Estuaries and Coasts (2012) 35:445–458
DOI 10.1007/s12237-012-9479-x

# Vegetation Cover and Elevation in Long-Term Experimental Nutrient-Enrichment Plots in Great Sippewissett Salt Marsh, Cape Cod, Massachusetts: Implications for Eutrophication and Sea Level rise

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Received: 20 July 2009 / Revised: 10 June 2011 / Accepted: 15 June 2011 / Published online: 26 January 2012

**Abstract** Nitrogen inputs restructure ecosystems and can interact with other agents of ecological change and potentially intensify them. To examine the effects of nitrogen combined with those of elevation and competition, in 2005 we mapped vegetation and elevation within experimental plots that have been fertilized since 1970 in Great Sippewissett salt marsh, Cape Cod, MA, USA and compared the resulting effects on marsh vegetation. Decadal-scale chronic nutrient enrichment forced changes in cover and spatial distribution of different species. With increasing enrichment, there was a shift in species cover primarily involving loss of *Spartina alterniflora* and an increase in *Distichlis spicata*. Percent cover of near monocultures increased with nitrogen fertilization, owing mainly to the proliferation of *D. spicata*. The experimental fertilization prompted a shift from the short form of *S. alterniflora* to taller forms, hence increasing above-ground biomass, where this species managed to remain. Chronic enrichment increased upper and lower limits of the elevation range within which certain species occurred. The shift to increased cover of *D. spicata* was also associated with faster accretion of the marsh surface where this species was dominant, but not where *S. alterniflora* was dominant. Interactions among nutrient supply, elevation, and competition altered the direction of competitive success among different species of marsh plants, and forced changes in the spatial distribution and composition of the salt marsh plant communities. The results imply that there will be parallel changes in New England salt marshes owing to the widespread eutrophication of coastal waters and the increasing sea level rise. Knowing the mechanisms structuring marsh vegetative cover, and their role in modification of salt marsh accretion, may provide background with which to manage maintenance of affected coastal wetlands.

**Keywords** Vegetation cover · Salt marsh · New England · Long-term nutrient enrichment · Eutrophication · Sea-level rise

## Introduction

Production and zonation of salt marsh vegetation are affected by nitrogen availability, elevation, and its associated edaphic characteristics, sea level rise, grazing, and other factors (Valiela and Teal 1974; Howes et al. 1981, 1986; Bertness 1991a, b, Gehrels et al. 2005). Earlier enrichment experiments demonstrated that growth and production of salt marsh vegetation and production were primarily limited by nitrogen supply (Valiela and Teal 1974; Valiela et al. 1975, 1978; Sullivan and Daiber 1974; Chalmers 1979; Haines 1979), and that the limitation was mediated by sediment redox (Howes et al. 1981, 1986). These enrichment experiments found that more nitrogen fostered changes in biomass, morphological characteristics of species, and changed vegetation composition of species, sometimes favoring opportunist species with a high affinity for higher nitrogen supply (Valiela et al. 1985a). More recent enrichment, competition, and zonation experiments corroborated the earlier findings that increased nitrogen supply shifted competitive success of salt marsh species, and hence composition of marsh swards (Levine et al. 1998a, Rogers et al. 1998). Most enrichment experiments reported span at most a few growing seasons. The question remains as to

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whether short-term results are broadly applicable to longer decadal time scales.

New England salt marshes often include creek bank, low- and high-marsh habitats. Vegetation in these habitats differs in relation to elevation within the tidal range, degree of water logging, redox potential, salinity, pH, and nutrient availability in sediment and pore water as well as other aspects (Warren and Niering 1993; Portnoy and Valiela 1997; Howes et al. 1986). Such contrasts lead to the recognizable plant zonation (Warren and Niering 1993, Donnelly and Bertness 2001;Thursby and Abdelrhman 2004; Silvestri et al. 2005). Within each habitat, interspecific competition also plays a significant role in establishing zonation of species (Valiela et al. 1978; Bertness and Ellison 1987; Bertness 1991a, b; Pennings et al. 2003, 2005). The competing species sort themselves into monospecific and mixed stands along this elevation gradient. *Spartina alterniflora*, the dominant plant species in New England salt marshes, is most often found in monospecific stands at lower elevations and in mixes at higher elevation ranges (Redfield 1972). Biomass and productivity of *S. alterniflora* decreases as elevation increases from creek bank to high marsh (Howes et al. 1986, Morris et al. 2002). This difference in productivity is associated with ecophenotypic growth forms, ranging from a tall (1–3 m) to a short form (10–40 cm; Shea et al. 1975; Valiela et al. 1978; Howes et al. 1986; Ornes et al. 1998). Other common species, such as *Spartina patens* and *Distichlis spicata*, are mostly found within higher elevation marsh habitats (Chapman 1960). Although in many marshes, each salt marsh plant species or form is poised within a reasonably well-defined intertidal vertical profile (Warren and Niering 1993), much heterogeneity has been reported for species in both different and similar areas (Bockelman et al. 2002; Silvestri et al. 2005), revealing some complexity in the interactions of the many controls on salt marsh vegetation.

Because most species of marsh plants are reasonably narrowly poised at certain tidal ranges (Warren and Niering 1993, Valiela and Rietsma 1995), rising sea level will inevitably force changes in the distribution of marsh vegetation. In the Western Atlantic, rates of relative sea level rise are approximately 2.0–2.5 mm year$^{-1}$ (Reed 2002), with local differences related to geological factors. The strata of marsh plants could survive in the face of increased sea level rise by moving higher and land-ward, if sufficient accretion—largely by peat formation from marsh grass biomass, and to some smaller degree by particle trapping—takes place, so that salt marsh surfaces could maintain pace with sea level rise (Bertness 1988, Morris et al. 2002, Slocum et al. 2005, Valiela 2005, Langley et al. 2009). Sea level has increased significantly in the Cape Cod area of New England, and has been accompanied by accretion of salt marsh surfaces of about 12 cm since 1970 (Reddy et al. 2002, White et al. 2005a, b). Accretion has therefore taken place, but if nutrient supply increased or decreased (Morris et al. 2002, McKee et al. 2007, Langley et al. 2009, Cherry et al. 2009, Darby and Turner 2008, Turner et al. 2009) rates of biomass accumulation or sediment trapping, enrichment such as is taking place widely in the world's shorelines could alter the ability of marshes to keep up with sea level rise.

In this paper, we make use of detailed data on vegetation cover and elevations from experimental plots included in a long-term study conducted since 1970 in Great Sippewissett salt marsh (Valiela et al. 1973, 1985a) to define multi-annual changes in vegetation cover and their potential links to differences in nutrient supply and elevation shifts. The experimental plots have been chronically fertilized at different doses; each plot contains vegetation within the elevation gradient from creek bank to high marsh (Fig. 1). We use cover and elevation data collected in 2005 from the experimental plots with two principal aims. The first goal was, using data collected in 2005, to define how different rates of long-term (decadal-scale) chronic nutrient addition affected salt marsh vegetation growing at different elevations in a New England salt marsh.

The second goal was to define possible interactions of long-term nitrogen enrichment and elevation of the marsh surface and the resulting effect on the balance between accretion and sea level rise. From analyses of the cover and elevation data, we first assessed the response of cover and elevation range of the different marsh plants to

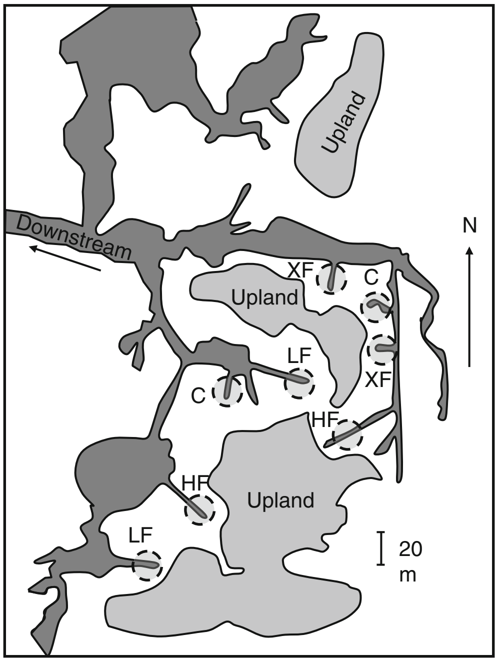

**Fig. 1** Map of experimental plots within Great Sippewissett salt marsh. Plots marked *C* are controls, the rest are fertilized with mixed fertilizer at three dosages [0.85 (*LF*), 2.52 (*HF*), and 7.56 (*XF*) g N m$^{-2}$ week$^{-1}$]. *Gray areas* upland hummocks, *dark gray* tidal streams

differences in nutrient supply rates. We then examined how the changed vegetation in turn was associated with altered marsh surface elevation and speculate on the implications of our findings in the face of widespread eutrophication and increasing sea level rise of coastal environments.

## Methods

### Site Description

We have fertilized experimental plots (10 m in radius, Fig. 1) within Great Sippewissett salt marsh on Cape Cod, MA, USA, since 1970 (Fig. 1). Each plot is bisected by a small creek and includes creek bank (30–50 cm above mean sea level; MSL), low marsh (50–70 cm above MSL), and high marsh (>70 cm above MSL). Although the relative proportion of these habitats varied across plots, at the start of the study all plots contained a reasonably similar distribution of species (Valiela et al. 1985a). Two replicate plots receive each of a series of the four different treatments: untreated controls (C) and three dosages [0.85 (LF), 2.52 (HF), and 7.56 (XF) g $\mathrm{N m^{-2}}$ $\mathrm{week^{-1}}$] of a mixed fertilizer (10%N, 6% $P_2O_4$, 4%$K_2O$; Valiela et al. 1973).

The fertilizer we used is a slow-release mix, mainly organic nitrogen, with much of the organic form as urea, with small amounts of nitrate and ammonium. Since this was the first experiment in nutrient enrichment of salt marshes, we had no previous history with which to constrain the dosages; we set fertilization doses at 10, 30, and 90 times the United States Department of Agriculture-recommended annual dosage for oats; the original intent was to capture a wide range of nutrient loads, reaching high enough levels as to test the upper limits of tolerance and responses of the salt marsh ecosystem to eutrophication.

Fertilized plots were treated biweekly during the growing season (between March and October from 1970 to 1997 and during May–September since 1997). The nitrogen inputs that were therefore applied to treated plots, if considered on a per-year and per-unit area basis, ranged from 12 to 1,572 kg total N $\mathrm{ha^{-1}}$ $\mathrm{year^{-1}}$ (Table 1). This large range of nitrogen loads fall roughly within a reported range of inputs of total nitrogen of 27 to 1,880 kg total N $\mathrm{ha^{-1}}$ $\mathrm{year^{-1}}$ found to be entering many of the world's coastal environments, including salt marshes (Table 10.5 in Bianchi 2007). Fortuitously, the range of salt marsh fertilization we chose long ago matched the nitrogen inputs to which estuarine ecosystems have been exposed, according to more recent studies.

### Estimation of Vegetation Cover

To estimate and map vegetation cover in all plots, we used a visual estimation technique. Comparisons of methods concluded that visual method is more time efficient than point intercept methods, and may, in fact, give better estimates of cover (Mueller-Dombois and Ellenberg 1974). The field procedure was to set up lines that extended from a permanent post at the center of each plot to the periphery. The lines were marked at 0.5-m intervals and were separated by 2.50 m at the perimeter of the plot. We then mapped the vegetation patches within 0.5-m intervals from the center to the outer margin of the plot and then repeated the procedure until we had covered the entire circular plot. To describe the vegetation in the plots, we specified spatial extent location of patches of monocultures or mixes of different species or of short and tall forms of *S. alterniflora*. Within each patch, we distinguished cover categories in bins of 10% cover.

We initially verified our visual estimates of cover by surveying 27 replicate 1 $m^2$ plots by both the visual and conventional point-intercept methods. Values of cover obtained by the visual method compared quite well to those obtained using the point-intercept method (Fig. 2), providing assurance that the more time-effective visual method was a reliable approach.

To spatially analyze vegetation maps, we digitized and georeferenced all field maps in ArcView 9.1. Polygons of all

**Table 1** Rates of delivery of total nitrogen, per unit area, from the fertilization treatments for the Great Sippewissett marsh plots, shown as a rate of fertilization per meter square per year on the plots, and for comparison with nitrogen loads to larger land units, expressed as kilogram total N per hectare per year

| Treatment | Fertilizer dose ($\mathrm{g\ N m^{-2}\ year^{-1}}$) | Nitrogen load ($\mathrm{kg\ N ha^{-1}\ year^{-1}}$)[a] |
|---|---|---|
| C | 0 | 12 |
| LF | 0.85 | 182 |
| HF | 2.52 | 532 |
| XF | 7.56 | 1,572 |

[a] Including atmospheric deposition on the marsh surface, from Bowen and Valiela (2001)

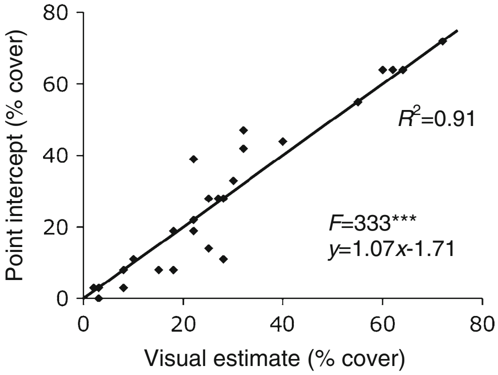

**Fig. 2** Comparison of point intercept method with visual estimates of cover. Data shown are the visual estimates of percent cover in a 1 $m^2$ patch versus cover values determined with a 36-point-intercept method

mapped patches were drawn in Arcmap and the relative percent covers of all species associated with them were assigned to each. The percent cover of each patch and its area were calculated with the Spatial Analyst tool provided by ArcView.

### Elevation Measurements

To obtain a detailed description of the topography of each plot (so that we could then relate detailed local elevation to vegetation cover), we conducted detailed elevation surveys in all plots. During winter 2005–2006, we measured elevation within each of the plots using water as a leveling device (accuracy to 1 cm, Evgenidou and Valiela 2002). This method uses changes in height of water within a measured tube connected to a reservoir to determine the relative difference in elevation from one point to the next. To provide a detailed survey of topography over the entire plot, we took elevation measurements along up to 21 radial transects recording relative elevation points at meters 1, 3, 4, 5, 6, 7, 8, 9, and 10 for even radii and 2, 4, 5, 6, 7, 8, 9, and 10 for odd radii. If major changes in topography occurred between pairs of measurements, additional data points were collected along transects.

We related the relative elevation measurements we collected for each plot to the elevation of the other plots by converting all topographical data to mean sea level by a series of steps. First, during three different spring tides, we placed wooden stakes painted with Elmer's Glue All. We added food coloring to the glue so that we would clearly see the exact level of the high tide in each plot. After incoming tidal waters washed off the colored glue, we measured the height of tidal flooding to within 0.25 cm. We then determined the absolute elevation of the marsh surface at the point of each tide gauge by taking the difference between the known height of the high tide and the height of flooding at the tide gauge. The elevation of the marsh surface at the center point of each plot relative to the elevation at the wooden stakes was then measured with the water-leveling device. Finally, the average elevation of the center point according to calculations made from all wooden stakes that flooded at each of the three tides surveyed was determined. This measurement was then standardized to mean sea level for all plot centers using National Oceanic and Atmospheric Administration datum for station 8447355 (Monument Beach), using the present epoch 1983–2001.

All raw elevation data were digitized using programs developed with Matlab 6.5 software. We used these programs to calculate all relative elevation points and link them to mean sea level. In addition, the programs linearly interpolated data to create detailed contour maps of each plot and output elevation data into a format that was imported into ArcView 9.1 to facilitate comparisons of elevation and vegetation data.

To ascertain if local increases in elevation were associated with the species present, and to assess whether *S. alterniflora* or *D. spicata* were involved in raising elevation of the marsh surface, we measured elevations along replicate transects from outside each plot into areas within the plots that were dominated by *S. alterniflora* or by *D. spicata*. The replicated transects included measurements inside and outside each plot, at five 1-m interval within the plots, and five measurements at 1-m interval beyond the boundary of the plots.

## Results

We reduced the field data on cover and elevation to geographic information system-based maps such as the examples shown in Fig. 3, which affords a comparison of a control plot with a plot subject to the highest fertilizer dose (XF). These two examples highlight contrasts in vegetative cover, as well as in elevations, between plots. It is difficult to perceive, from maps or cover data, the remarkable changes in vegetative cover that have taken place in these plots; Fig. 4 helps convey the changes in a XF plot. The entire area in this image was initially (in 1971) short *S. alterniflora*, which remains relatively uniform at about 10–15 cm in height today outside the plot (Fig. 4, foreground on lower part of image). In contrast, the *S. alterniflora* growing inside the plot (white stakes indicate the edge of the plot, Fig. 4) has been stimulated to grow to over 1 m tall (area in right center, Fig. 4). In addition, *D. spicata*, which originally was present only as scattered shoots to the left of the image, near the marsh elder fringe on the high tide mark, has proliferated to 100% cover in the center of the plot, displacing other species, including *S. alterniflora*. Surprisingly, marsh elder (*Iva frutescens*) shrubs that normally grow only at the upper high tide margin of salt marshes (Thursby and Abdelrhman 2004) in Cape Cod, have in recent years encroached, as a second replacement, on space that was colonized by *D. spicata* at the expense of *S. alterniflora* (Fig. 4, left, center). This paper describes and discusses these dramatic changes in vegetative cover under the different experimental enrichment regimes, as seen in data collected during the 2005 growing season.

Cover in the control plot included two kinds of patches: monocultures of taller *S. alterniflora* at lower elevations near creek banks, and mixes of shorter *S. alterniflora* and *S. patens* at higher elevations on the marsh platform (Fig. 3, left, top). In the XF plot, the spatial heterogeneity was more marked with monoculture patches of tall *S. alterniflora* at lower elevations, monocultures of *D. spicata*, with some *I. frutescens* and patches of mixed species (Fig. 3, left bottom) at higher elevations.

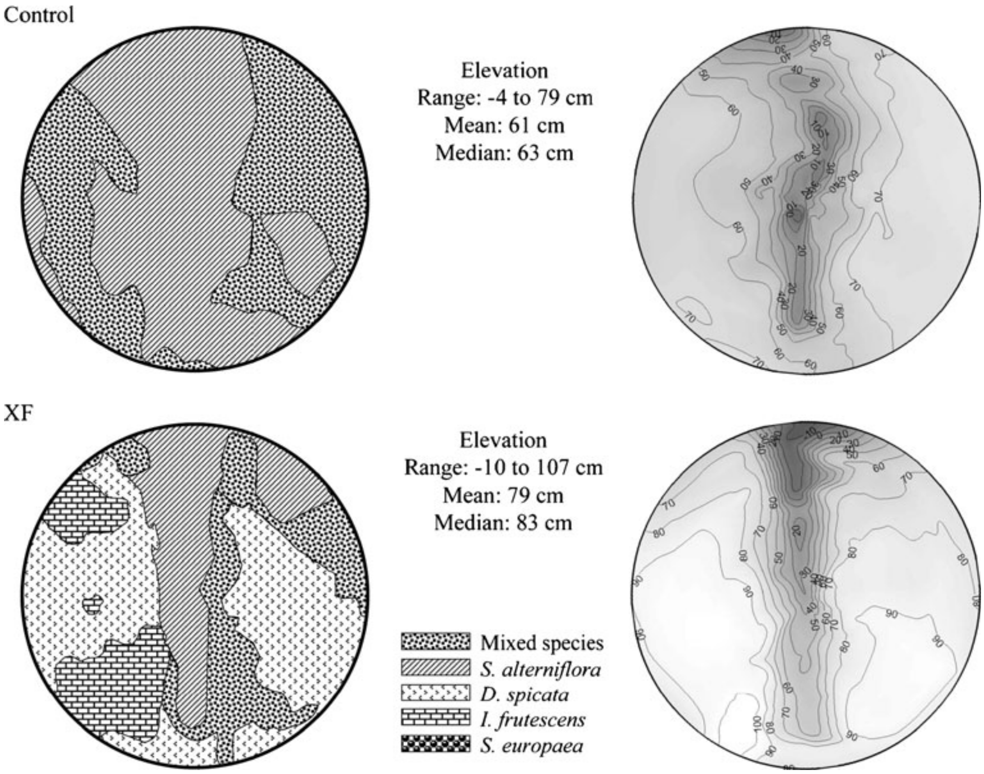

**Fig. 3** *Left* simplified outline of vegetation in a sample control and a XF treatment plot. Vegetation on the plot is shown as patches of mixed species (<80% predominance of any one species) and patches of near monocultures of specific taxa (>80% cover of one species). *Right* elevation contour maps of the same control and XF treatment plots shown on the *left*. All elevations are reported in centimeter, where MSL= 0.0 cm

C and XF plots showed similar topography, with a low creek in the middle, a sloping creek bank, grading to a near-flat marsh platform. Elevation of the plots differed to some degree from one plot to another (Fig. 3, right). In 2005, mean elevation of the XF plot was, on average, 18 cm higher than that of the C plot. Lowest elevations in C and XF plots were similar, but maximum elevation was substantially higher (by 28 cm) in the XF plot. More detailed cover and elevation maps for all the plots were included in Fox (2007), and will also be available at http://ecosystems.mbl.edu/sippewissett/index.html.

**Fig. 4** View of experimental marsh plot treated with the XF dosage, showing the marked responses of vegetation that have occurred after decades of chronic nutrient enrichment

The substantial differences in responses of vegetation (species cover, species mixes vs. monocultures, and spatial heterogeneity), and elevation of the surface of the plots—suggested by the two example plots in Fig. 3 and the image in Fig. 4—were substantiated by comparisons of data from the entire set of plots, which follow below.

## Vegetation Response

### *Shifts in Species Cover*

After 35 years of chronic enrichment treatments, vegetation cover in the Great Sippewissett plots showed marked shifts. Based on results from previous published work, reviewed above, we infer that larger nitrogen supply substantially altered competitive outcome. For example, considering entire plots, the higher fertilization doses were associated with about 40% lowered cover of *S. alterniflora* (Fig. 5, left, first panel), and about tenfold increased cover of *D. spicata* (Fig. 5, left, third panel). These responses were similar to reports from elsewhere (Traut 2005). There was no evident net long-term effect of fertilization on cover of *S. patens* (Fig. 5 left), even though in earlier experiments we detected some shorter term, time-dependent responses by *S. patens* to nitrogen supply (Rietsma et al. 2011).

Effects of enrichment on species composition were most evident if data are shown in stacked form (Fig. 5, right). *S.*

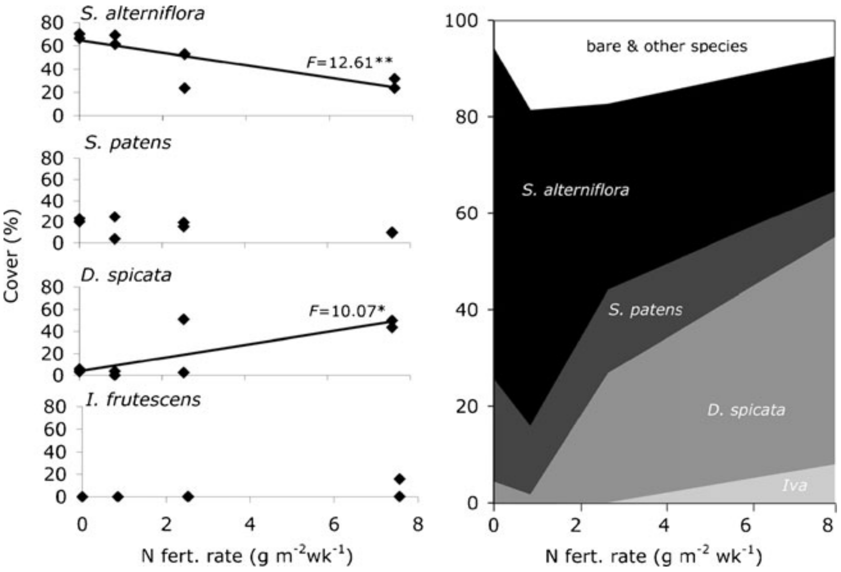

**Fig. 5** *Left* Total percent cover of *S. alterniflora*, *S. patens*, *D. spicata*, and *I. frutescens* shown versus rate of nitrogen fertilization dose (g m$^{-2}$ week$^{-1}$). *Right* stacked version of the graph on the *left*

*alterniflora* dominated in plots where nitrogen supply was low, but at the highest fertilization rates *D. spicata* expanded considerably, largely at the expense of *S. alterniflora*. *S. patens* cover remained virtually unchanged and *I. frutescens* appeared only in higher fertilization treatments.

### Alteration of *S. alterniflora* Forms

Cover of ecophenotypic taller and short forms of *S. alterniflora* changed with increasing fertilization (Fig. 6, top). Cover of short form *S. alterniflora* decreased significantly with higher fertilization rates, while cover of taller forms of *S. alterniflora* increased. The short form was converted to taller forms of *S. alterniflora* even at the lowest fertilization regimes. The sensitivity of *S. alterniflora* forms to nitrogen supply follows earlier reports (Valiela et al. 1978, 1985a), and was also found by Gallagher et al. (1988), Seliskar et al. (2002), and Morris et al. (2002).

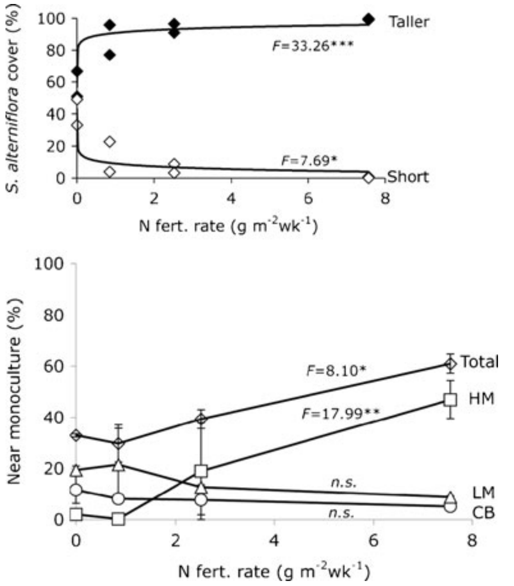

**Fig. 6** Top: Percent contribution of total cover by the short and taller ecophenotypes of *S. alterniflora* versus rate of nitrogen fertilization dose (g m$^{-2}$ week$^{-1}$). Data were log transformed for statistical analysis. *Bottom* mean percent of plot covered by near-monoculture, total, and divided into three elevations: creek bank 30–50 cm (CB), low marsh 50–70 cm (LM), and high marsh>70 cm (HM). A near-monoculture was considered any mixture of species of which 80% or greater was one species

### Changes in Occurrence of Other Species

In addition to the shifts in cover and form of the major vegetation species, there were losses and gains of minor species associated with fertilization. *Aster tenuifolius* and *Limonium carolinianum* appeared not uncommonly in mixed vegetation patches in the high marsh of control plots, but were absent in fertilized plots (Table 2). In contrast, the higher fertilization treatments stimulated presence of *Atriplex patula* and *I. frutescens*. These minor species might have reacted to either the higher nitrogen supply or to the increased elevation of the fertilized plots (see below).

The number of total species present decreased in control plots and increased in the highest treatment plots during the 35 years of experimental treatments (Table 3; Valiela et al. 1985a; Hersh 1996). Each of the four species lost over this period, *Salicornia virginica*, *Salicornia bigelovii*, *Plantago juncoides*, and *Triglochin maritima* were high-marsh species. The loss of high-marsh taxa is surprising in view of the increased elevation we report below as associated with fertilization, but seems related to the overwhelming response of *D. spicata*, a species that, more than any other, expanded opportunistically where *N* supply increased.

**Table 2** Species found in one plot of control treatment (0 gN m$^{-2}$ wk$^{-1}$) in 1976, 1996, and 2005 in creek banks (CB), low marsh (LM) and high marsh (HM) habitats

| Species | Habitat | 1976 (Valiela et al. 1985a, 1985b) | 1996 (Hersh 1996) | 2005 |
|---|---|---|---|---|
| *Spartina alterniflora* | CB, LM | X | X | X |
| *Spartina patens* | HM | X | X | X |
| *Distichlis spicata* | HM | X | X | X |
| *Salicornia europaea* | HM | X | X | X |
| *Salicornia virginica* | HM | X | X | - |
| *Salicornia bigelovii* | HM | X | X | - |
| *Aster tenuifolius* | HM | X | X | X |
| *Limonium carolinianum* | HM | X | X | X |
| *Gerardia maritima* | HM | X | X | – |
| *Plantago juncoides* | HM | X | – | – |
| *Triglochin maritima* | HM | X | – | – |
| Total | | 11 | 9 | 6 |

"X's" indicate that the species was present in that year

### *Shifts in Monocultures and Mixes*

So far, we have discussed overall cover per plot, but in reality, the various taxa occurred in spatially heterogeneous patches that varied from near monoculture to highly mixed mosaics. For this study, we defined as "near-monoculture" any patch with greater than or equal to 80% cover by a single species.

Larger nitrogen supply increased cover of near-monocultures for entire plots ("Total" data in Fig. 6, bottom). Near-monoculture patches were about 30% of the plots in C plots and ranged up to more than 60% in XF plots (Fig. 6, bottom). The trend to more near-monocultures, however, was most pronounced in high marsh, rather than in low marsh or creek banks. Near-monocultures of *D. spicata*, a high marsh plant, made up nearly 45% of the total area of plots subject to the XF treatments (Fig. 6 and Fig. 3) and gained plot area cover at the expense of low-marsh plants such as *S. alterniflora*. This again highlights the apparent advantage that high nutrient supply conferred on an opportunistic species such as *D. spicata*.

## Responses of Marsh Surface Elevation

Specific elevation played an independent as well as a dependent role on the effects of fertilization and shifts in salt marsh vegetation cover. Small local elevation differences initially setup the vegetation strata within the experimental plots, but the long-term treatment led not only to changes in vegetation but also altered topography of the plots. Below, we define the changes in marsh platform elevation and examine possible mechanisms involved.

### *Effect of Fertilization on Marsh Surface Elevation within Plots*

Mean elevation of the entire area of the experimental plots was quite variable, as evident in Fig. 3 (right panels). In general, however, elevations increased significantly with increasing enrichment (Fig. 7, top). The data included in Fig. 7 are averages for the entire plot. To examine some possible mechanisms that could have been responsible for the changes in height of salt marsh surfaces, below we carry out a more detailed analysis of the elevation and cover information.

We partitioned maps of the entire plots (such as shown in Fig. 3) into areas with different percent covers of *S. alterniflora* and *D. spicata*, and then plotted the mean elevation of those areas versus the percent cover of each species (Fig. 7, middle and bottom). To some degree, the data for *S. alterniflora* and *D. spicata* are mirror images but they do suggest that more *D. spicata* was associated with higher elevations, while there was no such correlation for cover of *S. alterniflora*.

To get more specific evidence as to the relative role of *S. alterniflora* and *D. spicata* on elevation of the marsh surface, we made use of the measured elevations along transects from inside the plots through the plot boundary to outside the plots (Fig. 8). We first note that in C plots, where no fertilizer was added, the surface of the marsh surface inside plots sloped lower from outside the plots toward the tidal creeks that bisected the plots (Fig. 8, top row of panels). The elevations in the LF plots were quite similar to those of C plots (Fig. 8, second row), as if the doses were insufficient to prompt much change. Differences in elevation between inside and outside plots were more prominent in the HF and XF treatments (Fig. 8, third and fourth row), but there were further details of interest. Elevations within HF and XF plots were higher, but only in one HF plot and the two XF plots plots where *D. spicata* had become a dominant contributor to cover. One HF plot was located at a distance of about 10 m away from the high marsh fringe where *D. spicata* initially grew and this distance may have impaired colonization by the vegetative growth used by this

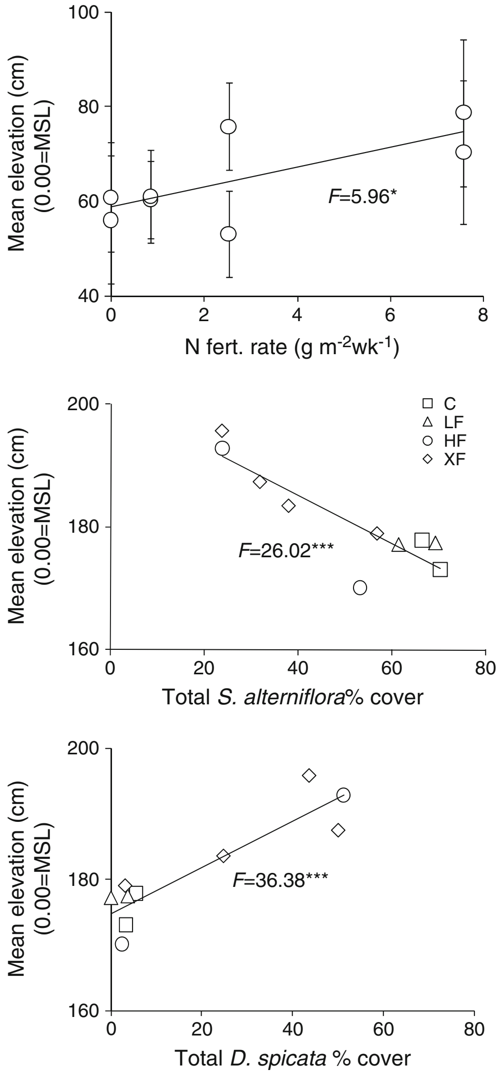

**Fig. 7** *Top* mean (±SD) elevation plotted versus rate of nitrogen fertilization (g m$^{-2}$ week$^{-1}$). *Error bars* represent standard deviations. *Middle* **and** *bottom* **mean elevation plotted versus total** *S. alterniflora* **percent cover and total** *D. spicata* **percent cover.** *XF* **diamonds,** *HF* **circles,** *LF* **triangles,** *C* **circles**

species. In any case, where *D. spicata* was dominant, we found higher marsh elevations by some 5–20 cm (Fig. 8) prominently nearer the tidal creeks.

To statistically assess, first, the relationship of fertilization treatment to inside–outside contrasts in elevation and second, its association with either *S. alterniflora* or *D. spicata*, we calculated the difference in elevation between inside and outside the plots from the specific transect data. We first plotted the contrasts in inside–outside elevations versus the fertilization rate (Fig. 9, top). Larger fertilizer doses were variable but associated with greater differences in elevations: the larger the dose, the larger the relative rise in height within the plot.

Second, to see if change in marsh platform elevation within the plots were associated with specific taxa, we separately plotted the differences in elevation between inside and outside for areas with *S. alterniflora* and areas with *D. spicata* canopies (Fig. 9, middle and bottom). There were no significant rises in marsh elevation within plots associated to canopy cover of *S. alterniflora* (Fig. 9, middle), but, in contrast, there were significant rises where cover of *D. spicata* was greatest. These results suggest that growth of *S. alterniflora* had minor effects on elevation of the marsh platform, even after more than three decades of chronic fertilization and even though growth of *S. alterniflora*, as evident in Fig. 3, was greater than in areas outside the plots or in C plots. Increases in percent cover of *D. spicata*, favored by large nutrient additions, were, in contrast, associated with significant rises in elevation of the marsh platform. We therefore find meager or no evidence that *S. alterniflora* was likely to facilitate encroachment by *D. spicata.* Rather, we conjecture that something intrinsic to *D. spicata* might be behind its ability to expand its cover.

## Interaction of Nutrient Supply and Elevation on Vertical Distribution of Salt Marsh Species

To highlight the adjustments in elevations associated with the higher dose of nutrient addition on the vertical distribution of the major plant species, we plotted, as examples, cover for each species versus elevation in XF and C plots (Fig. 10). The other fertilization treatments furnished shifts in cover that were intermediate within those of C and XF treatments and are not shown in Fig. 10.

Chronic, high supply of nutrients lowered cover of *S. alterniflora* (Fig. 10, first panel), except at the lowest level (where the opportunistic competitor, *D. spicata* could not grow well; Fig. 10, fourth panel). Fertilization increased cover of the glasswort, *Salicornia europaea*, in most elevations (Fig. 10, second panel), but cover of *S. patens* was relatively unchanged (Fig. 10, third panel). Cover of *D. spicata* increased substantially across most of the tidal range, except at the very bottom (Fig. 10, fourth panel). Cover of *I. frutescens* followed the patterns of *D. spicata*, and, as discussed above, only appeared after *D. spicata* had established a thick thatch that raised elevation of the sediment surface.

Fertilization regime did not change mean elevation at which we recorded taller and short *S. alterniflora* (Fig. 10, black diamonds, top), or *S. patens*, *D. spicata*, *S. europaea*, and *I. frutescens* (Fig. 11, black diamond). There were significant shifts, however, in the upper and lower ranges at which species were found (Figs. 11 and 12, gray circles). These shifts in upper and lower elevations were affected by fertilization regime.

Taller *S. alterniflora* and *S. patens*, for example, did grow somewhat higher in the intertidal range when exposed to larger nutrient supply (Fig. 11 top and Fig. 12 top). The species that showed the broader expansion in vertical range,

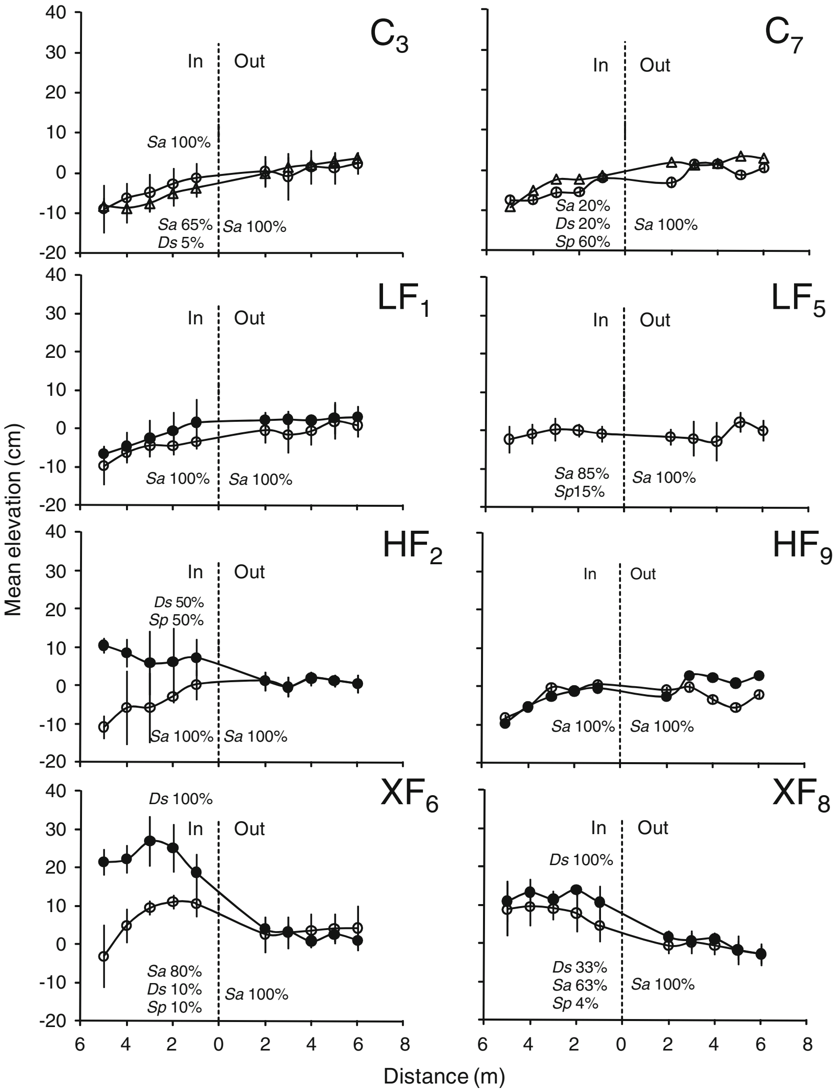

**Fig. 8** Mean (±SE) elevation along replicate transects that ran from outside to inside experimental plots subject to *C* (*top row of panels*), *LF* (*second row*), *HF* (*third row*), and *XF* (*fourth row*) fertilization treatments. In each panel, we show data for transects drawn through higher (*black circles*) and lower (*open circles*) marsh areas; for more specific identification of the composition of the canopy, percent cover for *S. alterniflora* (Sa), *D. spicata* (Ds), and *S. patens* (Sp) is provided for each inside and outside sections of the transects. The subscripted numbers under *C*, *LF*, *HF*, and *XF* are just to identify plots that were initially selected as replicates for each treatment

however, was *D. spicata*, a species that more than doubled its vertical range in elevation, expanding particularly downward (Fig. 11, second panel) so that it replaced *S. alterniflora* as shown earlier in Fig. 4 (right). To some extent, then, added nitrogen permitted *D. spicata* to grow into low-marsh habitats, previously the near-exclusive domain of *S. alterniflora*, and the new canopy then proceeded to foster higher rates of accretion in the colonized areas. We do not know the mechanism underlying the expansion of *D. spicata* at the expense of *S. alterniflora*; we conjecture that the mechanism may involve differential effectiveness in use of the added nitrogen, a notion that needs confirmation, and in addition, we note that the expansion was not prevented by the lower elevation of the areas previously supporting *S. alterniflora*.

Fertilization enabled *S. europaea* to grow about 30 cm lower than its normal range (Fig. 11, third panel), into the creek banks where tall *S. alterniflora* usually dominated. *S. europaea* made opportunistic use of relatively small, local bare patches where tall *S. alterniflora* died back.

*I. frutescens* was initially largely absent from the experimental plots, but grew into HF and XF plots (Fig. 11, fourth panel). This species exclusively invaded sites where elevation of the marsh platform was substantially raised by the accumulation of thatch and sediment that took place under the swards of *D. spicata* that were fostered by the added nitrogen, similar to results reported by Bertness et al. (1992).

## Interspecific Interactions in Response to Nitrogen and Elevation Changes

To discern how interspecific interactions were affected by differences in elevation and nutrient supply, we plotted total cover of *S. alterniflora* versus total cover of *S. patens* and *D. spicata*, and of *D. spicata* versus *S. patens*, stratifying the data into fertilizer doses—C, LF, HF, and XF—and elevation range—simplified into three categories, creek bank (30–50 cm above MSL), low marsh (50–70 cm above MSL), and high marsh (>70 cm above MSL; Fig. 12).

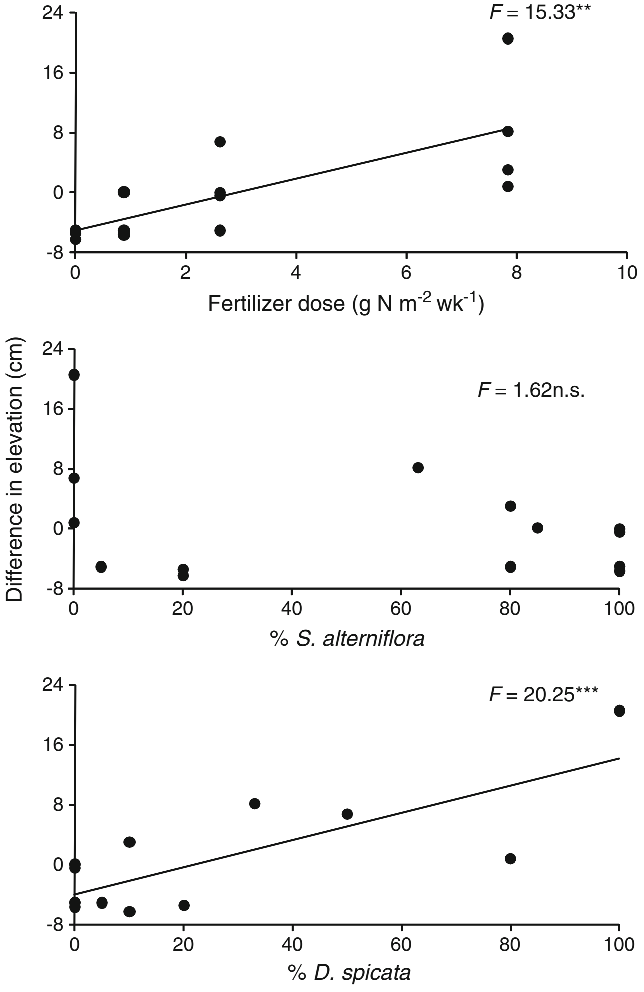

**Fig. 9** Mean inside to outside difference in elevation from data of Fig. 7 for each plot. The differences in elevation are plotted versus the fertilizer dose received by the plots (*top panel*, $y=1.66x-4.91$, $R^2=0.52$, $F=15.33$, $P=0.002$), as well as versus the percent cover of *S. alterniflora* (*middle panel*, $y=0.06x+3.0$, $R^2=0.11$, $F=1.62$, $P=0.23$), and vs. the percent cover of *D. spicata* (bottom panel, $y=3.27x+22.96$, $R^2=0.61$, $F=20.25$, $P=0.001$) recorded along the transects

To a greater or lesser degree, the three salt marsh species seemed to be competing for space or cover since there were negative associations between covers of the pairs of grasses (Fig. 12). Cover of *S. alterniflora* was higher on creek banks, diminished in low marsh, and was least within high-marsh elevations (Fig. 12, top two panels). The opposite was true for both *D. spicata* and *S. patens* (Fig. 11, top two panels). The responses to enrichment were evident within each elevation, with greater cover of *D. spicata*, the species that expanded its cover as well as elevation range when supplied with larger nutrient inputs, largely at the expense of *S. alterniflora* (Fig. 12, top panel). The extent of cover of *S. patens* was less-affected by the response of *D. spicata* to increased nutrient supply (Fig. 12, bottom). Cover by *S. patens* was variable but never equaled that of the other two species and was not favored at low elevations.

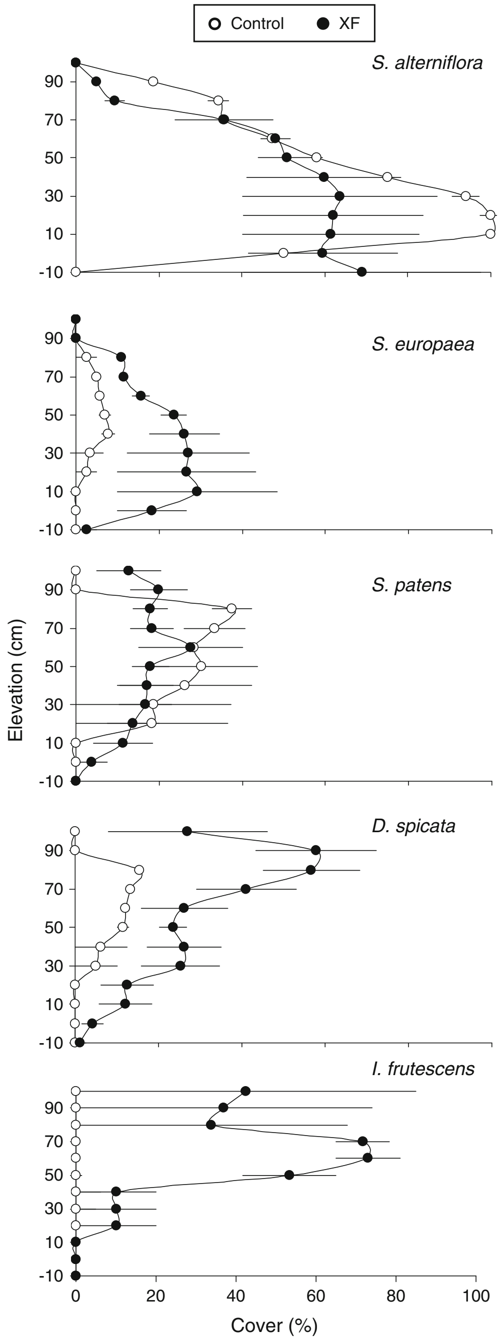

**Fig. 10** Percent cover (×±SD) for major plant taxa in XF and C plots, shown for bins of different elevations within the tidal range

## Discussion

Nutrients and environmental characteristics such as elevation and seawater inundation are major contributors to production and zonation of salt marsh vegetation. The extended duration of this study provided insight into the interaction between these processes and how they combine to effect the composition and zonation and potential future success of salt marsh vegetation.

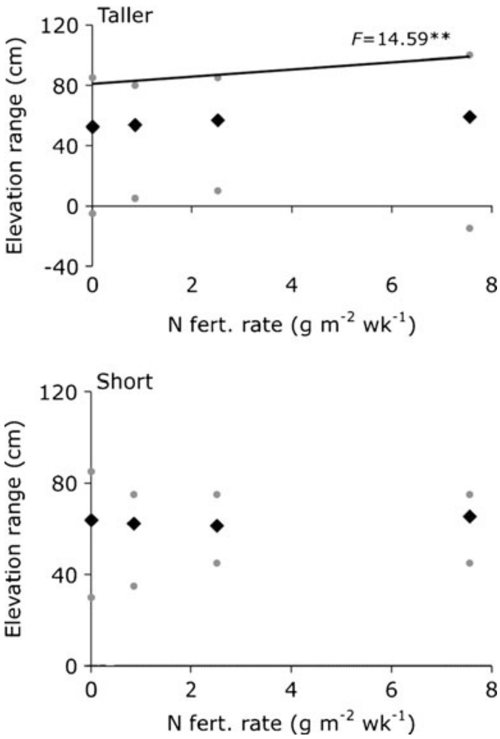

**Fig. 11** Mean elevation and range at which taller (*top*) and short (*bottom*) *S. alterniflora* ecophenotypes occurred versus fertilization rate (g m$^{-2}$ week$^{-1}$). Mean elevation (*black diamond*) is the weighted average elevation at which each form occurred, after normalizing for differences in percent cover at each elevation. Elevation ranges (*black dots*, *gray lines*) represent the mean of the upper and lower limits at which a species occurred. *Bars* represent standard error. Elevation reported relative to MSL=0.0

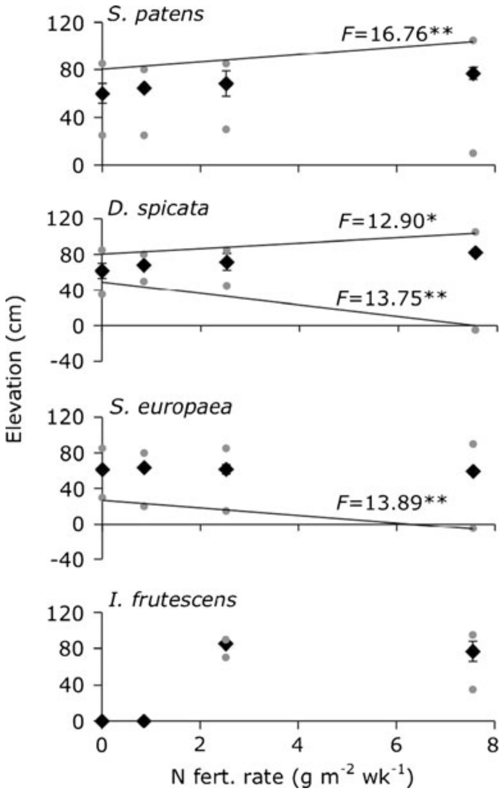

**Fig. 12** Mean elevation and mean elevation range at which *D. spicata*, *S. patens*, *S. europaea*, and *I. frutescens* occurred versus rate of nitrogen fertilization (g m$^{-2}$ week$^{-1}$). Mean elevation (*black diamond*) is the weighted average elevation at which each species occurred. Elevation ranges (*black dots*, *gray lines*) represent the mean of the upper and lower limits at which a species occurred. *Error bars* represent standard error. Elevation is reported relative to MSL=0.0

*D. spicata* gained most area cover among dominant species under fertilized conditions. In New England marshes, *D. spicata* can be occasionally found at lower elevations so that it is apparent that some other factor besides elevation constrains cover by this species. In our plots, *D. spicata* not only outcompeted *S. alterniflora* in the higher-marsh elevations, but also was the only species in our study to increase the upper and lower limits of its range of occurrence. There are probably several mechanisms underlying the remarkable responses of *D. spicata* to enrichment, including dominance in cover and increased surface accretion under *D. spicata* canopies. First, proliferation of *D. spicata* could have resulted from increased tolerance for greater submergence under larger nutrient supply (Suding et al. 2005). Second, typically, there is an accumulation of thick undercanopy thatch where *D. spicata* grows, so that surfaces may rise. Third, from previous work, we know that *D. spicata* produces biomass with considerably lower decomposition rates than *S. alterniflora* (Valiela et al. 1976, 1985b), so that elevation rise under *D. spicata* may be a result of slower decay. Fourth, some of these mechanisms may also confer higher particle trapping capabilities (Morris et al. 2002) and more organic biomass accumulation to marsh areas dominated by *D. spicata*. The latter may be more important, since δ$^{13}$C profiles in sediment cores from Cape Cod suggest that accretion is largely from undecomposed below-ground biomass of C4 plants, rather than phytoplankton or macroalgal particles (Kinney 2010).

Short-form *S. alterniflora* was converted to taller forms with fertilization as found previously (Valiela et al 1978; Hersh 1996). Nitrogen enrichment somewhat raised the vertical limit of the taller forms of *S. alterniflora*, to a degree expanding its potential range within the intertidal excursion. Nonetheless, cover of *S. alterniflora* decreased in our plots, in contrast to conclusions of a survey of 32 different enrichment experiments involving *S. alterniflora* by Pennings et al. (2005). Pennings et al. (2005) reported that in all cases, *S. alterniflora* outcompeted other major taxa and was the only species that consistently increased in cover. As one example that is, in contrast, consistent with our findings, Levine et al. (1998a) found that in lower elevations, *S. alterniflora* outcompeted *D. spicata*.

Our results may differ from previous experiments reviewed by Pennings et al. (2005), for perhaps two reasons.

First, the Great Sippewissett experimental plots included the entire range in elevation, from creek banks to high marsh. This experiment therefore included areas where *S. alterniflora* was at an advantage and some areas where it was not. Second, the contrast between our results and those of others has to do with the whole plot and decadal scale of our work, as in the case of *S. alterniflora*. Most studies in Pennings et al. (2005) were run on short-term basis; we report decadal-scale chronic enrichments, where the longer-term competitive and other outcomes might become evident, for example the increased accretion by *D. spicata*, which favored its expansion over areas previously dominated by *S. alterniflora*. In earlier reports of vegetation change in the Great Sippewissett plots, we also reported increases in biomass of *S. alterniflora*, prompted by fertilization, during the first 2–4 years of fertilization (Valiela et al. 1975). In smaller-scale manipulative experiments in Great Sippewissett marsh, Rietsma et al. (2011) demonstrated significant multiyear changes under different regimes of nutrient enrichment and competitive pressures. Shifts in salt marsh species dominance therefore take place at multiyear time steps and long-term observations are needed to reveal the slower responses.

At a whole-plot scale, responses by *S. patens* were variable and minor. Cover of *S. patens*, although variable, did not trend up or down during subsequent years, unlike results of other enrichment studies (Levine et al. 1998a, b; Pennings et al. 2005). Levine et al. (1998a, b) found that *S. patens* decreased under fertilized conditions when paired with *D. spicata* and *S. alterniflora*. In our plots, although *S. patens* was to some degree outcompeted by *D. spicata* in the high-marsh habitat, *S. patens* cover increased toward the upper limits of its range significantly, potentially offsetting its decrease in the low marsh to *S. alterniflora*. Despite an increase in vertical range, competition with enriched *D. spicata* decreased cover by *S. patens* in high marsh and its expansion into lower elevations was minimal, likely due to competition with *S. alterniflora* (Levine et al. 1998a).

There has been much theoretical discussion about how perturbations—such as increases in nutrient supply might or might not alter spatial distributions or exclusive or shared use of resources. Our findings as to the trends in monoculture use of marsh patches do not support speculations, since in low marsh there was no trend detectable with increased supply of the limiting nutrient, while high-marsh areas showed increased dominance of monoculture, with higher nutrient disturbance.

Our finding that there was some rises in salt marsh elevations that were associated with increased nutrient supply bear comparison with earlier reports. As Darby and Turner (2008) and Turner et al. (2009) note, this matter is an important issue in that the future of coastal wetlands will surely see increased eutrophication and sea level rise. Turner et al. (2009) emphasized that enrichment of salt marshes did not lead to rise in accretion of the experimental plots we discuss here.

Some time ago, we found that in high-marsh areas of our plots, standing crops of below ground biomass decreased with increased nutrient supply but not in low marsh. Moreover, low marsh annual below-ground production did not show significant decreases (Valiela et al. 1976). Unfortunately, we are unsure whether the cores studied by Turner et al. (2009) were taken from areas of high or low marsh, as this distinction seems important. In addition, the calculations done in that paper depend on the assumption that the fertilizer contained about 21% of insoluble ash and so the authors corrected apparent accretion by subtracting the rise owed to the presumed accumulation of ash. This correction may or might not be appropriate, since the ash may not be insoluble. For example, there is considerable Fe in the ash in fertilizer we used, but if Fe is exposed to an anoxic environment such as salt marsh sediment, a substantial part becomes reduced and soluble: for example only 24% of Fe added as fertilizer remained after several years in the plots (Giblin et al. 1986). Other elements in the ash likely suffered similar fates so it seems premature to reach early conclusions in this case. Because of the importance of these accretion issues in the future of coastal wetlands, these relationships merit further study.

The results summarized in the results above bear on two major issues in global change of coastal environments: widespread eutrophication (Bricker 1999) and accelerating sea level rise (Valiela 2005). In regard to eutrophication, our results suggest that chronic enrichment of salt marshes, at least in New England, will shift species covers, favoring opportunistic taxa that can proliferate under high nutrient supplies. To the degree that different marsh grass species have consequence for ecological services, there will be changes in marsh functions. In addition to the shift in dominance within the different habitats, salt marsh vegetation likely will tend toward monocultures of some of the newly dominant taxa, fewer taxa in lower tidal elevations, and perhaps more species along the upper part of the tidal excursion. Previous studies also demonstrate that production and biomass will likely increase under enriched nutrient regimes.

In regard to sea level rise, our results suggest that the predicted increases in sea level rise for New England will force land-ward “migration” of the bands of salt marsh vegetation, as long as there are no land-side barriers that prevent such movement. If sea level rise is accompanied by enrichment of tidal waters, the ensuing increase in cover of species such as *D. spicata* may force accretion rates that could perhaps compensate for higher-than-current rates of sea level rise. Where rising sea level becomes a serious issue threatening maintenance of coastal wetlands, it may be possible to consider salt marsh fertilization as a fallback management method to aid salt marsh accretion.

**Acknowledgments** In a project with a history of several decades, many people, agencies, and institutions made essential contributions. The owners of salt marsh parcels in Great Sippewissett marsh, the Arnold Gifford family during the early years, and more recently the Edward Hughes family, as well as Salt Pond Inc., and the Massachusetts Audubon Society, have been exceedingly forward-looking, helpful, and accommodating by allowing us to establish and maintain the experimental plots within their properties. We are indebted to many colleagues that shared the work and aims for the many decades behind this effort. Foremost, we thank John Teal, who steadfastedly made us focus on important aspects during the early decades of the Great Sippewissett salt marsh project. We owe a substantial debt to Brian Howes and Dale Goehringer and their students at the School of Marine Sciences and Technology, University of Massachusetts, Dartmouth, for their continuing efforts in maintaining the experimental plots. We also thank Carley Schacter for assistance in the field, and Daniel Steinberg, Frederic Jaffre, and Alfredo Aretxabaleta for help with ArcGIS and Matlab. This work was supported, over the years, by many private and federal sources, of which we here only note NSF grants DEB-0516430, DEB-0914795, and OCE-0453292, and NOAA grant NA07NOS4200025 to IV.

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