et al. 1999; Gardner et al. 1991). Seawater cations completely occupy the exchange sites on silts and clays at the salt water end of an estuary, effectively outcompeting ammonium. Consequently, ammonium is largely free in solution at the salt water end of an estuary, while at the freshwater end of the estuary ammonium is largely sorbed onto exchange sites (Seitzinger et al. 1991; Rysgaard et al. 1999). Thus, diversions that lower salinity also increase ammonium availability. In addition, seawater cations compete with ammonium for carriers on the

root membrane and decrease the efficiency of ammonium uptake, that is, the half-saturation constant for ammonium uptake increases at higher salinities (Morris 1984). This explains why vegetation can be nitrogen-limited in an environment rich in ammonium.

A study of the fate of nitrogen in the Great Sippewissett Marsh in Massachusetts showed that of the $^{15}\text{NH}_4^+$ injected experimentally into vegetated marsh sediment, 25% was lost rapidly through nitrification-denitrification, 40% remained even after 7 years, and 54–77% of the export was accounted for by denitrification (White and Howes 1994). There is evidence that plant biomass is the major sink for free NH_4^+ and that in the absence of plants the balance is shifted in the direction of nitrification-denitrification (Morris 1991). But the study by White and Howes (1994) demonstrated that the bacteria compete effectively with salt marsh plants for NH_4^+ . The stoichiometry of heterotrophic denitrification (Patrick and Reddy 1976): $24\text{NO}_3^- + 5\text{C}_6\text{H}_{12}\text{O}_6 + 24\text{H}^+ \rightarrow 12\text{N}_2 + 30\text{CO}_2 + 42\text{H}_2\text{O}$ can be applied to the nitrogen load to place some limit on organic carbon consumption, but it is complicated by the fact that not all carbon sources support equivalent rates of denitrification (deCatanaro and Beauchamp 1985).

Kaplan et al. (1979) estimated denitrification in the Great Sippewissett Marsh consumes $0.2\text{--}3.5 \text{ mg NO}_3\text{-N m}^{-2} \text{ d}^{-1}$ ($0.04\text{--}0.7 \text{ g m}^{-2}\text{year}^{-1}$, assuming a 200 day warm season), fed largely by nitrate in ground water, and accounts for $<0.1\%$ of belowground production. To put this in the context of the Mississippi River, the diversion at Caenarvon discharges 7.8×10^5 to $1.5 \times 10^6 \text{ kg NO}_3\text{-N year}^{-1}$ into an 848 km^2 wetland at concentrations ranging from 1.2 to 1.8 mg l^{-1} before entering Breton Sound (Hyfield et al. 2008). This is equivalent to a $\text{NO}_3\text{-N}$ load per unit marsh area ranging from 1 to $2 \text{ g m}^{-2}\text{year}^{-1}$ (71 to $142 \text{ mmol N m}^{-2} \text{ year}^{-1}$), which represents only $1.1\text{--}2.4 \text{ g C m}^{-2} \text{ year}^{-1}$ of primary production. In contrast, potential rates of denitrification at Caenarvon, measured in wetland sediments spiked with $1,750$ and $3,500 \text{ mg NO}_3\text{-N m}^{-2} \text{ d}^{-1}$, were of 57 and $87 \text{ mg N m}^{-2} \text{ d}^{-1}$ (equivalent to 21 and $32 \text{ g N m}^{-2}\text{year}^{-1}$), respectively (Delaune and Jugsujinda 2003). Van Zomeren et al. (2011) found that within 12 h of spiking a 10 cm water column over sediment with $^{15}\text{NO}_3\text{-N}$, the 2 mg l^{-1} concentration had dropped below detection, and 64% of the label was unaccounted for in plant or sediment, and probably was denitrified. The details differ, but in general, nitrification-denitrification is a major sink for NH_4^+ in wetlands and denitrification rapidly removes a majority of NO_3^- at the expense of carbon roughly in the ratio of 30 moles of carbon to 24 moles of nitrate.

Effects on Productivity and Community

Plant production in coastal wetlands is limited primarily by nitrogen availability as well as by stresses from flooding, salinity, and sulfides (Mendelsohn and Morris 2000). There are important interactions among these factors that affect plant growth and biomass partitioning among roots, rhizomes, and leaves. Nutrient enrichment increases flood tolerance in some wetland species like baldcypress (*Taxodium distichum*) (Effler and Goyer 2006) and bulrush (*Schoenoplectus americanus*) (Langley et al. 2013), and increases salt tolerance in others like *Spartina alterniflora* (Cavaliere and Huang 1979). *Spartina patens*, perhaps the most common plant in coastal Louisiana, is a species whose salt tolerance does not increase with increasing nutrient availability, but it does benefit from reduced salinity (Merino et al. 2010, Fig. 1). There was no growth response to nutrients when the salinity exceeded 35 ppt but nutrients increased growth three-fold when salinity was less than 5 ppt (Fig. 1). The ratio of belowground to aboveground biomass was not affected by either nutrients or salinity and was a constant $0.23:1$. Delaune et al. (2005b) reported a doubling of *S. patens* aboveground biomass in greenhouse treatments with additions of 10 g N m^{-2} and, like Merino et al. (2010), found a greater absolute response at 0 than at 8 ppt salinity.

Experience has shown that tree growth is enhanced in forested wetlands used to treat municipal effluent. At the discharge site of the Hammond Assimilation Wetland (HAW), growth of baldcypress was five-fold higher than in reference sites in the Maurepas swamp (Day et al. 2012), and increased primary production and sediment accretion in these sites have been sustained for decades (Day et al. 2004; Hunter et al. 2009). Basal diameter growth of baldcypress seedlings transplanted to treatment subunits ranged from $18.1 (\pm 2.6) \text{ mm}$ nearest the outfall to $8.0 (\pm 0.9) \text{ mm}$ at a distance 700 m downstream and $6.4 (\pm 0.9) \text{ mm}$ in a reference site near the HAW (Lundberg et al. 2011). However, this response is dependent on a favorable hydroperiod; flooding stress can prevent nutrients from enhancing tree growth (Keim et al. 2012).

The input of mineral sediment, fresh water, and nutrients will likely change plant community composition in fresh or brackish, peat-dominated wetlands, resulting in a complex cascade of events. An increased rate of mineral input may result in a marsh community that can vertically accrete faster and is more resilient to disturbance, provided that the soil organic matter is preserved. However, the creation of freshwater wetlands by diversions can result in weaker soils because low salinity marsh soils are generally weaker than higher salinity marsh soils (Howes et al. 2010; Morton and Barras 2011). On the other hand, lower salinity marshes have

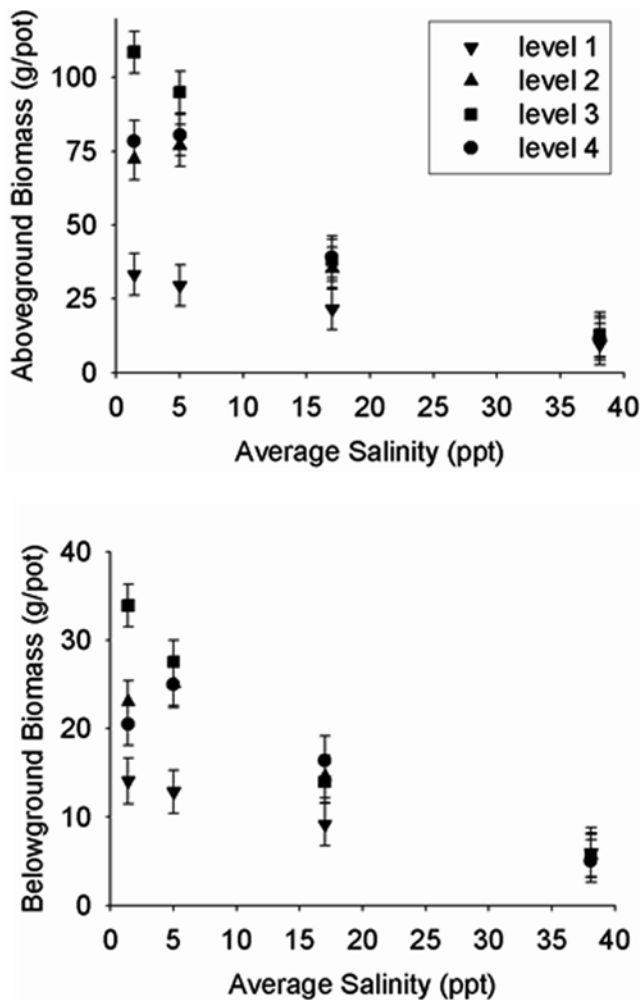


Fig. 1 The above- and belowground biomass of *Spartina patens* grown at different salinities and at different levels of nutrients, harvested after 144 days of treatment in a greenhouse. Nutrient levels were (1) 0.5 & 0.024, (2) 1.46 & 0.07, (3) 2.43 & 0.12, and (4) 3.89 & 0.19 mg N cm⁻³ & mg P cm⁻³ of soil, respectively. (Modified from data in Merino et al. (2010))

the capacity to recover from disturbance via the spread of perennial, rhizomatous plants such as *Typha*, *Panicum*, and *Phragmites* that convert open water to emergent marsh (van der Valk 1981), whereas salt marshes lack such capacity. One solution would be to pulse diversions to allow periodic salt intrusion from late summer through spring.

Plant species do not benefit equally from nutrient enrichment, and it can be anticipated that river diversions will modify plant community composition; this will be most pronounced at the freshwater end of the system. Nitrophilous species such as *Phragmites* and *Typha* could in many cases replace established species (Rickey and Anderson 2004). Moreover, river diversions will reduce salinity, and this too will shift species composition in places away from species typical of salt or brackish water habitats (e.g., *Spartina* spp.) to less salt-tolerant species. Diversions or wastewater inputs can increase flooding, which may stress existing vegetation

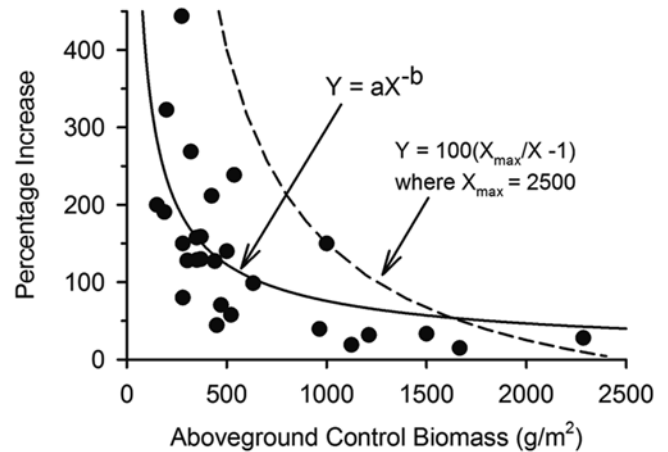


Fig. 2 The relative increase in dry standing biomass of *Spartina alterniflora* after 1 or more years of fertilization with nitrogen or a combination of nitrogen and other nutrients relative to the maximum biomass observed during a growing season on control plots. Also shown are the best fit of a power function (—, $a=9,377$, $b=0.7$, $r^2=0.41$) and a theoretical curve (---) generated by assuming each control plot's biomass was increased to a hypothetical maximum of 2,500 g m⁻². Updated from Morris (1991). (Sources: Gallagher 1975; Valiela et al. 1975; Patrick and DeLaune 1976; Haines 1979; Mendelsohn 1979; Buresh et al. 1980; Cavalieri and Huang 1981; Silliman and Zieman 2001; Gratten and Denno 2003; Tyler et al. 2003; McFarlin 2004; Olcott 2011; Morris et al. 2013; and Zhang et al. 2013)

and select for more flood-tolerant species, confounding nutrient effects. Other indirect effects have been observed in treatment wetlands and river diversion sites, including increased herbivory (e.g., nutria "eating out" marshes, Shaffer et al. 1992; 2009).

The growth of vegetation in response to nitrogen fertilization of salt marshes decreases as the *in situ* control biomass increases. The relationship can be described reasonably well with a power function (solid line in Fig. 2). When the control biomass is very high, 2,500 g m⁻² of dry standing biomass, very little can be gained in the way of added production from fertilization, but at a low control biomass there is a large potential for increasing productivity, provided that salinity and flooding stresses are relatively low. If nitrogen alone were able to raise the biomass to a hypothetical maximum of 2,500 g m⁻², the predicted relationship would appear as depicted by the dashed line in Fig. 2.

There is a large gap between the empirical fit of the power function and the hypothetical maximum (Fig. 2). This gap must result because of co-limitation by other factors, and these can be categorized as one or a combination of stresses and limitations, including osmotic stress, hypoxia, herbivory, disease, soil chemistry (toxicity and/or micronutrient deficiencies), and perhaps others. The relative importance of these will depend on the salinity, climate, weather, and elevation relative to the tidal frame. The productivity of roots and rhizomes can be expected to follow a similar trend, that is, their relative responses to nutrients should depend on

their status with respect to all of these other limitations and stresses, and this at least partially explains the disparate results from fertilization studies of belowground biomass.

Effects on Belowground Biomass—Empirical Studies

Plant developmental processes and growth are greatly affected by nutrient availability. With few exceptions, the absolute production of roots and shoots increases with nutrient loading. This is supported by numerous experimental studies and field observations (e.g., Stevenson and Day 1996; Shipley and Meziane 2002; Day et al. 2006; Ravit et al. 2007; Hillman 2011). Buresh et al. (1980) reported an increase in belowground macro-organic matter of 5.5 to 6.3 kg m⁻² 4 months after fertilizing a Louisiana *Spartina alterniflora* marsh with N and P. Haines (1979) reported a trend of increased belowground macro-organic matter in fertilized compared to control plots during the last 6 months of a fertilization study in Georgia salt marsh. Valiela et al. (1976) reported increases of cumulative total belowground biomass from ‘regrowth cores’ in Great Sippewissett marsh high fertilization (HF) sites of 127% in low marsh and 111% in high marsh. In plots treated with urea at 20% the HF rate, cumulative belowground biomass increased 177% in low marsh and 32% in high marsh. Of the total belowground biomass, the greatest response was seen in rhizomes. Haines and Dunn (1976) also reported an increase in rhizome biomass following nutrient treatment. Zhang et al. (2013) reported a 33% increase in belowground biomass of *Spartina alterniflora* in fertilized mesocosms in Jiangsu province, China.

The nutrient effect on roots, however, is not universally the same. Tyler et al. (2007) reported that the effect of fertilization on belowground biomass differed between San Francisco and Willapa Bay estuaries: there was no effect in San Francisco Bay in either edge or meadow plots, but a 108% increase in fertilized Willapa Bay meadow plots relative to controls. Boyer et al. (2000) reported no significant change in belowground biomass of fertilized *S. foliosa* in a constructed marsh in the Tijuana Estuary. Darby and Turner (2008a) reported decreases in live root and rhizome biomass on field sites fertilized with nitrogen and phosphorus, with the greatest decreases associated with reference sites supporting the greatest belowground biomass. In a Louisiana marsh fertilized monthly from April through August, Darby and Turner (2008b) found no change in total belowground *S. alterniflora* biomass, but a 40 to 60% reduction in live biomass. Nyman (2014) reviewed the literature concerning river diversions within the context of the delta lobe cycle and concluded that nutrients were not the cause of wetland loss at the Caernarvon river diversion. Langley et al. (2013) found that the response of *Spartina patens* belowground biomass was dependent upon relative elevation:

at elevations 5–15 cm below mean sea level, biomass was about 100% greater in fertilized treatments, but the response declined with increasing relative elevation. Likewise, Priest (2011) found that nutrient additions increased belowground biomass of *S. alterniflora* in a North Carolina mesocosm study at all elevations from -20 to 53 cm NAVD88, but the response was greatest (+115%) at the lowest elevation.

Biomass Partitioning—The Theory

Plant root:shoot ratios decline as nutrient loading increases (Morris 1982; Ågren and Ingestad 1987; Hilbert 1990; Ericsson 1995; Ågren and Franklin 2003, Darby and Turner 2008a, b; Hillmann 2011). This has led to some confusion about the effect of nutrients on belowground organic matter production. If added nutrients decrease belowground production, as some studies show, then soil strength will decrease with the loss of root structure, and the additive effect of roots on soil volume would be diminished (Darby and Turner 2008a; Turner 2010).

The observation that root:shoot ratios are variable and subject to control by nutrient availability inspired a well-known theory in the plant literature known as the functional balance model. The theory is based on the concept that there exists a functional balance between roots and shoots. This is an idea that can be traced to a paper by Brenchley (1916), who stated ‘the plant makes every endeavor to supply itself with adequate nutrient, and as if, when the food supply is low, it strives to make as much root growth as possible’. Much later, Davidson (1969) stated that the root mass multiplied by the rate of absorption is proportional to leaf mass multiplied by the rate of photosynthesis. These models are discussed in an excellent review by Bastow Wilson (1988). Thus, if nutrient uptake and carbon fixation are balanced, then $\alpha\rho W_L(t) = \mu W_R(t)$ (1).

Where W_L and W_R are the weights of leaves and roots at time t , respectively, α is the optimal concentration of tissue-nitrogen, ρ is the specific rate of primary production, and μ is the specific nitrogen uptake rate. From Eqn. 1 the root:shoot ratio is simply $W_R / W_L = \alpha\rho/\mu$ (2).

For *Spartina alterniflora*, the value of the specific-production term (ρ) is about 0.16 d⁻¹ at 20°C (Morris 1982), net of respiration, though we will use half that value because we will lump leaves and rhizomes and assume that these organs have a constant weight ratio of 1:1. The maximum uptake term (μ) or V_{\max} for specific ammonium uptake has a value of 3.26×10^{-3} d⁻¹ at 20°C (Morris 1980). If the ideal nitrogen concentration in tissue is 2%, then the root:shoot ratio should be, from Eqn. 2, about $(0.02 \times 0.08) / 3.26 \times 10^{-3} \approx 0.49:1$. This is the theoretical minimum root:shoot ratio, where shoots are defined as leaves plus rhizomes. If leaf weight and rhizome weight are equal, then the ratio of root:leaf would be about 1:1.

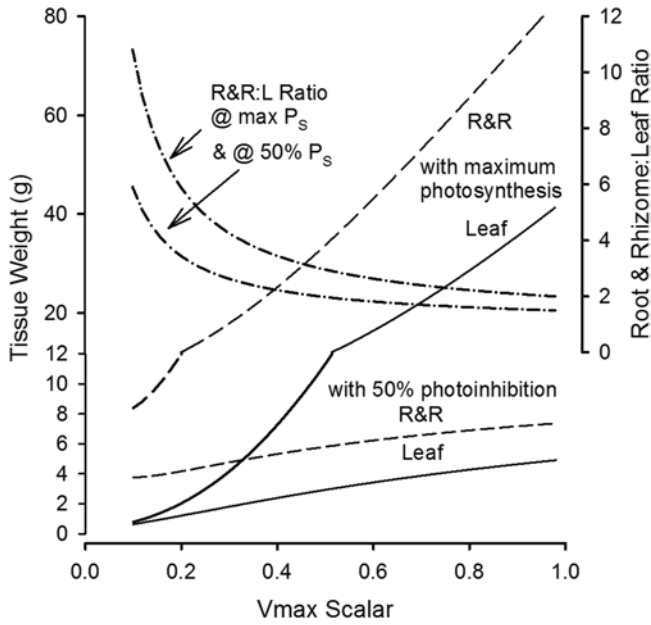


Fig. 3 Simulation of leaf and root + rhizome (R&R) growth (Eqns. 7 and 8) when the specific nitrogen uptake rate was scaled from 0.1 to 1.0 of V_{max} . The resultant leaf (—), root + rhizome (--- R&R) weights and ratios of root + rhizome to leaf weight are shown after 100 days of simulated growth under conditions of either maximum photosynthesis ($\rho = 0.16 \text{ d}^{-1}$ of leaf weight) or photoinhibition ($\rho = 0.08 \text{ d}^{-1}$)

The total rate of production

$$(dW_T / dt) \text{ is } dW_T / dt = dW_L / dt + dW_R / dt = \rho W_L \quad (3)$$

Substituting for W_R from Eq 2 and rearranging gives

$$\rho W_L = (1 + \alpha \rho / \mu) dW_L / dt \quad (4)$$

Solving the integral of Eq. 4 $\left(\int dW_L / W_L = \frac{\rho}{(1 + \alpha \rho / \mu)} \int dt \right)$ (5)

gives the leaf weight at time t $W_L(t) = W_L(0) e^{\frac{t \rho}{(1 + \alpha \rho / \mu)}}$ (6)

and from Eqn. 1 the root weight at time t is

$$W_R(t) = (\alpha \rho / \mu) W_L(t) \quad (7)$$

The specific rate of nitrogen uptake (μ) is variable, depending on the concentration of available nitrogen, oxygen, salinity, and other variables, and follows Michaelis-Menten kinetics (Morris 1980; Bradley and Morris 1990, 1991):

$$\mu = V_{max} N / (N + k_m) \quad (8)$$

Parameter V_{max} in Eqn. 8 is the maximum specific uptake rate; N represents the concentration of available nitrogen, and k_m is the half-saturation constant. The term $N / (N + k_m)$ can vary between 0, when $N = 0$, and 1 when the nitrogen concentration is high. Thus, $\mu = V_{max}$ when the nitrogen concentration is non-limiting. In what follows, we will explore the effect of changes in N by using a single scalar as a substitute for $N / (N + k_m)$.

The effect of nitrogen limitation on the growth of roots and leaves can be illustrated by scaling nitrogen uptake from 0 to 100% of V_{max} (Fig. 3). For example, the solutions of Eqns. 6 and 7 when applying a scalar of 1.0, simulating high nitrogen availability, resulted in a constant (over time) ratio of roots + rhizomes:leaves of 2:1 at maximum photosynthesis. Total plant weight increased to 124 g and root weight (exclusive of rhizomes) to 41 g in 100 days. Scaling the uptake parameter to 50% of its maximum value (Fig. 3), simulating nutrient-limited growth, resulted in a ratio of roots + rhizomes:leaves of about 3:1, final plant weight of 45 g, and final root weight of 22 g. Thus, the roots + rhizomes:leaves quotient decreased from 3 to 2 when we simulated a high level of nitrogen availability, but the increase in aboveground production was so great (41 vs 11 g) that, even with a lower root:shoot ratio, the absolute production of roots was almost 2x greater. Conversely, nutrient limitation results in an increase in the partitioning of photosynthate into root growth, which reduces leaf growth and, ultimately, total plant and root growth.

Scaling back the rate of photosynthesis (D) by 50% greatly reduced the nitrogen effect. (Fig. 3). Total plant weight was reduced to 12 and 9 g at full and half V_{max} , respectively. Interestingly, root weight was marginally greater at half V_{max} , 2.9 vs 2.5 g, than at full V_{max} , though total belowground biomass (roots plus rhizomes) was 5.8 and 7.4 g at full and half V_{max} , respectively. This reduced rate of photosynthesis also lowered the ratio of roots + rhizomes:leaves, especially at low V_{max} . These results illustrate the complexity of environmental interactions that are possible and their control of plant development.

Plant growth data published by Shipley and Meziane (2002) provide another good example. Experimental results from more than 20 plant species showed that the mean ratio of root:total plant weight decreased, total plant weight increased, and root weight increased 70% with increasing nutrient supply when plants were grown in high light. In low light, root weight was independent of nutrient supply, which is consistent with the model's predictions.

The effects of a step change in nutrient status show that a reduction in root biomass is possible theoretically after raising nutrient levels from a limitation to a surplus, but the reduction is fleeting and is not necessarily seen in rhizomes (Fig. 4). The theoretical results (Fig. 3) and the type of long-term growth studies discussed by Shipley and Meziane (2002) are equilibrium studies. Plantings were raised from start to harvest in the greenhouse or *in silico* in differing, but constant nutrient environments. We simulated what could happen when a plant, growing at a nitrogen-limited rate (at 40% of V_{max}) experiences a step increase in nitrogen availability (Fig. 4). The plant growing in equilibrium at a low nitrogen supply developed a root biomass of 3 g by day 50.

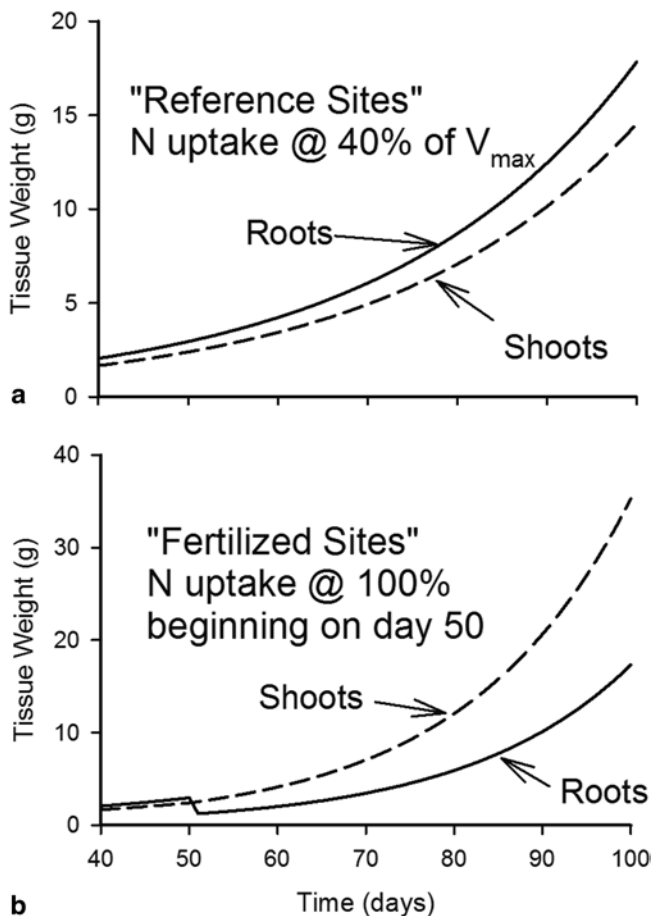


Fig. 4 Simulated time series of (a) nitrogen-limited growth with V_{max} (see text) scaled back 40% and (b) when V_{max} was scaled up from 40 to 100% on day 50 and beyond. Shoots are the sum of leaves plus rhizomes

Following the step up to high nitrogen supply, root biomass dropped to 1.25 g as the plant adjusted to a higher μ (Fig. 4b). By day 100 the root biomass of the nitrogen-limited plants increased to 17.8 g, leaves + rhizomes (shoots) increased to 14.5 g (Fig. 4a), and those of the 'fertilized' plants to 17.3 g and 35.3 g, respectively, (Fig. 4b).

A change in equilibrium following a step increase in nutrient supply (Fig. 4b) could explain discrepancies in short-term field fertilization experiments, but we emphasize that the resulting decrease in simulated root biomass extends only to roots. There is no reason to believe that rhizome biomass should decline. Rhizomes are the anatomical equivalents of the branches on a tree; they are horizontally growing, subterranean stems; they give rise to and support the leaves, and they probably respond to nutrients much like the branches of a tree. This was the rationale for aggregating leaves and rhizomes in the root-equilibrium model described above.

Effects on Sediment Organic Matter

The capacity of highly organic marshes to respond to sea-level rise would be compromised if the rate of belowground decomposition were to increase (Swarzenski et al. 2008) or, more specifically, if nutrient enrichment were to decrease the stability of the extant inventory of refractory organic matter. The long-term accretion of organic matter will decrease if the decay of refractory carbon increases or its production decreases. It is possible that nutrients, particularly the electron acceptor nitrate, may destabilize the extant inventory of soil organic matter. However, there are two sides to the equation. Organic matter accumulation and the volume of soil that it generates are primarily functions of the production of refractory organic matter and its stability. They are equivalent to primary production plus net import-export and minus the decomposition of the labile portion or organic production. The labile fraction of primary production does not increase sediment volume.

Nitrate is an energetically favorable electron acceptor, close to O_2 in energy yield (Fenchel and Blackburn 1979), and river diversions that are rich in NO_3 could actually stimulate the decay of organic matter that typically would resist decay under anaerobic conditions. However, this should only be a significant factor in peat marshes where organic matter makes up the majority of soil volume. Furthermore, these highly organic marshes represent a mature stage of the deltaic cycle (Gosselink 1984) that are likely unsustainable without significant mineral input. Wetland loss is a natural part of the growth and decay of a delta lobe, where losses from an old lobe eventually are balanced by accretion of land in a new lobe (Coleman 1988).

The production of refractory organic matter, as opposed to labile organic matter, is a question of litter quality, and litter quality is a function of species and nutrition. Decomposition is primarily a function of the quantity and quality of organic matter, and factors such as the availability of electron acceptors, temperature, and nutrients that affect the rate of decomposition. Where freshwater diversions reduce salinity, the dominant electron acceptor may change, altering the balance between sulfate reduction and methanogenesis (Kelley et al. 1990). The intrusion of salt water into freshwater wetlands or, conversely, the conversion of brackish to freshwater marsh will determine the availability of sulfate, the dominant terminal electron acceptor in anaerobic marine systems (Howarth and Teal 1979; King 1988), potentially altering the rate of decomposition of soil organic matter (Reddy and DeLaune 2008). However, the greater efficiency of sulfate reduction over methanogenesis is not enough to offset the greater quality of organic matter in fresh marshes over that in saline marshes (Kelly et al. 1990; Nyman and DeLaune 1991).

Another factor that may impact soil organic matter is the significant difference in the composition and decomposition of plants typical of tidal freshwater marshes and salt marshes (Odum and Heywood 1978). This difference affects both litter quality and the fraction of organic matter that is refractory. *Spartina alterniflora*, for example, has a relatively high lignin content and low nitrogen:lignin ratio (Marinucci et al. 1983; Valiela et al. 1984) and therefore decays more slowly and produces a higher fraction of refractory organic matter than a typical freshwater plant. Of the dominant plants in coastal Louisiana, *Spartina patens* produces the most refractory organic matter (Nyman and DeLaune 1991). Thus, river diversions that convert *S. alterniflora* marshes into *S. patens* marshes should increase refractory organic matter whereas diversions that convert *S. patens* marshes into fresher marshes should decrease refractory organic matter.

Morris and Bradley (1999) found that rates of CO₂ flux from the marsh sediment surface increased with nutrient enrichment (N and P), but it is not clear if this was from increased respiration of living roots and rhizomes, higher respiration from the decay of increased production and turnover of belowground biomass, or higher respiration from the decay of extant refractory soil organic matter. Field studies of decomposition often confuse these effects. Bragazza et al. (2006) found that the decomposition rate of recently formed litter from peat bogs increased along a gradient of atmospheric nitrogen (as nitrate) deposition, but in a peatland where plant growth was N-limited, increased N-supply led to an increase in the net accumulation of soil carbon (Aerts et al. 1995).

The focus in much of the decomposition literature has been on the effect of litter quality in terrestrial systems. Melillo et al. (1982) found that the initial lignin:nitrogen ratio was negatively correlated with the initial decomposition rate of leaf litter from six hardwood species. Other studies supported the result that lignin content of litter has a negative effect on the initial decomposition rate (Osono and Takeda 2004; Zhang et al. 2008). Talbot and Treseder (2012) found that litter nitrogen content in the model plant *Arabidopsis thaliana* had a positive effect on total mass loss because it increased the loss of lignin, nitrogen, and soluble organic carbon. Lignin content had a negative effect. However, another study found elevated litter and soil nitrogen had a minor, if any, effect on decomposition, and nutrient limitation of decomposition was not predictable from nutrient limitation of primary production (Hobbie and Vitousek 2000). Gentile et al. (2011) concluded that, while litter quality controls the short-term dynamics of decomposition and soil organic matter accumulation, long-term soil organic carbon storage cannot be predicted based on initial litter quality or, by extrapolation, nutrient supply. They concluded that the formation and stabilization of soil organic matter is controlled more by the quantity of litter input and its interaction with the soil matrix than by litter quality.

Aerts and de Caluwe (1997) manipulated the leaf litter chemistry of four *Carex* species by nitrogen fertilization and found that increased tissue nitrogen did not necessarily lead to higher litter decomposition rates. They speculated that high atmospheric nitrogen deposition may lead to a shortage of phosphorus in the organic substrates available to bacteria and fungi. Indeed, there is evidence that phosphorus limits microbial activity in some marshes (Sundareshwar et al. 2003), but this is not universal and its significance for overall decomposition and carbon sequestration is uncertain. Aerts and de Caluwe (1997) observed that increased nutrient supply led to faster release of N and P from litter in most species and a higher rate of nutrient cycling. This positive feedback between nutrient supply rate and the rate of nutrient cycling was reinforced by an increase in litter production in response to increased nutrient supply.

The evidence from terrestrial systems suggests that the addition of nutrients increases soil organic matter (Prescott 2010). After a decade of experimental NO₃ deposition, organic matter and N increased, 12 and 9% respectively, in forest floor and mineral soil. Apparently NO₃ deposition exerts a negative effect on microbial activity in this forest ecosystem by depressing the lignolytic activity by microbial communities and leading to the accumulation of forest floor and soil organic matter (Zak et al. 2008). A factorial experiment involving eight temperate sites, seven substrates, and nitrogen fertilization showed that nitrogen had neutral or negative effects on decomposition rate and that the nitrogen effect was independent of initial lignin concentration (Hobbie 2008).

Fungi, especially the white-rot fungi, are the primary degraders of lignin in terrestrial systems (Martínez et al. 2005; Sinsabaugh and Follstad Shah 2012), while bacteria dominate in anaerobic aquatic systems (Benner et al. 1986). Most fungi are obligate aerobes capable of degrading lignin to CO₂, but are incapable of growing on lignin as a sole carbon and energy source (Griffin 1994). Their dependence on oxygen partially explains the high accumulation rate of soil organic matter that we observe in anaerobic soils. Enzymes such as phenol oxidase require molecular oxygen for their activity and, therefore, are rarely active in anaerobic environments. Freeman et al. (2004) showed that the activities of hydrolase enzymes that have no oxygen requirement are also extremely limited in peatlands as a consequence of the inhibition of these enzymes by phenolic compounds and oxygen constraints on phenol oxidase. Thus, limitations on phenol oxidase activity promote conditions that inhibit decomposition (Freeman et al. 2004).

Nitrogen addition increases the incorporation and stabilization of organic matter into humus through a combination of chemical reactions and enzyme inhibition (Prescott 2010). High levels of inorganic N suppress lignin oxidation by white rot basidiomycetes and generally enhance cellulose

hydrolysis (Waldrop et al. 2004). Frey et al. (2004) found that active fungal biomass was lower in fertilized compared to control hardwood and pine stands, while active bacterial biomass was not greatly affected by N additions. This shift in microbial community composition was accompanied by a significant reduction in the activity of phenol oxidase, a lignin-degrading enzyme produced by white-rot fungi. Similarly, a basidiomycetous fungus isolated from decaying sea grass had no lignin peroxidase activity when grown in high-nitrogen medium (Raghukumar et al. 1999).

Although lignocelluloses are recalcitrant to anaerobic biodegradation, they will slowly degrade, presumably by bacteria, but there appear to be differences among plant species. After 294 days in the laboratory under anaerobic conditions, 16.9% of the lignin and 30.0% of the polysaccharide components of lignocellulose derived from *Spartina alterniflora* were degraded, but only 1.5% of the lignin and 4.1% of the polysaccharide components of lignocellulose derived from *Rhizophora mangle* were degraded (Benner et al. 1984). Benner et al. (1991) also reported differential decomposition of the submolecular components of lignin. Kirk and Farrell (1987) attributed the very limited anaerobic metabolism of lignin during extensive incubations to nonlignin components or metabolism of abiotically derived subcomponents. Prescott (2010) questioned the selective preservation model, and argued that microbial and biochemical transformations of plant compounds into novel recalcitrant compounds, rather than selective preservation, lead to the creation of stable organic matter. Soil organic matter is a complex chemical buffet of products and byproducts, and the bacterial and fungal consumers are finicky diners.

Effects on Marsh Elevation

Coastal wetlands maintain equilibrium with sea level, within limits, by inputs of mineral sediments and in situ organic soil formation (Reed 1995; 2002; Morris et al. 2002). Critical variables that determine accretion rate and elevation are the concentration of suspended sediment in flood water over the marsh surface, primary productivity, decomposition of sediment organic matter, relative elevation or flood duration, and kinetic energy. In estuaries where relative sea-level rise is high, as in the subsiding Mississippi Delta, the concentration of suspended sediment in flood water and mineral sedimentation are critical to sustaining healthy marshes. When flooding with sediment laden water is low, relative marsh elevation declines. Evidence from empirical studies shows that vegetation typical of coastal wetlands thrive when sedimentation rates are raised experimentally (Croft et al. 2006; Fragoso and Spencer 2008). Wetlands downstream of diversions at Caernarvon, West Pointe a la Hache, and Bonnet Carré (Lane et al. 2006; Day et al. 2009; Day et al. 2013) and marshes affected by Atchafalaya River discharge (Day et al.

2011) all have higher vertical accretion rates, high below-ground biomass, and/or greater aboveground growth. The effectiveness of sediment diversions for marsh restoration in the Delta will depend on the concentration of sediment, the volume of discharge, and the manner and effectiveness of sediment distribution. Impounded wetlands are isolated from surface flow and will not benefit from diversions unless they are hydrologically reconnected.

Summary

Among the proposed solutions for reversing wetland loss in the Mississippi River Delta is the creation of water diversions or utilization of siphons to reintroduce suspended sediment carried in the River. However, diversions will introduce significant quantities of nutrients as well as sediment, and this has raised concerns about the effect of nutrients on the wetlands, particularly on the production and stability of sediment organic matter. Contradictory results from experimental field studies have fueled these concerns. The effects of nutrients are complex. They influence plant community composition, herbivory, biogeochemistry, and plant growth and development. Sediment and freshwater diversions will change some wetland plant communities, and highly organic wetland soils will transition to minerogenic sediments.

To understand the effect of nitrogen on soil organic matter, it is useful to consider its fate as well as its effects on both decomposition of organic matter and primary production. The majority of nitrate added to a wetland will be denitrified at the expense of a fraction of the labile organic carbon. The balance between organic production and decomposition will determine the change in volume of soil organic matter, and the aboveground plant production will affect sedimentation. The net effect of the organic matter balance and the mineral input determines wetland soil accretion.

With respect to plant development, increasing nutrient availability is associated with a decrease in the root:shoot ratio, though numerous studies document that the absolute production of roots and rhizomes increases with nutrient enrichment (Haines and Dunn 1976; Stevenson and Day 1996; Shipley and Meziane 2002; Ravit et al. 2007; Hillmann 2011). This also is supported by the functional balance theory of plant development (Davidson 1969; Bastow Wilson 1988; Fig. 3). It was shown theoretically that a step increase in nitrogen availability can temporarily decrease the standing stock of roots as a new equilibrium is established, but there is no reason to think that rhizomes should be similarly affected.

The consequences and stability of the extant inventory of refractory organic matter (e.g., lignin) are entirely different from the consequences of the decomposition of labile organic matter. Labile organic matter does not add new

volume to soil; it decomposes relatively quickly and the speed of its decay matters little. However, the production of refractory organic matter and its stability do matter. In terrestrial soils where fungi are the dominant degraders of lignin (Martínez et al. 2005), it has been shown that nitrate inhibits the activity of the lignin-degrading enzyme phenol oxidase (Raghukumar et al. 1999; Waldrop et al. 2004), leading to an increase in soil organic matter in sites of high nitrate deposition (Zak et al. 2008). The phenol oxidase enzyme is not active in anoxic environments like wetland soils. The activity of hydrolase enzymes, which have no oxygen requirement, is inhibited in wetlands by phenolic compounds that build in concentration as a consequence of the constraints on phenol oxidase (Freeman et al. 2004). Knowledge of the effect of nitrate on anaerobic soils is incomplete, but the balance of evidence supports the efficacy of diverting water and sediment from the Mississippi River to restore and stabilize its wetlands. The need for action to restore the wetlands is urgent, and with a thoughtfully designed monitoring scheme in place, plans to divert sediment laden water into the wetlands should proceed.

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