## Chapter 5

# PLANT COMMUNITIES OF TIDAL FRESHWATER WETLANDS OF THE CONTINENTAL USA AND CANADA

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**Abstract**: Tidal freshwater wetlands (TFW) occur along the Gulf of Mexico, Atlantic, and Pacific coasts of the continental USA and Canada. Plant communities vary spatially across elevation, latitudinal, and disturbance gradients and temporally with season, between years, and over longer time scales. Patterns on a local scale are determined by seed availability, germination requirements, seed bank strategies, and tolerance of seeds and seedlings to stresses. Regional (estuarine) patterns involve tolerances to salinity and sedimentation, as well as hydrologic stresses. Latitudinal patterns may be a response to climatic gradients along the Atlantic coast and rainfall gradients on the Pacific coast. Annual species, which are important vegetation components, vary considerably. Causes of distribution changes or extirpations of rare/threatened species are poorly understood and impact of invasive species varies with location. Comparisons among Atlantic, Gulf, and Pacific coasts are limited by lack of data. Relatively little is known about tidal freshwater swamps or about West coast TFW.

Species names follow a widely used US Department of Agriculture (USDA) web site (www.itis.usda.gov/index.html). In a few cases, a species name or variety is not accepted by ITIS; such taxa are designated as (NA) or not listed.

**Keywords:** annuals, Atlantic coast, seedling establishment, Gulf coast, high marsh, hydrologic gradient, invasive species, low marsh, marsh, marsh types, Pacific coast, precipitation patterns, rare species, salinity gradient, seeds, seed germination, seed banks, seedlings, swamp, tidal patterns, tidal freshwater wetland types

## INTRODUCTION

Along tidal rivers of North America, tidal freshwater wetlands (TFW) are dynamic landscape elements. They were used by Indians, European colonists, and later by settlers (see: Chapters 3 and 13). Where they still exist, TFW are vibrant, colorful, diverse, and highly productive (see: Chapter 10). They provide, for example, wildlife habitat and open space in often increasingly urbanized surroundings.

In this chapter, we restrict our discussion to (1) the extent of TFW in the East along the Atlantic coast from the Canadian Border (St. Lawrence River) to the northern Gulf of Mexico, and in the West along the Pacific coast from Washington State south to California (Fig. 1). We also compare (2) three geographical areas, Atlantic, Gulf, and Pacific coasts, and examine (3) plant community dynamics including temporal and spatial patterns. The spatial considerations include local, regional, and geographical comparisons. The importance of disturbance and of seed banks to vegetation dynamics is considered within a local context. These are followed by (4) species of special interest, including annuals, as well as rare and invasive (also see: Chapter 9) species, and (5) conclusions and suggestions for future study.

## GENERAL COMPARISONS

Tidal wetlands of North America are influenced by diverse geology, topography, and climate and experience variable tidal regimes (Odum et al. 1984, Emmett et al. 2000, Mitsch & Gosselink 2000). Brief descriptions of the extent of TFW, habitats and wetland types, climate, and tide characteristics are found in this section (for discussions of sedimentation and geomorphology, see: Chapter 4). Within an estuary, sites typically fresh water (by definition <0.5 ppt, Odum et al. 1984) may experience periodic influxes of saltier water

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Edited by A. Barendregt, D.F. Whigham, A.H. Baldwin;

***Figure 1.*** TFW found along the Pacific, Atlantic, and Gulf Coasts of North America. Locations are for those rivers (R) reviewed for Chapter 5. River abbreviations are from north to south. (A) Pacific coast: **PuS** - Puget Sound (Washington); **Col** - Columbia R (border Washington, Oregon); **SFB** - San Francisco Bay-Delta Estuary (California); **Sac** - Sacramento R (California); **SJo** - San Joaquin R (California). (B) Atlantic coast: **StL** - St. Lawrence R (Quebec, Canada); **MeB** - Merrymaking Bay (Maine); **Mer** - Merrimack R (Massachusetts); **Nor** - North R (Massachusetts); **Hud** - Hudson R (New York); **Del** - Delaware River (New Jersey, Delaware); **DelB** - Delaware Bay; **Mau** - Maurice R (New Jersey); **Rar** - Raritan R (New Jersey); **Mul** - Mullica R (New Jersey); **GEH** - Great Egg Harbor R (New Jersey); **CSB** - Chesapeake Bay; **Nan** - Nanticoke R (Delaware, Maryland); **DuCr** - Dueling Creek (Washington, DC); **Ptx** - Patuxent R (Maryland); **Pam** - Pamunkey R (Virginia); **Mat** - Mattaponi R (Virginia); **PAS** - Pamlico/Albemarle Sound (North Carolina); **CpF** - Cape Fear R (North Carolina); **Ata** - Atamaha R (Georgia); **Sat** - Satilla R (Georgia); **Sav** - Savannah R (Georgia); **StJ** - St. John's R (Florida). (C) Gulf Coast: **Suw** - Suwanee R (Florida); **Mis** - Mississippi R (Louisiana); **Atc** - Atchafalaya R (Louisiana).

due either to drought, storms, or other climatic influences. Accordingly, through time, as well as spatially, salinity gradients may exist. These perturbations increase disturbance level and result in increased plant species richness and are important to the vegetation dynamics of TFW, and thus, are included, albeit briefly, in this chapter.

## Extent

TFW occur on the Atlantic, Gulf, and Pacific coasts of North America. They are best developed in the East along the Atlantic coast from New Jersey to Georgia and along the northern Gulf of Mexico coast and in the West in Alaska (Chapters 13-16). These are areas where there is adequate rainfall to maintain freshwater flow in rivers, a flat topography along the river to the ocean that makes possible broad drowned river valleys permitting extensive TFW to develop and have a significant tidal range (Mitsch & Gosselink 2000). Furthermore, extensive development of TFW does not occur along steep and rocky coastlines in eastern Canada (except along the St. Lawrence River) and in northern New England. Similarly, mountains restrict the size and drainage of most estuaries along the Pacific coast and coastal ranges that run parallel to inland ranges further reduce the extent of most watersheds that can reach the coast. Thus, only a few systems, such as the Puget Sound, Columbia River (Garono et al. 2003), and San Francisco Bay-Delta estuaries, are large enough to support TFW. According to Field et al. (1991), TFW cover an estimated 131,000 ha on the Atlantic coast, mostly in the Mid-Atlantic States, 47,000 ha along the Gulf coast, mostly in Louisiana, and only 14,700 on the Pacific coast (Table 1) where, as indicated, TFW south of Alaska are restricted.

There are, however, considerable discrepancies among the available data on the extent of TFW. For example, estimates range for: New Jersey from 89,000 ha (Odum et al. 1984) to 3,889 ha (Tiner 1985) or 6,195 ha (K. Walz pers. comm.); New York along the Hudson River from 400 ha (Odum et al. 1984) to 715 ha (T. Howard pers. comm.), not including 325 ha of tidal swamps; and for Maryland, where estimates are not so disparate, from 42,361 (McCormick & Somes 1982) to 55,659 (Tiner & Burke 1995). Published estimates for the Pacific coast are also quite variable; ranging from 14,771 ha (Table 1) to 57,000 ha (Field et al. 1991). Reasons for variable estimates depend on the databases and techniques used to make the estimates. For some basins, underestimates of the actual coverage occur because TFW dominated by trees and shrubs (i.e., swamps) are not included, yet TFW swamp habitats may be quite extensive. Along the Atlantic coast, for example, substantial tidal swamps occur along the St. Lawrence River, Connecticut River (R. Tiner pers. comm.), in Delaware Bay (G. Moore, D. Snyder pers. comm.), Chesapeake Bay (McCormick & Somes 1982, Peterson & Baldwin 2004a), and the St. John's River in Florida (R. Virnstein pers. comm.).

Present-day estimates do not represent the historical extent of TFW. As much as 20% of the original TFW have been lost to development on the Atlantic coast (Mitsch & Gosselink 2000). Likewise, extensive development of wetlands has occurred along the Pacific coast, recent compared to the

***Table 1.*** Area (ha) of coastal freshwater wetlands by region (USA), including tidal marshes and swamps, and non-tidal and non-specified areas; also given are regional percentages. Data are from Field et al. (1991).

| | **MARSHES** | | | **SWAMPS** | | |
|---|---|---|---|---|---|---|
| **Region** | **Tidal** | **Non-tidal** | **Not Specified** | **Tidal** | **Non-tidal** | **Not Specified** |
| New England | 728 | 4,856 | 18,009 | 567 | 93,604 | 281,135 |
| Mid Atlantic | 14,326 | 18,251 | 17,604 | 24,767 | 294,166 | 244,673 |
| South Atlantic | 24,929 | 240,667 | 7,284 | 65,761 | 1,484,792 | 222,577 |
| Gulf of Mexico | 36,219 | 698,852 | 146,820 | 10,805 | 2,214,480 | 161,834 |
| Pacific | 5,706 | 72,196 | 931 | 9,065 | 66,004 | 155,035 |
| Atlantic coast | 39,983 | 263,774 | 42,897 | 91,095 | 1,872,561 | 748,385 |
| Gulf of Mexico | 36,219 | 698,852 | 146,820 | 10,805 | 2,214,480 | 161,834 |
| Pacific coast | 5,706 | 72,196 | 931 | 9,065 | 66,004 | 155,035 |
| Total | 81,908 | 1,034,822 | 190,647 | 110,965 | 4,153,046 | 1,065,254 |
| **Percentages** | | | | | | |
| Atlantic coast | 49 | 25 | 23 | 82 | 45 | 70 |
| Gulf of Mexico | 44 | 68 | 77 | 10 | 53 | 15 |
| Pacific coast | 7 | 7 | 1 | 8 | 2 | 15 |

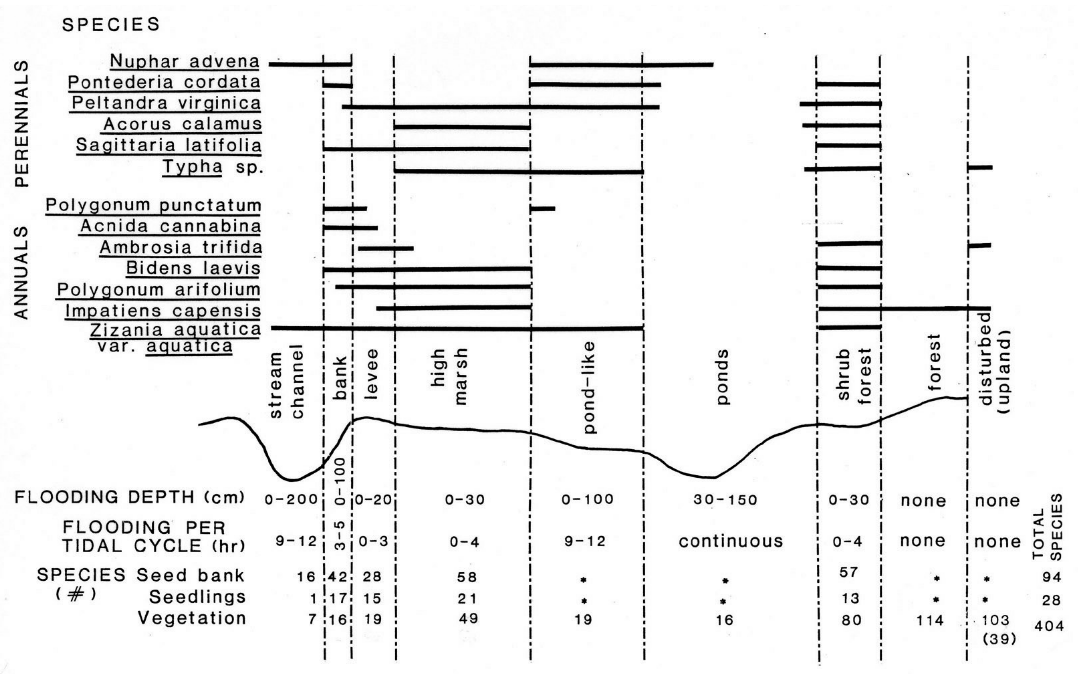

***Figure 2.*** Diagrammatic representation of major habitats along an elevation gradient and distribution patterns for dominant tidal species in a Delaware River TFW (From Leck et al. 1988; reproduced with permission).

Atlantic coast, has resulted in the loss of >70% of the tidal wetlands in Puget Sound (Washington) and >95% in the San Francisco Bay-Delta (California) (Atwater et al. 1979, Levings & Thom 1994). However, in some estuaries where not impeded by surrounding development or geomorphology, wetland area has expanded related to increase in tide range caused by river channelization and sea level rise (e.g., upper Delaware River; Chapter 13).

***Table 2.*** Characteristic plant species of tidal freshwater marshes along the Atlantic and Gulf of Mexico coasts. Species listed are those that occurred at three or more* representative sites. Representative sites are in Canada (Québec) and in USA (Massachusetts, Connecticut, New York, New Jersey, Maryland, Virginia, Delaware, Washington, DC, Georgia, and Louisiana). Life forms are annual (A) and perennial (P). The total number of species reported averaged 45 per study and ranged from 9-101 species (N = 11). The percentage of all species that were annual averaged 30% and ranged from 11-50% (N = 10).
Sources: Chabreck 1972, Tiner 1977, Whigham & Simpson 1975, Baillargeon 1981 cited in NWWG 1988, Doumlele 1981, Birch & Cooley 1982, Bowden 1984, Couillard & Grondin 1986, Leck et al. 1988, Caldwell & Crow 1992, Barrett 1994, Bélanger & Bédard 1994, Tiner & Burke 1995, Baldwin & DeRico 1999, Perry & Hershner 1999, Baldwin et al. 2001, Edinger et al. 2002, Neff 2002, Baldwin & Pendleton 2003, Leck & Leck 2005, MANHP 2005, A. Baldwin (pers. obs.).

| Species | Life form |
|---|---|
| *Acorus calamus* | P |
| *Amaranthus cannabinus* | A |
| *Bidens laevis* | A |
| *Calamagrostis canadensis* | P |
| *Carex lacustris* | P |
| *Cuscuta gronovii* | A |
| *Hibiscus moscheutos* | P |
| *Impatiens capensis* | A |
| *Leersia oryzoides* | P |
| *Lythrum salicaria* | P |
| *Mikania scandens* | P |
| *Nuphar lutea* | P |
| *Peltandra virginica* | P |
| *Pilea pumila* | A |
| *Polygonum arifolium* | A |
| *Polygonum punctatum* | A |
| *Polygonum sagittatum* | A |
| *Pontederia cordata* | P |
| *Sagittaria graminea* | P |
| *Sagittaria latifolia* | P |
| *Sagittaria rigida* | P |
| *Schoenoplectus fluviatilis* | P |
| *Schoenoplectus tabernaemontani* | P |
| *Sium suave* | A |
| *Spartina cynosuroides* | P |
| *Typha angustifolia* | P |
| *Typha latifolia* | P |
| *Typha* spp. | P |
| *Zizania aquatica* | A |
| *Zizaniopsis miliacea*+ | P |

* *Alternanthera philoxeroides* was important in wetlands of the southeast Atlantic and Gulf of Mexico coasts, but reported at only two reviewed sites.
\+ Important only in southeast Atlantic and Gulf of Mexico coasts.

## Habitats and types of TFW

There are two broad categories of TFW. Those dominated by herbaceous species are 'marshes', while those dominated by woody species are 'swamps' (Tables 2-4). Swamps may be dominated by shrub (scrub-shrub swamps) or tree (swamps) species, but they also have many of the herbaceous species that occur in marsh habitats (Table 4). In swamps, the areas between woody plants are called 'hollows' and are topographically lower than the 'hummocks' on which woody species and a variety of additional herbs and vines occur (Rheinhardt & Hershner 1992). Distribution of marshes and swamps across elevation gradients is associated with decreasing hydroperiod (i.e., frequency, depth, and duration of flooding). Typically, there are three or four, fairly distinct, habitats based on hydroperiod (Fig. 2). Nearest the tidal streams are 'low marsh' habitats, which grade into 'high marsh', and then scrub-shrub swamp and swamp. However, in some locations, low to high marsh patterns are not obvious, and instead there is an elevation-dependent vegetation mosaic (Darke & Megonigal 2003). Mosaic vegetation, even in a limited area, may be due to multiple causes, with constraints related to habitat, geography (resulting, e.g., in species isolation where TFW are discontinuous), and vegetation history (Barrett 1994). Varied and complementary life forms and varied survival value of alternate regeneration modes (seed bank vs. buds), influenced differentially by hydrologic processes, allow for coexistence (Barrett 1994).

An interesting feature of TFW along the Gulf of Mexico is the imperceptible change from low marsh to high marsh and random appearance of plant associations (see: Chapter 15). In still other places, there can be a sharp change from low to high marsh, from marsh to swamp, or from wetland to terrestrial vegetation. Small-scale variation within any one habitat can be dramatic and simple designation, as low and high marsh, does not accurately reflect the complexity of TFW (Simpson et al. 1983a, Pasternack et al. 2000).

Additional TFW habitats may be distinguished, the extent of which is not well documented. Pond and pond-like areas are found in areas diked or otherwise altered by humans (Simpson et al. 1983a) or beaver (*Castor canadensis*) (M. Leck pers. obs.) and have floras dominated by floating (Lemnaceae), submerged (e.g., *Ceratophyllum demersum*), or emergent (e.g., *Zizania aquatica*) macrophytes. Along the Hudson River (NY) (also observed elsewhere) are freshwater intertidal mudflats, exposed at low tide and completely inundated at high tide by 0.9-1.2 m of water, and intertidal rocky or gravelly shores (Tiner 1985, Barrett 1994, Edinger et al. 2002, Kiviat & Stevens 2002). Characteristic species of the mudflats include *Heteranthera reniformis*, *Orontium aquaticum*, *Sagittaria graminea*, *S. rigida*, *S. subulata*, *Schoenoplectus americanus*, and *Zizania aquatica*. Characteristic species of the rocky or gravelly shores are *Amaranthus cannabinus*, *Bidens bidentoides*, *Brassica nigra* (an exotic), *Cardamine pensylvanica*, *Orontium aquaticum*, *Plantago cordata*, and *Polygonum hydropiperoides.* Rocky shores along the Merrimack River (Massachusetts) are dominated

***Table 3.*** Species of freshwater tidal swamps occurring at three or more representative Atlantic and Gulf of Mexico sites. Life forms are annual (A), perennial (P), and woody (W). Representative sites are in Canada (Québec) and UDA (New York, New Jersey, Maryland, Delaware, Virginia, North Carolina Florida, and Louisiana). The total number of species reported per study averaged 45 species and ranged from 21-78 total species (N = 8). Within a single river system the average number of species was 13 and ranged from 1-39 species (N = 8). Soil organic matter content ranged from 10-80% (N = 4) and salinity ranged from 0-21 ppt (N = 8).
Sources: Penfound & Hathaway 1938, Cauboue 1972, Whigham & Simpson 1975, Conner & Day 1976, Hoffnagle 1980, Conner et al. 1981, Doumlele et al. 1985, Couillard & Grandin 1986, Leck et al. 1988, NWWG 1988, Rheinhardt 1991, 1992, CZR Inc. 1999, Darst et al. 2002, Edinger et al. 2002, Light et al. 2002, Peterson 2003, Leck & Leck 2005, A. Baldwin (pers. obs.), M. Leck (pers. obs.).

| Type | Species | Life form |
|---|---|---|
| Trees | *Acer rubrum* | W |
| | *Carpinus caroliniana* | W |
| | *Fraxinus pennsylvanica* | W |
| | *Fraxinus profunda* | W |
| | *Liquidambar styraciflua* | W |
| | *Magnolia virginiana* | W |
| | *Nyssa aquatica* | W |
| | *Nyssa biflora* | W |
| | *Pinus taeda* | W |
| | *Taxodium distichum* | W |
| | *Ulmus rubra* | W |
| Shrubs | *Alnus rugosa* | W |
| | *Alnus serrulata* | W |
| | *Cephalanthus occidentalis* | W |
| | *Cornus amomum* | W |
| | *Cornus foemina* | W |
| | *Ilex verticillata* | W |
| | *Ilex vomitoria* | W |
| | *Lindera benzoin* | W |
| | *Rosa palustris* | W |
| | *Viburnum dentatum* | W |
| | *Viburnum nudum* | W |
| Vines | *Amphicarpaea bracteata* | P |
| | *Apios americana* | P |
| | *Dioscorea villosa* | P |
| | *Parthenocissus quinquefolia* | W |
| | *Smilax laurifolia* | W |
| | *Smilax rotundifolia* | W |
| | *Toxicodendron radicans* | W |
| Herbs | *Boehmeria cylindrica* | P |
| | *Cicuta maculata* | P |
| | *Impatiens capensis* | A |
| | *Leersia oryzoides* | P |
| | *Onoclea sensibilis* | P |
| | *Osmunda cinnamomea* | P |
| | *Osmunda regalis* | P |
| | *Peltandra virginica* | P |
| | *Pilea pumila* | A |
| | *Polygonum arifolium* | A |
| | *Polygonum punctatum* | A |
| | *Polygonum sagittatum* | A |
| | *Saururus cernuus* | P |
| | *Sium suave* | P |
| | *Symplocarpus foetidus* | P |
| | *Thalictrum pubescens* | P |
| | *Zizania aquatica* | A |

by *Amaranthus cannabinus*, *Schoenoplectus pungens*, or *Spartina pectinata* (Caldwell & Crow 1992), while along the Delaware River (New Jersey) *Symphyotrichum puniceum*, *Lythrum salicaria*, *Polygonum punctatum*, and *Vernonia noveboracensis* are common and *Bidens bidentoides*, a rare species, is predictable (M. Leck pers. obs.).

TFW may be broadly categorized into three types (Mitsch & Gosselink 2000). Along the Atlantic and Gulf coasts most TFW are 'mature marshes' that are approximately 500 years old and have a well-developed substrate with 10-15% to 30-40% organic matter. Such TFW are typically dominated by diverse annual and perennial herbaceous species (Table 2; Odum et al. 1984, Simpson et al. 1983a) that vary spatially (Fig. 2) and temporally (Whigham & Simpson 1992). FTW along the East coast are likely quite recent, less than 300 years, with probably most of them originating and growing with soil erosion associated with deforestation and agriculture (Orson et al. 1992, Hilgartner & Brush 2006). Until colonial times, areas now TFW in the Chesapeake estuary, for example, were open water (Pasternack & Brush 1998 and references cited, G. Brush pers. comm.).

On the Pacific coast, most TFW are also of the mature type (Table 4). In the Pacific Northwest, the older TFW are approximately 300 years old because of large Holocene earthquakes and tectonic land subsidence (Atwater 1987), while some some deeper sediments in the San Francisco Bay-Delta date to approximately 6000 years (Atwater et al. 1977, 1979, Fairbanks 1989, Malamud-Roam & Ingram 2004). The amount of soil organic matter varies greatly, depending on location and salinity influences, with reported ranges between 5-25% (Thom et al. 2002), 9-60% (Josselyn 1983), or around 50% (Atwater et al. 1979).

The second type of TFW is referred to as 'floating marshes' that occur along the Gulf coast. These have a diverse flora that may be dominated by *Panicum hemitonum*, *Sagittaria lancifolia*, or *Eleocharis baldwinii* and *E. parvula* (Mitsch & Gosselink 2000; see also Sasser & Gosselink 1984, Swarzenski et al. 1991). The substrate, a thick organic mat with living roots, rises and falls with the tide and thus, floating marshes are not affected by hydroperiod or by sedimentation. 'Active marshes,' the third type, are also located along the Gulf coast. These have formed in the past 25 years on emerging islands in the active deltas of the Mississippi and Atchafalaya Rivers and have a number of colonizing species that occupy specific niches. At the water edge *Colocasia esculenta* dominates, with *Salix nigra* on the levees; on extensive back-island mud flats are *Schoenoplectus deltarum* or *Sagittaria latifolia*, and in between occur *Typha latifolia* and a seasonally varied mix of annual and perennial species (Mitsch & Gosselink 2000; see also White 1993).

## Climate

A major factor contributing to differences between Atlantic and Gulf coasts and the Pacific Coast is rainfall pattern. On the Atlantic coast, precipitation is fairly evenly distrib-

***Table 4.*** Plant species occurring at two or more representative sites on the Pacific coast of North America. Representative sites are from Skagit Estuary in Puget Sound (Washington), the Columbia River (Washington and Oregon), and the San Francisco Bay – Delta region (California). Life forms are annual (A) and perennial (P). For San Francisco Bay freshwater tidal marshes, approximately 20 of 90 total species are annuals (22%); data are unavailable for Puget Sound and Columbia River marshes.
Sources: Nomenclature is based on Hickman (1993) and ITIS. Some older names are listed in parentheses. Other sources are Atwater et al. (1979), Burg et al. (1980), Christy & Putera (1992), and V. Parker, L. Schile, J. Callaway & M. Vasey (pers. comm.).

| Species | Life form |
|---|---|
| *Agrostis alba* (NA) | P |
| *Argentina egedii* ssp. *egedii* | P |
| *Aster douglasii* (NA) | A |
| *Aster subspicatus* (NA) | A |
| *Bolboschoenus maritimus* (NA) | P |
| *Carex lyngbyei* | P |
| *Deschampsia cespitosa* | P |
| *Distichlis spicata* | P |
| *Eleocharis macrostachya* (*palustris*) | P |
| *Euthamia occidentalis* | A |
| *Jaumea carnosa* | P |
| *Juncus balticus* | P |
| *Sagittaria latifolia* | P |
| *Schoenoplectus acutus* | P |
| *Schoenoplectus americanus* (*olneyi*) (NA) | P |
| *Schoenoplectus californicus* (NA) | P |
| *Schoenoplectus tabernaemontani* (*validus*) | P |
| *Triglochin maritimum* | P |
| *Typha angustifolia* | P |
| *Typha latifolia* | P |

uted throughout the year, but on the Pacific coast, especially areas of California with Mediterranean climate, rainfall occurs primarily during the winter (Table 5), permitting considerable swings in salinity. Pacific coast estuaries large enough to maintain tidal conditions can shift from relatively freshwater conditions in winter to well-mixed estuaries and more saline conditions (e.g., from 4-30 parts per thousand (ppt)) during summer months in northern San Francisco Bay; Conomos et al. 1985), thereby creating wetlands with mixtures of freshwater and halophytic species. Regionally, in the Mediterranean-climate part of the Pacific Coast, these salinity influences result from reduced river flow permitting salinity to move farther upriver, combined with a lack of summer rainfall to remove it from the soil.

Local Pacific coast climates are strongly influenced by the California Current System that is structured by strong temporal variability, with a cold year-round strong southward current and a northward undercurrent (Hickey & Banas 2003) and by the north Pacific High Pressure System. Nutrients, temperature, and salinity are also influenced, resulting in nutrient-rich, wind-driven upwelling near the coast and a general trend of increasing salinity and temperature southward along the coast (Hickey & Banas 2003). Seattle, Washington, for example, averages 975 mm precipitation, with about 9% of that falling in the summer months (Table 5), while San Francisco averages less than 500 mm with only 1.6% falling in the summer. The cold ocean moderates maritime conditions further by generating coastal fog or low clouds, which can be a critical source of moisture during the summer months. Furthermore, along the northern Pacific coast, the slight influence of salinity can be ameliorated by summer rainfall, creating tidal high marshes dominated by freshwater species like *Typha latifolia* and *Schoenoplectus acutus*, and low marshes dominated by species like *Carex lyngbyei,* that can tolerate some salinity. Farther south, the dry Mediterranean-climate summers in California can result in some salt accumulation in high marsh areas. The salinity results from evaporative concentration when high tides and summer rainfall are insuffient to remove the salts from the wetland soils. Where marshes may receive rare tides with low salinity, conditions create mixed marshes with freshwater species, like *Schoenoplectus acutus* and *S. californicus,* dominating low marshes where more tidal flushing occurs, and high marshes often grade into saltier habitats that are dominated by halophytes, like *Distichlis spicata* and *Jaumea carnosa*. Farther upriver, high marsh areas remain fresh and are often invaded by shrubby woody species like *Salix lasiolepis*, *Cornus sericea*, and *Cephalanthus occidentalis* var. *californicus*.

Water flow in streams and rivers peaks in late winter and spring because of winter rains and snowmelt from the surrounding mountains. Climatic influences on regional and restricted watersheds can shift the magnitude and location of oligohaline-freshwater boundaries as the water level in rivers drops. In California, the combined summer flows of the Sacramento and San Joaquin Rivers drop to roughly 13% of average peak winter rates (Conomos 1979). These conditions are aggravated in systems like the San Francisco Bay-Delta, where over 80% of freshwater inflows are diverted for urban and agricultural uses (Monroe & Kelly 1992) and the patterns and magnitude of flow have been drastically changed (Arthur et al. 1996).

In the East, precipitation exceeds 1000 mm (Table 5), with more than 25% falling during the summer. However, periods of persistent drought result in variable salinity, especially where rivers have smaller watersheds with little freshwater input to the estuary. Along the Merrimack River, the limit of salt may vary 10 km (Caldwell & Crow 1992) with drought and along the Hudson River the salt line can shift >23 km (T. Howard pers. comm.). In addition, large storms (e.g., hurricanes and northeasters) can push brackish water into TFW (e.g., Cape Fear River estuary, Hackney & Yelverton 1990). Near the freshwater-oligohaline transition zone in the Mattaponi River (Virginia), for example, the long-term average was 0.5 ppt, but salinity averaged 2.8 in 1999, ranging from 0.0-15.9 ppt (Darke & Megonigal 2003).

The impact of hurricanes (e.g., Katrina in August 2005 and Rita in September 2005) on TFW, where violent wave action and salinity surges occurred, was considerable (see e.g., Neyland 2007 and websites[1],[2]).

***Table 5.*** Precipitation averages (mm) for representative Atlantic, Gulf, and Pacific coast locations. Shown are total precipitation, months having the highest and lowest values, and the percent of the yearly total that falls during the summer (JJA = June, July, and August). Data are from Williams (1994).

| | **Annual total** | **Highest** | | **Lowest** | | **J J A** |
|---|---|---|---|---|---|---|
| ***Location*** | **mm** | **Month** | **mm** | **Month** | **mm** | **%** |
| **Atlantic coast** | | | | | | |
| Montreal (Canada) | 1036 | Jan | 97 | April | 66 | 25.2 |
| New York, New York (USA) | 1095 | Aug | 107 | Feb | 76 | 26.7 |
| **Gulf coast** | | | | | | |
| New Orleans, Louisiana (USA) | 1539 | Jul | 163 | Oct | 71 | 29.2 |
| **Pacific coast** | | | | | | |
| Seattle, Washington (USA) | 975 | Nov/Dec | 150 | Jul | 20 | 8.6 |
| San Francisco, California (USA) | 483 | Jan | 114 | Jul | 0 | 1.6 |

### Tidal Cycles

Tides and tidal cycles vary considerably (Odum et al. 1984, Mitsch & Gosselink 2000) and where tidal water is constricted due to river morphology (broad at the mouth), tidal amplification occurs upstream. Amplification may not be obvious from tide charts; e.g., along the Hudson River at New York City (East River location, at sea level, tide is 1.2 m, while at Albany 217 km upriver, at 83.8 m above sea level, tide is 1.5 m). In addition, presence of barrier islands, such as the Outer Banks, prevents tidal influence up rivers in North Carolina causing a gap in TFW along the Atlantic coast (except the Cape Fear River system). Similarly, along the California coast, due to insufficient freshwater flow during summer, many rivers form sand bars that block tidal flow (Gordon 1979).

Tides are semi-diurnal on the Atlantic coast and diurnal along much of the Gulf coast. Amplitude varies along the Atlantic coast: 1-5 m - St. Lawrence River ((NWWG 1988); 1.5 m - Hudson River (Troy, NY); 2.6 m - Delaware River (Trenton, New Jersey/Crosswicks Creek); 0.85 m - Nanticoke River (Sharptown, Delaware); and 1.35 m - Cape Fear River (North Carolina). On the Gulf coast, e.g., Louisiana /Atchafalaya Delta, where lunar impact is small, tides are irregular, of low amplitude (<0.5 m), and wind-driven (Mitsch & Gosselink 2000). In addition to Louisiana, wind tides influence extensive areas of the Pamlico/Albemarle Sound of North Carolina (R. Rheinhardt pers. comm.) and even in other areas where tides are lunar there may be an important wind component. Lunar tide effect, especially where impact is small and irregular, may be eliminated by storm runoff and/or winds.

Along the Pacific coast, the tidal cycle is mixed semi-diurnal, with two high and two low tides a day (24.84 hr), with a significant disparity in the heights of each high tide and each low tide (Conomos 1979, Emmett et al. 2000). The smallest fluctuations are in southern California (1.75 m) while the largest occur in the Puget Sound (3.45 m) (Emmett et al. 2000).

## TEMPORAL PATTERNS IN PLANT COMMUNITIES

Tidal freshwater plant communities vary seasonally, between years, and over longer temporal scales. They also change spatially, locally across elevation gradients, as well as regionally and geographically.

### Within-year variation

Remarkable seasonal changes occur in Atlantic coast TFW over the course of a year, as well as through the growing season, dependent on the diverse plant species found within them (Tables 2, 3, 6). Many TFW herbaceous species die back to the soil surface during winter, so that the wetland has a flat, barren appearance, with a layer of decomposing plant material that decreases in thickness as spring approaches. Also during winter, channel edges are scoured clear of litter. Beginning in March or April, the high marsh gradually becomes green as seeds of annual species (e.g., *Impatiens capensis, Polygonum arifolium*) germinate in response to warming temperatures, often yielding high densities of seedlings, which grow quickly in the high light environment with increasing photoperiod (Parker & Leck 1985, Leck 2003). At the same time, perennials (e.g., *Acorus calamus, Peltandra virginica*) begin growth. Vegetation development takes longer in low marsh locations that are inundated for longer periods of time and have lower densities of seeds in the seed bank.

Canopy development in the high marsh is dynamic. Leaves and shoots of perennials (e.g., *Acorus calamus*, *Leersia oryzoides*, *Peltandra virginica, Phalaris arundinacea*) typically grow more rapidly than the seedlings of annuals and reach maximum height and biomass to form a canopy early in the summer (e.g., June in the mid-Atlantic region) (Odum 1988, Whigham & Simpson 1992). By mid to late summer, the stems of many annual species emerge above the perennials to form a canopy often >1 m tall, with certain species (*Amaranthus cannabinus, Ambrosia trifida, Zizania aquatica*) exceeding 2 m. Some perennials die back as they are overtopped by annuals that continue to grow, experience thinning, and eventually reach maximum biomass later in the season (e.g., September). As autumn approaches, annuals cease growth, set seed, and senesce, resulting in increased light closer to the soil surface, and permitting a second growth period for perennials, such as *Peltandra virginica*, that had died back earlier in the growing season. Swamps similarly display seasonal changes with herbaceous species beginning to grow before leaves of trees and shrubs emerge.

The seasonal changes in canopy and species are also seen in a changing palette of colors. Most early flowering plants have green flowers (e.g., *Acorus calamus, Peltandra virginica, Phalaris arundinacea*), but as the season progresses, there can be impressive floral displays, pink or white of *Hibiscus moscheutos,* magenta of *Lythrum salicaria,* orange of *Impatiens capensis,* and light yellow of *Zizania aquatica* in anthesis. Growth of the orange stems of the parasitic vine, *Cuscuta gronovii*, can be extensive in mid to late summer. In autumn, the TFW turn yellow- or red-brown, studded with yellow flowers of *Bidens laevis* and *Helenium autumnale* or the lavender of *Symphyotrichum puniceum*. In swamps, there are also senescing leaves of woody species that provide reds (*Acer rubrum, Nyssa sylvatica*), yellows (*Alnus, Fraxinus* spp.), and purples (*Liquidambar styraciflua*). During winter, the high marsh turns brown following the first killing frosts. In swamps, browns are often brightened by the lingering red fruits of *Ilex verticillata,* a shrub.

Many TFW species in the Northeast flower and/or disperse seed in late summer or autumn, including *Impatiens capensis,* which occurs in a variety of moist habitats, but has delayed seed production in a TFW (Simpson et al. 1985). Some exceptions flower early, including *Phalaris arundinacea* whose non-dormant seeds are shed in late June (Leck 1996) and low-growing, early-flowering annual species like *Gratiola neglecta, Lindernia dubia,* or *Ludwigia palustris*.

In Pacific coast TFW, dominants are typically perennial graminoids or species with grass-like shoots (Table 4). Most of these are of large stature (e.g., *Schoenoplectus acutus, S. americanus, S. californicus, S. tabernaemontani, Phragmites australis,* and *Typha latifolia*; 2-3 m) that emerge early in the spring at around the same time deciduous woody dominants begin to flower or leaf out (*Cephalanthus occidentalis, Cornus sericea, Salix lasiolepis*). Although annuals and perennials of smaller stature make up a majority of the species richness of these TFW, for the most part they remain in the understore. Accordingly, seasonal changes mostly reflect growth periods with the wetland greening up in spring and turning brown during autumn.

## Inter-annual variation

In addition to the seasonal patterns of flowering and seed dispersal, species composition has been found to vary between years in Mid-Atlantic TFW (Fig. 3), usually due to variations in abundance of annual species that often comprise half or more of the species and account for the greatest number of individuals (Fig. 4; Parker & Leck 1985, Leck & Simpson 1987, 1995, Whigham & Simpson 1992). Inter-annual variation of annual species occurs, in part, because of differences in seed production, variable germination of micro-sites due to spatial variation in litter, surface topography, and to variations in local climatic conditions. Because annuals must be recruited each year, conditions that alter germination, seedling establishment, or growth of a species result in varied abundances and fluctuations in vegetation composition (Leck & Simpson 1995, Baldwin et al. 2001). On the Pacific coast, inter-annual variation in annuals and smaller statured perennials may reflect habitat disturbance, such as woody detritus in the Pacific Northwest (Maser & Sedell 1994) and fire in California (M. Vasey, L. Schile, V. Parker & J. Callaway pers. comm.).

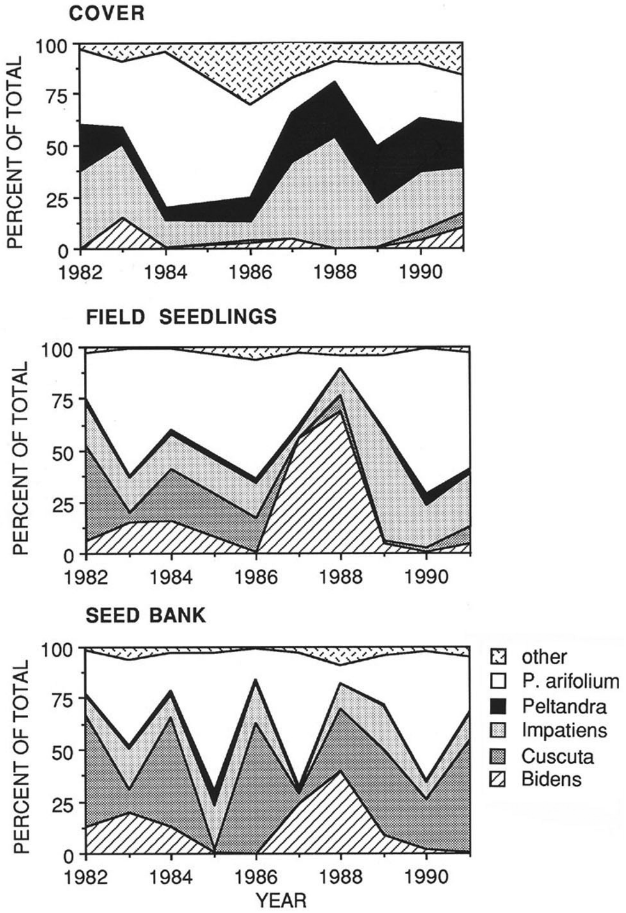

***Figure 3.*** Comparisons of species importance among three life history stages (seed bank from greenhouse emergence and field seedlings and cover). Shown are data (% of totals) for *Bidens laevis*, *Cuscuta gronovii*, *Impatiens capensis*, *Peltandra virginica*, *Polygonum arifolium* and other species for a Delaware River high marsh site (From Leck & Simpson 1995; reproduced with permission).

## Long-term variation

Vegetation of TFW also changes over longer periods (see: Chapter 13). Field and Phillip (2000) reported that the overall percentage of low marsh habitats along the Delaware River increased from 9% in 1977/78 to 34% in 1997/98 while high marsh habitats decreased in area. They attributed changes to sea level rise and lack of sediment accretion. In another Delaware River study, vestiges of former sedge-swamp vegetation occurred in seed bank samples at a depth of 30-32 cm (Leck & Simpson 1987, Leck & Leck 2005), attributed to tide level rise and sedimentation that caused the loss of an alder-sedge-dominated community. The dynamic nature of estuaries may also be seen in data from the Altamaha and Satilla estuaries in Georgia. Along the Altamaha, the acreage of TFW changed from 808 ha in 1953 to 626 in 1974 and 793 in 1993. Along the Satilla, TFW occupied 232 ha in 1953, 114 in 1974 and 147 in 1993 (Smith & Chalmers 2001). In southern Maine in Merrymaking Bay, stabilization of tidal wetlands during the past 50 years is related to forest recovery within the watershed (Lichter et al. 2006).

Long-term changes can also occur in response to the intrusion of brackish water into fresh water portions of tidal rivers. Perry and Hershner (1999) documented an increase in the abundance of *Spartina cynosuroides*, an oligohaline species, from 1974 to 1987, possibly due to an increase in salinity resulting from ground water removal by a nearby paper mill (R. Rheinhardt pers. comm.). Changes are not uniform along the Atlantic coast, however, and Higinbotham et al. (2004) found no evidence of brackish intrusion along the Altamaha and Satilla Rivers in coastal Georgia between 1953 and 1993.

Anthropogenic effects on TFW have been substantial (see: Chapters 13, 14). During colonial times, TFW in North and South Carolina were diked and used for growing rice (Prevost 1986) and are now managed for duck habitat. In New England, losses occurred following dam construction that eliminated tides, and elsewhere wetlands were used for many purposes, including landfills, roads, and industrial sites. These impacts substantially reduced the extent of TFW and also altered plant composition (Leck et al. 1988, McKee & Baldwin 1999, Crain et al. 2004).

In San Francisco Bay-Delta, the remaining TFW are generally island remnants within larger shipping channels, adjacent to diked former wetlands that are managed for agriculture or duck habitat. Diversion of water for agriculture or to cities farther south in California threatens the dynamics of the remaining wetlands. Low water flow and levee breaks bring brackish water into areas formerly exclusively fresh.

# SPATIAL VEGETATION PATTERNS AND FACTORS RESPONSIBLE FOR THEM

Vegetation patterns of TFW can be examined over spatial and temporal scales. At the local scale the most obvious differentiation occurs across elevation gradients related to changes in hydrology, but other factors, such as herbivory and substrate, may be locally important. At the regional scale, differences are mostly due to within-estuary variation in hy-

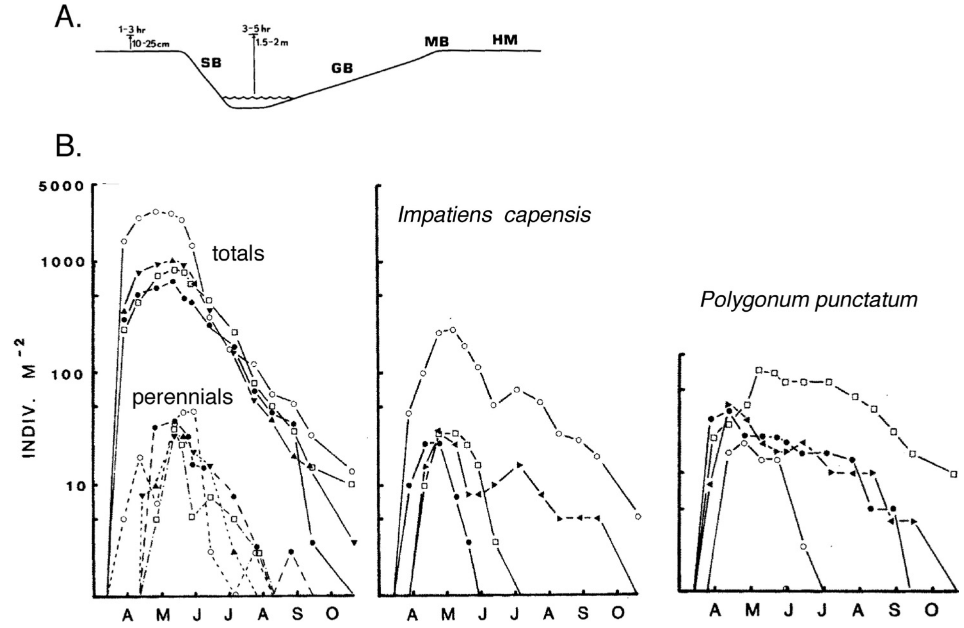

***Figure 4.*** Channel cross-section (A) with inundation zones noted and seasonal patterns (B) in numbers of individuals ($m^{-2}$) found in steep bank (●, SB), gentle bank (☐, GB), midbank (▲, MB), and high marsh (○, HM) zones (n=10). Field data shown are for site totals and numbers of perennials, *Impatiens capensis* and *Polygonum punctatum* (From Parker & Leck 1985; reproduced with permission).

drology and salinity, especially in the portion of the estuary that is closest to the boundary between fresh and salt water. Latitudinal variations in the characteristics of TFW and differences between Atlantic and Pacific coasts are mostly due to differences in climate.

## Local vegetation patterns

Vegetation patterns at the local scale are influenced by physical and biotic factors to which species have varying tolerances. Accordingly, across an elevation gradient and with disturbance, the relative importance of physical and biotic influences varies. Moreover, environmental cues that vary spatially influence seed germination, seed banks, and seedling establishment and are, therefore, fundamental to understanding vegetation patterns.

### *Elevation gradients*

Elevation gradients, which determine inundation regime, occur over varying scales. Gradients can be short (over m) or long (over km); in swamps elevation of hummocks above hollows may be small in scale (cm).

Closest to the subtidal portion of the elevational gradient, low marsh habitats, with longer inundation periods, are dominated by perennials, e,g., *Nuphar lutea* and *Sagittaria subulata* (Fig. 2). Submergent macrophytes, e.g., *Elodea* species, which dominate permanently flooded locations (Capers 2003a), may occasionally be found among these low marsh perennials. Annuals, such as *Polygonum punctatum,* and *Zizania aquatica,* may also occur and dominate locally. In contrast, high marsh at higher elevation usually has a greater number of annual and perennial species. Likewise, swamps, near the upper limit of the inundation gradient, are dominated by hardwood trees and support diverse shrub and herb flora (Table 3). Where there is adequate light, the hollows of swamps and scrub-shrub habitats may have many of the same species that occur in the high marsh (Rheinhardt 1992). Hummocks themselves are habitat for another group of herbs, represented by *Carex* spp., grasses (e.g., *Cinna arundinacea*), ferns (e.g., *Osmunda cinnamomea*, *O. regalis*, and *Thelypteris palustris*), and forbs (e.g., *Viola cucullata*).

Distribution patterns along the tidal gradient are determined by tolerances of individual species to inundation regime (Figs. 2, 3, 5). For example, high marsh species transplanted into low marsh locations did not survive nor did low marsh species transplanted into a high marsh location (Parker & Leck 1985). On the high marsh, biotic stresses (competition) dominate while in low marsh habitats, physical stresses (inundation) are more important and impact species to differing degrees (Fig. 4). Overlap of species distributions is common, however, resulting in the lack of distinct zones in some TFW, especially in swamps. Moreover, diverse communities may be interspersed with extensive almost pure patches of, e.g., *Acorus calamus, Ambrosia trifida, Schoenoplectus fluviatilis, Typha* spp., or *Zizania aquatica*. However, it should be noted that multiple vegetation types may be relics of chance colonization events followed by habitat pre-emption that results in, e.g., mixed dominants and large unexplained variance (Barrett 1994).

Overall, species richness on the Atlantic and Pacific coasts increases from low to the high marsh and swamp habitats, with the highest richness occurring in swamps or scrub-shrub habitats because the hummock and hollow topography provides a greater richness of microhabitats (Rheinhardt 1992, Peterson & Baldwin 2004a, Tanner et al. 2002). In a study that compared responses to hydroperiod (Fig. 5), annuals appeared to have more variable responses while perennials were unaffected or growth was promoted (Baldwin et al. 2001). In upper Chesapeake Bay, the number of species increased with distance inland from one to 14 (Pasternack & Brush 2002). In addition, sandy, dry levee sites had many species while frequently flooded sites were usually monospecific.

Low marsh areas in Pacific coast TFW typically have few species, such as *Schoenoplectus acutus, S. americanus,* or *Carex lyngbyei*. Often on mudflats, small annual species can be found, like *Lilaeopsis masonii* or *L. occidentalis*. A slight increase in elevation causes a sharp increase in the number of species, including *Ludwigia peploides, Mimulus guttatus, Polygonum punctatum,* and *P. persicaria*. In shrub or tree swamp habitats, *Alnus rubra*, *Myrica gale,* and *Picea sitchensis* to the north, and *Cephalanthus occidentalis* var. *californicus, Cornus sericea, Populus fremontii* and *Salix lasiolepis,* to the south, also provide heterogeneous patches that support higher species richness (Tanner et al. 2002). The diverse assemblages of many Pacific coast wetlands reflect

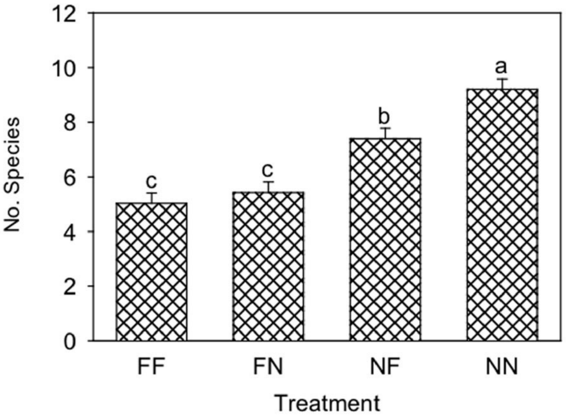

***Figure 5.*** Effects of hydroperiod on number of plant species. Species richness was determined in marsh sods exposed to four hydrologic regime treatments in the greenhouse. Treatments were: continuously flooded for five months (FF); flooded for 35 days followed by a period of four months when not flooded (FN); not flooded for 35 days followed by a flooded period of four months (NF); and not flooded for five consecutive months (NN) (When not flooded, water level was 10 cm below the soil surface). Plotted values are means ± SE of number of plant species in experimental units throughout the duration of the study. Means with different letters are significantly different (Tukey-Kramer test). Effect of date and date x hydrologic regime were not significant (P>0.05) (From Baldwin et al. 2001; reproduced with permission).

rapid shifts from brackish-saline to freshwater conditions, spatially heterogeneous patterns of elevations, seasonal freshwater influences, soil conditions, and disturbance (Simenstad et al. 2000b).

### *Disturbance*

Various levels and kinds of disturbance produce patches for colonization. These may be caused by death of annuals or by herbivory, scouring due to water and ice, removal or deposition of litter and flotsam, sedimentation, or salt pulses (e.g., Odum et al. 1984). Such patches provide habitat for replacement by annuals or less often by perennials (Parker & Leck 1985). The influences of flood disturbance, which varies both longitudinally and perpendicularly to the channel, are not well appreciated (Barrett 1994). Barrett also distinguishes between flood stress and flood disturbance and suggests that they are more important than gap size. Although no clear pattern of succession has been documented in TFW (Mitsch & Gosselink 2000), if disturbances are sufficiently large as occur in man-made wetlands, directional changes (succession) may occur (Leck 2003).

Of the various agents of disturbance that influence vegetation development, ice appears to have received little attention (exceptions include Bélanger & Bédard (1994) and Ewanchuk & Bertness (2004)). Moving ice may scour litter away from edges of tidal channels and river shores where the most successful plants are annuals or strongly rhizomatous perennials (Caldwell & Crow 1992, M. Leck pers. obs.). Where scouring by ice (and water) is important, annuals, whose seeds can find protection in the micro-relief of the marsh surface or rocky shoreline and strongly rhizomatous perennials, are most successful (Caldwell & Crow 1992). Moreover, along the St. Lawrence River, where ice can remain for five months each year, it plays an important role in sedimentation and may actually serve as a protective agent (Serodes & Troude 1984).

Disturbance by intense herbivory can have significant impact on vegetation. Along the St. Lawrence River, snow geese (*Chen caerulescens atlantica*) lower production of *Schoenoplectus americanus*, enhance that of *Zizania aquatica*, and have no effect on *Sagittaria* species (Giroux & Bédard 1987), thus altering community composition (M. Jean pers. comm.). Geese grubbing, coupled with ice disturbance, decreased productivity but increased richness in a brackish wetland study (Bélanger & Bédard 1994). In the Delaware and Chesapeake estuaries, grazing by non-migratory Canada geese (*Branta canadensis*) can have a significant detrimental effect on *Zizania aquatica* populations (Baldwin & Pendleton 2003, Nichols 2003). Beaver (*Castor canadensis*), muskrat (*Ondatra zibethicus*, nutria (*Myocastor coypus*), and possibly non-native carp (*Cyprinus carpio*) can significantly reduce biomass and richness (Ford & Grace 1998, Evers et al. 1998, Connors et al. 2000, Baldwin & Pendleton 2003).

On the Pacific coast, disturbance results from processes associated with flooding and drought. Major rare floods remove aboveground accumulations of plant debris, open up habitats, shift substrates, and provide establishment opportunities for many species. In the Pacific Northwest, a primary source of disturbance in tidal wetlands is large downed wood, such as tree trunks, brought in by floods (Maser & Sedell 1994). Such detritus modifies local sites in a variety of ways, sometimes creating ponds, other times increasing sedimentation, disturbing sites to form new channels, and serving as a substrate for establishment of woody species (Maser & Sedell 1994, Simenstad et al. 2000b). In California, fire introduced in early spring can provide sites for colonization in wetland habitats by removing dense accumulated litter. Smaller species respond rapidly, increasing in frequency and abundance in the subsequent few years (M. Vasey, L. Schile, V. Parker & J. Callaway pers. obs.).

Large-scale TFW disturbances, including human activities, such as physical alteration of wetlands and wetland creation as part of mitigation activities, create altered habitats for opportunistic species. Vegetation development, and, thus, succession, in constructed wetlands depends on the availability and dispersability of seeds, sediment quality, hydrologic conditions, growth forms of colonizing plants, water currents and deposition of litter, and by the vegetation itself (Neff 2002, Leck 2003, Leck & Leck 2005, Leck & Schütz 2005). Seed banks with very high densities of seeds and species richness develop quickly (Baldwin & DeRico 1999, Leck 2003). Other anthropogenic impacts, such as oil spills, have the potential to affect recruitment of annuals from the seed bank and subsequent community composition (Leck & Simpson 1992).

Additional factors influence TFW vegetation development in disturbances. These include: characteristics of seeds, seed banks, and seedlings (Leck & Simpson 1994, Neff & Baldwin 2005); availability of suitable substrate that can be colonized in, e.g., newly prograding deltas (Gosselink 1996 cited in Mitsch & Gosselink 2000), swamps (Peterson & Baldwin 2004a), or constructed wetlands (Neff 2002, Leck 2003, Leck & Leck 2005); as well as salinity (Baldwin et al. 1996) and other stresses (biotic and physical gradients) (Baldwin et al. 2001, Parker & Leck 1985).

Vegetation patterns in some TFW seem to follow a different trajectory than patterns in terrestrial habitats where annual species are replaced by perennials that are in turn replaced by woody species. In fact, the continuing importance of annuals (60.5% of cover over 10 years in a reference wetland and >50% cover in most channel edge and midpoint locations of a constructed wetland after 10 years; Leck & Simpson 1995, Leck 2003) indicates the importance of processes like disturbance due to tide rise and sedimentation that have resulted in a habitat unsuitable for establishment of perennials, such as *Carex* species or woody plants. In contrast, along the Connecticut River, Barrett (1994) found annuals to be less important than along the Delaware River and five of eight vegetation types were dominated by perennials. Sedge-dominated communities are also found in Maine (C. Crain pers. comm.). Differences among river systems in the relative importance of annuals suggest differences in substrates, levels of disturbance, or other factors that deserve study. It also appears, if TFW are similar to salt marshes, that plants create a hospitable environment for themselves and that only some dramatic change, such as disturbance, flooding, or salinity, can shift species composition (Hackney et al. 1996, Baldwin & Mendelssohn 1998).

## *Seed banks: strategies, composition, and relationship to vegetation*

Mid-Atlantic and a few Gulf coast studies of seed dispersal, germination, seed bank dynamics, population dynamics of seedlings in the field, and studies of vegetation patterns have provided insights regarding the linkage between the seed bank and extant vegetation on a local scale.

### Dispersal

Seed dispersal is mostly by water, but wind and animal dispersal also occur (Middleton 1999, Neff & Baldwin 2005). Distribution can, in part, be explained by buoyancy. For example, *Impatiens capensis* and *Peltandra virginica* have seeds that float for months and are widely dispersed. However, low marsh and stream bank habitats are characterized by species, e.g., *Zizania aquatica*, whose seeds do not float and are adapted to remain in place after falling from the parent plant. *Zizania* seeds sink rapidly and have bristles which secure them in the substrate. In contrast, reduced or no bristles in intertidal varieties of *Eleocharis obtusa* var. *peasei, E. olivacea* var. *reductiseta,* and *Schoenoplectus smithii* var. *smithii* are interpreted as reducing the chance of dispersal by epizoochory and of seeds being stranded in litter at the high tide line where it is not continuously wet enough for survival of seedlings (Ferren & Schuyler 1980).

Secondary dispersal of wind-dispersed seeds may also be by water (e.g., *Salix* spp., *Acer saccharinum*; A. Baldwin, M. Brock, M. Leck, pers. obs.) and dispersal of seedlings of some species is exclusively by water (e.g., *Lythrum salicaria, Pontederia cordata*; Schulthorpe 1967). Dispersal of seeds (and rhizomes), entrapped and transported by ice (Caldwell & Crow 1992), appears not to have been studied. However, despite an abundance of propagules, colonization may not be from seeds or seed banks. Capers (2003a) found that for submerged species in channels, 60% of establishment was from plant fragments and 16% from vegetative growth.

### Germination requirements and seed bank strategies

Most germination and seedling establishment occur in spring and several factors control the transition from seeds in the seed bank to seedling establishment (Leck 1996). Soil seed banks are of three types: transient, <1 yr; short-term persistent, 1 - 5 yr; and long-term persistent, >5 yr (Thompson et al. 1997). Seed characteristics and germination responses, first reported by Thompson and Grime (1979), are related to seed bank strategies. Our studies similarly found that large-seeded species (*Impatiens capensis, Polygonum arifolium*), which did not require light for germination and that germinated at low temperature following stratification (5° C), had transient seed banks (Leck & Simpson 1993, Leck 1996, Leck & Brock 2000). Another transient species, *Peltandra virginica*, also large-seeded, had no seed dormancy but was prevented from germinating until spring by an impermeable fruit coat and a requirement for high (>10° C) germination temperature (Leck 1996). In contrast, species with small seeds that require light and alternating temperatures for germination were persistent in the seed bank (*Bidens laevis*). However, even species with persistent seed banks can have a sizable proportion of a year's seed production germinate the spring following dispersal (Leck & Simpson 1995). Long-term persistent seed banks do occur (e.g., *Dulichium arundinacium, Ranunculus sceleratus*) and may contribute to the vegetation when soil disturbance occurs (Leck & Simpson 1987, 1993). Because of the importance of annuals and of species with transient or short-term persistent seed banks, there is considerable depletion of the seed bank during spring germination and seed density can be reduced by as much as 97% in surface samples (Leck & Simpson 1987).

### Tolerances of seeds and seedlings

Along elevation/hydrological gradients tolerances to hypoxic conditions vary. Species in low marsh and stream channel locations have seeds that germinate under anoxic conditions (e.g., *Pontederia, Zizania*) (Leck 1996). *Peltandra virginica* seeds, in contrast, are able to germinate under both aerobic and anoxic conditions, but buoyancy affects their distribution. *Peltandra virginica* fruits, made buoyant (and drying-resistant) by a layer of mucilage that covers the seed, are dispersed to high marsh locations, away from tidal channels where the large buoyant seedlings are easily dislodged by water movement (Whigham et al. 1979, Leck & Simpson 1993, Leck 1996). Young plants are frequently observed in high marsh locations. Another species capable of germinating under both aerobic and anoxic conditions is *Phalaris arundinacea*, but it does not occur in inundated channel bottoms. Established plants occur along levees and, in constructed wetlands, along the upland edge and on higher microhabitats (e.g., bases of *Lythrum salicaria* plants) (M. Leck pers. obs.). Although seeds can germinate when inundated, seedlings do not develop roots and, therefore, establishment is deterred. Also, it is possible that, like *Peltandra virginica*, seedlings float, preventing establishment in channels.

In contrast to these species, *Impatiens capensis* seeds cannot tolerate prolonged anoxia (Leck 1996). In the high marsh, seedlings are often found in slightly elevated microhabitats, e.g., at the bases of perennials or where litter has accumulated (M. Leck & R. Simpson pers. obs.). Differences in seedling tolerances along an elevation gradient can be seen in Fig. 2. *Impatiens capensis*, with large seedlings tolerated the biotic competition (max. 4607 seedlings $m^2$) on the high marsh, but not the physical stresses associated with the tidal channel (Parker & Leck 1985, Leck & Simpson 1993).

*Polygonum punctatum*, in contrast, did not survive on the high marsh, but dominated along channels. In tidal swamps, shade-tolerant and shade-intolerant species may grow in close proximity (R. Rheinhardt pers. comm.). Varied tolerances of seedlings, together with microsite influences on germination, create the complex vegetation patterns observed.

However, even in a given high marsh location, *Bidens laevis* seedlings did not survive to reproduce during some years (Fig. 3). A requirement for higher alternating temperatures (Leck et al. 1994) means that it may germinate somewhat later than *Impatiens capensis* or *Polygonum arifolium* that germinate at lower temperature, have high densities, and larger seedlings, against which it must compete. *Bidens laevis* seedlings are relatively small (Leck & Simpson 1993). The occurrence of suitable establishment conditions may therefore be more problematic than for other large-seeded annuals.

Germination of annuals from undisturbed soil samples in a greenhouse study was earlier than for perennials (two peaks were at 78 and 83 year days, and 108 and 115 respectively) (Leck et al. 1989). Also in the field, perennials did not persist through the growing season and in the greenhouse *Sagittaria latifolia* germination was 1-1.5 months later than most other species (Parker & Leck 1985, M. Leck pers. obs.).

Other factors affecting germination and establishment include salinity and nutrients. Germination of *Phalaris arundinacea* was reduced ~20% by 50% sea water and increased ~33% by 5 mM $KNO_3$ (S. Massingill pers. comm.). In a study of oligohaline wetlands in the Mississippi delta, Baldwin et al. (1996) found that salinity did not affect seed viability, but it did inhibit germination. Increased salinity can reduce the abundance of species dependent on seedling recruitment in TFW, but would allow continued growth of species able to grow by vegetative means.

An environmental factor, about which little is known, is the effect of a mud coating on seedlings. This may be a greater problem for smaller seedlings and in areas where there is much sediment carried by tides. It is known, however, that added sediment on the soil surface can reduce germination. Peterson and Baldwin (2004b) found that density and richness of seedlings emerging from TFW sediments decreased significantly as sediment input increased from 0 to 2 cm depth, with reductions caused by as little as 0.5 cm of sediment.

### Relationship of the seed bank to vegetation

Several studies have examined the relationship between the seed bank and vegetation patterns. Existing vegetation (seedlings and vegetation cover) usually reflects the composition of the seed bank (Leck & Simpson 1995). Species richness was similar in a reference TFW site between seed bank, field seedlings, and vegetation in three habitats (Leck & Simpson 1987), but was greater in seed bank than vegetation in a constructed wetland (Leck 2003).

Annuals accounted for the varied composition of three life history stages over 10 yr at a high marsh site related to year-to-year population fluctuations (Fig. 3). Another study showed that seed rain, seed bank, seedlings, and seed production patterns varied among species, across sites along an elevation gradient for a species, and between years (Leck & Simpson 1994). Relationships between life history stages are complex. For some species, e.g., *Ambrosia trifida,* <1% of seeds survived to seedlings, and even fewer survived to maturity. In contrast, 91% of mature *Polygonum punctatum* plants were recruited from seed rain.

## Regional (estuarine) patterns

Within an estuary, vegetation patterns and species richness also change in response to variation in importance of fluvial and marine effects. At a landscape scale, upstream plant distribution is determined more by competitive ability or tolerance to shading and downstream by tolerance to physiological stress (Crain et al. 2004). This mimics the distribution along elevation gradients described above.

Along the Mattaponi River (Virginia), a tributary of Chesapeake Bay, communities closer to the downstream end of the tidal fresh zone had more species that can also occur in oligohaline habitats, while the dominant species of upriver sites near the upper limit of the tidal effect were almost entirely freshwater species (Darke & Megonigal 2003); the two sites were only 19 km apart. On the nearby Pamunkey River (Virginia) TFW, while sizable, occur on the inside of only a few wide bends in the river, but alternate with tidal swamps that occur within the next upriver bend, and oligohaline wetlands that occur within the next downriver bend, distances of <1 km (R. Rheinhardt pers. comm.). Differences in composition may also be related to salt pulses associated with storm events or periods of drought (Peterson & Baldwin 2004a, b), which are considered below.

In the Nanticoke River watershed (Maryland and Delaware), Peterson and Baldwin (2004a) found that seed banks of marshes and of hummocks and hollows in swamps varied linearly along the river and its tributaries. Specifically, taxa and seedling density decreased with increasing distance upstream in swamp hollows and hummocks, but increased or remained constant in marshes. The observed variation across the tidal landscape in swamps may have been due to periodic saltwater pulses in the lower reaches of the tidal fresh water zone that stunted trees and shrubs and created a high light environment capable of supporting a well-developed herbaceous understore and subsequent seed bank. Along the Pamunkey River, however, the stunted nature of trees >35 km upriver appears associated with hydrologic stress (R. Rheinhardt pers. comm.).

The impact of salinity on species richness deserves more attention, given the potential occurrence of salt pulses and to projected estimates of sea level rise. In a study of oligohaline marshes on the Connecticut River, Warren et al. (2001) found that richness was consistently higher in mid-salinity than at either the lowest or highest salinity sites (seven locations ranging from fresh/oligohaline to polyhaline). Similarly, Senerchia-Nardone and Holland (1985) found a greater number of species occurred at the more brackish of two sites, which were located on opposite banks of the river.

Sedimentation regimes may differ within an estuary. In the St. Lawrence Estuary (Canada), upstream TFW receive water with little sediment and do not experience the sediment deposits characteristic of wetlands farther down the estuary (Serodes & Troude 1984). In a Delaware River study, Field and Phillip (2000) reported decreases in high marsh area and increase in low marsh over 20 yr in all sites except the most upstream one. These differences within the estuary were attributed to changes and differences in sedimentation over time and with location.

Other within-estuary effects have been observed in species range changes in the Delaware estuary. More species, both brackish and freshwater, have extended ranges since 1950 while fewer species have reduced ranges, and several intertidal endemics, notably *Amaranthus cannabinus, Bidens bidentoides*, and *Sagittaria subulata* have had no range change (Schuyler et al. 1993). Possible reasons for expanded ranges include seasonal shifts in chlorides and dissolved solids, adverse environmental impacts caused by industrial development, increased impact of brackish water, habitat elimination, and introduction of brackish species in ballast dumped in freshwater areas. These explanations are, however, only hypotheses and the causes of range expansion are poorly understood (Schuyler et al. 1993).

In addition to hydrology and sedimentation, species vary in their tolerances to salinity, dependent in part on growth strategies (Howard & Mendelssohn 1999b). In estuaries, TFW in the oligohaline transition boundary may experience periodic salt-water pulses during storms and, over a longer period, during periods of low water flow (e.g., late summer and early autumn). Responses to salinity, and the resultant impact on structure and composition of vegetation, depend on the ability of individual species to recover and the intensity and duration of the stress. Competitive displacement due to physical factors and biotic interactions played important roles in a New England transplantation study that examined species tolerance of salt and oligohaline species along elevation and salinity gradients (Crain et al. 2004). However, in the absence of competition, the 10 test species grew best in the lowest salinity wetlands.

Thus, the salinity gradient may change spatially and temporally, depending on water flow, wind, and tidal factors. A small increase during drought one summer may alter plant composition for several years (Odum et al. 1984) and in tidal swamps, where trees are already at the edge of their tolerance range, the change may be permanent (R. Rheinhardt pers. comm.). The impact of salinity in systems where freshwater flow is regulated by dams can be seen in the distribution of certain salt-tolerant species (i.e., *Distichlis spicata, Spartina patens*) across a salinity gradient (Crain et al. 2004).

On the Pacific coast, fluctuations in seasonal rainfall strongly influence marsh wetlands at oligohaline boundaries. During a severe 2 yr drought, many species responded not only with declines in growth, but also shifts in elevation (Atwater et al. 1979). Similarly, where former wetlands had been reclaimed for agriculture, levee breaks in the California Delta island system further diverted freshwater flow patterns, bringing brackish water farther inland. For example, a break in the Jones Track levee during June 2004 resulted in a 5 ppt salinity increase in the western Delta, a usually freshwater region (S. Siegel pers. comm.).

Crain et al. (2004) note a paradox – the highest species richness occurs where competition is highest. This, too, is observed in TFW along elevation gradients (Fig. 2). In some estuaries, however, the transition zones from fresh to salt water may have the highest plant species richness due to combinations of species overlapping in tolerances **(**L. Schile, V. Parker, M. Vasey & J. Callaway pers.obs.). Underlying mechanisms have not been studied and comparative data for multiple sites are lacking.

## Geographic effects

On the Atlantic coast from the St. Lawrence River in Canada to Florida, the composition of the vegetation of TFW, not unexpectedly, changes with latitude, but no systematic comparison has been made. Thus, patterns and causes of latitudinal variation are poorly understood. In the north, the presence of ice and scouring by ice influence patterns of sediment distribution that, undoubtedly have profound biological effects (Lavoie et al. 2003). The most widely distributed species appear to be *Zizania aquatica*, an annual distinguished as var. *brevis* in the north and var. *aquatica* in the south, and the perennials *Peltandra virginica, Pontederia cordata,* and *Sagittaria latifolia*.

Along the Pacific coast, *Juncus balticus, Potentilla anserina* spp. *pacifica, Schoenoplectus acutus, Typha angustifolia,* and *T. latifolia* are found in all three estuaries that have been examined (Table 5). Other TFW species include *Athyrium filix-femina* var. *cyclosorum*, *Epilobium ciliatum*, *Juncus effuses*, *Oenanthe sarmentosa*, and *Urtica dioica*.

Interestingly, relatively more salt-tolerant species, such as *Carex lyngbyei,* dominate low marshes than high marshes along the Pacific coast. However, as Mediterranean-climate conditions intensify southward along the California coast, freshwater species such as *Schoenoplectus acutus* and *Phragmites australis* dominate low marsh areas where more tidal flushing occurs, while more halophytic species, such as *Distichlis spicata* and *Jaumea carnosa*, dominate the higher portions of marshes that are less frequently flooded and accumulate salt (4 – 10 ppt). TFW in Washington and Oregon often are dominated by *Carex lyngbyei*, *Eleocharis palustris*, *Schoenoplectus americanus*, and *S. tabernaemontani*. *Carex lyngbyei* frequently forms pure stands in both low and high marsh areas (Eilers 1975, Jefferson 1975, Burg et al. 1980, Ewing 1986). In the Columbia River estuary, TFW can be found as far as 164 km from the mouth of the river and are principally dominated by *Carex lyngbyei*, *S. americanus* and *S. tabernaemontani*, with woody forests or swamps encroaching from higher ground in many sites (Jefferson 1975, Christy & Putera 1992).

Away from the Pacific Maritime climatic influence in the San Francisco Bay-Delta, TFW are dominated by *Schoenoplectus acutus* and *S. californicus*, which often exceed 3 m in height. *Typha* species (*T. angustifolia*, *T. latifolia* and hybrids) are also frequent in freshwater tidal areas, as is *Phragmites australis*. *Schoenoplectus americanus* is abundant in wetlands with a slight saline influence and can range from 30 to 200 cm tall depending on wetland location (L. Schile & V. Parker pers. obs.); however, it is replaced by *Bolboschoenus maritimus* in brackish tidal wetlands. In addition, Pacific coast TFW contain a number of other widespread species, including *Calystegia sepium*, *Epilobium ciliatum*, *Juncus balticus*, *Lythrum californicum*, *Mimulus guttatus*, *Oenanthe sarmentosa*, and *Polygonum punctatum*. In slightly brackish conditions, additional species include *Distichlis spicata, Euthamia occidentalis*, *Pluchea odorata*, and *Potentilla anserina* ssp. *pacifica*.

As in Atlantic coast areas, few complete lists of species are available for most of the Pacific coast, making it difficult to compare floristic patterns. The Delta region of California is reported to have over 90 native wetland species, while over 130 have been found on Browns Island, an oligohaline ancient wetland located at the confluence of the San Joaquin and Sacramento Rivers (Knight 1980) (146 species are listed in Mason 1957). Some, like *Bidens laevis*, *Phragmites australis*, *Polygonum punctatum*, *Sagittaria latifolia*, *Typha angustifolia*, and *T. latifolia* are widespread species found across North America. Other species, including dominants, are either restricted to the Pacific coast (e.g., *Potentilla anserina* spp. *pacifica*) or even more locally restricted (*Lilaeopsis masonii*) (Mason 1957, Hickman 1993).

The prevalence of tidal freshwater swamps in the East appears related to geomorphology and to the presence of coastal plain from New Jersey south. However, they occur along the Connecticut and St. Lawrence Rivers, e.g., but have received little attention (R. Tiner pers. comm.). On the Pacific coast, swamps are present although their extent is more limited and are primarily located in Oregon and Washington, reflecting rainfall patterns.

Certain species (*Aeschynomene virginica*) occur in coastal tidal Pine Barrens rivers (Maurice River), but not along the Delaware River; others are not found along the Maurice River system (e.g., *Gratiola virginana, Elatine americana*), but occur along the Delaware River; while still others occur in both river systems (*Bidens bidentoides, Bidens frondosa* var. *anomala* (Ferren 1975). Another floristic study of TFW species (Ferren & Schuyler 1980) found that the Delaware and Raritan River systems were similar, but different from the Mullica and Great Egg Harbor River systems, which originate in the Pine Barrens and were similar to each other. The Delaware and Raritan systems had affinities with both the Hudson system to the north and the Chesapeake to the south. Brackish species, however, were collected in both groups, indicating the importance of salinity in distribution patterns.

## SPECIES OF SPECIAL INTEREST (ANNUALS, RARE AND INVASIVE SPECIES)

### Annuals

Why are annuals such an important component of TFW in Atlantic coast estuaries? It may be that annuals are maintained by the continuing disturbance caused by sea level rise and sedimentation (Orson et al. 1992; Chapter 13), coupled with frost heaving in winter. Another factor may be the morphology and growth phenology of the dominant perennial species (e.g., *Acorus calamus*, *Peltandra virginica*), which form a relatively open canopy that dies back completely to the ground during the winter. This canopy architecture allows recruitment and growth of annual seedlings. In contrast, seedling recruitment is rare in wetlands dominated by dense perennial grasses, such as *Phragmites* and *Spartina,* or by *Typha* spp. that have a dense canopy that persists through the winter (Baldwin & Mendelssohn 1998).

Along the Pacific coast, TFW are dominated by large herbaceous species (*Schoenoplectus* spp., *Typha* spp. and *Phragmites*), as well as a few shrubs. Annual species do not form dominant patches, but a number of annuals, including *Calystegia sepium*, *Polygonum persicaria*, and *P. punctatum* are prevalent in the community. These species, other annuals, and short-lived perennials all increase in frequency and abundance with disturbance. Interestingly as noted earlier, Barrett (1994) found a ‘paucity’ of annuals in Connecticut River sites compared to the Delaware River, suggesting that this could be related to a delay in the onset of the vegetative season.

### Rare species

Status and distribution of estuarine endemics and rare species deserves discussion. Limited data, based on dissimilar data sets, suggest an increase in rare species (Federal or state-listed, or species of concern) with decreasing latitude: 0 species along the St. Lawrence River (Québec, Canada), 9 in three Connecticut River sites and 27 in New Jersey (M. Jean pers. comm., Barrett 1994, see: Table 6). However, perhaps due to relative isolation and more extreme winter climate, a dozen endemic varieties are reported from the St. Lawrence region (*Bidens tripartida* var. *orthocoxa* (not listed by ITIS), *Cicuta maculata* var. *victorinii*, *Deschampsia caespitosa* var. *intercotidalis* (NA by ITIS), *Epilobium ciliatum* var. *ecomosum*, *Gentiana crinita* var. *victorinii* (NA), *Gratiola neglecta* var. *glaberrima* (NA), *Helenium autumnale* var. *fylesii*,

***Table 6.*** Rare, threatened, and endangered plant species of New Jersey tidal freshwater marshes. Life forms are annual (A) and perennial (P). Also indicated is occurrence in brackish marhes (x). Source: NJ Department of Environmental Protection rare species database, courtesy D. Snyder and E. Williams (pers. comm.).

| Species | Life Form | Brackish |
|---|---|---|
| *Aeschynomene virginica* | A | x |
| *Bidens bidentoides* | A | x |
| *Bidens eatoni* | A | |
| *Callitriche palustris* | A | |
| *Cardamine longii* | A? | |
| *Cuscuta polygonorum* | A | |
| *Cyperus engelmannii* | A | |
| *Cyperus polystachyos* | A | |
| *Elatine americana** | A | x |
| *Eriocaulon parkeri* | P | |
| *Eryngium aquaticum* var. *aquaticum* | P | |
| *Fuirena squarrosa* | P | |
| *Gratiola virginiana* | A | x |
| *Heteranthera multiflora* | A? | x |
| *Hydrocotyle verticillata* var. *verticillata* | P | x |
| *Isoetes riparia* var. *riparia* | P | x |
| *Limosella australis* | A | |
| *Micranthemum micranthemoides* | A | x |
| *Myriophyllum tenellum* | P | |
| *Nelumbo lutea* | P | |
| *Sagittaria calcyina* var. *spongiosa* | P | |
| *Sagittaria subulata* | P | x |
| *Schoenoplectus maritimus* | P | x |
| *Schoenoplectus smithii** | A | x |
| *Utricularia biflora* | P | |
| *Utricularia gibba* | P | |
| *Wolffiella gladiata* | P | |

* Species added based on Leck & Leck (2005).

*Lycopus americanus* var. *laurentianus*, *Mimulus ringens* var. *colpophilus*, and *Zizania aquatica* var. *brevis*) (Baillargeon 1981 cited in NWWG 1988).

Comparison of tidal rare, endangered or threatened species in New Jersey found similar numbers in freshwater and brackish, and fewest in salt marshes. Of the 27 TFW species (Table 6), 11 also occur in brackish tidal wetlands, but none also occur in salt marshes. However, three of the estuarine endemics, *Amaranthus cannabinus*, *Bidens bidentoides* and *Sagittaria subulata* are recorded for the Delaware estuary, none appears not to have been widely studied (Schuyler et al. 1993). Certain rare species of TFW habitats, such as *Eriocaulon parkeri*, have been extirpated along some rivers (e.g., Delaware River) (Schuyler et al. 1993), but may occur regionally along others (Mullica and Maurice Rivers) (JCNERR 1999, M. Leck pers. obs.). Causes of extirpations and distribution changes may be related to habitat loss or degradation, but are not well understood (Schuyler 1986).

Recent studies suggest that many rare species depend on open patches created by disturbances. Griffith and Forseth (2003) found that *Aeschynomene virginica* established and reproduced best in patches where vegetation was removed either experimentally or by muskrats (*Ondatra zibethicus*). Leck and Leck (2005) reported 11 rare/endangered species that found suitable establishment niches during the first 4-5 yr following construction of a created wetland compared to one species in reference sites. Barrett (1994) reported that rare species in Connecticut River sites appeared more often in species-poor vegetation types.

Along the Pacific coast, freshwater and brackish tidal wetlands are typically dominated by only a few species, but may contain a large number of rare or less frequent species. Some species are rare due to habitat loss (e.g., *Hibiscus lasiocarpus*), but others may be of more recent evolutionary origin or restricted to specific habitats (*Lathyrus jepsonii* var. *jepsonii*, *Lilaeopsis masonii*). *Sagittaria sanfordii*, for example, was reported to cover extensive areas in the San Francisco Bay-Delta freshwater tidal areas prior to agricultural development of the region, but now is rare (Mason 1957, CNPS 2001). Other rare species include *Carex interrupta, Epipactis gigantea, Lindernia dubia, Rorippa columbiae,* and *Scirpus cyperinus* in Oregon and Washington, and in transition to brackish wetlands, *Cordylanthus mollis* ssp. *mollis* and *Cirsium hydrophilum* var. *hydrophilum* in California.

## Invasive species

In the East, non-native species (or varieties), including *Phalaris arundinacea* and *Phragmites australis*, may form dense populations that contribute to vegetation changes (see: Chapter 9). The most important invasive in TFW in New England, as well as in Mid Atlantic estuaries, appears to be *P. australis* (Farnsworth & Meyerson 1999, 2003, Rice et al. 2000, Leck 2003). An increase in invasiveness seems likely because McCormick and Ashbaugh (1972), Good and Good (1974), or Whigham and Simpson (1975) did not report it as an important community type in three Delaware River TFW. Moreover, McCormick and Ashbaugh report several other species having high frequency and/or cover in stands with *P. australis*. Evidence suggests that increased invasiveness is due to expansion of an introduced genotype because rapid invasion along the lower Connecticut River estuary appeared not to be related to tidal restriction or disturbance (Warren et al. 2001).

In contrast to and despite its reputation, *Lythrum salicaria* in a Delaware River-constructed wetland had no long-term impact on richness (Leck 2003, Leck & Leck 2005). In fact, *L. salicaria* may be uncommon probably because dense colonies decline allowing establishment of native species (Lavoie et al. 2003 and references cited therein). In addition, *Lythrum salicaria* and *Phragmites australis*, as well as *Butomus umbellatus*, are not important in St. Lawrence River TFW, especially in downriver areas, possibly due to the high-amplitude tides and to the species-poor, but dense, populations of native species that resist invasion (Lavoie et al. 2003).

Invasive species represent a considerable problem in many of the Pacific coast wetlands, especially in Oregon and Washington. *Amorpha fruticosa, Iris pseudacorus*, *Lythrum salicaria*, and *Phalaris arundinacea* are considered noxious weeds and invade disturbed as well as undisturbed wetlands (Apfelbaum & Sams 1987, Glad & Halse 1993, Christy & Putera 1993). While these species also occur further south in the San Francisco Bay-Delta region (Raven & Thomas 1970, Knight 1980, Grossinger et al. 1998), they are not yet a problem. Moreover although the San Francisco Bay-Delta estuary has been considered one of the most invaded estuaries in the world (Cohen & Carlton 1998), the majority of the invasive species are invertebrates and fish. Invasive vascular plants such as *Lepidium latifolium*, and to a lesser degree, *Arundo donax* and *Eichhornia crassipes,* commonly invade and pose a long-term problem for restoration and management (Young et al. 1997, Grossinger et al. 1998, Renz 2002).

## CONCLUSIONS AND FUTURE STUDIES

The factors driving the structure of TFW result from a complex and dynamic interplay among abiotic and biotic processes (Pasternack et al. 2000). Elevation, as noted by Pasternack et al. (2000), is not a constant feature, but is variable and changes through time as a function of sedimentation that, in turn, is dependent on plant communities, distance to tidal inlet, distance to stream, elevation, and sea level rise, as well as animal activity. Observations indicate an underlying sensitivity of tidal freshwater plant communities to hydrogeomorphic conditions (Pasternack & Brush 2002). Along Atlantic and Pacific coasts of North America, threats to TFW are similar and include: reclamation for agriculture, filling, erosion, excess nutrients, altered hydrology, invasion of non-native plants, and nuisance animal species (Ehrenfeld 2000, Baldwin 2004) although rates of loss appear to have slowed in recent years in some areas (e.g., St. Lawrence River, M. Jean pers. comm.). Surprisingly little is known about TFW compared to their saline counterparts, particularly on the Pacific coast (Mitsch & Gosselink 2000). TFW are highly productive and provide refuge for many birds, fish, and invertebrates; however, they have been highly altered and destroyed, and have proven difficult to restore. Restoration efforts along the Pacific coast are increasing because of the recognition of these habitats as critical for salmon and other organisms (Healey 1982, Myers & Horton 1982). Subsidence of diked wetlands is a critical issue for restoration, especially in the freshwater end of the gradient where soils are predominantly organic (Atwater & Belknap 1980, Williams & Orr 2002). In the San Francisco Bay-Delta region, many restoration efforts have created tidal lakes due to high subsidence rates (3-5 m range) that occurred while the areas were diked. Adding material to raise elevations has met with some success in salt marsh areas (e.g., Williams & Faber 2001, Cornu & Sadro 2002), but in the San Francisco Bay-Delta TFW, the low density, high organic soils tend to compact because of their lower bearing capacity (Orr et al. 2003).

Based on data available from Atlantic (AC), Gulf (GC), or Pacific coast (PC) studies, we recognize the following emerging patterns:

- Hydrologic gradients drive horizontal distribution and, thus, zonation of vegetation (AC, PC).
- Sedimentation appears to be a driving force maintaining TFW (AC, GC)
- Seasonal inequalities in precipitation cause salinity impact at oligohaline boundaries (AC, PC).
- Seed banks and establishment vary locally and across the landscape (AC, GC).
- Seasonal and inter-annual variations occur in seed banks and vegetation due to the importance of annual species (AC).
- Dispersability, seed germination requirements, and seedling tolerances drive establishment patterns (AC).
- Animals are important constraints on vegetation structure (AC, GC).

We suggest that future studies of TFW consider the following: (1) The relative importance of stresses, including biotic (competition), physical (inundation, sedimentation), and chemical (salinity, eutrophication), across elevation, regional, and geographic gradients. How these stresses impact life history stages is especially important as TFW continue to be influenced by sea level rise. (2) Comparative ecophysiology studies would shed light on growth strategies and competitive abilities that relate to vegetation patterns. (3) The roles of annual species and mechanisms by which they are sustained. Are generalizations about the importance of annuals, based on Atlantic coast studies, broadly applicable? (4) How do intrinsic factors compare with extrinsic in the distribution of rare and invasive species within and among river systems? (5) Can understanding seed dispersal, as well as seed bank and seedling dynamics, help prevent degradation and further wetland loss, and enhance restoration efforts? (6) Responses of Pacific coast wetlands, which can be older than Atlantic coast wetlands (1000 vs. 500 yrs), to sea level rise and other perturbations deserve study. (7) More needs to be learned about tidal freshwater swamp distribution and vegetation dynamics.

Finally, the context of future research inevitably will incorporate the changes in global climate (e.g., Osborn & Briffa 2006) and the subsequent rapid sea level rise (Rignot & Kanagaratnam 2006) that will have ongoing impacts on all tidal ecosystems. Future studies need to establish careful baseline information on all aspects of their system to control for or directly study such influences. Sadly, we are just beginning to investigate TFW at a time when global climate and sea level changes cause background manipulation of processes before overall understanding of these systems is possible.

## ACKNOWLEDGEMENTS

C. Crain (for New England), G. Edinger and T. Howard (Hudson River), M. Jean (St. Lawrence River), L. Kelley, G. Moore, S. Siegel, D. Snyder, K.S. Walz, E. Williams (New Jersey), and R. Virnstein (Florida) provided data and insights. Colleagues, students, family, and friends over the years have contributed to the work on which this paper is based. R. Rheinhardt and R. Tiner provided thoughtful comments that improved this chapter. H. Lord prepared the map. We are grateful to all. Rider University provided support.