

**DECOMPOSITION AND MINERALIZATION IN MARSH VEGETATION:
A REVIEW OF CONCEPTS, WITH APPLICATIONS TO SAN ANTONIO BAY**



REPORT SUBMITTED TO:

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EXECUTIVE SUMMARY

This document presents 1) a general overview of the processes of decomposition and mineralization, 2) some characteristics of decomposition and mineralization in marsh ecosystems, and 3) conceptual models of decomposition and mineralization in major marsh types of the San Antonio Bay. Decomposition and mineralization are complex ecological processes. Only a general overview of which is presented in this document.

Decomposition and mineralization are two of the primary processes controlling ecosystem productivity and function. The rates of these two processes are functions of many factors: physical, chemical, and biological. Six major factors are: 1) size of the detritus particles, 2) chemical composition of the detritus, especially the relative amounts of carbon and nitrogen, 3) moisture content, 4) temperature, 5) oxygen supply (a major limiting factor in marsh ecosystems), and 6) composition of the biotic community feeding on the detritus. Each of these factors affects the dynamics of decomposition and mineralization within the marsh ecosystem, but external factors also have substantial effects. Marshes and tidal flats receive detritus and nitrogen in surface runoff from terrestrial uplands and from the bay during high tides and storm surges. These external inputs, along with atmospheric inputs, are added to internal inputs from production of litter and animal detritus from the marsh and tidal flat communities.

The supply of organic matter is the single most important factor affecting decomposition and mineralization dynamics. This organic matter is supplied to the marsh from three primary sources: 1) transport from higher elevation systems, 2) production within the marsh, and 3) transport from lower elevation systems. Of these three sources, internal production by the marsh vegetation is generally the most significant. Productivity of marsh vegetation, and hence litter production, is largely a function of moisture supply, water salinity, and depth of inundation. All three of these factors are both temporally and spatially dynamic, hence marsh productivity and resulting decomposition and mineralization rates can fluctuate substantially over short spatial distances and among years.

Annual aboveground productivity varies widely in coastal salt marshes along the Atlantic and Gulf coasts (200-3700 g/m²), surface litter values from 100-1100 g/m², and reported annual decomposition rates of 20-45% of annual aboveground production. Vegetation data have been collected since 2014 from 13 marsh communities fringing San Antonio Bay. Three species (*Spartina alterniflora*, *Spartina patens*, and *Distichlis spicata*) were the most common dominant species in these marshes. Annual aboveground biomass in the marshes dominated by these three species ranged from 310 to 1650 g/m², surface litter from 0 to 1260 g/m², and estimated decomposition rates of 40-50%.

Both depth of standing water and salinity varied among the San Antonio Bay marshes spatially and temporally. The *Spartina alterniflora* marshes had the deepest inundation averaging (over sites and years) 33 cm, with *Distichlis spicata* marshes having a mean of 22 cm, and *Spartina patens* marshes the shallowest average inundations (8 cm). Surface water salinity in the marshes varied widely during the study, ranging from 1.3 ppt in 2017 on the east side of the Delta (near the mouth of the Guadalupe River) to 15.8 ppt on the west side of the bay in 2020.

Overviews of litter decomposition and nitrogen dynamics in marsh plant communities are presented, based on studies reported in the literature. Data from these studies, combined with site-specific data from the San Antonio marshes, were used to develop five conceptual models of vegetation decomposition and mineralization dynamics in San Antonio Bay marshes. Each of the conceptual models consists of 1) a fate and transport component illustrating the pathways by which aboveground plant biomass moves through the plant-soil-water marsh system and 2) a fate and transport component illustrating the movement of nitrogen through the plant-soil-water marsh system.

The conceptual models represent the three major marsh types around San Antonio Bay (*Spartina alterniflora*, *Distichlis spicata*, *Spartina patens*). *Spartina alterniflora* marshes are represented by one conceptual model (North ANWR site), a marsh directly exposed to the open bay. *Distichlis spicata* and *Spartina patens* marshes are each represented by two conceptual models, one illustrating conditions of the respective marshes exposed to open bay conditions (West Delta site) and one illustrating conditions of the respective marshes occurring in a closed basin environment (South ANWR site). The purpose of the conceptual models is not to provide precise site-specific estimates of decomposition and mineralization dynamics because much of the input data used in the conceptual models are literature values from studies conducted in other coastal marshes. Instead, the purpose of the conceptual models is to illustrate the basic concepts associated with the vegetation decomposition and mineralization component of San Antonio Bay marshes.

Several general conclusions are presented based on the estimates generated by the conceptual models. *Spartina alterniflora* marshes had the highest estimated loss of annual aboveground plant biomass to bay waters (50%), as would be expected from their topographic position. Loss of annual aboveground plant biomass into adjacent waters was estimated to average 34% in the *Distichlis spicata* marshes and 20% in *Spartina patens* marshes. The conceptual models also suggested that all three marsh types functioned as organic matter sinks (i.e., soil organic matter increasing over time) and organic matter nitrogen sinks. Available soil nitrogen was estimated to be highest in *Spartina patens* marshes, intermediate in *Distichlis spicata* marshes, and lowest in *Spartina alterniflora* marshes. The conceptual models also indicated that there are likely to be substantial differences between Delta marshes and closed basin marshes in respect to both organic matter and nitrogen dynamics.

Five suggestions for data improvement are also presented. These suggestions primarily are concerned with providing site-specific data that would be most effective in improving the precision of the conceptual model results.

1.0 INTRODUCTION

All ecosystems require an adequate supply of energy and nutrients in order to continue to function. The ultimate source of energy for most ecosystems is sunlight, i.e. solar energy. Plants convert solar energy into stored energy in the form of plant tissue, primarily carbohydrates. These carbohydrates can be broadly separated into two forms, labile (non-structural) and structural (non-labile). The labile carbohydrates consist mostly of relatively short-chain carbohydrates, such as sugars and starches, that are primarily used for respiration (i.e., energy source for the plant tissues), either in the short-term or stored for later use. Structural carbohydrates are used to build structure and consist mostly of longer-chain carbohydrates such as cellulose, hemicellulose, and lignin.

In almost all ecosystems, organisms other than green plants are also dependent on the carbohydrates produced by green plants for their energy supply. Some organisms feed directly on the living plants, consuming the labile carbohydrates only (e.g., mycorrhizal fungi, aphids, and humming birds) or both labile and structural carbohydrates (e.g., most herbivores). Other organisms feed on the herbivores (carnivores) or a combination of plants and herbivores (omnivores). However, a substantial amount of plant material, and the energy contained in its biomass, is not consumed while the plant tissue is alive. Instead, the plant tissue dies and is added to the ecosystem in the form of plant litter. This detritus, the litter combined with dead animal tissue and animal waste products, becomes the energy source for saprophytic consumers, including invertebrates and microbes. Through the processes of decomposition and mineralization, most of this detritus is eventually broken down into its constituent elements and the remaining energy released back into the environment.

The productivity and sustainability of an ecosystem is dependent on a continuous input of energy and supply of nutrients. Decomposition of detritus is a major process in the resupply of these nutrients and in the supply of the energy to many of the organisms critical to the recycling of these nutrients. Although each nutrient has its role in maintaining ecosystem productivity, nitrogen is often the most important ecologically. Because of its ecological importance, nitrogen is the nutrient discussed in this document.

1.1 Overview of Controlling Factors

The breakdown of detritus involves two parallel processes, one physical and the other chemical. The physical process (decomposition) is primarily one of decreasing the size of the individual detritus particles. As the process of decomposition occurs, there is an associated process of chemical change. A major part of this chemical change is the chemical breakdown of structural carbohydrates, with the subsequent release of carbon dioxide (CO₂) and mineral elements into elemental or ionic forms (mineralization).

The rate of decomposition and mineralization is a function of many factors: physical, chemical, and biological. Six major factors are: 1) size of the detritus particles, 2) chemical composition of the detritus, especially the relative amounts of carbon and nitrogen, 3) moisture content, 4) temperature, 5) oxygen supply, and 6) composition of the biotic community feeding on the detritus.

During decomposition, the sizes of the individual detritus particles are reduced. This reduction in size is partially an abiotic process (e.g., physical breakdown from wetting and drying or from freezing and thawing, wind breakage, wave action) and partially a biological process. The primary biological process is feeding by detritivores. During feeding, the sizes of the particles are reduced by physical action of chewing by larger detritivores (mostly invertebrates) and by chemical action by microbes (both free-living and within larger detritivores). As particle size decreases, the surface area of the particles increases relative to the mass of the particles. This increase in surface area results in more rapid rates of microbial and chemical processes.

Plant detritus consists of both labile (e.g., starches, sugars) and non-labile (structural) carbohydrates. Structural carbohydrates include cellulose, hemicellulose, and lignin. During metabolism by detritivores, particularly microbes, long-chain structural carbohydrates are broken into progressively shorter-chain carbohydrates. This is an oxidation process whereby oxygen is combined with carbohydrates (CHO-) during respiration to form carbon dioxide (CO₂) and water, and to provide the energy source for the microbes. The rate of this oxidation (respiration) process is controlled by a number of chemical and physical factors. Two important chemical factors are the amount of nitrogen available in relation to the amount of carbon in the detritus and the amount of oxygen available.

Microbes and other detritivores feed on detritus. The carbohydrates in the detritus provide the energy for the organisms but the organisms also require nitrogen (as well as other nutrients) for growth (i.e., production of proteins in their tissues). Efficient decomposition occurs when there is a proper balance between carbon (C), from the carbohydrates, and nitrogen (N), mostly from plant and animal proteins, in the detritus. A C:N ratio of about 10:1 is often used as the division between efficiently decomposed materials and materials that are more difficult to decompose. As the ratio decreases (N becomes more abundant), the rate of decomposition increases (other factors remaining constant). As the ratio increases (C becomes more abundant), the rate of decomposition slows.

When oxygen is abundant, aerobic decomposition takes place and the rate of decomposition is not limited by oxygen. When the supply of oxygen is substantially reduced, anaerobic conditions begin to dominate the decomposition process. Anaerobic decomposition tends to be slower than aerobic decomposition and often produces toxic by-products. A common cause of anaerobic conditions is water saturation.

Although an overabundance of water results in anaerobic conditions and a resulting shift in decomposition dynamics, lack of water also has a negative effect on decomposition. The rate of decomposition is dependent on the growth and respiration rates of the decomposer community, both microbes and invertebrates. An optimum moisture level is required for the most efficient rate of decomposition. As the detritus and surrounding litter layer becomes drier, decomposition slows. If the detritus and surrounding litter become too wet, the supply of oxygen is reduced, anaerobic conditions begin to develop, and the rate of decomposition slows.

Decomposition is primarily a respiration process. Respiration is a chemical process and chemical processes are temperature dependent. At low temperatures (e.g., at or below freezing), microbial respiration, and hence decomposition, is minimal in most environments. As temperatures increase, the rate of decomposition also increases. The optimum temperature level for decomposition depends somewhat on the composition of the decomposer community and on the supply of adequate moisture but in general, the higher the temperature the more rapid the decomposition rate, up to the point where high temperatures begin to affect the physiology and structure of the organisms.

Different types of decomposer organisms have different efficiencies for decomposing various types of detritus. Therefore any environmental factor that affects the composition of the decomposer community can have an effect on decomposition rate and the products produced. Shifts in composition of the invertebrate population can affect the rate at which detritus is reduced in size and the order in which various materials are reduced. The invertebrate community also produces by-products that enter into the detritus component and the composition of these by-products may vary by composition of the invertebrate community. Different types of microbes are more effective in decomposing various types of detritus than other types of microbes and they differ in how they respond to changes in environmental conditions. Saprophytic fungi are generally more effective in decomposing high C detritus than are most types of bacteria for example.

Each of these factors, plus others not mentioned, have potentially substantial effects on the decomposition and mineralization process. Which factors are more important at a particular site and at a particular time depends on the overall ecological conditions at that site and at that time. In coastal environments, where there is a continuous interaction between wet and dry sites and wet and dry conditions at individual sites, the complexity of the process increases even more.

1.2 Spatial Landscape Components

The San Antonio Bay landscape can be separated into five major spatial components relative to nutrient and decomposition dynamics: 1) river and stream, 2) open bay, 3) terrestrial upland, 4) marshes and flats, and 5) atmosphere. All five components are linked and the nutrient and decomposition dynamics in each are affected, at least to some degree, by those in the other components. Decomposition and mineralization in marshes and flats is the emphasis of this document.

The Guadalupe River and small streams around the edges of San Antonio Bay have a major impact on nitrogen dynamics of the Bay because of 1) inputs of freshwater into the Bay, 2) dissolved nitrogen in various chemical forms in the river and stream water, and 3) sediments and organic matter transported into the Bay. The river and streams receive nitrogen loadings from upstream, from litter deposition along river and stream banks, from overland flow of sediments and litter, from agricultural runoff and subsurface drainage, and from atmospheric deposition.

The open bay receives nitrogen inputs from each of the other spatial components in various forms, including dissolved nitrogen, organic matter, and sediments. These water-borne inputs are mixed in the bay water column and moved around and across the bay by tides and currents. Changes occur in the chemical form of nitrogen in both the water column and sediments. Aquatic animals and plants accumulate nitrogen and deposit nitrogen as waste products and dead tissue.

Decomposition and mineralization occurs at various rates throughout the terrestrial uplands in response to inputs of litter, animal detritus, atmospheric deposition, and moisture levels. Surface runoff and subsurface leaching from the uplands is a potential source of detritus and nitrogen inputs into the rivers and streams, marshes, and flats. During periods of flooding and storm surges, detritus and nitrogen inputs are moved in the opposite direction, from the bay or rivers and streams to the uplands.

Marshes and flats receive detritus and nitrogen inputs as surface runoff from terrestrial uplands and from the bay during high tide and storm surges. These external inputs, along with atmospheric inputs, are added to internal inputs from production of litter and animal detritus from the marsh and tidal flat communities.

Atmospheric deposition occurs as dry deposition and in rainfall across all the spatial components. Some organic particles can be transported from the land and water components to the atmosphere during storm events and, in the case of the uplands and the marshes, during fire events. A more common method of nitrogen transfer from the land and water components to the atmosphere is transfer in gaseous forms during decomposition and mineralization.

2.0 PLANT PRODUCTION IN MARSHES AND TIDAL FLATS

Decomposition and mineralization dynamics are dependent, first of all, on the supply of organic matter. It is the organic matter that is being decomposed. The amount and the physical and chemical characteristics of this organic matter substantially affect the decomposition process within the marsh.

Organic matter is supplied to marshes from three primary sources: 1) transport from higher elevation systems, 2) production within the marsh, and 3) transport from lower elevation systems. There is also, in most cases, a substantial amount of un-decomposed organic matter in the marsh, but this material originated from one or a combination of the three primary sources. Some organic matter can be supplied to the marsh by atmospheric deposition, but this amount is generally small.

Transport of organic matter from higher elevation systems into the marsh is common and the amounts can be significant. Major sources include debris carried by overland flow (surface runoff) into the marsh and water transport from river, stream, or channel flows through the marsh as these waters move into the estuary or bay system. Some organic matter is transported into the marsh from uplands by animal movement. This animal-transported material is often in the form of animal wastes or dead tissues.

Transport of organic matter into the marsh from lower elevation systems occurs by tidal flows and storm surges. Water moving into the marsh from the adjacent bay or other estuarine system carries with it both particulate and dissolved organic matter, as well as floating plant and animal material. As the waters recede, some of the organic matter is trapped by the marsh vegetation and remains in the marsh. Tides and storm surges can also export organic matter from the marsh into higher elevation communities as water levels rise and into lower elevation marshes or the open bay as the waters recede. In addition, the movement of animals into and out of the marsh results in inputs and export of organic material.

Although substantial amounts of organic matter can be transported into the marsh from both higher and lower elevation systems, most marsh organic matter is produced within the marsh. The largest contribution to marsh organic matter is from production by marsh vegetation (net primary production). Net primary production (NPP) varies in response to fluctuations in a number of factors. Important control factors include species composition of the plant community, nutrient level, salinity, depth and frequency of inundation, and frequency and intensity of disturbances.

The most common salt marsh vegetation along the Atlantic and northern Gulf coasts are *Spartina* (cordgrass) marshes. Three species are most common: *Spartina alterniflora* (smooth cordgrass), *S. cynosuroides* (big cordgrass), and *S. patens* (marshhay cordgrass). Big cordgrass does not occur much south of the Sabine River (Gould 1975). *Spartina spartinae* (gulf cordgrass) is a common species along, and somewhat inland of, the Texas coast often forming extensive, almost monospecific, stands. However, it occurs at slightly higher elevations than *S. alterniflora* and *S. patens*, on sites that are only infrequently flooded by estuarine waters.

Juncus roemerianus (black needlerush) is a common and productive species in eastern coastal marshes, often forming almost monoculture stands. However, it is not a common species in Texas coastal marshes (Correll and Johnston 1970). *Schoenoplectus* [*Scirpus*] *americanus* (Olney bulrush) is somewhat of an ecological equivalent of *J. roemerianus* in San Antonio Bay and other marshes along the central Texas Coast. *Phragmites australis* (common reed) is a species that is replacing *Spartina*, especially *S. patens*, in some coastal marshes along both the Atlantic and Gulf Coasts. It is a common species in the marshes of San Antonio Bay, especially on the Guadalupe River Delta, but it has undergone a major decline in many of the marshes around San Antonio Bay during the past ten years.

Spartina alterniflora, *S. patens*, and *Distichlis spicata* are the primary dominant species in the salt marshes of San Antonio Bay. Although these are also the primary dominant species all along the southern Atlantic and northern Gulf Coasts, the marshes along the central Texas Coast have been reported to be less productive than those further east and this lower productivity has been attributed to higher salinity levels in the more western, and more arid, marshes (Britton and Morton 1989). However, data collected in the marshes of San Antonio Bay (McLendon et al. 2020) indicate that the sampled *S. alterniflora* marshes were less productive than most *S. alterniflora* marshes in more eastern locations but

aboveground production in *S. patens* marshes around San Antonio Bay were higher than those in Louisiana and New Jersey (Table 2.1).

Table 2.1 Annual net primary productivity (NPP; g/m²) in coastal marshes.

Location	Dominant Species	NPP	Reference
Salt Marshes			
New Jersey	<i>Spartina alterniflora</i>	200	Angradi et al. 2001
Delaware	<i>Spartina alterniflora</i>	445	Morgan 1961
North Carolina	<i>Spartina alterniflora</i> (tall)	1239	Blum et al. 1978
North Carolina	<i>Spartina alterniflora</i> (medium)	932	Blum et al. 1978
North Carolina	<i>Spartina alterniflora</i> (short)	337	Blum et al. 1978
North Carolina	<i>Spartina alterniflora</i>	925	Craft et al. 1988
North Carolina	<i>Spartina alterniflora</i>	770	Craft et al. 1989
North Carolina	<i>Spartina alterniflora</i> (7-10 ppt)	870	Craft et al. 1999
North Carolina	<i>Spartina alterniflora</i> (25-35 ppt)	643	Craft et al. 1999
Georgia	<i>Spartina alterniflora</i> (tall)	3700	Gallagher et al. 1980
Georgia	<i>Spartina alterniflora</i> (medium)	1300	Gallagher et al. 1980
Louisiana	<i>Spartina alterniflora</i> (tall)	2750	Pezeshki & DeLaune 1988
Louisiana	<i>Spartina alterniflora</i> (short)	1600	Pezeshki & DeLaune 1988
Louisiana	<i>Spartina alterniflora</i> (short)	1061	Buresh et al. 1980
Texas	<i>Spartina alterniflora</i> (short)	568	McLendon et al. 2020
New Jersey	<i>Spartina patens</i>	694	Windham 2001
Louisiana	<i>Spartina patens</i>	460	Ford & Grace 1998
Texas	<i>Spartina patens</i>	923	McLendon et al. 2020
Texas	<i>Distichlis spicata</i>	696	McLendon et al. 2020
Texas	<i>Paspalum vaginatum</i> (high salt)	298	McLendon et al. 2020
Texas	<i>Paspalum vaginatum</i> (brackish)	569	McLendon et al. 2020
North Carolina	<i>Juncus roemerianus</i>	690	Bellis & Gaither 1985
North Carolina	<i>Juncus roemerianus</i>	812	Christian et al. 1990
North Carolina	<i>Juncus roemerianus</i>	560	Foster 1968
North Carolina	<i>Juncus roemerianus</i>	796	Stroud & Cooper 1968
North Carolina	<i>Juncus roemerianus</i>	895	Waits 1967
North Carolina	<i>Juncus roemerianus</i>	792	Williams & Murdoch 1966
Georgia	<i>Juncus roemerianus</i>	2200	Gallagher et al. 1980
Florida	<i>Juncus roemerianus</i>	849	Heald 1971
Florida	<i>Juncus roemerianus</i> (low marsh)	949	Kruczynski et al. 1978
Florida	<i>Juncus roemerianus</i> (high marsh)	243	Kruczynski et al. 1978
Mississippi	<i>Juncus roemerianus</i>	390	Gabriel & de la Cruz 1974
Louisiana	<i>Juncus roemerianus</i>	3295	Hopkinson et al. 1980
Fresh-Brackish			
England	<i>Phragmites australis</i>	1446	Boar et al. 1989
New Jersey	<i>Phragmites australis</i>	917	Angradi et al. 2001
New Jersey	<i>Phragmites australis</i>	1855	Windham 2001
Texas	<i>Spartina spartinae</i>	543	Garza et al. 1994
Texas	<i>Spartina spartinae</i>	336	Scifres et al. 1980
Texas	<i>Leersia hexandra</i>	596	Scifres et al. 1980
Texas	<i>Paspalum lividum</i>	512	Scifres et al. 1980
Texas	<i>Typha domingensis</i>	383	Scifres et al. 1980

Plant productivity, and therefore potential detritus input, in marshes is affected by a number of factors. Salinity is a major factor affecting productivity, by its direct effect on the productivity of a particular species and its effect on species composition. Throughout its range, *S. alterniflora* marshes can be of three forms: tall, medium, and short. This difference in height, and a corresponding difference in productivity, can largely be attributed to salinity, with the taller and more productive form occurring within a marsh complex on the less-saline, generally higher elevation, sites. Marsh productivity is

generally enhanced by tidal flushing (Windham 2001), the rate of which increases with an increase in micro-topography. In North Carolina, the tall form is almost four times as productive as the short form but the tall form is only about twice as productive in Louisiana (Table 2.1). A difference in surface elevation of 10 cm can result in separation of the two forms in Louisiana (Pezeshki and DeLaune 1988). Net photosynthetic rate of the tall form on the higher elevation and less saline sites in Louisiana was 17.5 $\mu\text{mol}/\text{m}^2/\text{sec}$ compared to 11.4 for the short form (Pezeshki and DeLaune 1988), a 52% higher productivity rate for the tall form. The three forms appear to be environmentally controlled and are not genetically different.

Substantial annual fluctuations in primary production may occur in marshes, in part the result of higher water salinity during dry years because of less freshwater inputs. At five locations within a *Juncus* marsh along the North Carolina coast, annual plant biomass production increased by an average of 33% between a dry year and a following average rainfall year (average of 921 g/m^2 and 1222 g/m^2 , respectively; Christian et al. 1990). Differences in location of marshes in the same estuary can have a similar effect because of differences in freshwater inputs. Aboveground biomass averaged 870 g/m^2 in a *Spartina alterniflora* marsh in North Carolina where surface water salinity averaged 7-10 ppt compared to 643 g/m^2 in a nearby *S. alterniflora* marsh where surface water salinity averaged 25-35 ppt (Craft et al. 1999).

Dense stands of marsh plants can reduce light intensity in the lower layers of the plant canopy. Reduced light intensity can, in turn, affect species composition and reduce decomposition rate. Light levels of only 22% of upper canopy levels were measured 40 cm below the upper canopy surface in dense stands of tall *Spartina alterniflora* in Louisiana (Pezeshki and DeLaune 1988). In a *S. patens* marsh in Louisiana, 17% of ambient light reached the soil surface on plots with 460 g/m^2 of aboveground biomass (ungrazed) compared to 75% on grazed plots producing 112 g/m^2 of aboveground biomass (Ford and Grace 1998).

3.0 DECOMPOSITION RATES

High net primary productivity (2-4 kg dry matter/ m^2 /year), low rate of herbivory on *Spartina*, and water-saturated soils contribute to the development of large pools of detritus and soil organic matter in estuarine marshes (Craft et al. 1989). The amount of total plant detritus (standing dead + litter) in coastal marshes can approach or exceed the annual amount of plant material produced (Table 3.1).

Table 3.1 Annual aboveground primary production, standing dead, and litter biomass (g/m^2) in coastal marshes.

Location	Dominant Species	Production	Standing Dead	Litter	Total Plant Detritus	Reference
New Jersey	<i>Phragmites australis</i>	1855	1175	627	1802	Windham 2001
New Jersey	<i>Spartina patens</i>	694	28	596	624	Windham 2001
Louisiana	<i>Spartina patens</i>	460	----	---	1063	Ford and Grace 1998
Texas	<i>Distichlis spicata</i>	772	----	---	593	McLendon 2014
Texas	<i>Paspalum vaginatum</i>	840	----	---	448	McLendon 2014
Texas	<i>Spartina alterniflora</i>	255	----	---	114	McLendon 2014
Texas	<i>Spartina patens</i>	918	----	---	1027	McLendon 2014

Organic matter accumulation in marsh soils is dependent on hydroperiod and marsh age, with rates of organic matter accumulation greatest in marshes characterized by low tidal amplitude and irregular flooding (Craft et al. 1988). This organic material is a source of energy and nutrients for the estuarine food web and tidal export of detritus and nutrients from marshes can be important in maintaining the secondary productivity of estuarine ecosystems (Craft et al. 1989). Young *Spartina* marshes may obtain

primary production levels near those of mature *Spartina* marshes fairly rapidly, often within ten years (Craft et al. 1999). However, vertical structure, organic matter and nutrient accumulation, denitrification, and tidal export of nutrients may take longer to reach mature marsh levels (Craft et al. 1989).

In irregularly flooded marshes, a greater proportion of net primary productivity accumulates in the marsh and less is exported by tidal action than in frequently flooded marshes (Craft et al. 1988). Seven marsh communities on the western edge of San Antonio Bay were sampled in a dry July and again in September (McLendon 2014). Litter was present in all seven communities in July. All seven communities had standing water at the September sampling date and there was no litter present at five of the sites. There was an average 493 g/m² of litter present in the seven communities in July compared to 290 g/m² in September, a loss of 203 g/m² (40%), mostly from tidal flushing.

Annual decomposition rates in coastal marshes have been reported to be on the order of 20-50% (Table 3.2). These rates are generally enhanced by tidal flushing and, as is the case with upland plant communities, by low carbon to nitrogen (C:N) ratios in the detrital material (Windham 2001).

Table 3.2 Decomposition rates (one-year % mass loss) in coastal marshes.

Marsh Type	Dominant Species	Rate	Location	Reference
Salt	<i>Juncus roemerianus</i>	25	North Carolina	Christian et al. 1990
Brackish	<i>Phragmites australis</i>	21	New Jersey	Windham 2001
Brackish	<i>Spartina patens</i>	43	New Jersey	Windham 2001

A common method of estimating decomposition rates is by the use of litterbags. A difficulty in using litterbags is quantifying the amount of small-sized material that may be lost from the bags but that was not decomposed. This may potentially be even more of a problem in frequently flooded systems because the inflow and outflow of water may remove small particles of organic matter from the bags. Bouchard et al. (2003) found flushing loss in a shrub-dominated marsh to equal over half the amount estimated from litterbags in frequently-flooded location and 25% in an infrequently-flooded location. As much as 67% of annual production may not be accounted for in litterbag measurements of decomposition in *Juncus* coastal marshes in North Carolina (Christian et al. 1990).

Standing dead tissue in marshes may remain upright for more than one year. In North Carolina *Juncus* coastal marshes with annual primary production of 812 g/m², standing dead biomass averaged 1001 g/m² (Christian et al. 1990). However, the relative amounts of standing dead plant tissue and litter can vary substantially by species even within the same marsh. In a brackish marsh in New Jersey, 65% of the dead plant tissue of *Phragmites australis* was standing dead and 35% was litter on the soil surface whereas 5% was standing dead for *Spartina patens* and 95% was litter (Windham 2001).

A portion of annual production by plants in salt marshes is buried in sediments each year. This amount averages 12% in regularly flooded salt marshes in North Carolina and 20% in irregularly flooded marshes (Craft et al. 1988). Two *Spartina alterniflora* marshes in North Carolina had 19% and 24% annual accumulation of net primary production into soils (Craft et al. 1999). This equated to 288 g biomass/m² (115 g C/m²) and 274 g biomass/m² (159 g C/m²) respectively and 4.5 g N/m² and 2.2 g N/m² per year, respectively. On sites in a brackish *Spartina patens* marsh near the mouth of the Pearl River in Louisiana, sediment accretion rate was 1.82 mm/yr, which exceeded the shallow subsidence rate of 1.07 mm/yr, resulting in an increase in soil surface elevation (Ford and Grace 1998).

4.0 PLANT PRODUCTION IN SAN ANTONIO BAY MARSHES

4.1 Study Sites and Salinity Dynamics

Species composition and aboveground biomass data have been collected in 13 marsh communities around the edges of San Antonio Bay (McLendon et al. 2020). Data collection began in 2014 at four sites, two on the Guadalupe River Delta and two on the western edge of San Antonio Bay along the eastern edge of Aransas National Wildlife Refuge (Figure 4.1). A site on Welder Flats, located at the extreme eastern edge of San Antonio Bay, was added to the sampling design in 2017.

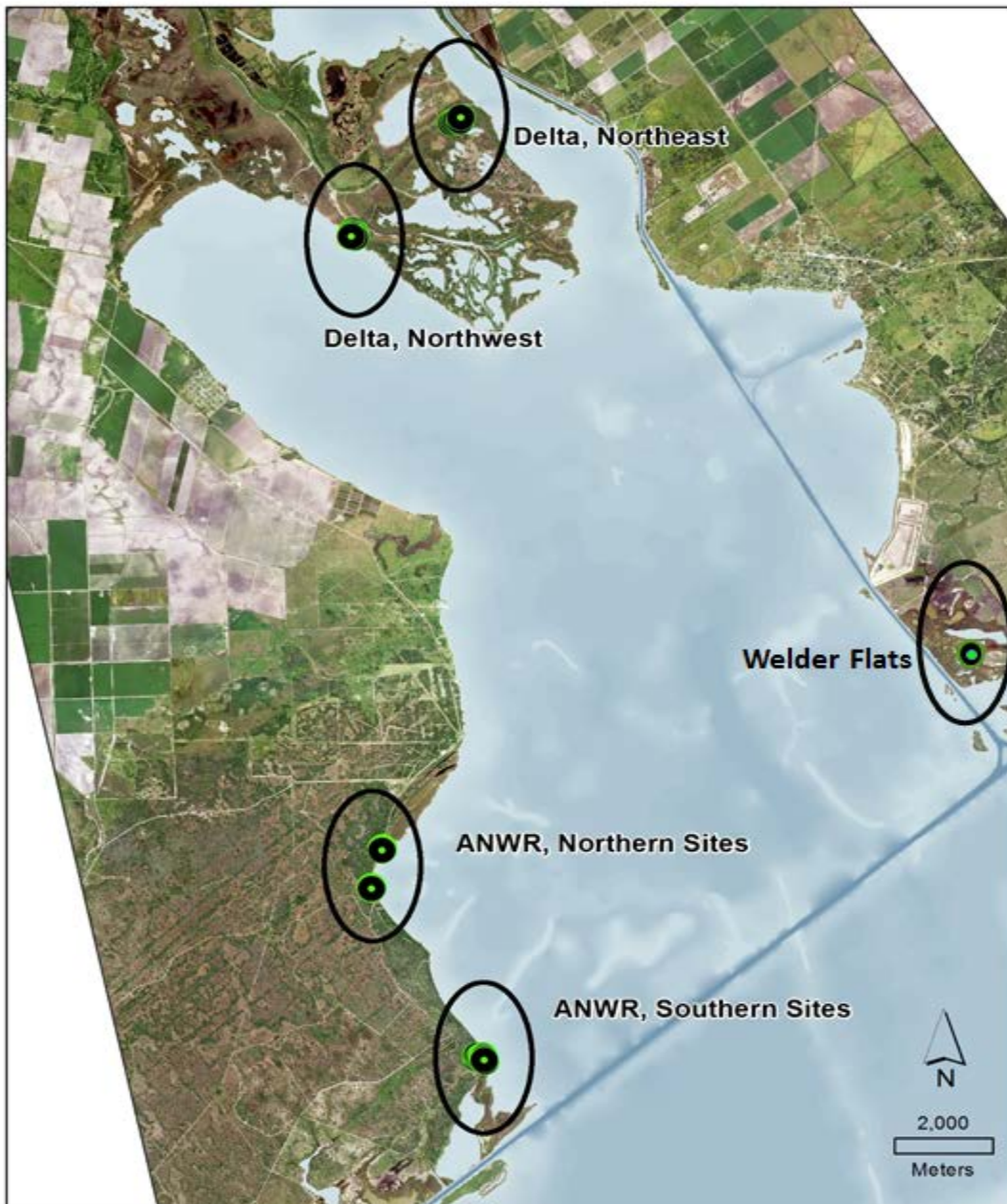


Figure 4.1 Location of the five vegetation sampling sites in marshes around San Antonio Bay.

San Antonio Bay is a relatively shallow bay, with average depths seldom exceeding 2.5 m (Booker and McLendon 2015a). Prevailing winds are generally from the southeast to the northwest, except during winter frontal passages when winds are from the north to the south. The major freshwater inflow into San Antonio Bay is from discharge from the Guadalupe River, the mouth of which is located immediately (200 m) to the northeast of the east Delta site. The combination of prevailing winds and freshwater inflow from the Guadalupe River results in a general counter-clockwise circulation pattern, with saline water entering the bay from the southeast (Espiritu Santo Bay) and moving northwest across the bay by wind and tidal action. Inflow from the Guadalupe River in the northeast (Guadalupe Bay) directs this northern flow to the northwest, from which it moves down the western side of San Antonio Bay and exits in the southwest corner of the bay (into Mesquite Bay).

The counter-clockwise circulation pattern is the primary factor affecting average salinity values in the bay and in those marshes adjacent to the open bay. In general, salinity decreases from north to south. The lowest values (5-9 ppt) tend to be in Guadalupe Bay, where the Guadalupe River discharges into the bay, and highest (15-25 ppt) along Matagorda Island along the southern edge of San Antonio Bay (Longley 1994). Guadalupe-Blanco River Authority (GBRA) recorded baywater salinity at a station about 2 km east of our South ANWR site (southwest San Antonio Bay) and at a station about 6 km northeast of our North ANWR site (northeast San Antonio Bay, near Seadrift). Bay water salinities in July 2014 ranged from 26-36 ppt at the south station and 9-22 ppt at the north station. Texas Parks and Wildlife Department (TPWD) collected water salinity data at a point near the southeast corner of the Delta and values varied between 1 and 34 ppt during 1988-2010, with average values in 2008-2010 of about 20 ppt (Guthrie et al. 2010). The TPWD site is about halfway between the mouth of the Delta and the GBRA site near Seadrift, which had average salinity values of about 20 ppt in July-September 2014.

Water salinity values in the marshes are generally less than those of the open bay because of dilution by freshwater from river discharge and overland flow of rainwater. Approximately 1.5 million acre-feet of freshwater entered San Antonio Bay annually 2014-2017. The average volume of water in San Antonio Bay (including Hynes and Guadalupe Bays) is about 147,000 acre-feet (Alireza Asadi, personal communication). Of the 1.5 million acre-feet of freshwater input, about 1.13 million acre-feet (74.5%) were from Guadalupe River discharge (based on USGS measurements of flows at the Tivoli gauge), 0.36 million acre-feet (24.1%) from direct rainfall into the Bay (including the Delta), and 0.02 million acre-feet (1.4%) as surface runoff (Booker and McLendon 2015b). Although surface runoff contributes only a small portion of the freshwater input into San Antonio Bay, much of this runoff flows through the marshes and therefore is an important source of freshwater to them.

The sampling sites differ in relation to exposure to open bay waters. Four of the sites (North ANWR, West and East Delta, Welder Flats) are located on tidal flats immediately adjacent to the open bay (Figure 4.2), as is one of the marsh communities (*Spartina alterniflora*) at the South ANWR site. The remainder of the marsh communities at the South ANWR site are separated from the open bay by a low (2 m) sand dune. Except during storms or unusually high tidal flows, the dune prevents bay water from moving inland. The site receives surface runoff from the surrounding uplands and from a swale that extends about 500 m upslope that drains the surrounding live oak woodland. A basin occurs between the end of the swale and the foot of the dune (Figure 4.3). This basin was dry at the beginning of data collection in July 2014, but was inundated to a depth of about 30 cm (1 foot) in September 2014, as a result of substantial rains received in the watershed in August 2014 (Figure 4.4). The basin remained inundated (25-50 cm depth) through October 2019. The basin was dry again by the summer of 2020. These differences in exposure to the bay, along with the elevation differences among communities at the South ANWR site, result in different patterns of salinity and inundation that, in turn, affect both plant productivity, species composition, and decomposition dynamics.



Figure 4.2 Marsh communities at the North ANWR (A) and West Delta (B) sites.



Figure 4.3 Aerial photograph of the South ANWR site (central area) and the drainage that flows into the central depression (light-colored seahorse-shaped feature). The dune is to the right of the central depression.

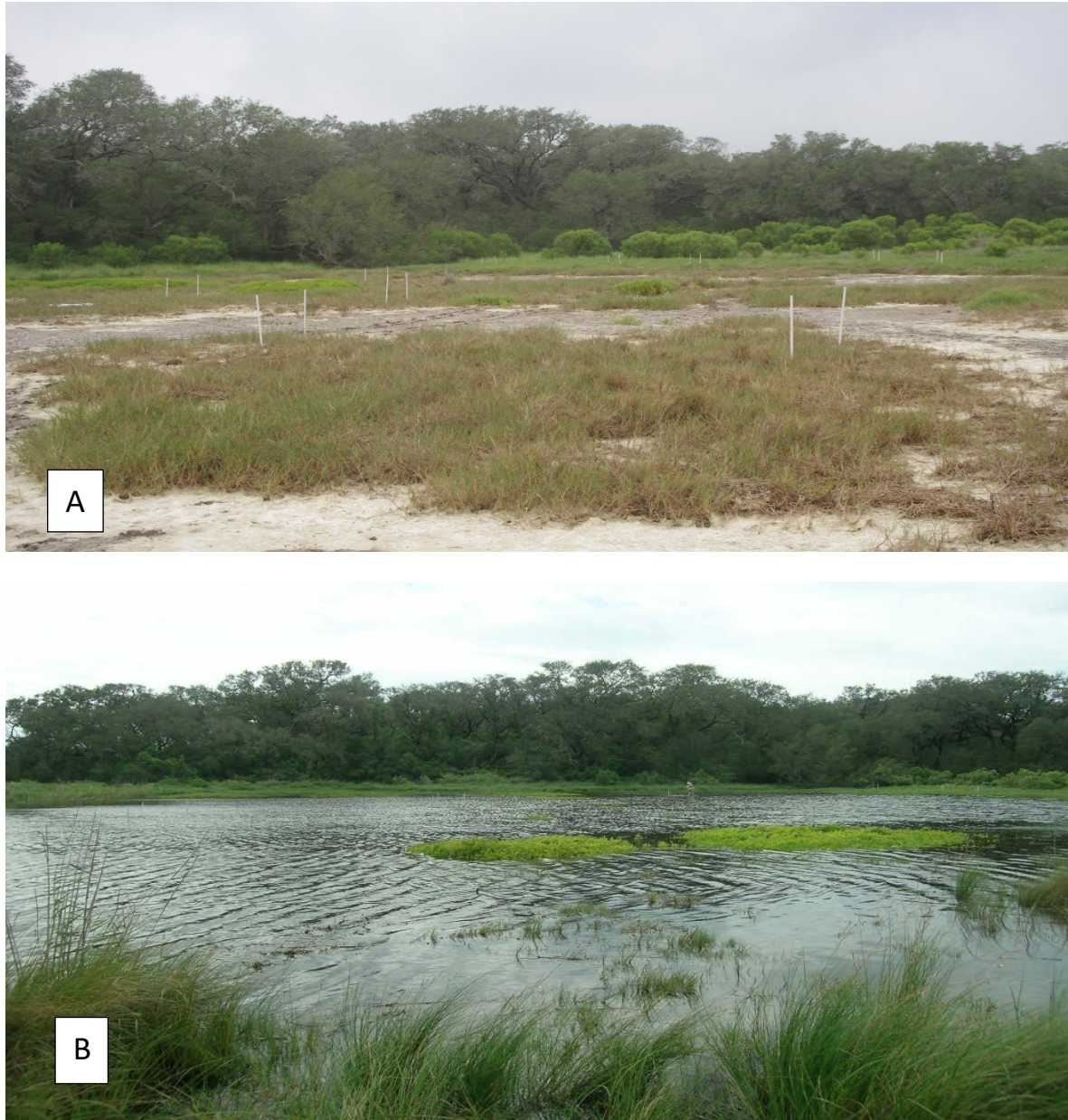


Figure 4.4 Central depression at the South ANWR site in July 2014 (A) and the same area in September 2014 (B).

Salinity measurements of standing surface water were made at most sites in 2016-2019 at the time of vegetation sampling. Average salinity in the marshes to the west (interior) of the dune decreased from 7.5 ppt in September 2016 to 5.1 ppt in September 2018, and then increased to 16.4 ppt in October 2019. The high mean in 2019 was the result of bay water flowing into the depression because extremely high tides over-topped the dune in September and October that year. Salinity values were lowest at the East Delta site, which is near the mouth of the Guadalupe River. Values averaged 1.4 ppt in 2017 and 2.9 ppt in 2018. Values at the West Delta and North ANWR sites averaged 6.7 ppt in 2016, 5.2 ppt in 2017, and 11.9 ppt in 2018. Salinities were relatively high in the *S. alterniflora* community on the bay side of the

dune at the South ANWR site, averaging 7.5 ppt in 2016 and 2017, 13.5 ppt in 2018, and 15.2 ppt in 2018.

Inundation depths were also measured in 2014 and in 2016-2019. Deepest inundations (23-44 cm overall means) occurred in the *Spartina alterniflora* marshes on the west side of San Antonio Bay and the marshes nearest the central depression at the South ANWR site (Table 4.1). The East Delta marshes had inundation depths about twice as deep as those in the West Delta marshes (11-12 cm and 4-6 cm, respectively). Marshes located on the dune at the South ANWR site tended to have inundation depths (6-9 cm) similar to those of the West Delta marshes. The Welder Flats sites were established in 2017 and inundation depth in 2017-2018 was similar to that of the West Delta sites in those years, but was more similar to the South ANWR dune sites in 2019.

Table 4.1 Mean inundation depth (cm) at the marsh vegetation sampling sites around San Antonio Bay.

Site	Marsh Community	2014	2016	2017	2018	2019	Mean
Sites Inland of Dune							
South ANWR	<i>Paspalum vaginatum</i>	31	31	49	25	45	36.2
South ANWR	<i>Paspalum-Phragmites</i>	29	15	31	21	37	26.6
South ANWR	<i>Distichlis spicata</i>	21	9	39	12	34	23.0
South ANWR	<i>S. patens-Phragmites</i>	10	1	14	4	18	9.4
South ANWR	<i>Spartina patens</i>	4	1	13	5	17	8.0
South ANWR	<i>S. patens-Distichlis</i>	8	0	11	2	11	6.4
Sites Open to Bay Water							
North ANWR	<i>Spartina alterniflora</i>	40	37	67	22	55	44.2
South ANWR	<i>Spartina alterniflora</i>	27	45	45	25	52	38.8
East Delta	<i>Distichlis spicata</i>	8	13	23	8	8	12.0
East Delta	<i>S. patens-Distichlis</i>	8	11	23	7	6	11.0
West Delta	<i>Distichlis spicata</i>	6	6	5	0	11	5.6
West Delta	<i>S. patens-Distichlis</i>	3	5	4	0	10	4.4
Welder Flats	<i>Spartina alterniflora</i>	--	--	0	5	17	7.3
Welder Flats	<i>Distichlis spicata</i>	--	--	0	7	18	8.3

Inundation data were not collected in 2015. Welder Flats sites were not established until 2017.

4.2 Species Composition

Twenty species have been recorded in the sample plots during the 2014-2019 study period. Of these, four species were most abundant, comprising an average of 94% of the total aboveground biomass sampled during 2014-2019 in the marshes open to the bay and 90% in the marshes in the dune basin (Table 4.2). Although some other species contribute lesser, but still significant, amounts of biomass in some years, it is these four major species that dominate aboveground biomass production, and therefore litter, in these marshes. *Distichlis spicata*, *Spartina patens*, and *S. alterniflora* are the major species in the marshes adjacent to open bay waters. *Schenoplectus americanus* has become a more important component in these marshes (Tables 4.2 and 4.3). *Spartina patens*, *D. spicata*, and *Paspalum vaginatum* are the major species in the dune basin marshes (Tables 4.2 and 4.3). *Phragmites australis* was initially an important species on the dune, but has declined over time. Several early- or mid-seral species, indicative of increased disturbance, increased following Hurricane Harvey.

Table 4.2. Species composition (% relative biomass) in marsh communities adjacent to open bay water (Open to Bay) or separated from the open bay by dune (Dune Basin), San Antonio Bay. Values are means over all plots in the respective locations (Open Bay or Dune Basin).

Location	Species	2014	2015	2016	2017	2018	2019	Mean
Open to Bay								
	<i>Distichlis spicata</i>	46.2	50.2	45.5	43.0	41.8	42.2	44.8
	<i>Spartina patens</i>	36.2	36.3	38.8	26.3	25.4	27.8	31.8
	<i>Spartina alterniflora</i>	16.8	12.8	11.2	20.3	26.1	12.3	16.6
	<i>Schenoplectus americanus</i>	0.0	0.1	4.1	7.3	4.3	17.0	5.5
	<i>Paspalum vaginatum</i>	0.7	0.5	0.4	2.1	1.9	0.6	1.0
	<i>Salicornia virginica</i>	0.1	0.1	t	0.6	0.5	0.0	0.2
	<i>Eleocharis</i> sp.	0.0	t	t	0.3	0.0	0.1	0.1
	<i>Cymodocea filiformis</i>	0.0	0.0	0.0	0.1	0.0	0.0	t
Dune Basin								
	<i>Spartina patens</i>	55.3	55.9	71.8	60.9	38.7	56.7	56.6
	<i>Distichlis spicata</i>	17.7	15.7	21.9	27.2	15.4	14.8	18.8
	<i>Paspalum vaginatum</i>	21.6	14.5	3.2	10.1	23.3	17.1	15.0
	<i>Phragmites australis</i>	4.7	7.1	1.7	1.5	0.9	0.7	2.8
	<i>Cynodon dactylon</i>	0.0	0.0	0.0	0.1	3.5	7.2	1.8
	<i>Suaeda conferta</i>	0.0	0.0	0.0	0.0	8.7	0.4	1.5
	<i>Ambrosia psilostachya</i>	0.4	3.1	0.8	0.1	3.0	1.1	1.4
	<i>Borrchia frutescens</i>	0.0	0.0	0.0	0.0	2.1	1.0	0.5
	<i>Eupatorium betonicifolium</i>	0.1	1.2	0.0	t	0.3	t	0.3
	<i>Salicornia virginica</i>	0.0	0.0	0.0	0.0	1.6	0.1	0.3
	<i>Eleocharis</i> sp.	0.0	0.4	0.6	0.0	t	0.2	0.2
	<i>Suaeda linearis</i>	0.0	0.0	0.0	0.0	0.8	0.6	0.2
	<i>Heliotropium curasscicum</i>	0.0	0.0	0.0	0.0	1.4	0.0	0.2
	<i>Sarcostemma cynanchoides</i>	0.2	t	0.0	0.0	0.3	0.1	0.1
	<i>Stenotaphrum secundatum</i>	t	t	t	0.1	0.0	0.0	t
	<i>Cynanchium barbigerum</i>	0.0	t	0.0	t	0.0	0.0	t
	<i>Schoenoplectus americanus</i>	0.0	t	0.0	0.0	0.0	0.0	t
	Unidentified forbs	0.0	2.1	0.0	0.0	0.0	0.0	0.4

A "t" indicates a trace amount (< 0.005).

Table 4.3 Species composition (% relative biomass) of the six most abundant species in the sampled marshes around San Antonio Bay, 2014-2019.

Marsh Community	Site	Species	Species Composition (%)						
			2014	2015	2016	2017	2018	2019	Mean
<i>Spartina patens</i>									
	South ANWR	<i>S. patens</i>	99.8	96.9	99.9	95.8	67.8	73.8	89.0
		<i>P. vaginatum</i>	0.0	0.0	0.0	0.0	12.1	10.5	3.8
		<i>D. spicata</i>	0.0	0.7	0.0	0.0	0.0	0.0	0.1
<i>S. patens-D. spicata</i>									
	South ANWR	<i>S. patens</i>	91.2	63.9	62.8	45.8	38.8	50.0	58.8
		<i>D. spicata</i>	4.6	8.1	11.2	34.9	0.0	0.0	9.8
		<i>P. vaginatum</i>	0.0	0.4	17.8	18.2	23.6	29.9	15.0
	West Delta	<i>S. patens</i>	89.1	89.1	80.0	63.0	83.5	55.5	76.7
		<i>D. spicata</i>	10.9	10.9	11.0	15.0	8.2	11.0	11.2
		<i>S. americanus</i>	0.0	0.0	8.8	22.0	8.3	33.5	12.1
	East Delta	<i>S. patens</i>	79.2	54.8	80.0	79.0	69.0	59.1	70.2
		<i>D. spicata</i>	19.7	42.9	19.0	12.7	21.1	29.6	24.2
		<i>P. vaginatum</i>	1.1	2.2	0.8	4.8	5.7	1.1	2.6
		<i>S. americanus</i>	0.0	0.0	0.2	3.4	4.2	10.2	3.0
<i>S. patens-Phragmites</i>									
	South ANWR	<i>S. patens</i>	91.7	73.1	97.4	95.9	60.4	93.9	85.4
		<i>P. australis</i>	8.1	19.4	2.4	4.1	3.0	3.1	6.7
<i>Distichlis spicata</i>									
	South ANWR	<i>D. spicata</i>	100.0	100.0	99.4	76.4	39.6	68.8	80.7
		<i>P. vaginatum</i>	0.0	0.0	0.6	23.6	60.4	31.2	19.3
	West Delta	<i>D. spicata</i>	100.0	100.0	91.0	73.4	90.0	49.6	84.0
		<i>S. americanus</i>	0.0	0.0	9.0	26.2	9.3	50.4	15.8
		<i>P. vaginatum</i>	0.0	0.0	0.0	0.0	0.4	0.0	0.1
	East Delta	<i>D. spicata</i>	96.6	99.0	97.2	87.7	86.6	89.0	92.7
		<i>S. americanus</i>	0.0	0.7	2.0	6.2	9.0	9.4	4.6
		<i>P. vaginatum</i>	3.4	0.3	0.8	5.1	4.0	1.3	2.5
	Welder Flats	<i>D. spicata</i>	----	----	----	97.9	97.1	100.0	98.3
<i>Spartina alterniflora</i>									
	North ANWR	<i>S. alterniflora</i>	99.5	99.3	99.7	99.4	99.6	100.0	99.6
	South ANWR	<i>S. alterniflora</i>	100.0	100.0	100.0	80.9	100.0	100.0	96.8
	Welder Flats	<i>S. alterniflora</i>	----	----	----	97.3	99.0	100.0	98.8
<i>Paspalum vaginatum</i>									
	South ANWR	<i>P. vaginatum</i>	100.0	100.0	0.0	0.0	0.0	0.0	33.3
<i>P. vaginatum-Phragmites</i>									
	South ANWR	<i>P. vaginatum</i>	83.5	65.4	6.9	4.0	14.7	0.0	29.1
		<i>P. australis</i>	12.7	21.8	31.9	20.0	0.0	0.0	14.4
		<i>D. spicata</i>	3.8	12.8	61.2	76.0	85.3	100.0	56.5

Welder Flats sites were not established until 2017.

4.3 Aboveground Production

Aboveground production averaged about 700 g/m² over six years (Table 4.4). Average values were generally higher in the three years preceding the hurricane. Aboveground production also varied by marsh type (Table 4.4). Marshes dominated by *S. patens* tended to be the most productive, averaging 700-1650 g/m² in pre-hurricane years (2014-2016) and 600-1300 g/m² following the hurricane. Means in the West Flat *S. patens*-*D. spicata* community were lower than in other *S. patens* marshes. Marshes dominated by *D. spicata* had annual means of 650-1200 g/m² in 2014-2016, compared to 350-1150 g/m² in 2017-19. Overall, *S. patens*-dominated marshes were about 25% more productive than were *D. spicata* marshes (981 and 781 g/m², respectively).

Table 4.4. Average annual total aboveground biomass (all species combined) in sampled marsh communities around San Antonio Bay.

Location	Marsh Community	2014	2015	2016	2017	2018	2019	Mean
Open to Bay								
North ANWR	<i>Spartina alterniflora</i>	370	589	652	310	500	313	456
South ANWR	<i>Spartina alterniflora</i>	177	37	23	47	10	24	53
Welder Flats	<i>Spartina alterniflora</i>	---	---	---	738	858	72	556
West Delta	<i>Distichlis spicata</i>	833	1119	1148	565	472	355	749
East Delta	<i>Distichlis spicata</i>	997	1210	1176	906	845	746	980
Welder Flats	<i>Distichlis spicata</i>	---	---	---	760	762	209	577
West Delta	<i>S. patens</i> - <i>D. spicata</i>	980	1292	1273	608	708	647	918
East Delta	<i>S. patens</i> - <i>D. spicata</i>	756	1630	1653	1217	1056	968	1213
MEAN		686	980	988	644	651	417	688
Dune Basin								
Upper Dune	<i>Spartina patens</i>	975	1291	1492	1297	837	1208	1183
Upper Dune	<i>S. patens</i> - <i>D. spicata</i>	846	907	757	793	844	1062	868
Upper Dune	<i>S. patens</i> - <i>P. australis</i>	1073	1358	1025	1240	1122	812	1105
Lower Dune	<i>P. vaginatum</i> - <i>P. australis</i>	1075	365	116	51	232	69	318
Depression	<i>Paspalum vaginatum</i>	137	458	0	0	0	0	98
West Flat	<i>Distichlis spicata</i>	771	646	688	1159	982	677	821
West Flat	<i>S. patens</i> - <i>D. spicata</i>	727	714	475	395	483	799	599
MEAN		801	820	659	705	643	661	713

It has been previously suggested that marsh communities in the San Antonio Bay area are less productive than marshes further east (Britton and Morton 1989), primarily because of lower precipitation and higher salinity levels. Our data from the San Antonio Bay marshes do not support this suggestion. The San Antonio Bay *S. alterniflora* marshes may be less productive than *S. alterniflora* marshes in Louisiana and along the Atlantic Coast (Table 2.1) but the *S. patens* marshes are more productive than reported for those in Louisiana and are as productive as many of the *S. alterniflora* marshes.

4.4 Litter Production

In most terrestrial plant communities, most of the annual litter production is from leaf and stem loss from the associated plants. This amount of annual litter production can be reasonably estimated by harvesting the aboveground biomass of herbaceous species and the leaves of deciduous woody species or, in the case

of evergreen woody species such as live oak, a portion of the annual production of leaves. In marshes, the measurement is more complicated.

Marsh plant communities produce litter in a similar manner as do terrestrial plant communities, i.e., annual production of herbaceous biomass plus leaves and stems from woody species. However, there are two major differences between marsh and terrestrial plant communities in relation to litter accumulation. First, some of the standing plant biomass produced in marshes does not remain in the marsh. Instead, a portion of this material generally is removed by tidal, wave, or storm surge actions. Secondly, material produced in other locations may be deposited into the marsh community by overland flow and by the same factors that can remove plant biomass from the marsh.

With the exceptions of storm events and exceptionally high tides, the litter input/export dynamics of the San Antonio Bay marshes can be simplified by separating the marshes into two types: closed systems (e.g., the dune basin at the South ANWR site) and marshes open to bay waters. Storms and exceptionally high tides affect input of litter into the marshes by transporting potentially large amounts of litter from other systems into the marshes. The export dynamics are affected in a similar manner by receding waters removing material from the marshes and into the bay. The amount of material deposited or removed by these events depends on the magnitude and duration of the storm or high tide events, as well as the spatial location of the marsh in relation to storm or tide patterns.

4.4.1 Marshes Open to Bay Waters

Five of the study sites support marshes that are open to bay waters. The included marshes consist of three *S. alterniflora* marshes, three *D. spicata* marshes, and two *S. patens*-*D. spicata* marshes (Table 4.4). These five sites received relatively little overland flow from the adjacent uplands. The Delta sites are on the low-elevation delta flat south of the Guadalupe River. Most surface flow occurs through deeper channels located throughout this flat landscape. Most upland surface flow at the North ANWR site passes through a *Phragmites* and mixed grass stand before entering a channel which directs the flow laterally into the bay before it moves across the *S. alterniflora* marsh. The Welder Flats marshes and the South ANWR *S. alterniflora* community are located on tidal mud flats receiving little upland flow because of either a low bluff (Welder Flats) or sand dune (South ANWR) blocking upland flows moving into the marshes. Because of these topographic features, input and export dynamics of these marshes are largely controlled by water movement from the bay into or out of the marshes. Exceptions occur following storm surges or very high tides when inundation depths exceed the topographic barriers and the receding waters drain back through these marshes.

Sampling began in 2014 (2017 at the Welder Flats site). There were substantial amounts of accumulated litter at all sites (except South ANWR) initially (Table 4.5). This high biomass was likely the result of minimal flushing of the litter debris in the immediately preceding years. The six years prior to the beginning of sampling (2008-2013) were dry, averaging 87% of the long-term annual mean. Therefore, non-tidal inundation was minimal. This allowed for the accumulation of undecomposed material. Assuming the 2014 standing biomass values were indicative of average conditions during the preceding dry period, average accumulated biomass equaled 89% of standing biomass (611 and 686 g/m², respectively; Table 4.5). This is similar to the value reported for an Atlantic Coast *S. patens* marsh (82%; Windham 2001).

Table 4.5 Litter and standing aboveground biomass (g/m²) in marsh communities open to bay waters, San Antonio Bay, 2014-2017.

Location	Marsh Community	Litter Biomass				Standing Biomass			
		2014	2015	2016	2017	2014	2015	2016	2017
North ANWR	<i>Spartina alterniflora</i>	114	12	0	0	370	589	652	310
South ANWR	<i>Spartina alterniflora</i>	17	0	0	0	177	38	23	47
Welder Flats	<i>Spartina alterniflora</i>	---	---	---	346	---	---	---	738
West Delta	<i>Distichlis spicata</i>	629	31	86	0	833	1119	1148	565
East Delta	<i>Distichlis spicata</i>	848	4	518	0	996	1210	1176	906
Welder Flats	<i>Distichlis spicata</i>	---	---	---	137	---	---	---	760
West Delta	<i>S. patens-D. spicata</i>	793	108	0	0	980	1292	1273	606
East Delta	<i>S. patens-D. spicata</i>	1263	0	241	0	757	1630	1653	1217

The amount of litter in relation to standing biomass in 2014 was less in the *S. alterniflora* marshes (24%) than in the *D. spicata* (81%) and *S. patens* (118%) marshes. High values (> 100%) for *S. patens* marshes have also been reported in Louisiana (Ford and Grace 1998). The lower values for *S. alterniflora* are likely the result of greater tidal flushing, with subsequent removal of litter, in these communities. The topographic gradient in San Antonio Bay marshes, as is the case in other coastal systems, is *S. alterniflora* at the lowest elevation (greatest water depth), followed by *D. spicata* communities and then *S. patens* communities at a slightly higher elevation (shallower depth of water). For example, the average depth of inundation measured in the *S. alterniflora* marshes at the time of sampling in 2014 and 2016 was 37.2 cm, compared to 7.1 cm in the *D. spicata* and 5.9 cm in the *S. patens* marshes.

Litter values declined substantially in the following years. This was likely the result of two factors. First, the buildup of old undecomposed litter from previous years had been removed in the 2014 sampling. Therefore, only new litter (new growth produced in the previous year) would be potentially present in subsequent years. The second factor is that almost all the plots were inundated in the subsequent years. The fluctuations in depth of water during these years likely removed much of the new litter each year. For example, the West Delta *D. spicata* marsh had an average of 833 g/m² standing biomass in 2014 (Table 4.5). If all this entered the detritus component as litter by the sampling date in 2015, there would have been 833 g/m² of litter present in 2015. However, there was only 31 g/m² present, or a loss of 802 g/m² (96%). The loss between 2015 and 2016 would have been 1064 g/m² (1119 g/m² standing crop + 31 g/m² litter in 2015 – 86 g/m² litter in 2016), or a 92% loss.

Regardless of the eventual spatial location of litter biomass, the sampled standing biomass values provide a quantification of litter production because the standing biomass, live and standing dead material, eventually enters the detritus component as litter. Therefore, potential annual litter production in the marshes open to bay waters is about 680 g/m² in dry years and 980 g/m² in wet years (pre-hurricane means, Table 4.4). *Spartina alterniflora* marshes produced about 600-750 g/m² annually under good conditions, *D. spicata* marshes 1100-1200 g/m², and *S. patens* marshes 1300-1600 g/m² of litter.

4.4.2 Marshes in the Dune Basin

Water transport of litter was very different into the dune basin marshes than in the marshes that were open to bay waters. Until 2019, there was little movement of bay water into the basin because of the blocking effect of the dune. Tides were very high in 2019 and bay water was flowing into the basin at the time of sampling that year. It is also probable that there was some movement of bay water into the basin during Hurricane Harvey in August 2017. Both of these events could have transported debris into and out of the basin. There are also two swales across the dune and it is possible that if depth of water in basin exceeded

the elevation of the dune crest at these two points water-borne litter could have been transported from the basin into the bay. In addition to the inflows in 2017 and 2019, there was probably outflow through these swales in August-September 2014 when the basin was filled (Fig. 4.4B). Standing water averaged 7 cm deep in September 2014 in the two plots nearest where the swales crested the dune.

However in most years, the basin functioned as a mostly closed system. Overland surface flow occurred into the basin from the surrounding oak woodlands and the drainage that extends inland from the northwest corner of the basin (Fig. 4.3). The drainage supports a well-developed cover of mostly herbaceous species. Therefore, runoff would need to be of sufficient magnitude to exceed the ability of that vegetation to trap the transported debris. In most years, especially the dry years prior to 2014, there is probably insufficient runoff to transport much debris into the central depression. Runoff from the oak woodlands on the uplands to the north and south of the basin flows through *D. spicata* and *S. patens* stands prior to entering the central depression. Some litter from the oak woodlands probably enters into these communities following major rainfall events.

Plant biomass data were collected in the South ANWR plots at two dates in 2014, July and September (Table 4.6). Litter was present in all seven communities in July, when conditions were very dry (Fig. 4.4A). No litter was present in September in the three lowest-elevation communities. Relatively deep (15-34 cm) standing water was present in these communities at that time (Fig. 4.4B) and it is most likely that any undecomposed litter was transported out of these plots by the water and deposited in surrounding, somewhat higher elevation, communities.

Table 4.6 Litter, standing crop biomass, and new growth biomass (g/m^2), and relative elevation (cm) in marsh communities in the dune basin, South ANWR site, at two sampling dates (July, September) 2014.

Location	Marsh Community	Litter Biomass		Standing Biomass (Jul)	New Growth (Sep)	Relative Elevation
		Jul	Sep			
Upper Dune	<i>Spartina patens</i>	845	1045	394	975	27-39
Upper Dune	<i>S. patens-D. spicata</i>	997	886	557	846	30-40
Upper Dune	<i>S. patens-P. australis</i>	1617	1245	768	1073	27-32
Lower Dune	<i>P. vaginatum-P. australis</i>	460	0	840	1075	9-14
Depression	<i>Paspalum vaginatum</i>	100	0	72	137	6-9
West Flat	<i>Distichlis spicata</i>	302	0	485	771	12-25
West Flat	<i>S. patens-D. spicata</i>	725	348	491	727	21-36

Relative elevation is the elevation above the bottom of the central depression.

Litter biomass declined between July and September 2014 in three of the *S. patens* communities and increased in one. Averaging over the four communities, mean litter biomass was $1046 \text{ g}/\text{m}^2$ in July and $881 \text{ g}/\text{m}^2$ in September, or a decrease of $165 \text{ g}/\text{m}^2$ (15.8%) over 70 days. Multiplying by 5.2 (365 days/70 days) results in an estimated annual loss rate of 82%. This seems a reasonable estimate based on data from other coastal marshes. Measured annual litter-bag mass loss in an Atlantic Coast *S. patens* marsh was 43% (Windham 2001), but as much as 50% of litter loss may not be accounted for in litter-bag measurements in frequently-flooded marshes. This would raise the actual rate in the marsh studied by Windham (2001) to 86%. The annual litter-bag loss rate in a salt marsh in North Carolina was 25%, but the authors of that study indicated that 67% of the actual loss was probably not accounted for (Christian et al. 1990). That would place the actual annual loss rate in that salt marsh at about 75%.

During the next three years (2015-2017), very little litter was present in any of the marsh communities at the South ANWR site (Table 4.7). Conditions were wet during this period, with depth of inundation

averaging 29 cm in the lowest three communities and 10 cm in the four upper-elevation communities in 2016-2017 (inundation data were not collected in 2015).

Table 4.7 Litter and standing crop biomass (g/m^2) in marsh communities in the dune basin, South ANWR site, 2014-2017.

Location	Marsh Community	Litter Biomass				Standing Biomass			
		2014	2015	2016	2017	2014	2015	2016	2017
Upper Dune	<i>Spartina patens</i>	1046	112	0	83	975	1291	1492	1297
Upper Dune	<i>S. patens-D. spicata</i>	886	58	17	81	846	907	757	793
Upper Dune	<i>S. patens-P. australis</i>	1245	34	27	76	1073	1358	1025	1240
Lower Dune	<i>P. vaginatum-P. australis</i>	0	26	10	0	1075	365	116	51
Depression	<i>Paspalum vaginatum</i>	100	11	0	0	137	458	0	0
West Flat	<i>Distichlis spicata</i>	302	14	0	0	771	646	688	1159
West Flat	<i>S. patens-D. spicata</i>	655	8	0	0	727	714	475	395

Coarse estimates of decomposition rates, or at least rates of litter loss, can be made by comparing litter biomass to previous-year standing biomass. This method assumes that all of the previous-year standing biomass enters the litter compartment by the following year and there is no input of litter from outside the community nor removal from the community other than by decomposition. Although this metric is only a broad first-approximation of litter loss (litter disappearance), it does suggest some interesting aspects related to decomposition rate when applied to the data from the dune basin marsh communities.

Between 2014 and 2017 there was very little residual litter (Table 4.8). Annual standing biomass averaged $703 \text{ g}/\text{m}^2$ and litter biomass averaged $22 \text{ g}/\text{m}^2$. There was more litter biomass in the upper dune communities than in the lower elevation communities and the annual litter loss rate was lower in upper dune communities. More litter biomass and lower litter loss may have been the result of higher productivity in the upper dune communities, and hence the maximum annual decomposition rate may have been exceeded. Alternatively, the higher litter biomass values may have been the result of water transport of some litter from the lower communities into the higher elevation communities.

Table 4.8. First approximation estimates of rate of litter loss in marshes in three locations in the dune basin, South ANWR site. Gross litter loss = (previous year standing crop) – (current year litter biomass), with values (means by location) taken from Table 4.7.

Location	Year	Previous Year Standing Biomass	Current Year Litter Biomass	(Previous – Current)	(Previous – Current)/ Previous
Upper Dune	2014-15	965	68	897	0.930
Upper Dune	2015-16	1185	15	1170	0.987
Upper Dune	2016-17	1091	80	1011	0.927
Upper Dune	Mean				0.948
Lower	2014-15	606	19	587	0.969
Lower	2015-16	412	5	407	0.988
Lower	2016-17	58	0	58	1.000
Lower	Mean				0.986
West Flat	2014-15	749	11	738	0.985
West Flat	2015-16	680	0	680	1.000
West Flat	2016-17	582	0	582	1.000
West Flat	Mean				0.998

Our data do not provide the information necessary to determine the fate of the standing biomass. The biomass could have been decomposed, at least in part, or it could have been transported out of the basin. Our data for 2014 (Table 4.6) indicates an annual decomposition rate of 82% in these South ANWR communities and adjusted rates for two Atlantic Coast marshes are 75% (Christian et al. 1990) and 86% (Windham 2001). The average of the three litter loss ratios (Table 4.7) is 0.977. Using the average of these three values (81%) as a reasonable estimate of decomposition rate, litter loss from export by water transport would be about 17% of annual production ($0.98 - 0.81 = 0.17$).

4.5 Nutrient Dynamics

Marshes are sites of nutrient transformation in estuaries, converting particulate materials into dissolved forms (Craft et al. 1988). The primary form of the particulate material is organic matter, although inorganic sources (e.g., deposition of erosion sediments from uplands or streamflow, mineral sediment deposition during storm events) can also be significant. The organic matter being decomposed and mineralized originates from three primary sources: 1) plants growing at the location plus animal detritus inputs at the location, 2) organic matter transported into the location from higher or upstream locations, and 3) organic matter transported into the location from lower elevations by tidal action and storm surges.

Nutrient content of organic material varies substantially. One major factor influencing the nutrient content is the concentration in the original material. Concentrations vary among plant species, plant parts, and individuals of the same species growing at different locations. For example, both nitrogen (N) and phosphorus (P) concentrations in live *Spartina alterniflora* plants varied with distance from stream edge to interior marsh in a salt marsh in Louisiana. Plants growing near the streambank contained an average of 0.9% N and 0.12% P in their aboveground tissue, compared to 0.7% N and 0.06% P in plants growing 16 m away from the streambank (Buresh et al. 1980). Concentrations of total N and $\text{NH}_3\text{-N}$ in the soil had the reverse pattern, with lowest concentrations 1.5 m from the streambank (0.43% total N) and highest concentrations (0.86%) 24 m from the streambank. These patterns of soil and plant tissue nitrogen concentrations suggest that the streambank plants were likely receiving substantial amounts of nitrogen from the stream water, which offset the lower concentrations in the streambank soil.

There are five primary components to nutrient pools in marsh communities: 1) nutrients contained in the aboveground live plant material, 2) nutrients contained in the aboveground detrital material, including both plant and animal tissues, 3) nutrients contained in belowground organic matter, including live roots and rhizomes and detrital material, 4) mineralized nutrients contained in the soil and sediments, and 5) nutrients contained in standing water (dissolved and particulate). Buresh et al. (1980) reported a standing crop aboveground biomass of 1061 g/m^2 in the *Spartina alterniflora* salt marsh they studied in Louisiana. N concentration of this material averaged 0.79% in June and 0.64% in September, or about 8.4 g N/m^2 in the aboveground plant tissue in June and 6.8 g N/m^2 in September. They also reported that belowground organic matter (macro) averaged 5494 g/m^2 (20 cm depth) at this site. The authors did not report how much of the 5494 g/m^2 belowground organic matter was roots and rhizomes, but a brackish marsh in coastal Louisiana dominated by *Spartina patens* had a root:shoot ratio of 1.11 averaged over a 13-month period, with a maximum of 2.28 in June (Ford and Grace 1998). Two *Spartina alterniflora* marshes in North Carolina had root:shoot ratios of 3.63 (643 g/m^2 aboveground, 2336 g/m^2 belowground) and 4.40 (870 g/m^2 aboveground, 3825 g/m^2 belowground) (Craft et al. 1999). Most of the belowground material (roots and rhizomes) was in the top 10 cm.

Salt marshes typically concentrate most of their roots and rhizomes in the upper soil (Table 4.9) to obtain oxygen for respiration (Craft et al. 1999). Root zone depth for a *Spartina patens* marsh in Louisiana was 30 cm (Ford and Grace 1998) and 40 cm for a *Spartina alterniflora* marsh in Louisiana (Casselmann et al. 1981). In the Louisiana *S. alterniflora* marsh, 65% of the root/rhizome biomass was located in the top 10 cm (Casselmann et al. 1981).

Table 4.9 Distribution of live root and rhizome biomass (g) in a *Spartina alterniflora* salt marsh in Louisiana (data from Casselman et al. 1981).

	Soil Depth (cm)								Total
	00-05	05-10	10-15	15-20	20-25	25-30	30-35	35-40	
Streamside (tall form)									
Roots	80	50	30	25	10	10	5	1	211
Rhizomes	400	215	100	85	70	30	25	10	935
Inland (short form)									
Roots	50	20	20	1	0	0	0	0	91
Rhizomes	130	70	50	45	20	1	0	0	316

Although a majority of root and rhizome biomass (live and dead) is commonly found in the upper 10 cm of coastal marshes, organic matter is generally high even at lower depths and in some cases can be higher at greater depths than in surface layers (Table 4.10). The relatively high organic matter content at lower depths may be the result of low decomposition rates resulting from lower oxygen contents and increased levels of toxic by-products.

Table 4.10 Organic matter (macro and humic) and nitrogen pools in five North Carolina salt marshes. Data taken from Craft et al. (1988).

Marsh	Soil Depth (cm)	Macro-OM (g/m ²)	Macro-OM N (g/m ²)	Macro-OM [N] (%)	Macro-OM C:N Ratio	Humic-OM (g/m ²)	Soil N (g/m ²)	Soil [N] (%)	Soil C (g/m ²)	Soil C:N Ratio
Oregon Inlet	00-10	3,535	25.73	0.73	62.8	150	137.8	0.17	2,066	15.0
Oregon Inlet	10-30	1,798	13.09	0.73	62.8	95	151.2	0.05	2,160	14.9
Snow's Cut	00-10	1,961	14.00	0.71	65.4	501	127.6	0.38	2,938	23.1
Snow's Cut	10-30	1,498	10.70	0.71	65.4	1,423	385.4	0.52	7,814	20.3
Pine Knoll	00-10	1,768	14.36	0.81	55.8	83	37.5	0.04	618	16.5
Pine Knoll	10-30	1,024	8.31	0.81	55.8	90	41.9	0.02	653	15.6
Texas Gulf	00-10	2,834	21.00	0.74	66.2	744	269.9	1.29	4,158	15.4
Texas Gulf	10-30	1,039	7.70	0.74	66.2	1,779	543.8	1.36	8,784	16.2
NC Phosphate	00-10	1,958	17.94	0.92	54.6	883	210.4	1.62	2,808	13.3
NC Phosphate	10-30	2,959	27.10	0.92	54.6	1,320	511.2	1.50	7,793	15.2
Mean	00-10	2,211	18.61	0.78	61.0	472	156.5	0.70	2,518	15.5
Mean	10-30	1,664	13.38	0.78	61.0	941	326.7	0.69	5,440	16.8

Macro-organic matter consists primarily of litter, root, and rhizome biomass. Averaged over five North Carolina salt marshes, the amount of macro-organic matter was greater in the top 10 cm of the marsh soil than in the next 20 cm (Table 4.10). This would be expected based on location of roots and rhizomes and the surface deposition of litter. However, the amount of humic organic matter is generally as high or higher in lower soil depths than in the surface 10 cm. Humic organic matter is organic matter in an advanced state of decomposition. These high amounts in subsurface layers results from a buildup of buried partially-decomposed material and slower decomposition and mineralization rates at depth. Net annual soil accretion rate in a *Spartina patens* marsh in Louisiana, for example, was 0.75 cm (Ford and Grace 1998). The average humic organic matter biomass in the five North Carolina salt marshes was 472 g/m² in the top 10 cm and an average of 470 g/m² per 10-cm in the 10-30 cm depth (Table 4.10).

Organic matter with carbon:nitrogen (C:N) ratios of 10 or less are easily and rapidly decomposed by microbial action. Decomposition is relatively slow when the C:N ratio increases above about 20. Salt

marsh macro organic matter tends to have high C:N ratios (greater than 50), suggesting relatively slow rates of decomposition and mineralization. These high C:N ratios are primarily the result of the large amounts of residual plant structural material contained in the litter. The smaller and the more labile portions of the litter are rapidly removed by action of decomposers and tidal removal, leaving proportionally higher amounts of high-C materials in the litter.

Decomposition and mineralization of organic matter is only one source of nitrogen in salt marsh ecosystems. Nitrogen fixation also occurs, primarily in the marsh soil and particularly in the upper 10 cm (Casselman et al. 1981). An annual nitrogen fixation rate of 5 g N/m² was observed in inland stands of *Spartina alterniflora* (short form) in coastal Louisiana and 15 g N/m² in streamside (tall) stands (Casselman et al. 1981). Most of the nitrogen fixation in salt marsh communities has been attributed to nonsymbiotic diazotrophic bacteria (Carpenter et al. 1978; Casselman et al. 1981), with blue-green algal fixation as a secondary source. Fixation rates were 4-8 times higher in the rhizosphere than on the soil surface of a Massachusetts salt marsh (80 mg and 10-20 mg N/m²/d, respectively; Carpenter et al. 1978). Nonsymbiotic diazotrophs are found in marsh soils, both on the surface and in vegetated subsurfaces, and as epiphytes on stems and leaves of marsh plants. Epiphytic nitrogen fixation in a Louisiana *Spartina alterniflora* marsh contributed about 6% of the total annual nitrogen fixation in that marsh (Casselman et al. 1981).

Diazotrophic nitrogen fixation has a high energy requirement. This energy source for the saprophytic diazotrophs in marsh soils is provided by root exudation of carbohydrates and by soil organic matter. The relationship between nitrogen fixation and root density in marsh soils results in the highest rates of nitrogen fixation occurring in the upper 10 cm of the soil, where root biomass and organic matter are the greatest, and then decreasing rates with increasing depth (Carpenter et al. 1978; Teal et al. 1979; Casselman et al. 1981). Of the total annual nitrogen fixed in a Louisiana *Spartina alterniflora* (tall form) marsh, over 80% was fixed in the soil profile (Table 4.11).

Table 4.11 Annual amounts of nitrogen fixed (g N/m²/yr) in a Louisiana *Spartina alterniflora* salt marsh (Casselman et al. 1981).

Mudflat Surface	<i>S. alterniflora</i> leaves/stems		Marsh Soil		Stream Sediments	Total
	Live	Dead	0-10 cm	10-20 cm		
1.56	0.03	0.66	7.70	3.18	0.33	13.46

In addition to total amount, the form of the nitrogen present in marsh soils is also ecologically important. Ammonium and nitrates are rapidly utilized by plants. Ammonium is the primary form of nitrogen produced by biological fixation (Smith 1996:206). Even in the presence of high total nitrogen concentrations in marsh soils, localized available nitrogen depletion can occur when plant uptake of ammonium exceeds the rate at which it becomes available (Casselman et al. 1981). Recent studies have shown that the C:N ratio of the available organic matter is one of only three factors (the other two being bacterial growth rate and nitrate:nitrite supply) controlling production of ammonium in coastal tidal systems (Kraft et al. 2014).

Soil organic matter and nutrient concentrations can vary substantially among coastal marshes as well as by depth, even in marshes within the same region (Table 4.12). In North Carolina salt marsh soils, the amount of soil carbon is often higher at 10-30 cm than at 0-10 cm, but nitrogen content generally decreases with depth. The dominant plant species also affects both organic matter and nitrogen content in these marsh soils. Phosphorus content also generally decreases with depth, but less so than nitrogen (Table 4.12).

Table 4.12 Bulk density (BD), pH, and nutrient levels (g/m²) and concentrations (%) in five North Carolina natural coastal salt marsh soils (Craft et al. 1988).

Marsh	Depth (cm)	BD (g/cm ³)	pH	Carbon (g/m ²) (%)		Nitrogen (g/m ²) (%)		Phosphorus (g/m ²) (%)		Dominant Species
Oregon Inlet	00-10	0.82	4.5	2,066	2.52	137.8	0.17	16.78	0.020	<i>S. alterniflora</i>
Oregon Inlet	10-30	1.50	4.0	2,160	0.72	151.2	0.05	26.97	0.005	<i>S. alterniflora</i>
Snow's Cut	00-10	0.34	4.5	2,938	8.64	127.6	0.38	19.39	0.057	<i>S. alterniflora</i>
Snow's Cut	10-30	0.37	3.4	7,814	10.56	385.4	0.52	34.64	0.047	<i>S. alterniflora</i>
Pine Knoll	00-10	1.03	6.1	618	0.60	37.5	0.04	61.31	0.060	<i>S. alterniflora</i>
Pine Knoll	10-30	1.36	6.5	653	0.24	41.9	0.02	130.70	0.048	<i>S. alterniflora</i>
Texasgulf	00-10	0.21	5.3	4,158	19.80	269.9	1.29	23.05	0.110	<i>J. roemerianus</i>
Texasgulf	10-30	0.20	5.4	8,784	21.96	543.8	1.36	22.44	0.056	<i>J. roemerianus</i>
NC Phosphate	00-10	0.13	4.8	2,808	21.60	210.4	1.62	19.38	0.149	<i>J. roemerianus</i>
NC Phosphate	10-30	0.17	5.0	7,793	22.92	511.2	1.50	22.66	0.066	<i>J. roemerianus</i>
Mean	00-10	0.51	5.0	2,518	10.63	156.5	0.70	27.98	0.079	
Mean	10-30	0.72	4.9	5,440	11.28	326.7	0.69	47.48	0.044	

Spartina coastal marshes are sources of organic materials and sinks for N and P in estuarine waters (Table 4.13; Craft et al. 1989). The marshes that Craft et al. (1989) studied were young marshes, with low pools of organic matter and nutrients. They suggested that the vegetation in young marshes rely on external sources of N (primarily NH₄-N) whereas mature marshes may be sources of NH₄-N for estuarine waters. Phosphate-P varies by season, with levels increasing as temperatures increase and uptake of PO₄-P is relatively low (1-2%) compared to fixation in the soil (Craft et al. 1989).

Table 4.13 Organic matter and nutrient concentrations (μmol/L) in marsh, estuary, inflow, and outflow waters of two North Carolina *Spartina* marshes (Craft et al. 1989).

Nutrient	Inflow	Outflow	Outflow - Inflow	Diff/ Inflow	Marsh	Estuary
Dissolved organic C	1170	1242	72	0.062	1453	1262
Particulate organic C	350	385	35	0.100	537	217
Dissolved organic N	30.8	38.4	7.6	0.247	44	40
Particulate N	40.7	43.2	2.5	0.061	54	62
NH ₄ -N	8.7	7.2	- 1.5	-0.172	11	14
Dissolved organic P	1.6	1.4	- 0.2	-0.125	0.6	1.4
Particulate P	2.7	2.5	- 0.2	-0.074	1.9	2.3
PO ₄ -P	4.5	2.3	- 2.2	-0.489	1.6	3.2

Soils in two North Carolina *Spartina alterniflora* marshes averaged 3.1% and 21.2% organic matter in the top 10 cm and 0.9% and 41.8% in the 10-30 cm depths (Craft et al. 1999). Constructed *Spartina alterniflora* marshes (22-26 years old) in the areas paired with the two natural marshes had lower soil organic matter (2.3% at 10 cm and 1.4% at 10-30 cm, and 8.9% at 10 cm and 1.1% at 10-30 cm; respectively). At least some coastal marshes in Texas have lower organic matter (1.8-2.9%) and nitrogen (0.6-0.7 mg/g) contents in soil than similar marshes along the Atlantic and upper Gulf Coast (Lindau and Hossner 1981).

Concentration of both N and P in tissue of *Spartina alterniflora* in Georgia salt marshes is highest in winter and early spring and decreases during summer because growth occurs at a higher rate than nutrient accumulation (Gallagher et al. 1980). June concentrations of both nutrients are also higher in *S. alterniflora* tissue in Louisiana salt marshes than are concentrations in September (Buresh et al. 1980). Nitrogen supply is a limiting factor in the growth rate of *S. alterniflora*, with the limitation more pronounced in high marsh locations than in creekbank locations (Gallagher et al. 1980). Creekbank plants accumulated 10.7 g N/m² during aboveground growth from minimum to maximum biomass compared to 2.1 g N/m² in high marsh plants.

Buresh et al. (1980) reported a N budget for a *Spartina alterniflora* salt marsh in Louisiana. Aboveground biomass (live and dead) contained 7 g N/m² in September, or 2% of total N in the system. Macro-organic matter (live and dead) in the top 20 cm contained 52 g N/m², or 14% of the total N. The remaining 84% (308 g N/m²) was contained in the soil, primarily in organic form and therefore unavailable for uptake by *S. alterniflora*. Less than 1% of the soil N (3 g N/m²) was inorganic N. Chalmers (1979) reported similar values for a *Spartina alterniflora* salt marsh in Georgia. Aboveground live *Spartina* biomass contained 6 g N/m² in September and 2.6% of total N in the system at the end of one year. Less than 1% of the total nitrogen in the soil was inorganic N.

Two *Spartina alterniflora* marshes in North Carolina contained 90.0 g N/m² and 151.9 g N/m² in the top 10 cm of soil and 26.8 g N/m² and 394.2 g N/m² respectively, at 10-30 cm soil depth (Craft et al. 1999). The corresponding carbon:nitrogen ratios were 21 and 23 at 0-10 cm and 48 and 29 at 10-30 cm. Carbon:nitrogen ratios > 20 are indicative of microbial immobilization of available soil N whereas C:N < 20 suggests that microbial needs are satisfied and sufficient N is available for plant uptake (Craft et al. 1999). The C:N values in these two marshes are above 20, suggesting that N is limited for plant uptake. The C:N value of 20 is a commonly accepted value for N becoming available to plants (Smith 1996). However between 20 and 30 C:N, there can be either N immobilization or N release, with N immobilization almost always occurring when the C:N > 30 (Tisdale and Nelson 1966).

Available phosphorus can also be a nutrient potentially affecting plant productivity. The N:P ratios in the soils of the two North Carolina marshes generally ranged from 1-17 (Craft et al. 1999). N:P ratios < 30-35 indicate that N rather than P is the primary limiting nutrient in these marshes (Craft et al. 1999).

Fertilization studies are one method of determining if nutrient supply is a major factor limiting growth of marsh plants. If application of fertilizer does not increase production, the supply of those nutrients is not likely to be a limiting factor, at least in the form supplied by the fertilizer. Conversely, if fertilization increases production, those nutrients were probably at low enough levels to limit plant growth. Buresh et al. (1980) fertilized plots in a *Spartina alterniflora* salt marsh in Louisiana and found that application of 20 g/m² of N in the form of ammonium sulfate increased aboveground production 28% over control plots (1357 and 1031 g/m², respectively), but addition of 20 g/m² of P (as trisodium phosphate) did not result in increased production (but did increase the P concentration of the tissue). The N fertilization also increased the height of the *S. alterniflora* (64 cm compared to 51 cm on control plots). These results indicate that plant production in at least that salt marsh community was N-limited. The N-treatment also increased belowground (0-20 cm) macro-organic matter by 15% (6322 g/m² on fertilized plots, 5494 g/m² on control plots). The increases in both the above- and belowground components occurred four months after fertilizer application, but tissue N concentration on the fertilized plots increased over control levels within a month of application. One month after application, tissue N concentration was 67% higher on fertilized plots than on control plots (1.35% and 0.81%, respectively). Four months after application, tissue N concentration was 15% higher on fertilized plots (0.86% compared to 0.75% on control plots) and this effect continued one year after application (1.06% on N-fertilized plots, 0.82% on control plots).

Of the N added by fertilization (20 g/m²), 57% was incorporated into tissue by the end of four months (28% in aboveground tissue and 29% in belowground tissues). The remaining 43% was: 1) incorporated into micro-detritus, 2) transferred below 20 cm, 3) removed by nitrification-denitrification, 4) removed by ammonia volatilization, or 5) removed by tidal water (Buresh et al. 1980). In a similar fertilization study in a *Spartina alterniflora* salt marsh in Georgia, half the applied nitrogen could not be accounted for and was assumed to have been removed by tidal action (Chalmers 1979).

Nitrogen concentration in marsh vegetation increases during decomposition (de la Cruz and Gabriel 1974; Hackney and de la Cruz 1980) because microbial proteins and exudates are bound by carbohydrates and phenolic plant constituents (de la Cruz 1975; Rice and Tenore 1981). In contrast, phosphorus concentrations tend to be higher in live plant material than in decomposing plant material (de la Cruz and Hackney 1977).

4.6 Evapotranspiration

Evapotranspiration in *Spartina alterniflora* salt marshes in Georgia averaged 3 mm/day during the summer and rainfall averaged 7 mm/day (Gallagher et al. 1980). Daily aboveground growth rates during this period averaged 7.5 g/m²/day. This equals a water-use efficiency (WUE; g water/g aboveground biomass) of 933 (rainfall) and a transpiration WUE of 310. Transpiration rates also vary by growth form. Mean stomatal conductance by *S. alterniflora* in Louisiana averaged 44% higher in the tall form compared to the short form (118 and 82 mmol/m²/sec, respectively; Pezeshki and DeLaune 1988).

Both productivity and transpiration rates were about equal between tall and short forms of *Spartina alterniflora* in Louisiana early in the growing season, but differences in both rates increased as the growing season progressed. This suggests that the short form, which grows under more stressed conditions, may have experienced lower nutrient uptake during the growing season or increased toxic effects of nutrient accumulation (Pezeshki and DeLaune 1988). Lower nutrient uptake in the short form may also be, in part, the result of lower nutrient supply in areas supporting the short form compared to areas supporting the tall form or shallower rooting depth in the short form (25 cm compared to 50 cm for the tall form; Buresh et al. 1980).

The increased stress to short forms may be the result, in part, of higher free sulfide and NH₄⁺-N levels in the lower-elevation soils supporting this form. Concentrations of both of these ions have been reported to increase with soil depth in soils dominated by the short form, with free sulfide concentration as much as four times as high in soils supporting the short form than adjacent soils supporting the tall form (Pezeshki and DeLaune 1988).

5.0 CONCEPTUAL MODELS OF DECOMPOSITION/MINERALIZATION

The conceptual models presented in this section are based on the site-specific data and the information from the literature presented in Section 4. Many of the values used in the models are estimated values derived from studies in coastal marshes from other areas. As a result, they are likely to be less accurate than site-specific values. However, they are reasonable estimates and serve to illustrate the processes and flows addressed in the models. Should more precise values become available, the current estimated values can be replaced by the more precise values. The purpose of these conceptual models is not to provide highly accurate values for the various components, but rather to illustrate the basic concepts associated with the plant decomposition and mineralization component of San Antonio Bay marshes.

5.1 *Spartina alterniflora* Marshes

These are the marsh communities most exposed to the open bay waters. They are continually flooded, at least at high tide, except for short and infrequent periods of unusually low tides. Some organic matter, sediments, and nutrients may be transported from adjacent higher elevation marshes or upland communities. The magnitude of these inputs relative to the inputs from tidal flows largely depends on site-specific characteristics. The *S. alterniflora* marshes in San Antonio Bay and the eastern side of St. Charles Bay tend to have channels of various depths that separate them from adjacent marshes of other types and from upland communities (Fig. 4.2A). Organic matter, sediment, and nutrient flows into these channels are mixed with water entering the channels from the bay and are subsequently diluted by tidal action. This likely minimizes inputs from uplands into the *S. alterniflora* marshes.

5.1.1 Plant Biomass Dynamics

Because of their location and the resulting continual, or almost continual, flooding, most litter produced in these marshes is flushed out into the open bay. Some build-up of litter can occur because of larger pieces of stems and leaves being trapped by upright stems, both live and dead. The fate of this material depends on the strength of water flow, both tidal and overland flow from adjacent uplands, and depth of inundation in the marsh. As inundation depth increases, more of the detritus material floats to the upper parts of the marsh vegetation structure. The upper stems and leaves have less ability to trap the detritus, resulting in more detrital material being transported out of the marsh and into the bay or into adjacent higher elevation communities, depending on the direction of the flow. Similarly, the stronger the flow rate, the more detritus is moved through the marsh and into the bay or adjacent higher elevation communities.

However, some litter produced in the *S. alterniflora* marshes does remain within the marsh. Our data suggest that this might be on the order of about 30% of annual plant aboveground biomass in well-developed *S. alterniflora* marshes in San Antonio Bay and 5% in decadent stands. Each year, part of this is decomposed and part is incorporated into the soil. Litter decomposition rates can be rapid in marshes (50% decomposition in 30-60 days; Bouchard et al. 2003) and direct burial of litter can also be substantial. In *S. alterniflora* marshes in North Carolina, 13-20% of annual aboveground plant biomass is incorporated (buried) into the soil (Craft 1997; Craft et al. 1999). Some standing dead material also enters the detritus chain, both while it remains attached to the live plant and as it is removed by tidal or storm action. As much as 20-34% of aboveground standing crop biomass is lost directly from the plant into standing water without entering the litter component (Pomeroy & Wiegert 1981:225; Christian et al. 1990; Windham 2001).

Most nutrients contained in litter and standing dead biomass are likely lost to these marshes because of transport into bay waters, either in organic matter or dissolved in tidal water. Most of these nutrients become inputs into the bay nutrient cycles, some of which may return to the marsh in tidal water. The nutrients that are available to the plants are primarily from anaerobic decomposition and mineralization of belowground plant parts, including buried litter, and from tidal (primarily) water moving into the soil. Under saturated conditions, water movement into the soil and among the various soil depths is a relatively slow process. That is one reason there is often a concentration of toxic materials in saturated soils. Oxygen is very limited in saturated soils and it moves slowly in the soil water system.

Belowground components of *Spartina alterniflora* consist of both rhizomes and roots. Root:shoot ratios reported for *S. alterniflora* marshes include 5.18 in Louisiana (Buresh et al. 1980) and 3.63 and 4.40 in two Georgia marshes (Craft et al. 1999). The Georgia marsh with the 3.63 ratio had aboveground biomass of 643 g/m² and 2336 g/m² of roots and rhizomes. Assuming a 3.63 root:shoot ratio and an aboveground biomass of 500 g/m² for the San Antonio Bay *S. alterniflora* marshes, results in an estimated

rhizome + root biomass of 1815 g/m². Casselman et al. (1981) sampled belowground biomass in two *S. alterniflora* marshes in Louisiana, one the tall form and the other the short form, and reported root + rhizome biomass of 1146 g/m² for the tall form and 407 g/m² for the short form.

In addition to the organic matter contained in the rhizomes and roots, the soil contains humic organic matter (organic matter in advanced stages of decomposition). Lindau and Hossner (1981) reported an average organic matter content of 2.4% in the marsh soils they sampled on the Texas Coast. *Spartina alterniflora* marsh soils in North Carolina had an average bulk density of 0.73 in the top 10 cm and 1.08 at 10-30 cm (Craft et al. 1988). Based on these bulk densities and organic matter contents, estimates of the humic organic matter content of the San Antonio Bay *S. alterniflora* soils are 2400 g/m²/10 cm depth and 7776 g/m² in the 10-40 cm depth (assuming the organic matter concentration and bulk densities were the same at 30-40 cm as they were at 10-30 cm).

Root turnover (death) rate in salt marshes has been reported to be 0.5 to 1.2 years (Blum 1993, White and Howes 1994), or an average of 0.85 years (= 1.18 annual replacement rate). Assuming a standing biomass of 1100 g/m² for the rhizomes and roots in the San Antonio Bay *S. alterniflora* marshes (Table 5.1), there would be an annual organic matter input of 1300 g/m² from roots and rhizomes.

Estimated humic organic matter in the upper 40 cm of the soil profile is 10,176 g/m² (Table 5.1). The annual input into this component consists of litter incorporated into soil (100 g/m²) plus rhizome and root biomass turnover (1300 g/m²), or a total of 1,400 g/m² into the top 40 cm of the soil. Macro-organic matter nutrient pools in constructed *S. alterniflora* marshes approximate those of natural marshes within about 30 years, but development of soil carbon and nitrogen pools takes considerably longer (Craft et al. 1988). Therefore the humic organic matter in the soils of the San Antonio Bay *S. alterniflora* may or may not be in equilibrium. The C:N ratios in *S. alterniflora* marsh soil humic organic matter (Table 4.10) are about 29% the magnitude of those in the macro-organic matter, suggesting that about 70% of the original carbon has been lost via decomposition in the humic material. A 70% reduction in weight of the estimated 1400 g/m² of macro-organic matter annually incorporated in the soil (Table 5.1) would result in the equivalent of 420 g/m² of humic biomass added to the top 40 cm each year. Under steady-state conditions, that would suggest a 4% annual turnover (decomposition) rate for humic organic matter.

Table 5.1 Plant biomass (g/m²) input values used in the conceptual mass-flow model of annual decomposition and mineralization dynamics in *Spartina alterniflora* marshes in San Antonio Bay.

Aboveground Biomass

Aboveground plant annual production:	500	(San Antonio Bay, Table 4.4)
Residual surface litter:	150	(30% of production; Litter:NPP Table 4.6)
Litter incorporated into soil (buried):	100	(20% of production; Craft et al. 1999)

Belowground Biomass

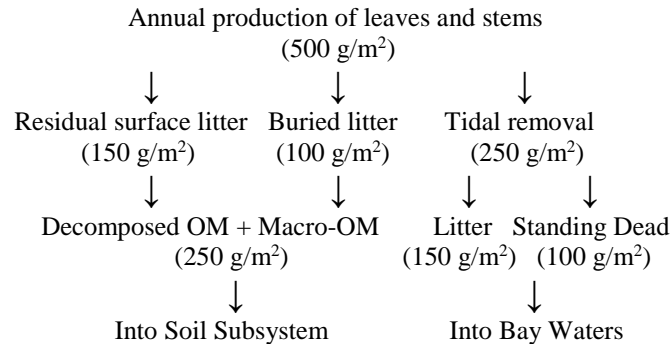
Rhizome + root standing crop (0-40 cm):	1100	(Craft et al. 1999; Casselman et al. 1981)
Rhizome + root annual turnover (0-40 cm):	1300	(1.18 * standing crop)
Humic soil organic matter (0-40 cm):	10176	(2.4% OM; Lindau & Hossner 1981)
Humic organic matter annual turnover:	420	(4% of humic soil organic matter pool)

Exported into Bay

Detritus directly from standing dead:	100	(20% of annual production; Windham 2001)
Detached litter:	150	(Annual production - litter & detritus)

There are two components to plant biomass dynamics in these marshes: production and loss (Table 5.2). Plant biomass is produced each year. Some of this biomass dies each year, some of which is lost from the plant and enters the detritus system and some remains attached to plant standing dead biomass. Some of the dead material is lost from the marsh by tidal or storm removal and some is added to the litter layer. Each year, some of the litter is lost from the marsh by tidal or storm removal, some enters the soil organic component, either as decomposed litter or as buried litter.

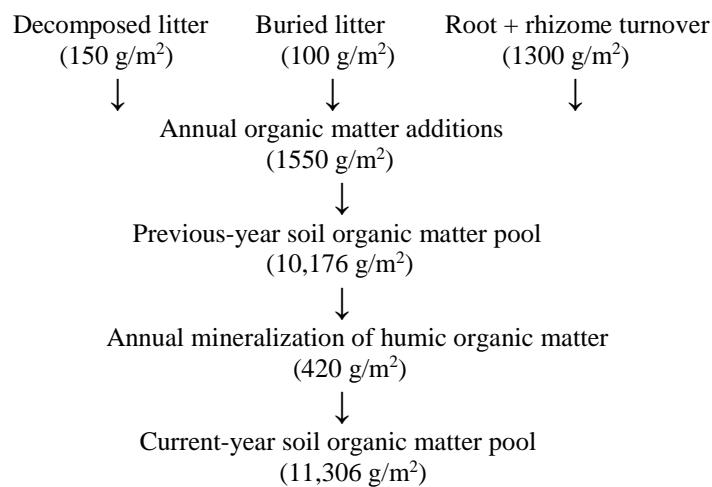
Table 5.2 Conceptual fate and transport flow pathways of aboveground annual plant biomass production in a typical *Spartina alterniflora* marsh around San Antonio Bay.



OM = organic matter.

Belowground biomass dynamics are similar to those of aboveground biomass in that they both are balances between production and loss. Two major differences in belowground from aboveground dynamics in the marshes are 1) the losses from tidal and storm transport are minor in the belowground system, except when sediments are transported out of the marsh, and 2) there is a large organic matter pool belowground that turns over relatively slowly.

Table 5.3 Conceptual fate and transport flow pathways of belowground plant biomass in a typical *Spartina alterniflora* marsh around San Antonio Bay.



The estimated belowground dynamics presented in the conceptual model suggest that humic soil organic matter content in the *Spartina alterniflora* marshes may not yet be in equilibrium. The estimates presented in Table 5.3 indicate an annual increase of 1,130 g/m² (annual organic matter additions – annual mineralization of organic matter), or an annual increase of about 11%. This suggests a moderate age for this conceptual marsh. Comparing humic contents between a 9-yr-old and a 13-yr-old constructed *S. alterniflora* marsh in North Carolina, the annualized increase was 21% per year (Craft et al. 1988). The humic content of the 13-yr-old marsh was 18% of the humic content of its paired natural *S. alterniflora* marsh.

5.1.2 Nitrogen Dynamics

Nitrogen is an important nutrient influencing the productivity of marsh ecosystems. It is used in the conceptual model as the illustration of the fate and transport of a nutrient. The dynamics of other nutrients will be similar to nitrogen in some respects and different in others.

The nitrogen (N) pool in a marsh at any particular time is equal to the N pool in the previous time step plus N inputs from external sources minus N exports from the marsh. In addition to the N pool, there are temporal changes in the N contents of the various components within the overall pool. For simplification in this conceptual model, the estimated N dynamics are restricted to the plant, soil, and water components (Table 5.4).

Table 5.4 Plant and water nitrogen input values used in the conceptual mass-flow model of annual decomposition and mineralization dynamics in *Spartina alterniflora* marshes in San Antonio Bay.

Freshwater Inputs Into Marsh

Annual overland flow (m ³ water/m ² marsh):	50	(Estimate: N ANWR <i>S. alterniflora</i> marsh)
Nitrogen concentration in flow water (ppm):	2.1	(San Patricio Co.; Ockerman 2002)
Annual N content of inflow (g N/m ² marsh):	105	
Average annual rainfall (cm):	87.2	(Austwell)
Nitrogen concentration in rainfall (ppm):	0.17	(San Patricio Co.; Ockerman 2002)
Annual N input from rainfall (g N/m ² marsh):	0.2	

Baywater Dynamics

Average depth of inundation (cm):	31	(San Antonio Bay; McLendon et al. 2019)
N concentration in baywater (ppm):	0.5	(Copano Bay; Ward and Armstrong 1997)
Average N content in standing water (g/m ²):	0.16	

Vegetation Aboveground Biomass

<i>Spartina alterniflora</i> biomass (g/m ²):	500	(San Antonio Bay, Table 4.4)
Nitrogen concentration in biomass (%):	0.8	(<i>S. alterniflora</i> in LA; Buresh et al. 1980)
Nitrogen content (g/m ²):	4	
Translocation of N to roots + rhizomes (g/m ²):	2	(50%; Pomeroy & Wiegert 1981)
Surface litter (g/m ²):	150	(Table 5.1)
Nitrogen concentration in litter (%):	0.5	(Gallagher et al. 1980; Craft et al. 1999)
Nitrogen content in surface litter (g/m ²):	0.8	

Belowground Organic Matter

Annual buried litter (g/m ²):	100	(Table 5.1)
Nitrogen content (0.5%; g/m ²):	0.5	
Root + rhizome standing crop (g/m ²):	1100	(Table 5.1)
Root + rhizome N concentration (%):	0.8	(Craft et al. 1988)
Root + rhizome N content (g/m ²):	8.8	
Annual root + rhizome turnover (g/m ²):	1300	(Table 5.1)
N content of root + rhizome turnover (g/m ²):	10.4	(N concentration = 0.8%)
Soil organic matter (0-40 cm; g/m ²):	10176	(Table 5.1)
N content of soil organic matter (g/m ²):	254	(2.5%; Foth & Turk 1972:145, Craft 1997)
Annual N in humus turnover (g/m ²):	10.5	(420 g/m ² x 0.025)
N content in mineral soil (g/m ² , 0-40 cm):	147.4	(mean of three <i>S. alterniflora</i> marshes)

Annual N Fixation

Mudflat and soil (g/m ² , 0-40 cm):	14.3	(<i>S. alterniflora</i> ; Casselman et al. 1981)
Epiphytic fixation on plants (g/m ²):	0.7	(<i>S. alterniflora</i> ; Casselman et al. 1981)

5.1.2.1 Nitrogen Dynamics in Marsh Waters

External input of N into the marsh system, excluding animal transport, is primarily by means of water flows. Freshwater input of N is by overland surface flow and precipitation. Surface flow varies, both spatially and temporally, in response to a number of environmental factors. For the purposes of the conceptual model, one of the seven watersheds surrounding San Antonio Bay is used as an example. Watershed 24606 includes most of the eastern half of the Aransas National Wildlife Refuge and has a shoreline of about 17.5 km (Booker and McLendon 2015b). Surface runoff from this watershed is estimated to be equal to 15-20% of rainfall in wet years and 5-7% in dry years (Booker and McLendon 2015b), or an average of about 12%. Watershed 24606 has an area of about 6.8 mi², or about 17,600,000 m². Average annual rainfall at Austwell is 872 mm. Assuming average conditions, total annual runoff from Watershed 24606 is estimated at about 15,400,000 m³.

Overland flow from this watershed into the bay is not spatially uniform. Instead, most of the flow is concentrated in a relatively small number of entry points (drainages, swales, and flats). Twenty major entry points may be a reasonable estimate for Watershed 24606. This would result in about 750,000 m³ of runoff water flowing through each point annually. The most extensive area of *Spartina alterniflora* marsh along the edge of Watershed 24606 is located about 4 km south of the Refuge headquarters and covers an area of about 15,000 m². In an average rainfall year, this marsh would therefore receive about 50 m³ of runoff water per square meter of marsh.

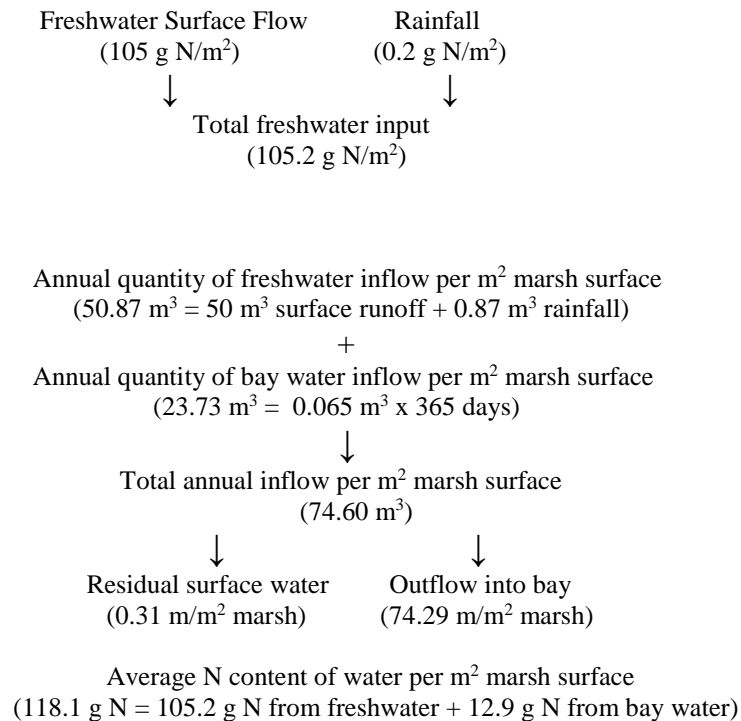
Nitrogen concentrations in surface runoff water at two locations on the central Texas Coast averaged 2.5 ppm total N from a mixed agricultural and rangeland area and 1.7 ppm from two rangeland areas in San Patricio County (Ockerman 2002). These two sites were adjacent to the Aransas River, about 10 miles (16 km) from its discharge point into Copano Bay. At a mixed agricultural and rangeland site in Kleberg and Nueces Counties, N concentration in runoff water averaged 1.3 ppm (Ockerman and Petri 2001). Runoff from this site entered Chiltipin Creek and then into Petronilla Creek before entering Baffin Bay about 12 miles downstream from Chiltipin Creek. These values compare with an inflow N concentration of 1.0 ppm in two North Carolina *Spartina* marshes (Craft et al. 1989).

Nitrogen concentration in rainfall averaged 0.38 ppm at eight locations centered northwest and southwest of Corpus Christi (San Patricio, Kleberg, and Nueces Counties; Ockerman and Livingston 1999; Ockerman and Petri 2001) and 0.17 ppm at three locations in eastern San Patricio County (Ockerman 2002). The eastern San Patricio County value (0.17 ppm) was used in the conceptual model because the sites nearer Corpus Christi were likely higher in nitrogen because of their proximity to petro-chemical and other industrial sites in Corpus Christi and Bishop.

Surface runoff and rainfall are inputs into the marsh. Bay water has both input and export functions. As tides and storm surges come in, bay water moves into the marsh and mixes with the resident water supply. As tides go out and storm surges recede, some of this water leaves the marsh and enters the open bay. Tides and surges therefore function as flushing mechanisms. High rainfall and high levels of surface runoff can also function as flushing mechanisms if the quantity of freshwater input exceeds the storage capacity of the marsh. A value of 0.5 ppm is used in the conceptual model for the average concentration of nitrogen in the bay waters adjacent to the marshes in San Antonio Bay. This is an average concentration reported for Copano Bay (Ward and Armstrong 1997).

In the conceptual model, these flushing actions are viewed in terms of a three-step process (Table 5.5). The first step is to calculate the concentration of the substance of interest, N in this case, in the current pool of marsh surface water. From this, the estimated content of the substance is quantified. The second step is to determine inputs of both water and the substance of interest into the marsh and recalculate the concentration and content of the substance in the resulting mixture. The third step is to determine export levels of the substance from the marsh and recalculate concentration and content of the substance in the marsh following export.

Table 5.5 Conceptual fate and transport of nitrogen in the water of a typical *Spartina alterniflora* marsh around San Antonio Bay. Values are annual totals.



The average difference between high and low tides in the San Antonio Bay area tends to be relatively small (6.5 cm at nearby Port O'Connor). Consequently, daily tidal flushing of standing water in the *S. alterniflora* marshes removes only a portion of the standing water in most of these marshes, although exceptionally high or low tides or storm surges occasionally result in the replacement of most of the standing water with bay water. An average tidal difference of 6.5 cm would potentially replace 21% of average standing water (31 cm) in the marshes.

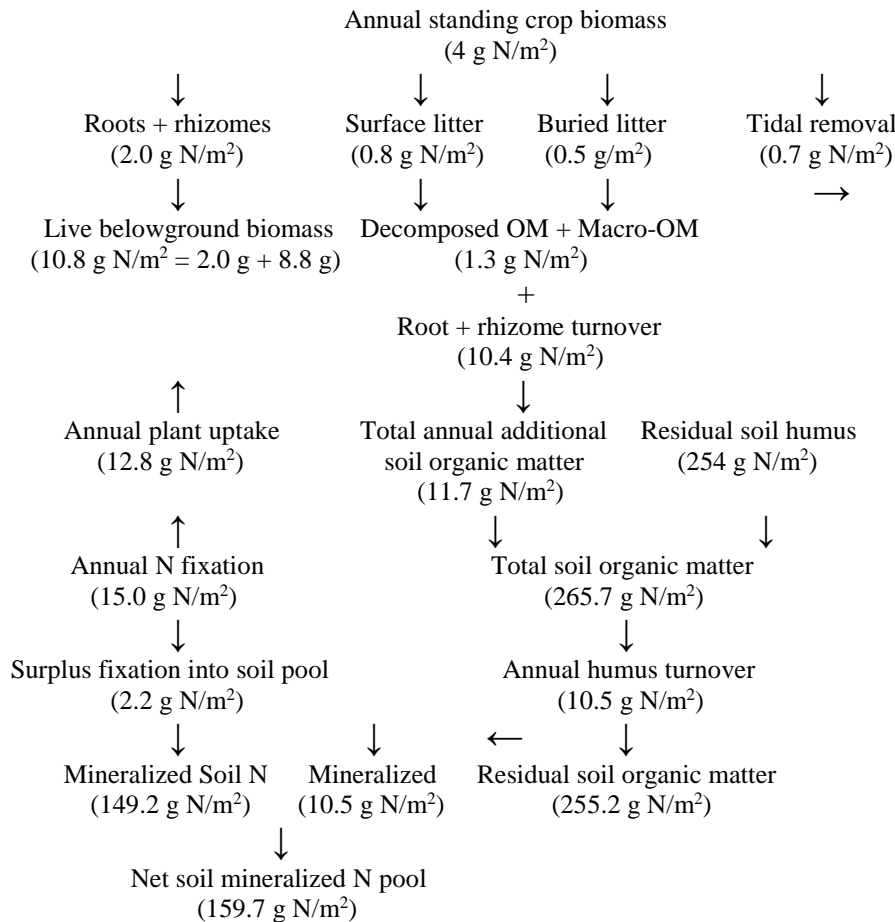
The estimated total annual inflow into the marsh is 74.60 m³ (Table 5.5). Assuming an average depth of surface water in the marsh of 31 cm, 99.6% of the water flowing into the marsh over a period of one year flows back out into the bay. The estimated average N concentration of the flow-through water is 1.6 ppm (= 118 g N/74.6 Mg water). This level of available N would be characteristic of late-seral, N-limited plant communities (McLendon and Redente 1992) and is similar to N concentrations (1.26-1.68 ppm) reported in North Carolina coastal marshes (Craft et al. 1989). Nitrogen limitation has been reported in some *S. alterniflora* marshes (Gallagher et al. 1980).

5.1.2.2 Plant-Soil Nitrogen Dynamics

Like most plants, *S. alterniflora* aboveground biomass varies in tissue N concentration by month and location. Average values reported in the literature include 0.7-0.9% in Louisiana (Buresh et al. 1980) and 0.8-1.0% in Georgia (Gallagher et al. 1980). A value of 0.8% was used in the conceptual model (Table 5.6). Of the amount of N utilized in production of aboveground biomass by *S. alterniflora*, as much as 54% is re-translocated back to belowground structures at senescence of aboveground tissue (Pomeroy and Wiegert 1981:180). Examples of N concentration in marsh litter include 0.53% for *S. alterniflora* in a North Carolina marsh (Craft et al. 1999), 0.44% for *S. alterniflora* in Georgia (Gallagher et al. 1980), and

0.63% for *Phragmites australis* litter in a New Jersey marsh (Windham 2001). An average value of 0.5% was used in the conceptual model (Table 5.6).

Table 5.6 Conceptual fate and transport flow pathways for nitrogen in annual plant production and standing crop biomass in a typical *Spartina alterniflora* marsh, San Antonio Bay.



Total soil N in *S. alterniflora* marshes (adjusted to 0-40 cm depth) has been reported as 116.0 g/m² in a Georgia marsh (Chalmers et al. 1979) and 169.9 g/m² (Craft et al. 1988) and 156.2 g/m² (Craft et al. 1989) in North Carolina marshes. The average of these three values is 147.4 g N/m².

5.1.2.3 Nitrogen Fixation

Nitrogen fixation also occurs in marshes. This occurs on the surface of mud flats, in the upper soil profile, and by epiphytes on plant stems and leaves. Annual N fixation (g N/m²) in a Louisiana *S. alterniflora* marsh were 1.56 on mudflats, 0.69 on plant stems and leaves, 7.70 in the 0-10 cm soil depth, and 3.18 in the 10-20 cm soil depth (Casselmann et al. 1981). Assuming the same linear decrease in fixation in the 20-30 and 30-40 cm soil depths as occurred between the 0-10 to 10-20 cm depths, results in an estimated annual fixation of 15.0 g N/m² over the 0-40 cm soil depth (12.7 g N in soil + 0.7 g N on plant tissue + 1.6 g N on mudflats). This value is similar to the 14.8 g N/m² fixation rate reported for a *S. alterniflora* marsh in Georgia (Pomeroy and Wiegert 1981:180).

5.1.2.4 Summary of Nitrogen Dynamics

The estimated N pools (per m² of marsh surface and to a depth of 40 cm) are: 12.8 g in live vegetation (above- and belowground biomass), 0.8 g in surface litter, 255.2 g in soil organic matter (humus + macro-organic matter), and 159.7 g mineralized soil N (Table 5.6), for a total N pool of 428.5 g N/m². Most (60%) of the N in the plant-soil subsystem is contained in soil organic matter. This compares to a value of 95% for coastal marshes in North Carolina (Craft 1997). Macro-organic matter (decomposed litter, buried litter, root and rhizome turnover) contributed 3% of the annual N pool in the conceptual model, compared to 2-22% in *S. alterniflora* marshes in North Carolina (Craft et al. 1988). Natural marshes along the Texas coast generally have lower soil organic matter contents than organic-rich marshes along the Atlantic Coast (Craft et al. 1998), therefore the lower contributions of macro-organic matter, and soil organic matter overall, in the conceptual model seems reasonable.

In natural marshes older than about 10 years, the rate of mineralization tends to be about equal to rate of N accumulation from new soil organic matter (Craft 1997). The estimated amount of N mineralized annually in the conceptual model was 10.5 g N/m² and the amount added in new soil organic matter was 11.7 g/m² (Table 5.6). The amount of annual mineralized N (10.5 g N/m²) is about the amount characteristic of natural coastal marshes (5-10 g N/m²; Craft 1997). The estimated plant N uptake was 12.8 g N/m², which is similar to the reported value of 10.7 g N/m² for a *S. alterniflora* marsh in Georgia (Gallagher et al. 1980).

5.2 *Distichlis spicata* Marshes

Distichlis spicata marshes generally form the vegetation zone on the inland-side of the *Spartina alterniflora* zone (Fig. 5.1). Around San Antonio Bay, depth of standing water in *D. spicata* marshes averages 12 cm, compared to 30 cm for *S. alterniflora* marshes (McLendon et al. 2020). Because of its higher elevation, *D. spicata* are in less direct contact with open bay water than are *S. alterniflora* marshes.



Figure 5.1 Ecotone between *Distichlis spicata* (left) and *Spartina alterniflora* (right) marshes.

Four *D. spicata* marshes are included in the validation study (McLendon et al. 2020). Two occur on the Delta (west side and east side), one occurs on Welder Flats, and one on the southeast side of Aransas National Wildlife Refuge (southwest side of San Antonio Bay). The Welder Flat marsh is separated from open water by a *S. alterniflora* community and has a short stretch of bare ground on the upland side. The Delta sites do not have adjacent *S. alterniflora* communities but are about 5-50 cm above normal surface of the bay (Fig. 4.2B). The South ANWR community is located on the edge of a shallow basin separated from open bay water by a low sand dune (Figs. 4.3 and 4.4). The first three marshes are sufficiently similar in topography to be represented by the same conceptual model. The West Delta *D. spicata* marsh is used as the basis for this model. This model is similar in many respects to the *S. alterniflora* model and consequently many of the same input values are used in this *D. spicata* model as were used in the *S. alterniflora* model. The conceptual model of the fourth *D. spicata* marsh (South ANWR basin) also has some of these same input values, both differs primarily in the lack of bay water impacts and lower productivity values.

5.2.1 West Delta *Distichlis spicata* Marsh

5.2.1.1 Plant Biomass Dynamics

The West Delta *D. spicata* marsh had an average annual aboveground biomass of 1033 g/m² in the pre-hurricane years (2014-2016; McLendon et al. 2020), all but 3% of which was from *D. spicata*. Because of the near-monoculture composition of the community in those years, the conceptual model is simplified as a single-species model. This level of aboveground production is about 84% of that reported for the species in Louisiana (1162-1291 g/m²; Mitsch and Gosselink 1994).

Root:shoot ratios for mature *D. spicata* include 0.84 (Seliskar and Gallagher 2000), 1.30 (Miyamoto et al. 1996), 1.94 (Seliskar 1987), and 4.40 (Evans et al. 2013). The average of these four values is 2.12, which would result in an estimated belowground (root + rhizome) biomass of 2190 g/m² (= 1033 g/m² aboveground biomass x 2.12).

The *Distichlis spicata* marshes of San Antonio Bay are not directly affected by tidal flushing as are the *S. alterniflora* marshes. However, *D. spicata* marshes generally do contain channels that connect to the open bay, at least some of which are kept open by alligator travel. In dry years, there is insufficient flow of water to flush litter from the marsh into the bay. Consequently, litter accumulates in the marsh. From data collected from the two *D. spicata* marshes sampled on the Delta (McLendon et al. 2019), annual standing crop of surface litter averages about 81% of the previous-year aboveground biomass in years when there is relatively little flushing of the marsh (i.e., dry years or years without storm surges). In other years, biomass of surface litter is equal to only about 2% of the previous-year aboveground biomass. The average, 42% is used as the residual surface litter in the conceptual model (Table 5.7).

Table 5.7. Plant biomass (g/m^2) input values used in the conceptual mass-flow model of annual decomposition and mineralization dynamics in the Delta *Distichlis spicata* marshes, San Antonio Bay.

Aboveground Biomass

Aboveground plant annual production:	1033	(San Antonio Bay, 2014-16; Table 4.4)
Residual surface litter:	434	(42% of production)
Litter incorporated into soil (buried):	145	(14% of production; Craft 1997)

Belowground Biomass

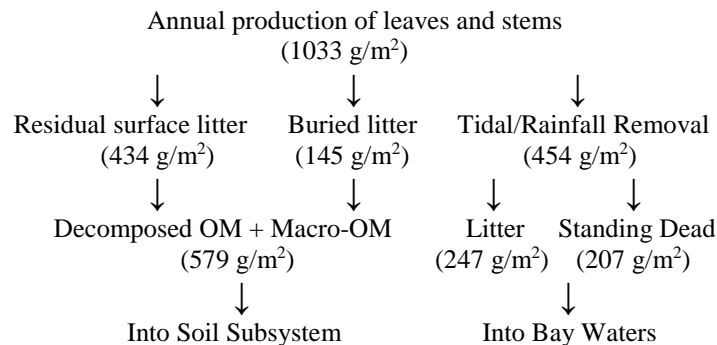
Rhizome + root standing crop (0-40 cm):	2190	(2.12 root:shoot ratio)
Rhizome + root annual turnover (0-40 cm):	2584	(1.18 * standing crop)
Humic soil organic matter (0-40 cm):	10176	(2.4% OM; Lindau & Hossner 1981)
Humic organic matter annual turnover:	420	(4% of humic soil organic matter pool)

Exported into Bay

Detritus directly from standing dead:	207	(20% of annual production; Windham 2001)
Detached litter:	247	(Annual production - litter & detritus)

An estimated $579 \text{ g}/\text{m}^2$ of organic matter enters the soil subsystem each year, on average (Table 5.8), or about 56% of annual plant production. The remaining 44% of annual production is estimated to be removed from the *Distichlis spicata* marsh and moved by water transport into bay waters. This transport can occur through tidal dynamics via the channels through the marsh or it can occur by surface flow following heavy rains. If a *Spartina alterniflora* marsh, or some other type of community, occurs between the *Distichlis spicata* marsh and the open bay, the estimated $454 \text{ g}/\text{m}^2$ of detritus would be transported through that marsh before entering the bay. In such a case, some of the detritus might be trapped in the other marsh community before moving into the bay. The residence time of this detritus in the bayside marsh could vary from days to months, perhaps even years at least in part.

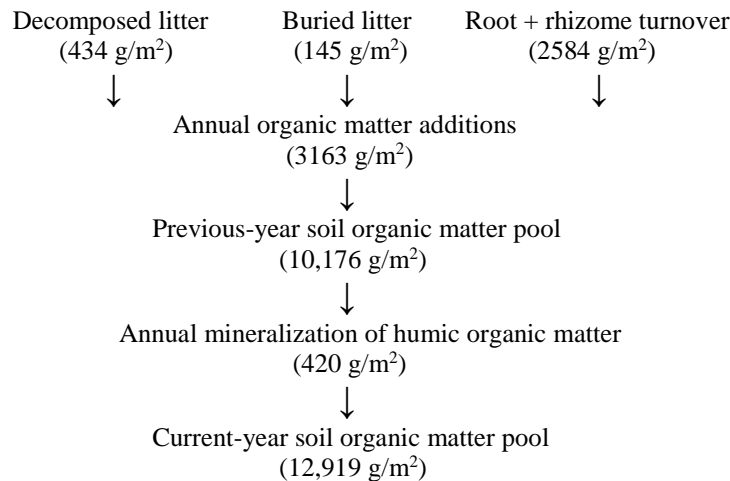
Table 5.8 Conceptual fate and transport flow pathways of aboveground annual plant biomass production in a *Distichlis spicata* marsh on the Guadalupe River Delta, San Antonio Bay.



OM = organic matter.

Belowground, an estimated 3163 g/m² of macro-organic matter is added to the soil each year (Table 5.9). Eventually, this organic matter is further decomposed into humus, while a portion of the humus pool is mineralized. As the humus pool increases over time, a larger amount will be mineralized each year.

Table 5.9 Conceptual fate and transport flow pathways of belowground plant biomass in a *Distichlis spicata* marsh on the Guadalupe River Delta, San Antonio Bay.



5.2.1.2 Nitrogen Dynamics

The *Distichlis spicata* marshes on which the Guadalupe River Delta conceptual model is based do not receive any substantial amounts of surface runoff from surrounding uplands. The Delta is flat and is dissected by shallow channels flowing into the bay. Any surface runoff that does accumulate flows rapidly into the channels with little effect on the marsh. Therefore, the freshwater inputs into the marsh consist of rainfall. As with the *S. alterniflora* marsh, average annual rainfall is 872 mm and contains about 0.2 g N/m² (0.17 ppm; Ockerman 2002).

Some bay water does flow into the *Distichlis spicata* marsh. Using an average high tide of 23 cm (Port O'Connor) and an average marsh surface elevation 27 cm, bay water would not flow onto the marsh surface under average tidal conditions. It would however flow over the marsh under particularly high tides and during storm surges. Bay water does enter the marsh by way of the channels, which range in depth from about 15-90 cm. Consequently, although the marsh surface may not have standing water under average conditions, the subsurface is saturated.

Excluding 2017 (hurricane) and 2019 (wet year), measured depth of inundation in the *Distichlis spicata* marsh plots on the west side of the Delta averaged 4 cm and on the east side averaged 8 cm (McLendon et al. 2020). The reason that standing water occurs in the plots is because of the concave nature of the marsh surface, which allows water to pond in these shallow depressions. The deeper inundation on the east side is likely the result of outflow from the Guadalupe River, the mouth of which is near the east Delta plots. For simplification, the assumption is made that the 4 cm of standing water on the west side is primarily bay water and the 8 cm of standing water on the east side is a 50:50 mix of river and bay water. Averaging these differences over the two sites (6 cm standing water that is 25% river water and 75% bay

water) and assuming N concentrations of 1.1 ppm in river water (Baird et al. 1996) and 0.5 ppm in bay water, the channel inflow water into the marsh is estimated to have a N concentration of 0.7 ppm.

An annual average of 0.25 cm of this inundation would be from rainfall (872 mm/365 days), leaving an average of 5.75 cm of channel (bay) water. This channel water would add 0.04 g N/m² of marsh surface, assuming a N concentration of 0.7 ppm in bay water.

Low tide at Port O'Connor averages 6.5 cm below average high tide. A decrease in channel water level of 6.5 cm would drain the 6 cm deep surface water on the plots. However this is not likely to happen in reality because of the distances the water would need to flow to fully drain. In some areas, the channels may be 50-200 m apart and may have 500-1000 m of channel length before they enter the bay. Therefore the assumption is made in the model that the 0.24 g N/m² from inflow (rainfall + channel water) remains in the marsh.

Plant and water nitrogen input values for the West Delta *Distichlis spicata* conceptual model are presented in Table 5.10. These values are combined with the conceptual fate and transport pathways for aboveground (Table 5.8) and belowground (Table 5.9) plant biomass to develop the conceptual fate and transport flow pathways for nitrogen in plant biomass in the West Delta *Distichlis spicata* marsh (Table 5.11).

Table 5.10. Plant biomass and nitrogen content input values used in the conceptual mass-flow model of annual decomposition and mineralization dynamics in the West Delta *Distichlis spicata* marsh.

Vegetation Aboveground Biomass

<i>Distichlis spicata</i> biomass (g/m ²):	1033	(San Antonio Bay, Table 5.7)
Nitrogen concentration in biomass (%):	0.86	(Bowman et al. 1985; Smith et al. 1992)
Nitrogen content (g/m ²):	8.9	
Translocation of N to roots + rhizomes (g/m ²):	4.4	(50% for <i>S. alterniflora</i>)
Surface litter (g/m ²):	434	(Table 5.7)
Nitrogen concentration in litter (%):	0.43	(50% of tissue N concentration)
Nitrogen content in surface litter (g/m ²):	1.9	

Belowground Organic Matter

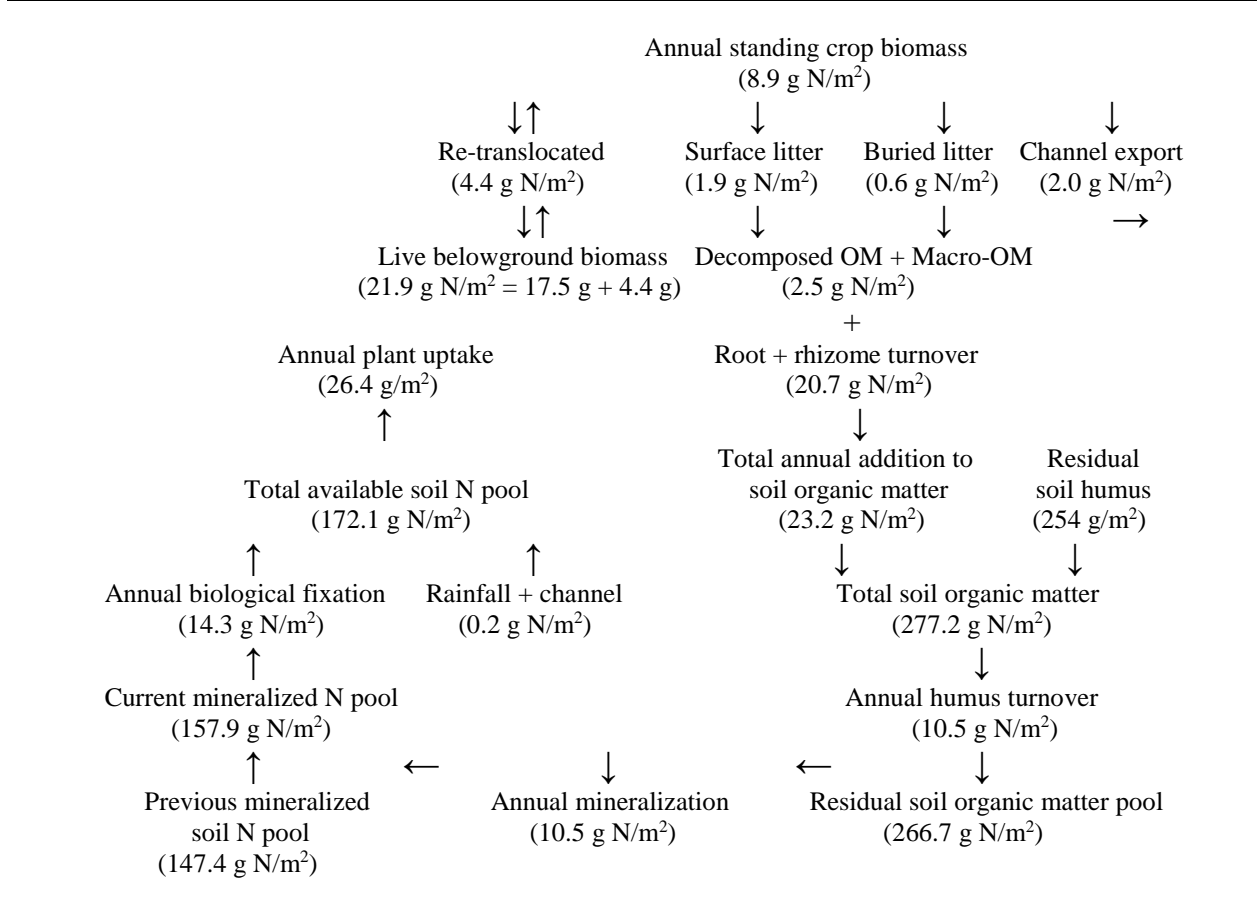
Annual buried litter (g/m ²):	145	(Table 5.7)
Nitrogen content (0.43%; g/m ²):	0.6	
Root + rhizome standing crop (g/m ²):	2190	(Table 5.7)
Root + rhizome N concentration (%):	0.8	(<i>S. alterniflora</i> ; Craft et al. 1988)
Root + rhizome N content (g/m ²):	17.5	
Annual root + rhizome turnover (g/m ²):	2584	(Table 5.7)
N content of root + rhizome turnover (g/m ²):	20.7	(N concentration = 0.8%)
Soil organic matter (0-40 cm; g/m ²):	10176	(2.4% OM; Lindau & Hossner 1981)
N content of soil organic matter (g/m ²):	254	(2.5% N; Foth & Turk 1972:145, Craft 1997)
N content of humus turnover (g/m ²):	10.5	(420 g/m ² x 0.025)
N content in mineral soil (g/m ² ; 0-40 cm):	147.4	(mean of three <i>S. alterniflora</i> marshes)

Exported to Bay or *S. alterniflora* Marsh

Detritus directly from standing dead (g/m ²):	207	(Table 5.7)
Detached litter (g/m ²):	247	(Table 5.7)
Total detritus exported (g/m ²):	454	
N exported in detritus (g/m ²):	2.0	(454 g/m ² x 0.043%)

Non-Organic Matter Inputs

Rainfall + channel water inputs (g/m ²):	0.2	
Mudflat + soil biological fixation (g/m ²):	14.3	(<i>S. alterniflora</i> ; Casselman et al. 1981)

Table 5.11. Conceptual fate and transport flow pathways for nitrogen in annual plant and water subsystems of the West Delta *Distichlis spicata* marsh, San Antonio Bay.

Based on the flows illustrated in the conceptual model (Table 5.11), this *Distichlis spicata* marsh is nitrogen limited, which is not an uncommon condition in coastal marshes (Chalmers 1979; Gallagher et al. 1980; Craft et al. 1999). Annual additions to the available N pool (annual mineralization, annual biological fixation, and rainfall plus channel water transport) sum to 25.0 g N/m², contrasted to an annual plant uptake requirement of 26.4 g N/m², or a 5.3% annual N deficit. The deficit is covered by the current the available N supply in the remaining mineralized N pool. Over time, this surplus would be depleted unless the annual supply of N increases. Based on the estimated values in the conceptual model, this depletion would take about 100 years. It is, of course, not likely that the flows and pool values used in the model will remain at these levels for that long a period.

Although the marsh plant community appears to be N limited, there appears to be an annual increase in the organic N pool. This is because organic matter loss by decomposition and mineralization is less than the supply of organic matter from the plant community. The previous year residual soil humus N pool was 254 g/m² in the model and the current year pool was 266.7 g/m², or an annual increase of 5%. This characteristic of marshes to be organic N accumulators has been shown in field studies (Craft 1997; Craft et al. 1988).

5.2.2 Closed Basin *Distichlis spicata* Marsh

The *Distichlis spicata* marsh at the South ANWR site is located in a closed basin. A sand dune between the basin and the open bay forms a barrier to free movement of bay water into the basin and overland flow water from entering the bay. These conditions existed until late-summer of 2017 when some breaching of the dune occurred during Hurricane Harvey. Subsequent high tides and wind-driven wave action has since reduced the dune to half its pre-hurricane height and the basin is now relatively open to tidal flows. The conceptual model presented in this section is based on pre-hurricane conditions.

In most ways, the basin *D. spicata* marsh is similar to the previously described *D. spicata* marsh. The major differences are related to water transport and the productivity of the plant community. Prior to the hurricane, the basin marshes received little inflow from the bay, but received substantial inflow in wet years from surface runoff from surrounding uplands. This runoff primarily entered the basin by way of a swale extending roughly northwest from the basin (Fig. 4.3).

During dry years, the central basin remains dry especially when there are multiple consecutive dry years, as was the case in the summer of 2014 (Fig. 4.4A). During wet years, the basin fills to a depth of 30-60 cm (Fig. 4.4B). Most of the years of field study at the site were wet years and because the site-specific data for this marsh were collected in these years, the conceptual model will be based on these wet conditions.

Average annual rainfall for 2014-2017 at the Austwell station was 115.4 cm (45.44 inches). This is not an unusual annual average. Annual rainfall averaged 124.4 cm (48.96 inches) over the six years from 2000 through 2007 and 116.1 cm (45.72 inches) for the five years from 1991 through 1995.

The sub-watershed draining into the South ANWR basin covers an estimated 25,000 m². An average annual rainfall of 115.4 cm would result in 288,500 kg of water falling on the sub-watershed. Estimated surface runoff in wet years is estimated to be 17% of annual rainfall (Booker and McLendon 2015b), or about 49,000 kg from the sub-watershed. At a N concentration of 1.7 ppm (Ockerman 2002), the runoff would contain an estimated 83.3 g N. The runoff would be concentrated in the basin, which covers about 20,000 m² (Fig. 4.3), of which about 20% is *Distichlis spicata* marsh. The *D. spicata* marsh has an average elevation of about 20 cm above the bottom of the central depression of the basin. Therefore most of the runoff water would eventually flow through the *D. spicata* marsh and into the central depression, carrying with it most of the dissolved N. Large amounts of suspended N, for example attached to sediments, would be filtered out of the runoff water and deposited in the marsh. Assuming that the suspended N constitutes 40% of the N in runoff water, an estimated 33.3 g N would be deposited in the *D. spicata* marsh each year, or about 0.008 g/m² annually.

5.2.2.1 Plant Biomass Dynamics

During four wet years (2014-2017), the *D. spicata* marsh averaged 816 g/m² of aboveground biomass annually (McLendon et al. 2020). During these years, depth of inundation in the marsh averaged 23 cm. Only small amounts of surface litter were found in the *D. spicata* marsh plots at the South ANWR site (McLendon et al. 2019). The largest amount (mean of 14 g/m²) was recorded in 2015, which was equal to 2% of the previous year aboveground production. It is probable that most of the litter produced in this marsh community is transported into the lower elevations toward the central depression in wet years. In 2014, the plots were sampled twice, first in July and again in September. The July sampling occurred during a dry period (Fig. 4.4A), while the September sampling occurred following substantial rains in August and September (Fig. 4.4B). In July 2014, there was an average of 302 g/m² of surface litter present in the *D. spicata* marsh plots, but none present in September 2014 (McLendon 2014). The surface of the plots was dry in July but had an average of 21 cm standing water in September. This suggests that

surface litter does accumulate during dry periods, but is removed by flotation and water transport during wet periods.

There was an average of 485 g/m² of aboveground biomass in the *D. spicata* marsh plots in July 2014 and 771 g/m² in September (McLendon 2014). Assuming half of the difference between July and September means would have been produced by September even under dry conditions, the estimated annual aboveground production in a dry year would be 628 g/m², or about 77% of average during wet years (816 g/m²). Using this estimate of 628 g/m² of annual aboveground biomass in dry years and 302 g/m² of surface litter in July 2014 results in an estimate of litter production being equal to 48% of aboveground biomass. This compares to the estimate of 44% for the West Delta *Distichlis spicata* marsh (Section 5.2.1.1). The estimate would be 2% of aboveground biomass in wet years, or an overall average of 25%.

Assuming 48% of annual litter production is either on the surface or flushed out by water, 52% is estimated to be either decomposed or buried each year. Allowing for 14% of aboveground production to be buried each year (Craft 1997), results in an annual decomposition rate of 38% (Table 5.12). The input values presented in Table 5.12 were used to develop the conceptual fate and transport flow pathways presented in Table 5.13.

Table 5.12. Plant biomass (g/m²) input values used in the conceptual mass-flow model of annual decomposition and mineralization dynamics in the closed basin *Distichlis spicata* marsh.

Aboveground Biomass

Aboveground plant annual production	816	(San Antonio Bay, 2014-2017; McLendon et al. 2020)
Residual surface litter:	204	(25% of production)
Litter incorporated into soil (buried):	114	(14% of production, Craft 1997)
Decomposed litter into soil:	310	(38% of production)

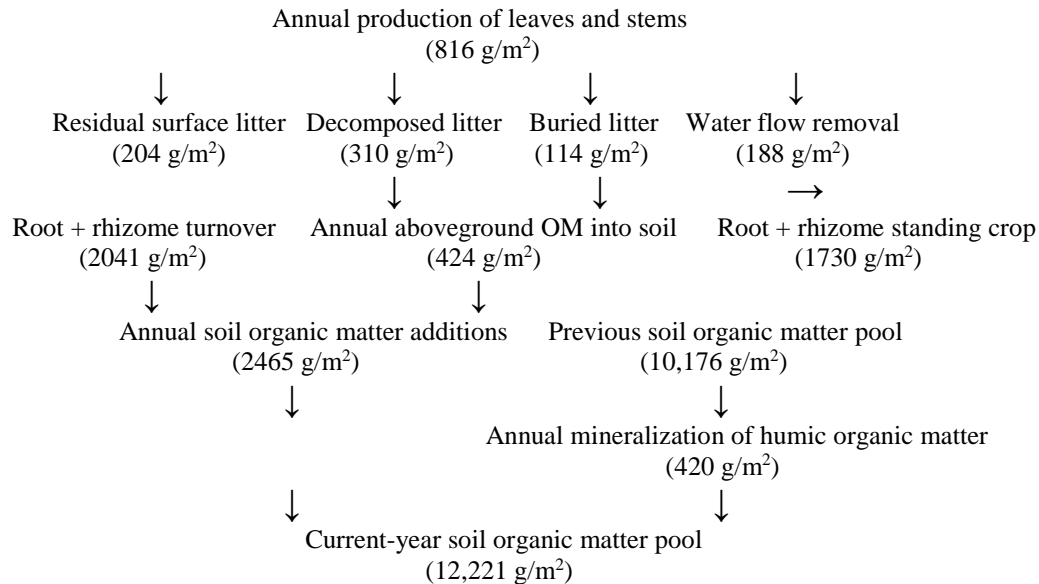
Belowground Biomass

Rhizome + root standing crop (0-40 cm):	1730	(2.12 root:shoot ratio)
Rhizome + root annual turnover (0-40 cm):	2041	(1.18 * standing crop)
Humic soil organic matter (0-40 cm):	10176	(2.4% OM; Lindau & Hossner 1981)
Humic organic matter annual turnover:	420	(4% of humic soil organic matter)

Exported to Adjacent Communities/Depression

Water transported litter:	188	(Production - surface/buried/decomposed litter)
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Table 5.13. Conceptual fate and transport flow pathways of above- and belowground annual plant biomass in the *Distichlis spicata* marsh in the closed basin at the South ANWR site, San Antonio Bay.



5.2.2.2 Nitrogen Dynamics

Plant and water nitrogen input values for the closed basin *Distichlis spicata* conceptual model are presented in Table 5.14. These values are combined with the conceptual fate and transport pathways for above- and belowground plant biomass (Table 5.13) to develop the conceptual fate and transport flow pathways for nitrogen in plant biomass in the closed basin *Distichlis spicata* marsh (Table 5.15).

Biological N fixation in marshes with perennial (or nearly perennial) standing water includes fixation by both soil organisms and by epiphytes on plant stems and leaves. At many of these sites, there is also N fixation on the surfaces of tidal mud flats. The closed basin *Distichlis spicata* marsh does not have tidal mud flats, therefore the annual N contribution estimated from this source (1.56 g/m²) was excluded from this conceptual model, and only 40% of the fixation by epiphytes in the *Spartina alterniflora* was included because of shallower inundation in the *Distichlis spicata* marsh (30 cm and 12 cm, respectively).

Table 5.14. Plant biomass and nitrogen content input values used in the conceptual mass-flow model of annual decomposition and mineralization dynamics in the closed basin *Distichlis spicata* marsh.

Vegetation Aboveground Biomass

<i>Distichlis spicata</i> biomass (g/m ²):	816	(San Antonio Bay; McLendon et al. 2020)
Nitrogen concentration in biomass (%):	0.86	(Bowman et al. 1985; Smith et al. 1992)
Nitrogen content (g/m ²):	7.0	
N translocation to roots + rhizomes (g/m ²):	3.5	(50% for <i>S. alterniflora</i>)
Surface litter (g/m ²):	204	(Table 5.12)
Nitrogen concentration in litter (%):	0.43	(50% of tissue N concentration)
Nitrogen content in surface litter (g/m ²):	0.9	

Belowground Organic Matter

Annual buried litter (g/m ²):	114	(Table 5.12)
Nitrogen content (0.43%; g/m ²):	0.5	
Annual decomposed litter (g/m ²):	310	(Table 5.12)
N concentration in decomposed litter (%):	0.43	
N content in decomposed litter (g/m ²):	1.3	
Root + rhizome standing crop (g/m ²):	1730	(Table 5.12)
Root + rhizome N concentration (%):	0.8	(<i>S. alterniflora</i> ; Craft et al. 1988)
Root + rhizome N content (g/m ²):	13.8	
Annual root + rhizome turnover (g/m ²):	2014	(Table 5.12)
N content of root + rhizome turnover (g/m ²):	16.1	(N concentration = 0.8%)
Soil organic matter (0-40 cm; g/m ²):	10176	(2.4% OM; Lindau & Hossner 1981)
N content of soil organic matter (g/m ²):	254	(2.5% N; Foth & Turk 1972:145, Craft 1997)
N content of annual humus turnover (g/m ²):	10.5	(420 g/m ² x 0.025)
N content in mineral soil (g/m ² ; 0-40 cm):	147.4	(mean of three <i>S. alterniflora</i> marshes)

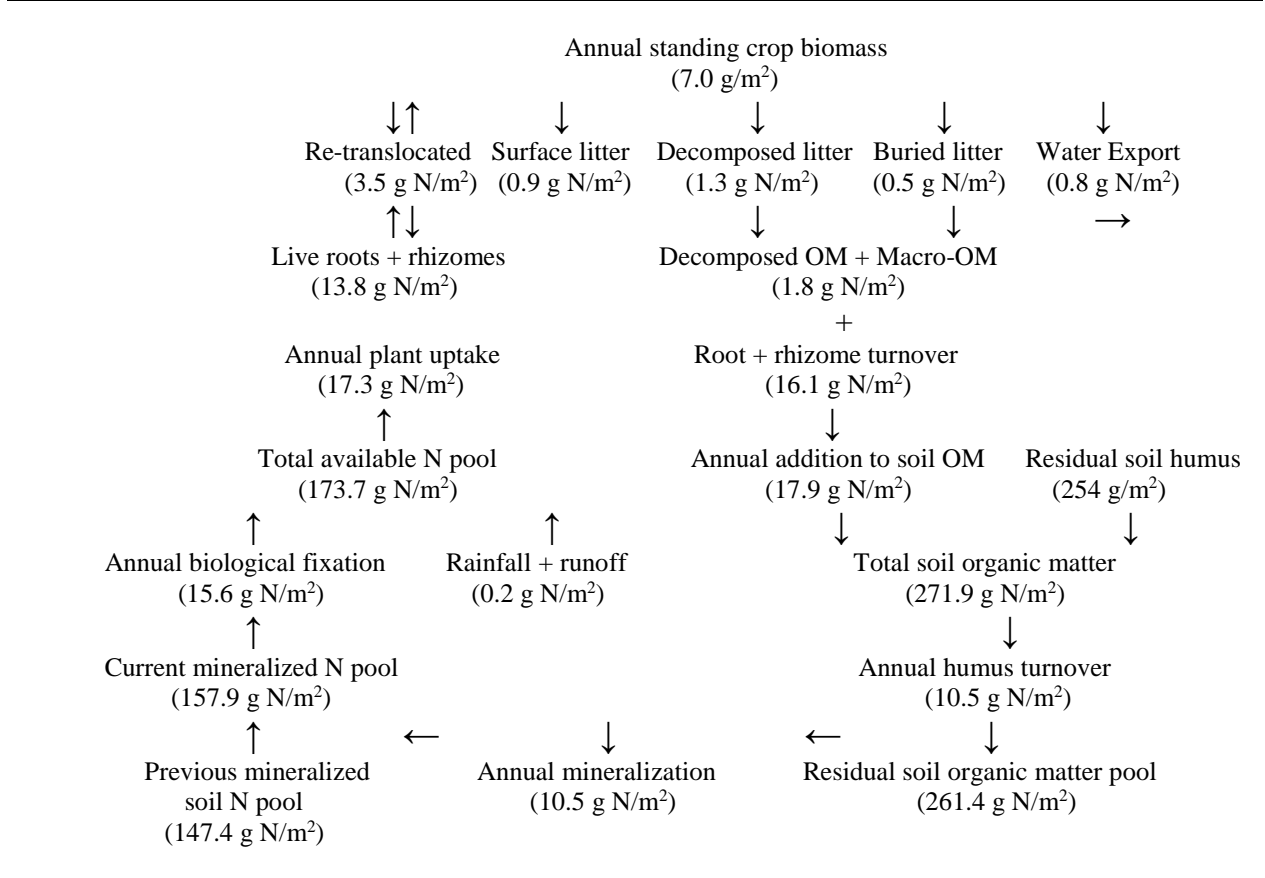
Exported to Adjacent Communities or Depression

Water transported litter (g/m ²):	188	(Table 5.12)
N concentration in litter (%):	0.43	(50% of tissue N concentration)
N content of water transported litter (g/m ²):	0.8	

Non-Organic Matter Inputs

N in rainfall (g/m ²):	0.2	(115 cm rainfall/m ² ; 0.17 ppm N)
N retained from surface runoff (g/m ²):	0.01	
Biological fixation in soil (g/m ²):	15.0	(estimated from Casselman et al. 1981)
Biological fixation by epiphytes (g/m ²):	0.6	(40% of fixation in <i>S. alterniflora</i> marsh)

Table 5.15. Conceptual fate and transport flow pathways for nitrogen in annual plant and water subsystems of the closed basin *Distichlis spicata* marsh, South ANWR site, San Antonio Bay.



Unlike the Delta *Distichlis spicata* marsh, the conceptual model suggests that the closed basin *D. spicata* marsh is not nitrogen limited. Total annual additions to the available N pool (annual mineralization, annual biological fixation, and rainfall plus runoff) are 26.3 g N/m^2 , compared to an annual plant uptake of 17.3 g N/m^2 . The primary reason for the difference in the N balance in the two marshes is the productivity of the two marshes. The lower plant production in the closed basin marsh requires less available soil N, but the N inputs into the two marshes are approximately equal ($25.0 \text{ g N/m}^2/\text{yr}$ in the Delta marsh and $26.3 \text{ g N/m}^2/\text{yr}$ in the closed basin marsh).

In the closed basin marsh, the soil N pool (organic and mineralized) is estimated to be 419.3 g N/m^2 and the plant system (above- and belowground) is estimated to contain 20.8 g N/m^2 . An additional 15.8 g N/m^2 is estimated to occur in the system as biologically-fixed N and N within soil water. Based on these estimates, the plant community in this marsh contains only 4.6% of the N in the plant-soil subsystem.

If indeed, as the values in the conceptual model suggest, this marsh is not N limited, some other factor or factors must be responsible for limiting the productivity of the plant community. In this case, it may likely be depth of inundation. Optimum depth for *D. spicata* is reported to be 5-7 cm (Shiflet 1963), although *D. spicata* was most productive in the San Antonio Bay validation plots when water depth was 6-13 cm (McLendon et al. 2020). At the time of vegetation sampling, water depth averaged 23 cm over the years 2014-2017 in the South ANWR *D. spicata* marsh, or 2-4 times the optimum depth for the species.

5.3 *Spartina patens* Marshes

Spartina patens marshes typically occur in the marsh zone directly above the *Distichlis spicata* zone, approximately 2 cm higher in elevation than the *Distichlis spicata* marsh, or 12-14 cm higher than the *Spartina alterniflora* marsh (Adams 1963). Around San Antonio Bay, depth of water averages 9 cm in *S. patens* marshes, compared to 12 cm for *D. spicata* marshes and 30 cm for *S. alterniflora* marshes (McLendon et al. 2020).

Three areas of *Spartina patens* marsh are included in the San Antonio Bay validation sampling: one on each side (east and west) of the Delta and one at the South ANWR site. The two Delta sites are similar in most respects and one conceptual model is used to represent both. *Spartina patens* is most abundant at the South ANWR site along the upper inland side of the dune that separates the basin from the open bay. It occurs as a near-monoculture on the south end of the dune and as the dominant species in mixtures with *Distichlis spicata* and *Phragmites australis* in the mid- and north ends of the dune. *Spartina patens* marshes also occur in less productive stands on the northwest corner of the basin. The *S. patens* marsh on the south end of the dune is used as the basis for the closed basin conceptual model.

5.3.1 West Delta *Spartina patens* Marsh

5.3.1.1 Plant Biomass Dynamics

The conceptual model was developed as a single-species model, given the dominance of the marsh vegetation by *S. patens*. The West Delta *S. patens* marsh averaged 1182 g/m² annual aboveground biomass in the pre-hurricane years (2014-2016), of which 86% was *S. patens* (McLendon et al. 2020). This is substantially higher than values reported for *S. patens* marshes in New Jersey (694 g/m²; Windham 2001) and Louisiana (460 g/m²; Ford and Grace 1998) but less than the peak live biomass value (1376 g/m²) reported for a *S. patens* marsh in Louisiana (Hopkinson et al. 1978).

Less of the annual litter production in *Spartina patens* marshes is flushed out by channel water than in adjacent *Distichlis spicata* marshes because the *S. patens* marshes are located at higher elevations on the Guadalupe River Delta and hence water depth across the *S. patens* marsh is less. In relatively dry years, accumulated surface litter biomass averaged 1028 g/m², or 118% of estimated previous-year aboveground biomass (McLendon et al. 2019). In wet years, accumulated surface litter biomass averaged only 58 g/m², or 5% of previous-year aboveground biomass. The mean of the two values (62%) was used as the residual surface litter proportion in the conceptual model (Table 5.16). The fate of the remaining 38% of annual aboveground production was assumed to have been a combination of entry into the soil, as decomposed litter and buried litter, and exported from the marsh by flushing through surface water channels. An estimated 24% of annual aboveground production was exported as litter from the *Distichlis spicata* Delta marsh by tidal action (247 g/m²; Table 5.8). Depth of standing water in the West Delta *S. patens* marsh averaged 73% of that in the West Delta *D. spicata* marsh (McLendon et al. 2019). This proportion (73%) was used to estimate the amount of litter exported by flushing from the *S. patens* marsh (18% = 0.24 x 0.73).

Table 5.16 Plant biomass (g/m^2) input values used in the conceptual mass-flow model of annual decomposition and mineralization dynamics in the Delta *Spartina patens* marshes, San Antonio Bay.

Aboveground Biomass

Aboveground plant annual production:	1182	(San Antonio Bay, 2014-16; McLendon et al. 2020)
Residual surface litter:	733	(62% of production)
Litter incorporated into soil (buried):	165	(14% of production; Craft 1997)
Litter exported by flushing:	263	(18% of production)
Current litter decomposed in current year:	21	(production - residual, buried, exported litter)

Belowground Biomass

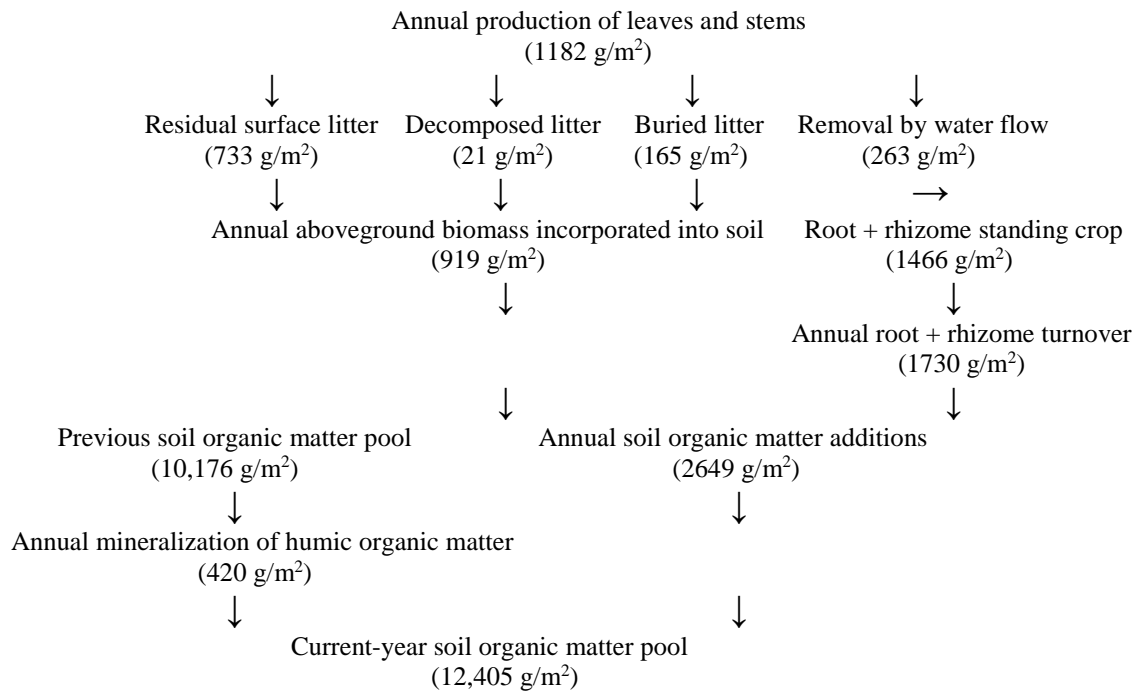
Rhizome + root standing crop (0-40 cm):	1466	(1.24 root:shoot ratio)
Rhizome + root annual turnover (0-40 cm):	1730	(1.18 * standing crop)
Humic soil organic matter (0-40 cm):	10176	(2.4% OM; Lindau & Hossner 1981)
Humic organic matter annual turnover:	420	(4% of soil organic matter pool)

Total amount of litter estimated to undergo decomposition annually was $754 \text{ g}/\text{m}^2$ (residual surface litter + current litter decomposed in current year; Table 5.16). This was equal to 64% of annual aboveground production. This compares to a value of 43% for a *Spartina patens* marsh in New Jersey (Windham 2001). A higher decomposition rate in the San Antonio Bay marsh seems reasonable because of warmer temperatures in Texas and the rate of decomposition in marshes, as in other ecosystems, increases as temperature increases (Ford and Grace 1998).

Root:shoot ratios have been reported for *Spartina patens* in Louisiana (1.11; Ford and Grace 1998) and New Jersey (1.37; Windham 2001) coastal marshes. In both cases, maximum rooting depth of *S. patens* was reported to be 30 cm. The root:shoot ratio used in the conceptual models for *S. patens* was 1.24 (Table 5.16), and average of the two reported values.

An estimated $919 \text{ g}/\text{m}^2$ of aboveground biomass enters the soil subsystem each year (Table 5.17), or 78% of annual aboveground production. This total includes the residual litter component which is gradually decomposed over the course of the year. To this addition from the aboveground plant system is added an estimated $1730 \text{ g}/\text{m}^2$ of belowground biomass annually, for a total organic matter input into the soil subsystem of $2649 \text{ g}/\text{m}^2$. Assuming an annual mineralization of $420 \text{ g}/\text{m}^2$ of humus, the total soil organic matter component is estimated to increase by about 22% per year.

Table 5.17 Conceptual fate and transport flow pathways of annual plant biomass production in a West Delta *Spartina patens* marsh, San Antonio Bay. Values are from Table 5.16.



5.3.1.2 Nitrogen Dynamics

Non-organic sources of N input into West Delta *Spartina patens* marsh are similar to those of the West Delta *Distichlis spicata*. An estimated 0.2 g N is supplied annually by rainfall. An annual average of 0.04 g N/m² was estimated to enter the *D. spicata* marsh by way of channel water and the average depth of surface water in the *S. patens* marsh is only about 73% of that of the adjacent *D. spicata* marsh (Section 5.3.1.1). Assuming that only 73% as much N enters the *S. patens* marsh by channel flow as enters the *D. spicata* marsh, this would equal 0.03 g N/m² annually.

Plant and water N input values are presented in Table 5.18. Aboveground biomass was estimated to have a tissue N concentration of 1.12%, which was the mean of three *Spartina* species: *S. alterniflora* (0.85; Buresh et al. 1980, Gallagher et al. 1980), *S. densiflora* (1.15; Jacobo et al. 2015), and *S. spartinae* (McAtee et al. 1979, Meyer 1982, Garza et al. 1994).

Table 5.18 Plant biomass and nitrogen content input values used in the conceptual mass-flow model of annual decomposition and mineralization dynamics in the West Delta *Spartina patens* marsh.

Vegetation Aboveground Biomass

<i>Spartina patens</i> biomass (g/m ²):	1182	(San Antonio Bay, Table 5.16)
Nitrogen concentration in biomass (%):	1.12	(mean of three <i>Spartina</i> species)
Nitrogen content (g/m ²):	13.2	
Translocation of N to roots + rhizomes (g/m ²):	6.6	(50% for <i>S. alterniflora</i>)
Surface litter (g/m ²):	733	(Table 5.16)
Nitrogen concentration in litter (%):	0.56	(50% of tissue N concentration)
Nitrogen content in surface litter (g/m ²):	4.1	

Belowground Organic Matter

Buried + decomposed litter (g/m ²):	186	(Table 5.16)
Nitrogen content (0.56%; g/m ²):	1.0	
Root + rhizome standing crop (g/m ²):	1466	(Table 5.16)
Root + rhizome N concentration (%):	0.8	(<i>S. alterniflora</i> ; Craft et al. 1988)
Root + rhizome N content (g/m ²):	11.7	
Annual root + rhizome turnover (g/m ²):	1730	(Table 5.16)
N content of root + rhizome turnover (g/m ²):	13.8	(N concentration = 0.8%)
Soil organic matter (0-40 cm; g/m ²):	10176	(2.4% OM; Lindau & Hossner 1981)
N content of soil organic matter (g/m ²):	254	(2.5% N; Craft 1997)
Annual N in humus turnover (g/m ²):	10.5	(420 g/m ² x 0.025)
N content in mineral soil (g/m ² ; 0-40 cm):	147.4	(mean of three <i>S. alterniflora</i> marshes)

Exported to Adjacent Marsh Community

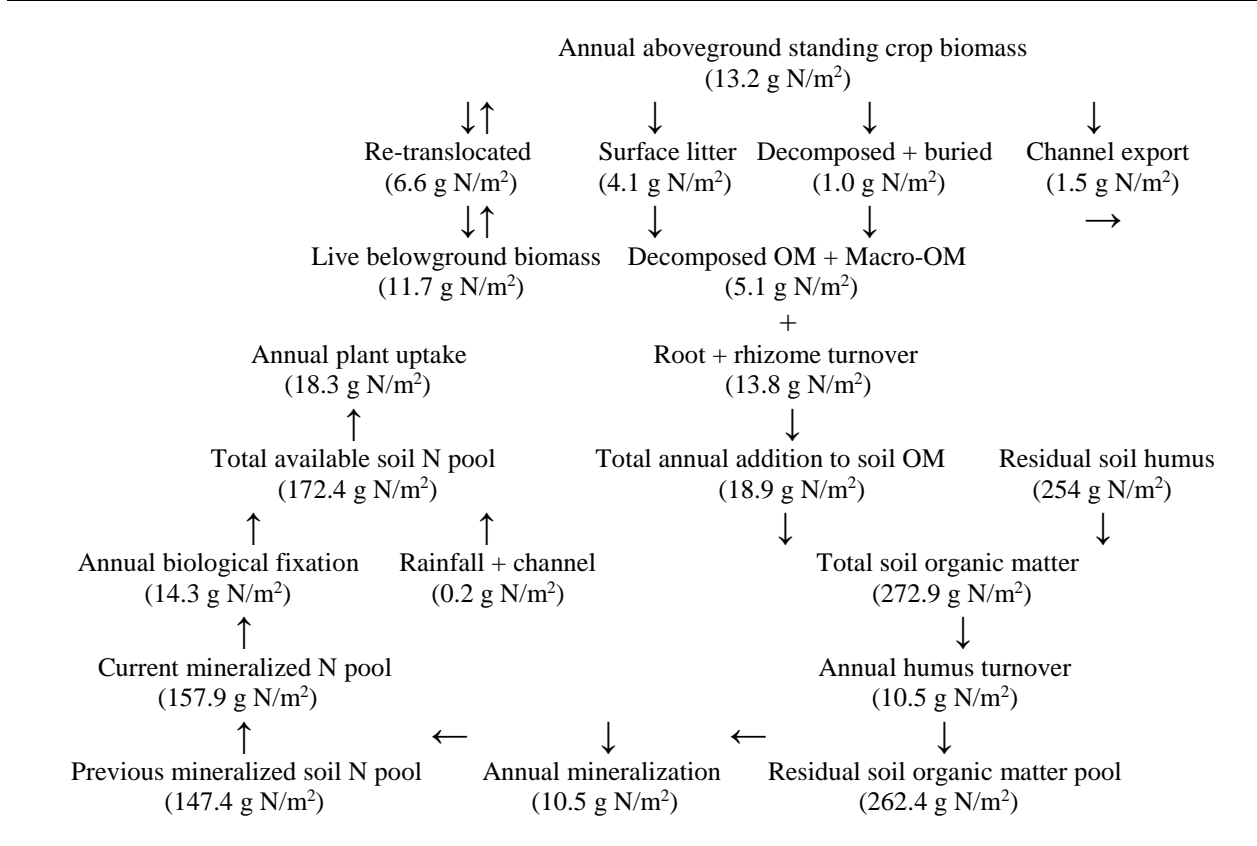
Water transported litter (g/m ²):	263	(Table 5.16)
N concentration in litter (%):	0.56	(50% of tissue N concentration)
N content in exported litter (g/m ²):	1.5	

Non-Organic Matter Inputs

Rainfall + channel water inputs (g/m ²):	0.2	
Mudflat + soil biological fixation (g/m ²):	14.3	(<i>S. alterniflora</i> ; Casselman et al. 1981)

Based on the flows illustrated in the conceptual model (Table 5.19), the West Delta *Spartina patens* marsh is not N-limited. Annual plant uptake is estimated to be 18.3 g N/m² and annual release of available N (mineralized soil N, biological fixation, rainfall and channel water N input) is estimated to be 25.0 g N/m². This is in contrast to the adjacent West Delta *Distichlis spicata* marsh (Table 5.11), which was estimated to be N-limited. The primary difference between the two marshes, as per the respective conceptual models, is belowground standing crop biomass. Root plus rhizome standing crop biomass in the *D. spicata* marsh was estimated to be 2190 g/m², compared to 1466 g/m² in the *S. patens* marsh. The respective tissue N contents were 17.5 and 11.7 g N/m².

Table 5.19. Conceptual fate and transport flow pathways for nitrogen in annual plant and water subsystems of the West Delta *Spartina patens* marsh, San Antonio Bay. Values are from Table 5.18.



5.3.2 Closed Basin *Spartina patens* Marsh

The South ANWR site *Spartina patens* marsh that occurs along the inland side of the dune is the highest elevation marsh in that closed basin system, with elevations 25-40 cm above the central basin and an average of 15 cm above the *Distichlis spicata* marsh at that site (Section 5.2.2). The *S. patens* marsh is best developed along the south portion of the dune, where it occurs almost as a monoculture of *S. patens*. That south part of the marsh is used as the basis for the conceptual model for the closed basin *S. patens* marsh.

The dune on the east side of the basin formed a barrier to most direct water flow from the basin into the bay and from the bay into the basin. The dune was weakened by Hurricane Harvey in 2017 and had eroded sufficiently by 2018 that bay water began flowing freely into the basin. Because of these hydrologic changes, the conceptual model of this marsh is based on conditions during 2014-2017, when the dune still functioned as a barrier.

Depth of water averaged 6 cm in the marsh between 2014-2017, ranging from an average of 1 cm in 2016 to 12 cm in 2017, one month after the hurricane (McLendon et al. 2020). Aboveground biomass averaged 1206 g/m² during these years, 97% of which was *Spartina patens*, and annual standing crop of surface litter averaged 291 g/m². In the closed basin *D. spicata* marsh, an estimated 23% of annual aboveground production was removed from the marsh by water transport (Table 5.12). The *D. spicata* marsh is located

at a lower elevation than the *S. patens* marsh and would therefore be expected to have a larger amount of surface litter flushed by surface water. The amount transported from the *S. patens* marsh was therefore estimated to be 18% of aboveground production, or 217 g/m². Buried litter was estimated to be 14% of aboveground biomass (Craft 1997), or 169 g/m². Estimated annual incorporation of decomposed litter is equal to total aboveground annual production minus the sum of standing crop, flushed, and buried litter. That estimate of decomposition is 529 g/m², or 44% of annual aboveground production. This compares to an annual decomposition rate of 43% in a New Jersey *Spartina patens* marsh (Windham 2001).

The same root:shoot ratio (1.24) and annual root and rhizome turnover rate (1.18) were used for the closed basin *S. patens* marsh as were used for the West Delta *S. patens* marsh. These result in estimates of 1495 g/m² average annual standing crop of roots and rhizomes and 1764 g/m² annual turnover of roots and rhizomes (Table 5.20).

Table 5.20 Plant biomass (g/m²) input values used in the conceptual mass-flow model of annual decomposition and mineralization dynamics in the closed basin *Spartina patens* marsh.

Aboveground Biomass

Aboveground plant annual production:	1206	(San Antonio Bay; McLendon et al. 2020)
Residual surface litter:	291	(San Antonio Bay; McLendon et al. 2019)
Litter incorporated into soil (buried):	169	(14% of aboveground production; Craft 1997)
Decomposed litter into soil:	529	(Production - surface, buried, flushed litter)

Belowground Biomass

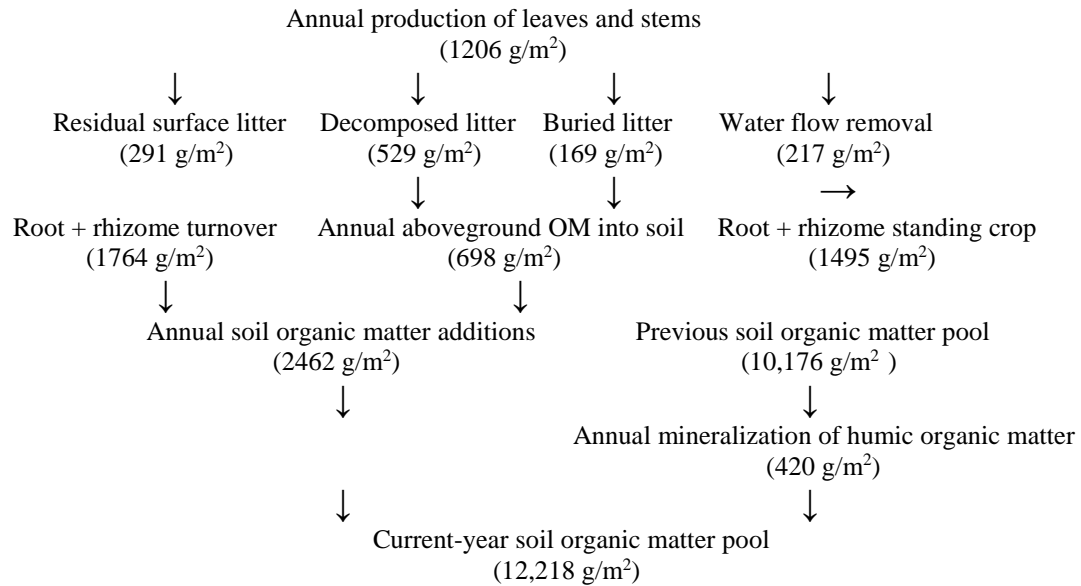
Rhizome + root standing crop (0-40 cm):	1495	(1.24 root:shoot ratio)
Rhizome + root annual turnover (0-40 cm):	1764	(1.18 * standing crop)
Humic soil organic matter (0-40 cm):	10176	(2.4% OM; Lindau & Hossner 1981)
Humic organic matter annual turnover:	420	(4% of humic soil organic matter)

Exported to Adjacent Communities/Depression

Water transported litter:	217	(18% of aboveground production)
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The above- and belowground input values (Table 5.20) were used to prepare the fate and transport flow pathways (Table 5.21).

Table 5.21 Conceptual fate and transport flow pathways of above- and belowground annual plant biomass in the *Spartina patens* marsh in the closed basin at the South ANWR site, San Antonio Bay.



Plant and water nitrogen input values for the closed basin *Spartina patens* conceptual model are presented in Table 5.22. These values are combined with the conceptual fate and transport pathways for above- and belowground plant biomass (Table 5.21) to develop the conceptual fate and transport flow pathways for nitrogen in plant biomass in the closed basin *Spartina patens* marsh (Table 5.23).

Because of its location on the upper portion of the dune, little runoff water flows into this *S. patens* marsh. Consequently, the only external source of N into the marsh is from rainfall. Likewise, the topographic position of this marsh excludes the presence of mudflats. Therefore, biological N fixation is limited to fixation in the soil.

Table 5.22. Plant biomass and nitrogen content input values used in the conceptual mass-flow model of annual decomposition and mineralization dynamics in the closed basin *Spartina patens* marsh.

Vegetation Aboveground Biomass

<i>Spartina patens</i> biomass (g/m ²):	1206	(San Antonio Bay; Table 5.21)
Nitrogen concentration in biomass (%):	1.12	(Mean of three <i>Spartina</i> species)
Nitrogen content (g/m ²):	13.5	
N translocation to roots + rhizomes (g/m ²):	6.8	(50% for <i>S. alterniflora</i>)
Surface litter (g/m ²):	291	(Table 5.20)
Nitrogen concentration in litter (%):	0.56	(50% of tissue N concentration)
Nitrogen content in surface litter (g/m ²):	1.6	

Belowground Organic Matter

Annual buried + decomposed litter (g/m ²):	698	(Table 5.20)
Nitrogen content (0.56%; g/m ²):	3.9	
Root + rhizome standing crop (g/m ²):	1495	(Table 5.20)
Root + rhizome N concentration (%):	0.8	(<i>S. alterniflora</i> ; Craft et al. 1988)
Root + rhizome N content (g/m ²):	12.0	
Annual root + rhizome turnover (g/m ²):	1764	(Table 5.20)
N content of root + rhizome turnover (g/m ²):	14.1	(N concentration = 0.8%)
Soil organic matter (0-40 cm; g/m ²):	10176	(2.4% OM; Lindau & Hossner 1981)
N content of soil organic matter (g/m ²):	254	(2.5% N; Craft 1997)
Annual N in humus turnover (g/m ²):	10.5	(420 g/m ² x 0.025)
N content in mineral soil (g/m ² ; 0-40 cm):	147.4	(mean of three <i>S. alterniflora</i> marshes)

Exported to Adjacent Marsh Community

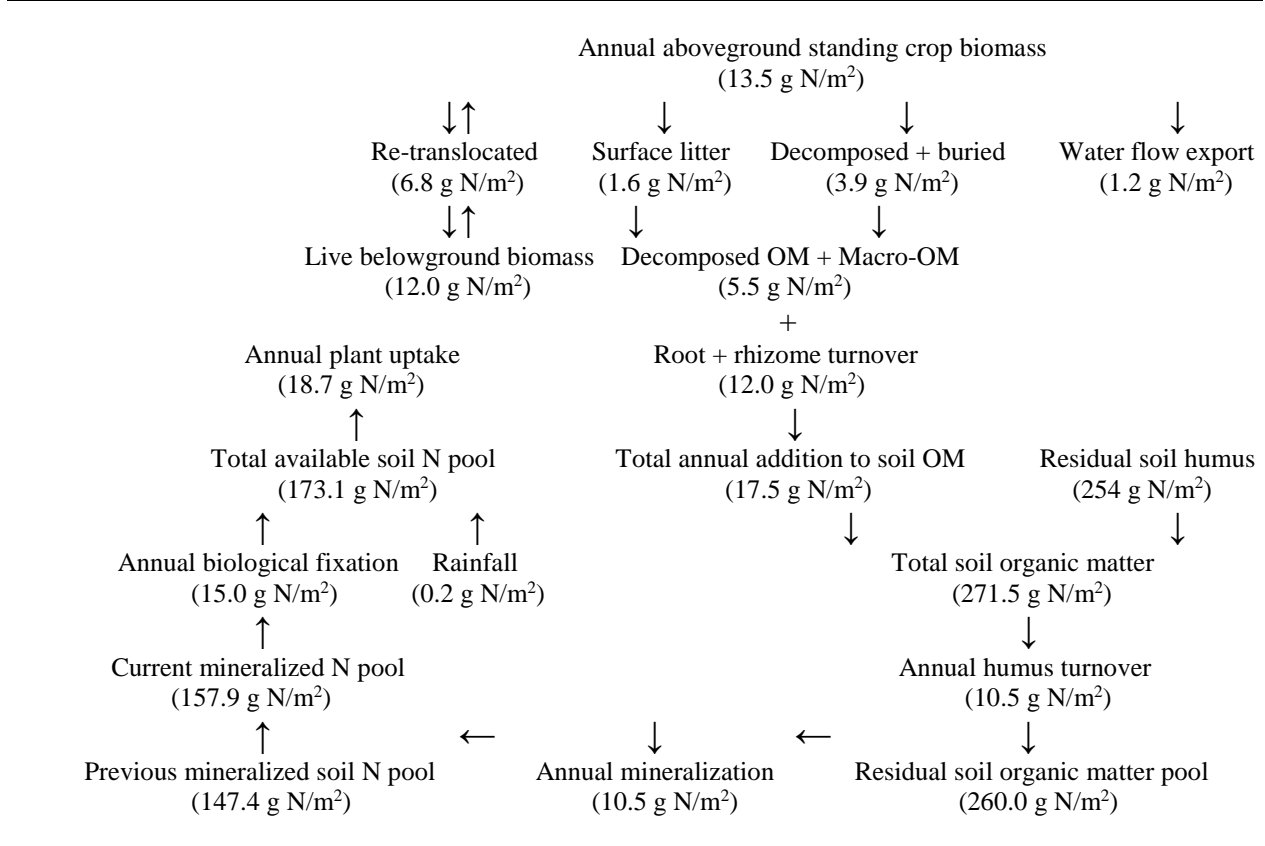
Water transported litter (g/m ²):	217	(Table 5.20)
N concentration in litter (%):	0.56	(50% of tissue N concentration)
N content in exported litter (g/m ²):	1.2	

Non-Organic Matter Inputs

Rainfall (g/m ²):	0.2	(115 cm rainfall/m ² ; 0.17 ppm N)
Soil biological fixation (g/m ²):	15.0	(estimated from Casselman et al. 1981)

Based on the flows illustrated in the conceptual model (Table 5.23), the closed basin *Spartina patens* marsh is not N-limited. Annual plant uptake is estimated to be 18.7 g N/m² and annual addition to the soil available N pool (annual mineralized N, biological-fixed N, N in rainfall) is estimated to be 25.7 g/m². The soil organic matter N pool is estimated to be increasing annually, but by a small amount (6.0 g N/m²; Table 5.23). This conceptual model is based on plant production during a wet period (2014-2017) and both aboveground production and root and rhizome biomass annual turnover will be less during drier years. These lower production levels will result in reduced organic matter input into the soil, and eventually lower mineralization rates.

Table 5.23. Conceptual fate and transport flow pathways for nitrogen in annual plant and soil subsystem of the closed basin *Spartina patens* marsh, South ANWR site. Values are from Table 5.22.



6.0 CONCLUSIONS

The aboveground biomass values used in the conceptual models (Section 5) are site-specific values taken from a seven-year data set. As such, they provide good estimates of aboveground production of the marsh vegetation. Estimates of belowground biomass were made from root:shoot values taken from the literature and applied to the aboveground biomass data. Therefore, the estimates of belowground biomass used in the conceptual model are reasonable, but are not site-specific. Rainfall and inundation depth data are also good. Rainfall data are from Austwell and inundation depths are site-specific, measured on the same dates as the vegetation sampling. Nitrogen concentration data in rainfall and surface runoff come from nearby San Patricio County. Soil and tissue N concentration data were taken from literature studies, some of which were as far away as North Carolina and Georgia, although they did come from *Spartina* marshes. Decomposition rate and litter fate data were both site-specific and literature values.

The purpose of the conceptual models was to provide a reasonable and realistic illustration of decomposition and mineralization patterns in the marsh vegetation of San Antonio Bay. The purpose was not to provide precise values for all components in the conceptual models. More precise values can occur as additional data, in particular site-specific data, become available. Suggestions are presented in the last part of this section as to types of data that would be useful in improving the estimates of the inputs into the conceptual models.

6.1 Comparisons Among Marsh Types

The *Spartina alterniflora* marsh had the highest estimated loss of aboveground biomass into bay waters (50%), which would be expected because of its location adjacent to the open bay and corresponding deep and permanent standing water. Another 20% of annual aboveground biomass production was estimated to be directly incorporated into the soil as buried litter and 30% was estimated to remain on the soil surface as litter and undergo slower decomposition. In contrast, 34% of annual aboveground biomass was estimated to be lost into adjacent waters in *Distichlis spicata* marshes and 20% in *Spartina patens* marshes. These lower loss rates were also the result of marsh zonation. Loss of plant biomass decreased as distance from open water increased. The zonation gradient also affected proportions of annual aboveground biomass entering the soil directly, as buried litter, and more slowly through decomposition of surface litter. Standing surface litter was estimated to account for 34% of annual aboveground production in the *Distichlis spicata* marshes compared to 43% in *Spartina patens* marshes.

The conceptual model estimates indicate that all three marsh types are functioning as organic matter nitrogen sinks, i.e., the organic matter nitrogen pools are increasing over time. The annual rates of increase are similar among the three types, but slightly higher (3.9% per year) in *Distichlis spicata* marshes, intermediate in *Spartina patens* marshes (2.8%), and least in *Spartina alterniflora* marshes (0.4%).

Annual available soil N pools (sum of annual mineralized N, biologically-fixed N, and N added from rainfall and surface flows) are estimated to be highest in the *Spartina patens* marshes (27.4 g N/m²), intermediate in the *Distichlis spicata* marshes (25.7 g N/m²), and slightly lower (25.3 g N/m²) in the *Spartina alterniflora* marshes. Annual plant uptake of N is estimated to be highest in *Distichlis spicata* marshes (21.9 g N/m²), intermediate in *Spartina patens* marshes (18.5 g N/m²), and least in *Spartina alterniflora* marshes (12.8 g N/m²).

6.2 Comparisons Between Delta and Closed Basin Marshes

The Delta marshes had higher estimated loss of aboveground biomass by flushing than did the closed basin marshes at the South ANWR site (33% and 21%, respectively) because of the existence of numerous channels and closer proximity to the open bay at the Delta site. As a result, the Delta marshes had lower proportions of estimated incorporation of annual aboveground into the soil (buried and decomposed litter) than did the closed basin marshes.

The conceptual models suggest that the Delta marshes are accumulating nitrogen more rapidly than the closed basin marshes at the South ANWR site. On average, the organic matter N pools in the Delta marshes are estimated to be increasing at a rate of 4.1% per year, compared to 2.6% annually at the South ANWR site. The Delta marshes also have larger annual additions of available soil N (27.0 g N/m²) and more annual plant N uptake (22.4 g N/m²) than do the South ANWR closed basin marshes (26.0 and 18.0 g N/m², respectively).

It should be remembered that these comparison values are conceptual model estimates. They are based on applications of reasonable data but much of the data used in the conceptual models is not site specific, therefore the results are only general estimates of actual conditions.

6.3 Suggestions for Data Improvement

As with most types of ecological data, multiple sampling periods will result in a better understanding of temporal dynamics than when data are collected at only one point in time. However, even one-time sampling of some of the variables used in the conceptual models would be extremely useful. The

suggestions listed below are certainly not exhaustive, but reflect a priority based on benefits from one-time collection of samples. The most useful site-specific data would be nitrogen concentrations, especially in the belowground system. Site-specific data related to decomposition dynamics and belowground biomass would also be very helpful.

1. Tissue N concentrations. Samples of aboveground biomass (stems, leaves, and standing dead) of the three major species (*S. alterniflora*, *S. patens*, *D. spicata*), surface litter, and belowground biomass (roots and rhizomes).
2. Belowground biomass: root and rhizome biomass. Samples divided into 10-cm depths. From these cores, rooting depth can also be determined.
3. Soil N concentrations. Soil cores taken, from which total soil N, soil organic matter content, and soil organic matter N concentration data can be collected.

Each of these three suggested collections can be made during a single sampling activity. Two additional collections, which would be very useful to improving the conceptual model estimates, would require two sampling trips. The first trip would place the sample materials at the sites and the second trip would collect the samples for analysis to determine the changes over time.

4. Decomposition rates. Litter bags would be placed at the soil surface and at a specified soil depth (e.g., 10 cm) in each of the five marshes. The bags would contain litter of known tissue N concentration (i.e., part of the litter collection from Item #1). The bags would be retrieved after a specified period (e.g., six months or one year) and then re-weighed and re-analyzed for N concentration. These data would provide information on both decomposition rate (surface and buried litter) and N changes during decomposition.
5. N mineralization. Resin bags would be placed at several depths in soil cores and then retrieved after a period of incubation (e.g., 3-6 months). The samples would be analyzed for available N content. These data would provide information on mineralization rates in the soils.

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