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Carbon sequestration in wetland soils:
Importance, mechanisms, and future prospects

Why soil?

Commonly referred to as “dirt,” soil is the unconsolidated matrix of organic and mineral matter that is found at the surface of the Earth and supports plant growth. Soils provide nutrients, minerals, and water to plants, and are habitats for a diversity of microbes, fungi, invertebrates, vertebrates, and plants. The organic matter in soils consists of the remains of once-living organisms and contains carbon (plus other elements), some of which has been sequestered (stored) for thousands of years. The amount of organic carbon in soils far exceeds the amount of carbon in the atmosphere, in terrestrial plants and animals, and in oceanic organic matter (Lal 2008).

Given the large amounts of carbon in soils and the role of rising atmospheric carbon dioxide (CO_2) levels in contemporary climate change, there is considerable interest in the mechanisms that transfer CO_2 from the atmosphere to long-term storage in soils and how environmental changes can affect rates of soil carbon sequestration. These questions are of scientific, political, and economic interest. For example,

- *How important is soil carbon sequestration in moderating increases in atmospheric* CO_2*?*
- *How can soil carbon sequestration be incorporated into carbon trading markets?*
- *Can management actions increase rates of soil carbon sequestration and also provide funds for ecosystem conservation?*

Here, I focus on carbon sequestration in wetland soils. Wetlands are especially interesting in this context because they cover a relatively small portion of the terrestrial land surface yet play a disproportionately large role in global carbon sequestration. I discuss the importance of wetlands as reservoirs of soil organic carbon, the mechanisms that lead to high carbon storage in wetland soils, and some possible ways that future environmental change may change rates of wetland carbon sequestration.

Soil carbon in wetlands and other ecosystems

Globally, soils contain 3258 Pg of organic carbon, with wetland soils holding 513 Pg (16%) of that total (Figure 1) [Pg = petagram = 10^{15} g = a million billion grams]. The majority of the wetland pool is stored in peatlands (primarily in the tropical and boreal regions) with a much smaller contribution from wetlands with mineral-dominated soils. The relatively high contribution of wetlands to the total soil organic carbon pool is remarkable since wetlands cover only ~4% of Earth’s land surface (Figure 1). Forests hold the largest store of soil carbon (1104 Pg, 34% of global total) and, like wetlands, their contribution to soil organic carbon storage is proportionately greater than their areal extent. In contrast, carbon storage in grass/shrublands and in deserts is low relative to the spatial coverage of these ecosystems.

The patterns of soil organic carbon storage and global area are reflected in the carbon density of each ecosystem type (that is, how much carbon is stored in a defined area). Wetlands have the greatest carbon density of any ecosystem type at 860 Mg ha^{-1} (Figure 1) [Mg = megagram = 10^6 g = a million grams; ha = hectare = 10,000 m^2]. Forests and grass/shrublands contain the most soil carbon on a global basis, but the carbon density in wetlands is ~three times greater than that in forests (265 Mg ha^{-1}) and ~six times greater than that in grasslands/shrublands (141 Mg ha^{-1}).

These observations raise the question of what characteristic(s) of wetlands promote such high carbon storage.

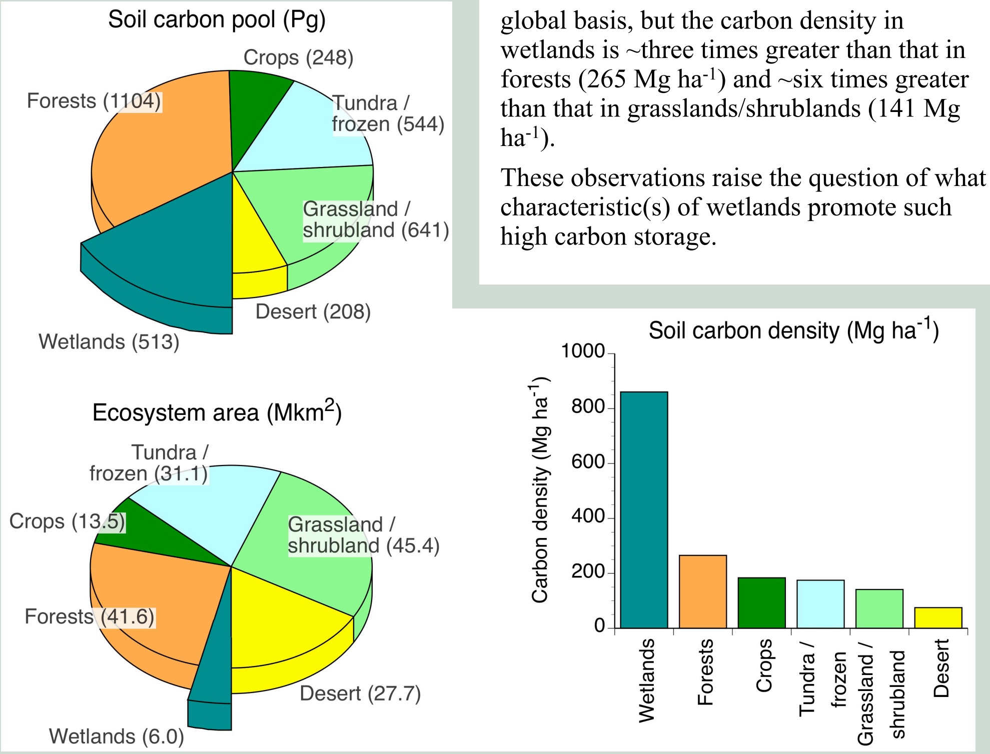
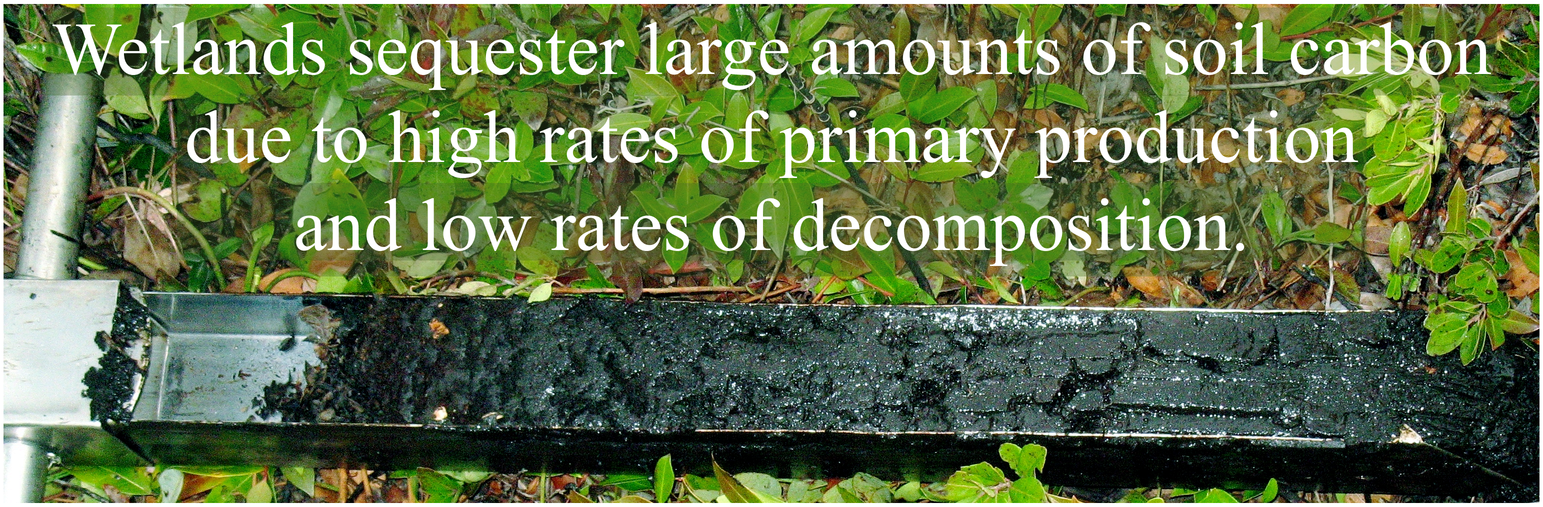


Figure 1: Carbon storage and global area of wetlands and other ecosystem types. Wetland soil carbon pools and ecosystem areas are from Bridgham et al. (2006). Values from Sabine et al. (2004) were used for all other ecosystem types. Soil carbon density is the soil carbon pool size divided by ecosystem area. For presentation, several biome types were grouped together; e.g., the “Forests” category contains tropical, temperate, and boreal forests. Pg = 10^{15} g, Mg = 10^6 g, Mkm² = 10^6 km², ha = hectare.

Wetlands sequester large amounts of soil carbon due to high rates of primary production and low rates of decomposition.



In any ecosystem, the accumulation of soil organic matter occurs when organic matter inputs are greater than losses. Primary production by wetland plants is typically the largest source of organic matter to wetland ecosystems, although inputs of external organic matter can be significant in some systems, especially those with a strong connection to rivers or estuaries that can deliver sediments and watershed-derived materials. Most of the organic matter inputs to a wetland will be broken down through a series of microbially-mediated reactions that yield CO_2 and/or methane (CH_4). Only the organic matter that does not completely decompose will accumulate as soil organic matter. Because CH_4 is a potent greenhouse gas, emissions of this gas to the atmosphere can offset some of the climatic benefits of wetland carbon sequestration, although this is not a significant issue in saline marshes and mangroves. Wetlands have high carbon densities relative to other ecosystems because they have high rates of primary production (carbon input) and low rates of decomposition (carbon loss).

Primary production

Wetlands are difficult environments for plants. Because oxygen (O_2) diffusion from the atmosphere into water-saturated soils is lower than the rate of O_2 consumption, the typical wetland soil is anoxic (i.e., contains no O_2) except for thin layers at the soil surface and in close proximity to plant roots. These anaerobic soils affect root metabolism, cell growth, and nutrient acquisition. Fluctuating hydrology (e.g., seasonal wet vs. dry periods) can cause temporal changes in water availability, soil O_2 concentrations, and nutrient availability. In coastal wetlands, plants must devote considerable energy to minimizing the uptake of sea salts and/or counteracting their effects on metabolism. Despite these challenges, many plants have physiological and anatomical adaptations that allow them to colonize wetland environments. The National Wetlands Plant List contains 8200 plant species that can be found in wetlands (Lichvar and Kartesz 2012); this is a not-insignificant fraction of the >90,600 species in the PLANTS Database of wetland and non-wetland plants (USDA NRCS 2013). Furthermore, wetlands on the whole are highly productive, with rates of annual net primary production that rival or exceed those of tropical forests and cultivated lands (Table 1). This generalization partially obscures considerable variability in primary production within and between specific wetland types. However, high rates of primary production are an important contributing factor to carbon sequestration in wetland soils.

Paradoxically, the wetland hydrology that leads to many of the aforementioned stresses is critical in driving high rates of wetland primary production. In wetlands, and in contrast with many dryland systems, the availability of water generally does not limit plant growth. Many wetlands can be considered pulsed systems with respect to hydrology. In tidal wetlands, the water level rises and falls once or twice daily. Many wetlands experience seasonal flooding. Precipitation patterns can drive temporal water level changes in rain-fed wetlands. In a conceptual subsidy-stress model that has been supported by data from bottomland forests, tidal wetlands, and other systems, primary productivity is maximized under a pulsed flow regime (Figure 2; Odum et al. 1995). These pulsed water inputs provide an energy subsidy to wetlands, delivering O_2-rich water, nutrients, and mineral sediments while also flushing accumulated toxins from soils. Pulsing also allows for periods of soil drying, increasing subsurface O_2 concentrations and leading to higher nutrient availability. These factors increase plant productivity. In contrast, flooded but stagnant wetlands experience the stresses associated with flooding but none of the benefits from a pulsed hydrology.

Ecosystem	Net primary production ($g\ C\ m^{-2}\ yr^{-1}$)
Wetlands	1300
Inland freshwater marsh	250-3000
Tidal salt marsh	65-1448
Northern peatland	150-972
Deepwater swamp	103-804
Tropical forest	620-800
Cultivated land	760
Boreal forest	430
Tundra	130
Desert	80
Temperate forest	65

Table 1: Rates of ecosystem net primary production (from Reddy and DeLaune 2008). Values for selected wetland types are from Mitsch and Gosselink (1993) and generally include only aboveground production.

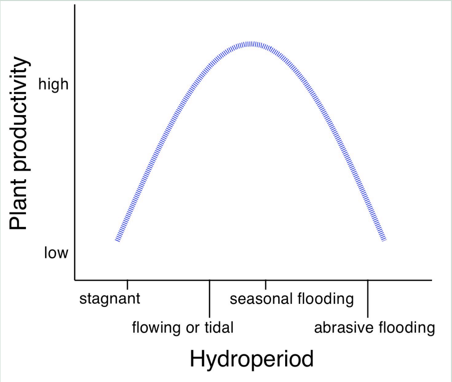


Figure 2: Conceptual model of the relationship between plant production and the frequency/intensity of flooding, showing maximal production when regular hydrological pulsing occurs (after Odum et al. 1995).

Warming temperatures, changing hydrology, rising atmospheric CO_2 concentrations, accelerating rates of sea level rise, and other changes are likely to alter rates of wetland carbon sequestration.

At the other end of the spectrum, productivity suffers when pulses are extreme enough to damage aboveground biomass and/or erode soils.

Wetlands are also highly productive because they are able to efficiently recycle nutrients such as nitrogen and phosphorus. Although wetlands are often referred to as “nature’s kidneys” since they play an important role in removing nutrients and pollutants from groundwater and surface water, most plant production in wetlands relies on internally recycled nutrients rather than new inputs. Furthermore, most wetlands are able to efficiently retain nutrients so that losses to adjacent waterways are minimal. This is analogous to tropical rainforests, which also are able to support high rates of primary production (Table 1) through highly-efficient nutrient recycling and regeneration.

Decomposition

Soil organic matter is a mixture of material that is in various stages of decay and includes contributions from wetland plants, soil microbes, soil invertebrates, and non-wetland sources (e.g., leaves from terrestrial trees that fall into a wetland). Fresh plant litter, which tends to dominate organic matter inputs to wetland soils, is a complex mixture containing cellulose, hemicellulose, and lignin (the major structural components of plant tissues) as well as proteins, lipids, and other biochemical components. The degradation of these compounds proceeds through a multistage process. Soil bacteria and fungi secrete extracellular enzymes that break large, complex biomolecules into smaller molecules (e.g., simple sugars, amino acids). These molecules can be assimilated by soil microbes and ultimately mineralized to CO_2 and/or CH_4.

The low availability of O_2 is the most important factor limiting rates of decomposition in wetland soils. Other factors including nutrient availability, the molecular composition of organic matter, temperature, and acidity also influence rates of decomposition, but these factors are not specific to wetlands (that is, they also affect decomposition in dryland systems). Decomposition rates are reduced in anaerobic soils for three reasons. Firstly, microbial metabolism shifts to less-efficient and slower pathways when O_2 is not available (Ponnamperuma 1984). In oxic (O_2-containing) soils of a typical dryland system (e.g., forest, grassland, or desert), soil microbes use O_2 as the electron acceptor when metabolizing organic carbon to CO_2. Like these aerobic microbes, humans also consume O_2, break down organic carbon (that is, the food you eat), and produce CO_2. In contrast, anaerobic wetland microbes use a series of alternate electron acceptors including oxidized forms of nitrogen, iron, manganese, sulfur, and carbon to metabolize organic carbon to CO_2 and/or CH_4. Each of these alternate pathways is less efficient than aerobic metabolism and leads to slower rates of decomposition. Secondly, the lack of O_2 in wetland soils limits the activity of phenol oxidase, an enzyme involved in the biodegradation of lignin and phenolic compounds. As a result, phenolic compounds accumulate and have the effect of limiting the activity of other enzymes that are responsible for some of the initial steps of soil organic matter degradation (Freeman et al. 2001). Thirdly, fungal activity is significantly reduced in anaerobic environments. Fungi that can degrade recalcitrant polymers such as lignin and tannins are rarely observed in peatlands (Thormann 2006), suggesting that the absence of this group of fungi may contribute to organic matter accumulation.

Carbon sequestration and environmental change

Wetlands can influence global environmental change by removing and sequestering atmospheric CO_2 and by emitting greenhouse gases such as CH_4 and nitrous oxide (N_2O). At the same time, changes in the environment can modify wetland carbon sequestration by affecting rates of plant production and soil decomposition. For example, warming of the atmosphere and soil will increase rates of decomposition, change plant species composition, and may lead to the drying-out of some wetland soils (Gorham 1991). Changes in hydrology due to this increased evapotranspiration, changes in precipitation, altered river flows, and purposeful drainage can affect plant production and accelerate rates of soil carbon decomposition (although CH_4 production will likely decrease) by decreasing soil water saturation and therefore increasing the penetration of O_2 into currently anoxic wetland soils (Laiho 2006). Elevated atmospheric CO_2 concentrations can stimulate plant production and soil organic matter accumulation in tidal wetlands (Langley et al. 2009). Rising sea levels can stimulate plant production in tidal salt marshes (Morris et al. 2002), but can depress plant production, organic matter accumulation, and CH_4 emissions in tidal freshwater marshes as saltwater moves into these historically freshwater environments (Neubauer and Craft 2009). For thousands of years, wetlands have been removing CO_2 from the atmosphere and sequestering it in soils. Understanding how rates of carbon sequestration and the fate of existing soil carbon will change in the face of individual and interacting environmental change factors is an area of considerable current research activity.

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Scott Neubauer is an Assistant Professor in the Department of Biology at Virginia Commonwealth University, a position he began in 2012 after having spent eight years as an Assistant Research Professor and the Assistant Director of the University of South Carolina's Baruch Marine Field Laboratory. He is an ecosystem ecologist and biogeochemist with broad interests in understanding the functioning of ecosystems (especially coastal wetlands) and their responses to environmental change at both global and local scales. He once considered becoming an astronomer (he could never wrap his head around the idea of infinity) or an astronaut (NASA didn't want him), but he is very happy spending his days playing in the mud.

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