

Sudden Vegetation Dieback in Atlantic and Gulf Coast Salt Marshes

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Value of Salt Marshes

Salt marshes rank as the most productive ecosystems on the planet (Fig. 1A and B). Biomass production can be greater than 3 kg dry matter/m²/year, which is 40% more biomass than tropical rainforests produce (5) (Table 1). Salt marshes provide multiple benefits to mankind. For example, coastal communities receive protection from storm surges and wave erosion. Models have suggested that the damage from Hurricane Katrina would have been dramatically reduced had the Gulf marshes been intact in 2005 (39). Salt marshes absorb excess nitrogen and phosphorus from sewage and fertilizer run-off into rivers, which, in turn, prevents algal blooms and hypoxia in coastal waters. Much of our hydrocarbon-contaminated run-off from industrial areas is detoxified and decomposed by microbial activity in salt marshes. In addition, these unique ecosystems provide habitat and shelter for many hundreds of species of shellfish, finfish, migratory and sedentary birds, and other marine animals (5). Costanza et al. (10) produced estimates that when adjusted for inflation by Gedan et al. (16) in 2007, found that tidal salt marshes generated over \$14,000/ha in waste treatment, habitat refuge, food production, and recreational value.

Despite the richness in animal species, the intertidal marshes of the salt marsh ecosystem are dominated by only a few plant species. Of these, the most prevalent plant species in a marsh are the tall and short forms of smooth cordgrass (*Spartina alterniflora* Loisel.). Tall and short forms of *S. alterniflora* are genetically identical and can convert from one phenotype to the other when environmental changes are imposed (43). Tall forms are healthier and more vigorous and colonize creek banks, whereas short forms are stunted and persist in areas of poor drainage (Fig. 2A and B). Both forms are found almost exclusively in the low marsh, which is defined as an area that floods daily. High marshes flood during lunar cycles and contain other salt-tolerant plant species such as *Distichlis spicata* (L.) E. Greene, *Spartina patens* (Ait.) Muhl, and *Juncus roemerianus* Scheele (5).

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History of Sudden Vegetation Dieback (SVD)

The first recorded account of a dieback in a U.S. salt marsh was in the early 1990s in the Florida panhandle where patches of *Sp. alterniflora* as large as 1 ha died (8). Much of the affected area has since recovered. A decade later, low marsh areas along Louisiana's coast began to exhibit extensive dieback (Fig. 3A to C). Estimates in the Gulf predicted over 150 km of coastline comprising more than 100,000 ha of salt marsh were affected (25). A large portion of the marsh died within 4 to 8 months. Green plants turned brown and died, giving rise to the name "Brown Marsh" (Fig. 3B and C). Many areas have yet to recover, while several new areas have been affected in recent years (Fig. 3A). In 2001, portions of the salt marshes of coastal Georgia also began experiencing dieback (Fig. 4A and B) (31). By 2002, Georgia experienced the largest dieback of salt marsh vegetation ever recorded, with an estimated 800 ha affected. Coinciding with these events in the South were sporadic SVD sites that appeared from the Chesapeake Bay to Maine (Fig. 5A to D) (1). Surveys suggested that more than 10% of the marshes on Cape Cod were affected and had turned to barren peat (38). Recent SVD events appear to be an Atlantic/Gulf Coast phenomenon (Fig. 6). Diebacks of this nature on *Sp. alterniflora* have not been noted along the Pacific Coast or in Asia. A dieback was observed in the UK in the 1950s, where over 200 ha of *Spartina townsendii* groves were completely denuded (18,20). The area eventually recovered (18,36).

Symptoms of SVD

SVD is characterized as a progressive decline that begins with thinning and/or browning of the aboveground foliage of *Sp. alterniflora* (1). Plant death results over a period of a few months, leaving barren areas of remnant peat (Fig. 7) (1,25,37). Along the Atlantic marshes, SVD is often associated with creek banks that are dominated by the tall form of *Sp. alterniflora* (Fig. 5B), whereas along the Gulf, SVD is observed in the inner marsh areas (Fig. 3A). A key characteristic of SVD is death of the rhizomes resulting in no new growth. Recovery can be very slow and may take many years, although some sites in Louisiana recovered within 2 years (25). Some creek banks in Connecticut have remained devoid of vegetation for 7 years, while others recovered after 3 years. Most of the Maine SVD sites have recovered (S. Adamowicz, *personal communication*). Affected areas can be proximal to one another or at random within an otherwise healthy

marsh with no obvious pattern in regard to hydrology or location. Most affected areas do not increase in size over time, which leaves a striking demarcation between what appears to be healthy plants and barren mud (Fig. 7). Occasionally, one can find stunted, declining plants on the perimeter of the dieback site. SVD may be confused with many other disorders known to affect marsh lands, but SVD is unique in that it is relatively sudden and results in rhizome death.

Possible Causes

Observers initially postulated several possible factors causing SVD, such as smothering from wrack (washed-up organic material brought in by the tide), sea level rise, drought, soil chemistry changes, herbivory, and plant pathogens (1). Many factors that were associated with one site were not found elsewhere. Several causes have been dismissed. For example, the smothering of marsh grass by large accumulations of wrack rarely kills the rhizomes, and in situations where there is death, the area is quickly recolonized the following year (42). Similarly, data suggesting sea level rise did not explain the sporadic appearance of SVD, and flooding experiments failed to reproduce dieback symptoms. Herbivory by geese, snails, and crabs can have serious impacts in SVD sites, but since they entail the removal of plant tissue, many have argued that

they should not be confused with SVD, where living plants die and turn brown (1). However, herbivory has been shown to be ecologically very important in expanding the size and delaying recovery of salt marshes from SVD (21).

Fungal pathogens. In many sites, SVD appeared to begin as specific foci of dieback, each radiating outward, culminating in a coalescence of foci to create large, irregular areas within the marsh system. This type of pattern suggested a contagious agent may be involved. In the UK in the 1950s, pathogens were suspected in a salt marsh dieback where *Spartina townsendii* suddenly died (18,19). Over 20 fungal species were isolated from dead rhizomes, but none of the fungi fulfilled Koch's postulates following pathogenicity tests. Although scientists concluded a parasite was not involved in the dieback, it is not clear if their conclusion would have been altered if live, dying tissue had been sampled instead of dead rhizomes or if selective media had been used.

A comprehensive assessment of the possible role of pathogens was conducted in Louisiana in 2002 following the dieback event (41). Samples, including roots and stems, were collected from several declining marsh sites. In addition, roots and stems were collected from a large mesocosm simulation study in which large intact turf samples from several marsh locations were subjected to different environmental treatments, e.g., rainfall, tidal fluctuations, and salinity, in an attempt to simulate the dieback phenomenon under controlled conditions (40). *Fusarium proliferatum* and *F. fujikuroi*, along with an undescribed species of *Fusarium*, all belonging to the *Gibberella fujikuroi* species complex (29), comprised the vast majority of fungi recovered from these samples, although *Rhizoctonia solani* was occasionally recovered as well. Briefly, more than 50 isolates from this collection were tested for pathogenicity and virulence by inoculating greenhouse-grown plants using several inoculation protocols including the use of colonized wooden toothpicks inserted into stems and application of water agar discs of the test fungi to freshly cut leaf scars. Also included in the pathogenicity tests were several isolates of *F. fujikuroi* that cause a black leaf spot on *Sp. alterniflora* (41) (Fig. 8). The toothpick inoculations provided measures of virulence in which the length of pith discoloration was measured, while the agar discs and other noninvasive inoculations were used to establish pathogenicity. A wide range of virulence was observed among the fungi that were tested, with symptoms ranging from slight discoloration at the infection court to plant death. The only pathogenic species were several species of *Fusarium* and *R. solani*. Interestingly, *F. fujikuroi*, the black leaf spot pathogen, was one of the most virulent pathogens.

A regional survey of Atlantic and Gulf SVD sites was initiated in 2006 to determine the *Fusarium* species composition (14; unpublished data). For this study, *Sp. alterniflora* was sampled from both SVD and healthy sites in Alabama, Connecticut, Delaware, Florida, Georgia, Louisiana, Maine, Maryland, Massachusetts, New York, and Virginia. None of the species originally recovered in Louisiana were found in high densities in any of the northern marshes. However, of 514 isolates of *Fusarium* spp. recovered, more than 75% shared morphological characteristics that putatively

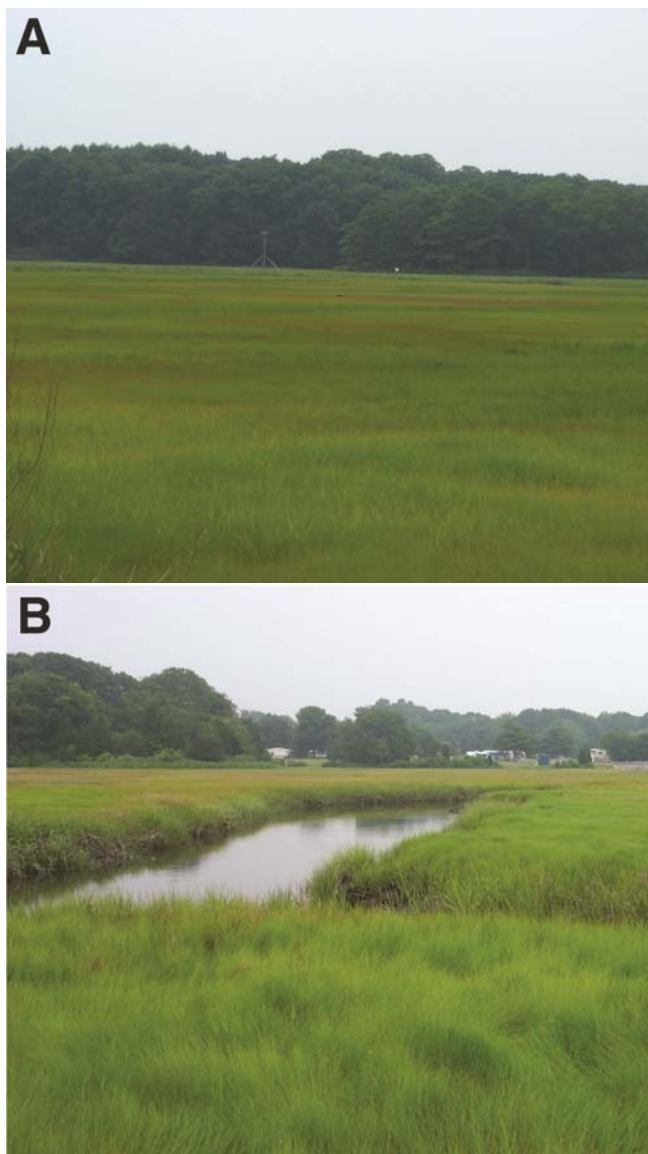


Fig. 1. Salt marshes in Madison, CT, unaffected by Sudden Vegetation Dieback. A, Mosaic zonation of a healthy marsh. B, Tidal creek in a healthy salt marsh.

Table 1. Primary production estimates from different natural and cultivated ecosystems

Ecosystems	Dry kg/m ² /year
Salt Marsh	3.30
Coral Reef	2.50
Tropical Rainforest	2.00
Sugarcane	1.73
Grassland	0.60
Corn	0.41
Wheat	0.34

^a Compiled from Bertness 2007 (5).

identified two groups as unidentified species. Furthermore, translation elongation factor 1 α (*tef*) gene sequences from this group formed a monophyletic cluster that did not include any other *Fusarium* species in the GenBank database. Sequences from the beta tubulin and calmodulin genes corroborated this finding (14). Isolates in this group were moderately virulent in pathogenicity tests and caused lesions on *Sp. alterniflora* stems. Based on these findings, this new species was named *F. palustre* (from the Latin *palus*, referring to the marsh habitat) (Fig. 9) (14). Importantly, *F. palustre* isolates were recovered from every SVD site.

The second largest group comprised isolates that were only slightly virulent on *Sp. alterniflora*, more variable morphologically than the *F. palustre* clade, resembling *F. incarnatum* (syn *F. semitectum*), and belonging to the *F. incarnatum-equiseti* species complex (30). Of the remaining isolates recovered from SVD sites, most were identified as *F. fujikuroi*, *F. equiseti*, *F. oxysporum*, *F. proliferatum*, or *F. solani*, while a few isolates of *F. graminearum* were recovered from a site in Delaware and *F. lactis* was identified from one site on Long Island, NY. All isolates were identified taxonomically and confirmed by taxonomic (24) and *tef* gene sequences (17). Intensive surveys conducted along the Connecticut and Cape Cod coastlines during 2007 to 2009 showed that colonies of *F. palustre* and *F. cf. incarnatum* were isolated more frequently from plants in SVD sites than in sites where no SVD was found (Table 2) (15). Although no evidence suggests that *Fusarium* is a

major incitant of SVD, its close association with stressed *Sp. alterniflora* in SVD sites suggests the hypothesis that it may exist as an endophyte with the potential for a pathogenic lifestyle on stressed plants. A current hypothesis suggests that *Fusarium* spp. may also function in the physiological disruption of sulfur-containing defense products in *Sp. alterniflora* (3,4,22).

Nematodes. The presence of root-knot nematodes (*Meloidogyne spartinae*) was first reported on roots of *Sp. alterniflora* in Florida (32), but until recently, interest in this nematode has been mostly taxonomic. However, in 2006, this nematode species was associated with *Sp. alterniflora* in SVD sites in Connecticut and Massachusetts (23) (Fig. 10A to C). The nematode was suspected as a factor in SVD for the following reasons: (i) the nematode's distribution was greatest on elevated creek banks where SVD was common; (ii) the nematode developed more quickly on plants along creek banks, and was specific only to *Sp. alterniflora* (the other sympatric species, such as *Sp. patens*, *Sp. cynosuroides*, *Juncus gerardii*, and *D. spicata*, were not affected by the nematode); and (iii) because of historical accounts on terrestrial plants of synergistic interactions between *Fusarium* spp. and root-knot nematodes (15,28). Inoculation tests satisfied Koch's postulates, but disease severity was marginal and mortality was never observed. When *Sp. alterniflora* was co-inoculated with *M. spartinae* and *F. palustre*, only a slight additive response in disease severity was observed, but no mortality (13). As an obligate parasite, *M.*

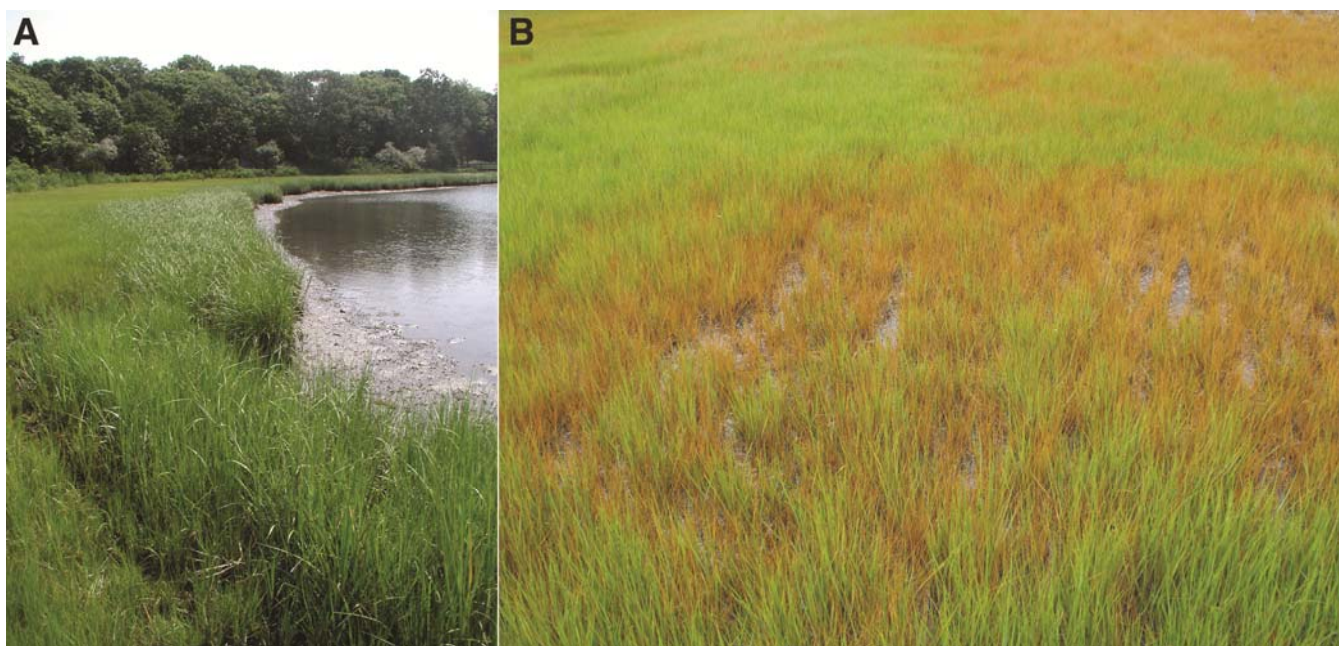


Fig. 2. A, Tall form of *Spartina alterniflora* on creek bank. B, Short form of *S. alterniflora* in salt pan.



Fig. 3. A, Sudden Vegetation Dieback (brown marsh) beginning to appear in a Louisiana marsh interior; B, showing the dying, browning *Spartina alterniflora*; C, remaining dead plants (courtesy C. Stagg).

spartinae may play a role in SVD as a predisposing stressor, but at present, its ecological contribution to SVD is unclear.

Herbivores. Much attention has been devoted to the influence of herbivores in SVD sites. Overgrazing can create “eat-outs”, which are areas in salt marshes that become denuded by intense herbivory (11). Grazers that were originally implicated in SVD are crabs, geese, and snails. Geese are unlikely agents since they can damage aboveground growth of *Sp. alterniflora*, but rarely kill rhizomes (1). In southern marshes where SVD had occurred, grazing by the salt marsh periwinkle snail, *Littoraria irrorata* Say, was shown to affect plant growth (34,35) (Fig. 11). Plants stressed by drought were found to be more susceptible to grazing by the snail. Silliman and colleagues (34,35) found that the snail obtained much of its nutrition from endophytic fungal species in *Phaeosphaeria* and

Mycosphaerella that colonized the damaged tissue. They proposed that the snail cultivated the fungi on dying tissue by initially scoring the tissue with their radula and allowing fungal saprophytes to colonize the wounds. However, SVD has occurred in many southern marshes where the snail did not occur. Many SVD sites are inhabited in very high densities by other invertebrates, including the purple marsh crab (*Sesarma reticulatum* Say) (9) (Fig. 12). High levels of marsh grass consumption can be attributed to herbivory by the purple marsh crab. A study on Cape Cod found that high densities of *Se. reticulatum* were strongly correlated with SVD sites (21). The increase in crab populations has been suggested to be a result of reduced predation (2,6). In most situations, herbivory has been shown to be ecologically important in expanding SVD sites and in restricting recovery, yet as with all putative

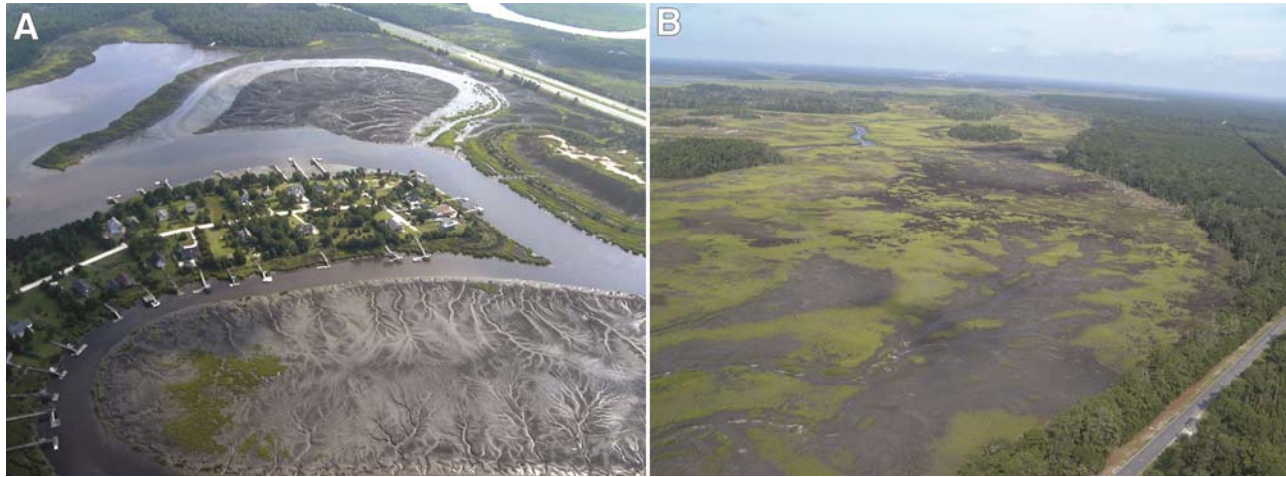


Fig. 4. A and B, Aerial views of Sudden Vegetation Dieback in Georgia salt marsh. (courtesy C. Rochester and M. Alber)



Fig. 5. Sporadic outbreaks of Sudden Vegetation Dieback in A, Popular Island, MD (courtesy L. Staver); B, Madison, CT; C, Lieutenant Island, Cape Cod, MA (courtesy S. Smith); and D, Drakes Island, Wells, ME (courtesy S. Adamowicz).

causes, experimental evidence demonstrating causality has been difficult to fulfill. Alternatively, Alber et al. (1) argued that herbivory resulted in the consumption of tissue and did not cause dieback and/or sudden death. In fact, the term *brown marsh symptoms* was coined because of the sudden appearance of dead standing biomass.

Abiotic stressors. Many wetland scientists favored the hypothesis that an abiotic stress preceded SVD, and one such proposed stressor was drought. Although most marshes flood daily, situations occur where tides can recede for extended periods of time and allow the soil to become aerobic. The major losses in marsh acreage in Louisiana coincided with one of the most intense droughts in the past 100 years (25). In Georgia, the time preceding SVD events (1999 to 2001) was the driest 3-year period on record (1). Major changes in soil chemistry occur when marsh soil becomes aerobic. Sulfides oxidize to sulfuric acid, and this results in soil pH values of 3 to 4, which in turn, causes the solubilization of heavy metals present in the soil. Mendelsohn, McKee, and colleagues (26,27) demonstrated that *Sp. alterniflora* was more sensitive to heavy metal toxicity than other sympatric species that did not decline during SVD events. Their conclusions were based upon

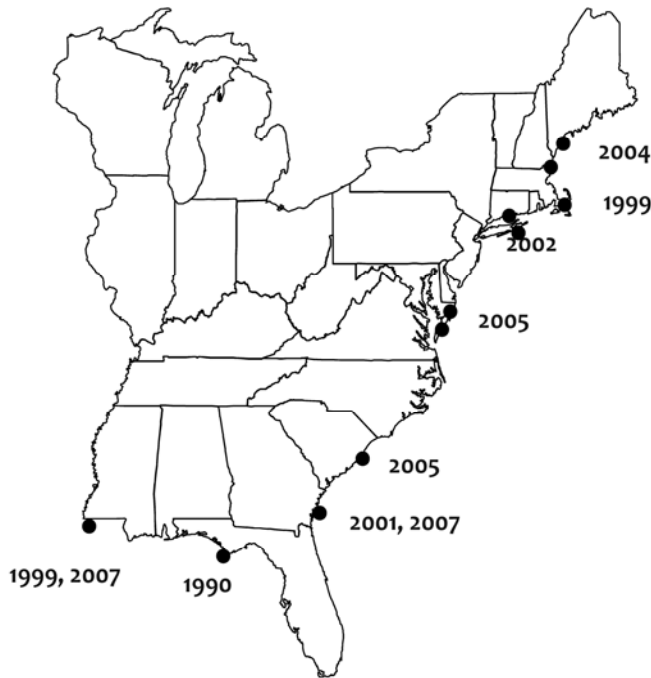


Fig. 6. Reported sites and dates of Sudden Vegetation Dieback along the Atlantic and Gulf coasts.



Fig. 7. Remnant peat left after *Spartina alterniflora* died following a Sudden Vegetation Dieback event.

the following lines of evidence: (i) plants in dieback areas during the brown marsh event had elevated metal ratios; (ii) marsh soils, when exposed to drought or aeration, generated higher acidities and greater metal concentrations; and (iii) *Sp. alterniflora* was much more susceptible to elevated metal concentrations than surviving species. Therefore, it was likely that the cause of plant mortality during the brown marsh event was metal toxicity, possibly exacerbated by water stress and fungal pathogens (27).

Although drought was associated with SVD in southern marshes (25,35), climatological data do not show an extended drought in most mid to north Atlantic marshes (1). However, tidal charts in New England show that wide fluctuations in average sea level began during the late 1990s (Fig. 13). These wide fluctuations from very wet to very dry conditions occurred when SVD was first noticed. It is not clear what effect this alteration in hydrology could have on the marsh ecosystem.

Most salt marsh plants are tolerant of the widely varying salinity natural to salt marshes. Brown et al. (7) showed that high salinity was not as damaging to the plant as was drought combined with high salinity. Although high salinity and drought are commonly associated with each other, increased salinity was not observed in most SVD sites (1). *Sp. alterniflora* is not only saline-tolerant, it continues to produce biomass in salinities up to 35 ppt (sea water) (44). As a stressor, however, salinity may predispose plants to disease (see below). Alber et al. (1) also conducted an analysis of temperature and precipitation trends in SVD sites using data from weather stations located nearby. No clear patterns were noted between SVD, rainfall, or temperature.

Interactions

Most wetland ecologists hold that drought alone or an interaction between drought and some other agent are the most likely scenarios that led to SVD in southern marshes. Many of the sus-



Fig. 8. (Left panel) Leaf spots incited by *Fusarium* spp.; (middle and right panels) stem rots caused by *Fusarium* spp.

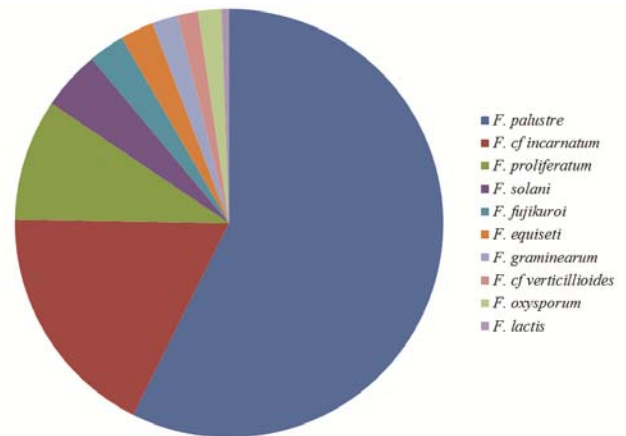


Fig. 9. Distribution of *Fusarium* spp. ($n = 514$) isolated from *Spartina alterniflora* plants removed from areas where Sudden Vegetation Dieback had occurred.

pected agents associated with SVD, such as pathogens, snails, and crabs, can be more damaging under drought conditions. Many of these scenarios were tested in greenhouse experiments described below (41). Having established that *Fusarium* species and *R. solani* could cause the same symptoms that were observed in the marsh, an experiment with virulent isolates was conducted in which two isolates of *F. proliferatum*, one isolate of *F. fujikuroi*, and one isolate of *R. solani* were tested under conditions that were associated with the marsh decline syndrome, including higher than normal salinity and water deficits. Briefly, flooded benches were adjusted to two salinity levels (23 and 38 ppt) with artificial sea water (Crystal Sea Marine Mix, Baltimore, MD) plus a fresh, deionized water control. Pots with drainage holes were submerged so the water was the same height as the soil line (submerged) or kept so the water level reached the bottom 3 cm of the pots (elevated). Two weeks later, plants were inoculated. Soil and plant water potential were monitored with tensiometers and a Scholander pressure chamber apparatus (PMS Instrument Co., Albany, OR), respectively. Plants were inoculated by placing a water agar plug of each test isolate onto nonwounded leaf scars at the second node above the soil surface and secured with a strip of plastic film. Blank agar plugs were used for the noninoculated controls. Disease severity was assessed at 4 weeks after inoculation by measuring the extent

of discolored pith tissue according to the following scale: 1, no symptoms; 2, discoloration at the inoculation site (IS); 3, discoloration in the internode immediately above the IS; 4, discoloration at the second node above the IS; 5, discoloration in the second internode above the IS; 6, discoloration at the third and higher nodes above the IS; and 7, plant death. Plant height also was measured (data not shown). The experiment was repeated once.

Soil water potential in the elevated pots varied from -0.02 to -0.05 MPa, and the submerged pots were saturated. Plant water potential values for the control (fresh water) and 23 and 38 ppt in the submerged treatments were -0.20 , -0.28 , and -0.31 MPa, respectively, and in the elevated pots were -0.40 , -0.46 , and -0.45 MPa, respectively. Results showed that the two *Fusarium* spp. were capable of causing severe symptoms in *Sp. alterniflora* and that these symptoms were greatly amplified with increasing salinity (Table 3). The salinity values used in this study were recorded in the marsh during the dieback event. *R. solani* was highly virulent in the fresh water treatment in both the raised and submerged pots, but virulence was not significantly different from the noninoculated controls in the 23 and 38 ppt treatments. This organism may be pathogenic in fresh water marshes, but it is probably not related to the dieback discussed here. There was a significant interaction ($P = 0.001$) between salinity and disease severity across

Table 2. Distribution of *Fusarium* isolates from *Spartina alterniflora* collected from healthy salt marshes and Sudden Vegetation Dieback sites in Connecticut and Massachusetts in 2007 to 2009

Location	Species ^a			
	Total ^b	<i>F. palustre</i>	<i>F. cf. incarnatum</i>	Other ^b
SVD sites				
Hammonasset Beach (CT)	62	32	11	19
Banca Marsh (CT)	24	22	1	1
Pleasant Point Marsh (CT)	16	11	1	3
West River (CT)	50	41	7	2
Neck River (CT)	24	20	1	3
Sippewisset Marsh (MA)	9	5	2	0
Lieutenant Island (MA)	10	9	1	0
Herring River (MA)	6	2	1	3
Total	195	140	25	10
Non-SVD sites				
Sherwood Island State Park (CT)	4	4	0	0
Milford Point (CT)	3	2	1	0
Mill Creek (MA)	1	0	0	1
Scorton Creek (MA)	3	3	0	0
Sesuit Neck (MA)	0	0	0	0
Great Meadow (CT)	1	1	1	0
Salt Pond Bay, (MA)	0	0	0	0
Ryder's Cove, (MA)	0	0	0	0
Total	12	10	2	1

^a Species were based on morphological characteristics.

^b *Fusarium solani* and *F. oxysporum*.

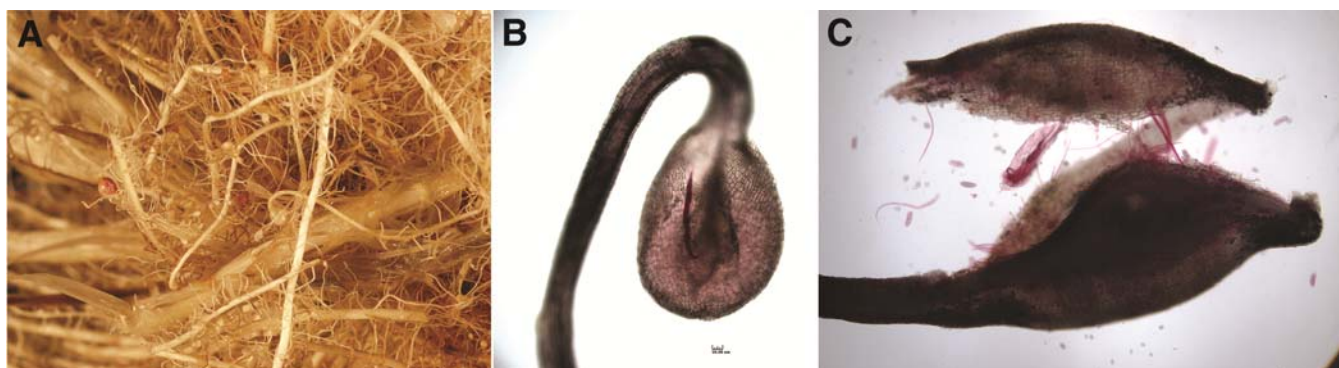


Fig. 10. Root-knot nematodes (*Meloidogyne spartinae*) on *Spartina alterniflora*: **A**, root galls on a naturally infected plant; **B**, root gall showing adult male (red) and bloated female both inhabiting the same gall; and **C**, crushed gall reveals different cohorts (eggs, first larval stage, and adults) of *M. spartinae*.

all isolates but not between plant water potential and disease severity ($P = 0.854$). However, the plant water potentials achieved in this greenhouse study were probably not as low as those recorded in the marsh during the dieback event, so we were not able to disregard reduced plant water potential as a stressor on the basis of this study. Nevertheless, moderate salinity alone appears to be sufficient to predispose plants to infection. We also recognize that these results were based on artificially inoculated plants that may not reflect the true endophytic relationship found in nature. However, given that *Fusarium* spp. are found in lower densities in healthy marshes than in stressed (13), it is reasonable to assume that stress, such as drought or salinity, would favor an increase in colonization and resulting disease.

In studies where increasing salinity (17.5, 35.0, or 70.0 NaCl ppt) was used to irrigate *Sp. alterniflora* grown in soil infested with *F. palustre* or in noninfested soil, fresh weights of *Sp. alterniflora* were inversely proportional to salinity (data not shown). We did not observe a significant interaction between salinity and inoculation with *F. palustre*, but plants were smallest when grown in infested soil under saline conditions (data not shown). Additional greenhouse studies were conducted with *Sp. alterniflora* in which drought, constant flooding, or normal tidal irrigations with and without inoculations with *F. palustre* were tested alone and in combination. Flooded plants were left in water for 3 days, drained for 1



Fig. 11. Dead stalks of *Spartina alterniflora* infested with the salt marsh periwinkle snail *Littoraria irrorata*.



Fig. 12. Adults of the purple marsh crab (*Sesarma reticulatum*) feeding on *Spartina alterniflora* in mesocosms.

day, and flooded again, and the drought treatments were imposed by allowing plants to go 3 to 5 days until leaves began to curl (indicator of drought). We believe that this stress was comparable to what a marsh system under severe drought might be exposed to. There was significantly more mortality in drought-treated plants when the soil was infested with *F. palustre* than with plants grown in noninfested soils (Fig. 14). Both fresh weight and disease ratings were affected more when plants were grown in infested soils and subjected to drought stress than if plants were grown in infested soil and irrigated normally (Fig. 15). Given that low incidences of *F. palustre* exist in marshes where no SVD was evident (13), we contend that the incidence of endophytic *Fusarium* spp. increases on stressed plants and that these otherwise weak pathogens then cause damage in the form of leaf spots, stem rots, and stunted growth. This scenario is equivalent to stalk rots of corn and sorghum in which water and high temperature stressors are required for these otherwise weak pathogens to cause disease. Schneider and Pendery (33) showed that *F. verticillioides* (syn *F. moniliforme*) is endophytic in corn unless plants are subjected to water stress early in the season, with symptoms developing several weeks after the water stress event. Similar findings were observed with *Fusarium oxysporum* f. sp. *asparagi* and *F. proliferatum* on asparagus (12).

The *Fusarium* species used in both of these experiments were readily isolated from healthy and diseased plants in the marsh and from the mesocosm experiment. One of the isolates, *F. fujikuroi*, which causes a black leaf spot, was widely distributed in Louisiana while *F. palustre* and *F. cf. incarnatum* were ubiquitous in Atlantic marshes. While there is ample evidence to implicate abiotic stressors as causal agents of the marsh decline, we cannot ignore the likely role played by these endophytic fungi. We conclude that plants were predisposed to infection by the severe environmental stressors that occurred in 1999 to 2000, and that there was a strong interaction between these predisposing events and the otherwise benign endophytes. The functions of these endophytes in non-stressed plants are not known. Symptoms in corn and *Sp. alterniflora* are virtually identical and include vascular and pith tissue discoloration and disintegration leading ultimately to weakened stems, premature leaf death, and lodging.

In New England, the purple marsh crab (*Se. reticulatum*) has hindered restoration efforts in many SVD sites, leading scientists to wonder why these invertebrates have recently reached such high densities. While predation release has been postulated as one reason (2), we also questioned if *Se. reticulatum* are more attracted to SVD sites than to non-SVD sites, possibly because stressed, diseased *Sp. alterniflora* was more palatable. To test this hypothesis,

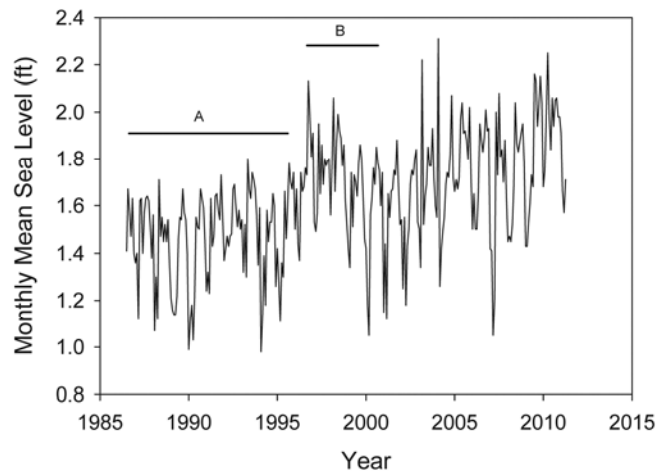


Fig. 13. Mean monthly sea level for New London, CT, over the past 25 years. The time period labeled "A" represents time preceding the first reports of Sudden Vegetation Diebacks (SVD). The time period labeled "B" represents when SVD appeared in New England.

preliminary studies were conducted where adult marsh crabs captured from an SVD site in Madison, CT, were reared in captivity in mesocosms. Consumption, based on estimates of the number of grass blades cut, was greater on *Sp. alterniflora* plants that were drought- and diseased-stressed than on nonstressed healthy plants. Although additional experimentation is needed, these preliminary findings suggest that a temporary drought and/or infection by *Fusarium* spp. may predispose plants to be more attractive to the purple marsh crabs.

Summary

The fact that SVD is in multiple marshes over large areas makes it of considerable ecological and societal importance. The ramifications of salt marsh loss in a vulnerable coastline are readily evident following coastal destruction by hurricanes. From 1999 to 2004, SVD has occurred sporadically from Maine to the Gulf Coast. The lack of a good working hypothesis for the cause of SVD initially hampered ecologists from distinguishing it from other disturbances in salt marshes. A key signature of SVD is that it occurs quickly (within one season) and there is little to no recovery the next year. In southern marshes, drought-mediated changes in soil chemistry were postulated to have precipitated the initial stress that led to the SVD event (brown marsh) in 1999. Investigations into the possible role of *Fusarium* in causing SVD led to the discovery of a new species, *F. palustre*, which has been associated with SVD sites from Maine to Louisiana. It may have an endophytic association with *Sp. alterniflora* similar to that of other *Fusarium* species and their hosts, e.g., *F. verticillioides* on corn, *F. thapsinum* on sorghum, or *F. proliferatum* on asparagus. Although the endophytic fusaria on *Sp. alterniflora* are probably not primary causal agents, they may function as pathogens in plants predisposed by stressors. The role of root-knot nematodes as potential contributors to the complex is still unclear. The unique obligate relationship that they maintain with living plants is problematic in attempts to determine their role in SVD sites. Herbivory by marsh crabs and snails continues to affect the recovery of salt marshes undergoing stress, but the difficulty in completing an analogous set of Koch's postulates in healthy marshes with these herbivores precludes the demonstration of causality. Creative experiments are needed.

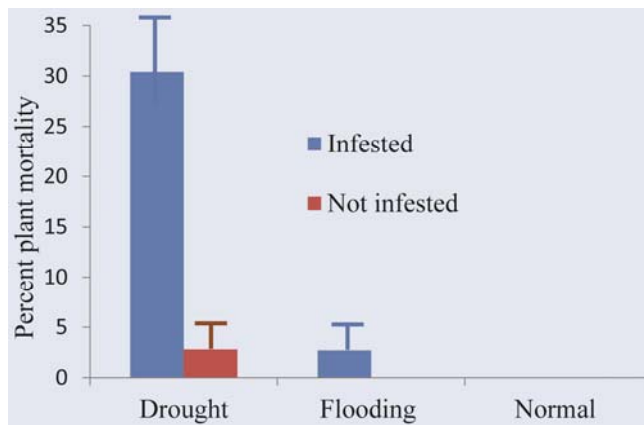


Fig. 14. Effect of drought, flooding, and normal irrigation on plant mortality of *Spartina alterniflora* grown in soil infested with *Fusarium palustre* or in noninfested soil.



Fig. 15. Effect of *Fusarium palustre* on plants exposed to drought.

Table 3. Effects of salinity and water deficits on disease severity caused in *Spartina alterniflora* caused by *Fusarium proliferatum*, *F. fujikuroi*, and *Rhizoctonia solani*

Isolate	Salinity of irrigation water (ppt) ^b	Disease severity ^a	
		Elevated ^c	Submerged ^c
<i>F. proliferatum</i> 1	0	2.6	3.0
<i>F. proliferatum</i> 1	23	3.4	3.6
<i>F. proliferatum</i> 1	38	5.8	5.4
<i>F. proliferatum</i> 2	0	2.8	3.2
<i>F. proliferatum</i> 2	23	4.4	4.2
<i>F. proliferatum</i> 2	38	6.2	6.4
<i>F. fujikuroi</i>	0	3.0	3.8
<i>F. fujikuroi</i>	23	5.2	4.8
<i>F. fujikuroi</i>	38	6.2	6.2
<i>R. solani</i>	0	4.8	4.8
<i>R. solani</i>	23	2.2	2.2
<i>R. solani</i>	38	1.8	1.4
Control	0	1.2	1.4
Control	23	1.6	1.4
Control	38	1.8	2.0
LSD ($P = 0.05$)		2.2	1.9

^a Disease severity was based on the following scale: 1, no symptoms; 2, discoloration at the inoculation site (IS); 3, discoloration in the internode immediately above the IS; 4, discoloration at the second node above the IS; 5, discoloration in the second internode above the IS; 6, discoloration at the third and higher nodes above the IS; and 7, plant death.

^b Deionized water was used to prepare artificial sea water as described in the text. Salinity is expressed in parts per thousand.

^c Pots with drainage holes were submerged so the water was the same height as the soil line (submerged) or kept so the water level reached the bottom 3 cm of the pots (elevated).

It is possible that stressors, such as eutrophication and/or sea level rise, may have made marsh plants more susceptible to temporary drought, which may explain why sudden dieback has not been reported previously. The increased reports of dieback in recent years may have the same etiology, but it is not clear if these recent events are extensions of the original SVD or precipitated by new, unidentified stressors. Alternatively, it may be that SVD is reported more frequently because people are more attuned to recognizing the phenomenon. Many questions remain as to the cause and nature of SVD; therefore, remediation efforts, including development of varieties of *Sp. alterniflora* with resistance or tolerance to biotic and abiotic stressors, will remain elusive until we obtain some clarity with regard to causation.

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