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Multiple disturbances in a *Spartina alterniflora* salt marsh: Are they additive?¹

Monica Goigel Turner²

Environmental Sciences Division, Oak Ridge National Laboratory,
Oak Ridge, TN 37831-6038

ABSTRACT

TURNER, M. G. (Env. Sci. Div., Oak Ridge Natl. Lab., Oak Ridge, TN 37831). Multiple disturbances in a *Spartina alterniflora* salt marsh: Are they additive? Bull. Torrey Bot. Club 115: 196–202. 1988.—The role of ecological disturbance has received much attention, but most studies consider single rather than multiple types of disturbance. An experiment was conducted to determine whether combinations of disturbances (clipping, trampling and fire) elicit additive responses from *Spartina alterniflora* Loisel. equivalent to the sum of responses to the individual disturbances. When combined, clipping and trampling had additive effects on aboveground standing stocks of *Spartina*, but combinations of fire with clipping or trampling had less effect than predicted. Effects on net aboveground primary production (NAPP) differed from effects on standing stocks. Clipping combined with trampling or burning reduced NAPP more than predicted, whereas the effect of burning and trampling on NAPP was additive. Thus, nonadditive responses to multiple disturbances can be identified and quantified, but the nature of the effect may differ with the parameter studied. Understanding such interactions is necessary to predict ecosystem dynamics in response to disturbances.

Key words: disturbance, multiple disturbances, Cumberland Island, *Spartina alterniflora*, clipping, trampling, fire, salt marsh.

Ecological disturbance has received much attention (e.g., Barrett and Rosenberg 1981; Mooney and Godron 1983; Sousa 1984; Pickett and White 1985; Rykiel 1985; Turner 1987a), but most studies only consider a single type of disturbance. The importance of the interaction of multiple influences on ecological systems has been acknowledged (e.g., Peterman 1980; Schowalter 1985), but discussions of multiple disturbances are rare (but see Lugo 1978). Ecosystems respond to complexes of disturbances that occur at different spatial and temporal scales (Delcourt

et al. 1983), and we must seek to understand their effects and interactions.

When two or more disturbances occur simultaneously, responses may be additive (i.e., the sum of responses to individual disturbances), or they may be nonadditive (i.e., greater or less than the sum of the responses to the single disturbances). Lugo (1978) suggested that combined ecological perturbations may interact in nonadditive ways, accelerate energy losses, and rapidly reduce a system's capacity to tolerate further perturbation. Other authors have acknowledged potential synergism among disturbances (White and Pickett 1985; Schowalter 1985), but no quantitative studies have been reported.

I conducted an experiment on salt marsh vegetation (*Spartina alterniflora* Loisel.) to determine whether pairwise combinations of three ecological disturbances (clipping, trampling and fire) acted in an additive manner. These three treatments represent disturbances which are exotic to the marsh and to which the species are presumably not adapted. The definition of disturbance used here is from White and Pickett (1985): "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate

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availability, or the physical environment.” The term “perturbation” is used synonymously with “disturbance” in this paper, because the disturbances were under direct control of the experimenter (White and Pickett 1985).

Study Site and Methods. The study site was located on Cumberland Island, Camden County, Georgia (30°48'N, 81°26'W). This 9404-ha island extends 25 km from north to south and at its widest point measures 9 km. The geology, soils, water resources, vegetation, and fauna of Cumberland were described by Hillestad *et al.* (1975). The island has low relief (5–8 m above sea level), except for dune areas that may reach elevations of 18 m. Major plant communities are typical for barrier islands of the Georgia coast (Johnson *et al.* 1974). The tidal land on the mainland side of the island is characterized by smooth cordgrass (*Spartina alterniflora* Loisel.). The upper margin of the marsh grades into a grass-forb community composed primarily of glasswort (*Salicornia virginica* L.), salt grass [*Distichlis spicata* (L.) Greene] and occasional stands of black needle rush (*Juncus roemerianus* Scheele).

The experimental treatments represent disturbances which are not naturally common in southeastern salt marshes. Burning is not common in Atlantic coastal marshes, but some *Spartina* spp. marshes are occasionally ignited by lightning fires (Davison 1984). Grazing ungulates were not native to the Georgia barrier islands (Johnson *et al.* 1974), but Cumberland is now inhabited by free-ranging feral horses that frequently graze the salt marshes (Lenarz 1983). The clipping and trampling treatments simulated two aspects of horse grazing.

Study plots were located in a large salt marsh on the southern end of the island. Homogeneous stands of short (<1 m) *Spartina alterniflora* were selected. Eight experimental treatments were replicated at two sites approximately 600 m apart. The eight treatments were composed of a three-way factorial arrangement with two levels (presence or absence) each of clipping, trampling and burning. Unburned plots were 10 × 20 m, and burned plots were 7 × 10 m because of difficulties in burning larger areas. All experimental plots were surrounded by a

1-m buffer zone and were contained within enclosures designed to exclude only horses, allowing free movement of other animals (such as raccoons) and tidal material.

Clipping was done in alternate months from July 1983 through November 1984 with a weed trimmer that cut the grass to a height of 10 to 15 cm. Grass clippings were left on the marsh surface and were lost in a few days through tidal action. Vestergaard (1985) found no difference in the response of marsh vegetation to mowing with and without clippings left on the marsh. Trampling was simulated biweekly. Holes (10 to 15 cm diameter) were dug with a trowel to a depth of 15–20 cm at 1-m intervals in the plots, representing the approximate size and depth of horse trample holes in the marsh (personal observation). The treatment was repeated during alternate weeks to prevent rhizome regrowth and sedimentation in the trample holes. Burning took place March 11, 1984 at each replicate. Conditions for burning were selected such that tidal amplitude was low (midway between full moon and new moon) and low tide occurred during midday, to allow for maximum drying. Stalks of standing dead were not spaced sufficiently close to carry the fire due to previous horse grazing, and additional fuel was spread over the site to provide fuel continuity. A bale of hay was added to each 100 m² burned. Only aboveground vegetation was consumed by fire; roots and rhizomes were not burned. Clipping and trampling treatments began on burned plots at the end of March 1984.

On each study plot, eight samples of aboveground vegetation were collected during alternate months. Unburned plots were sampled from July 1983 through November 1984; burned plots were sampled prior to burning, then during alternate months from May 1984 through November 1984. Prior to each sampling period, a lengthwise 9-m transect was established randomly in each plot with the constraint that no area was sampled twice during the study. Samples were collected systematically along one side of the transect at 3-m intervals. Aboveground vegetation was harvested in eight 0.25-m² circular clip plots to within 2 cm of the marsh surface. Aerial vegetation was washed, sorted into live and dead, and dried to constant mass at 60°C.

Net aboveground primary production (NAPP) was calculated for each study plot using the Smalley method (Smalley 1959). This method underestimates productivity because it does not account for decomposition or herbivory losses (Linthurst and Reimold 1978; Shew *et al.* 1981; Dickerman *et al.* 1986), but the method was adequate to compare relative rates of productivity among treatments. NAPP was calculated so that losses due to clipping were included. The difference between vegetation remaining after each clipping treatment and that present at the beginning of the next sampling period was used to compute NAPP for each interval.

Statistical analyses were done using SAS (SAS Institute 1982). Vegetation data were normally distributed ($P < 0.01$, Kolmogorov D -statistic), and parametric statistical procedures were subsequently used. To test whether the effects of combined perturbations were equal to the sum of the responses to the perturbations applied alone, contrasts (Snedecor and Cochran 1967) and estimates were used. The contrast measures the contribution to the total variance of the factors being compared and tests whether these contributions are the same using an F -statistic. The estimate then provides the numeric difference between the means, and a t -statistic can be used to determine its significance. The contrast and estimate yield the same level of significance. Testing for nonadditive effects was done using paired disturbance combinations.

Arithmetic addition of the disturbance effects is not appropriate for determining whether combinations are additive. For example, standing stock reductions of 60% in each of two treatments applied singly would sum to an unrealistic predicted reduction of 120%. A proportional relationship must be used to remove this bias. For example, to predict the standing stock of biomass on a clipped and trampled plot if the disturbances were additive, one would first compute the ratio of biomass on the clipped-only plot to biomass on the control (e.g., clipped/control = $90/150 \text{ g/m}^2 = 0.60$). This ratio would then be multiplied by the standing stock of biomass on the trampled plot to obtain the value predicted for the plot that was clipped and trampled (e.g., trampled biomass = 100 g/m^2 , and 0.60×100

= 60 g/m^2). This is equivalent to predicting the biomass present with both disturbances by multiplying the standing stock biomass in a control by the proportion of biomass remaining in each disturbed plot (e.g., $150 \text{ g/m}^2 \times 0.6 \times 0.667 = 60 \text{ g/m}^2$). To remove the arithmetic bias, therefore, testing for additivity among disturbances using linear contrasts required log transformed data. Continuing the clipped and trampled example above, the additive relationship to be tested can be written as:

$$(CL \cdot TR) / C = CLTR$$

where

CL = standing stock on clipped site,
 TR = standing stock on trampled site,
 C = standing stock on control site, and
 CLTR = standing stock on clipped and trampled site.

Using log biomass as the variable, this can be rewritten as:

$$\log CL + \log TR - \log C = \log CLTR$$

$$\log CL + \log TR - \log C - \log CLTR = 0.$$

The coefficient vector for the contrast is thus:

$$+1 \quad +1 \quad -1 \quad -1 \quad = 0.$$

Contrasts and estimates for the additivity of clipping and trampling were done for each sampling date. Tests that included the burn treatment were only done for the 1984 growing season, as burning occurred in March 1984.

Results. DISTURBANCES APPLIED SINGLY. Standing stocks of live *Spartina* biomass reached annual maxima during late summer, and peak standing dead occurred in early winter. All experimental perturbations caused declines in peak biomass (Fig. 1). Clipping and trampling each reduced peak biomass (occurring in September) by similar amounts: 20% in 1983 and 50 to 55% in 1984. Burning reduced peak biomass by 35% in 1984 (Turner 1987b).

Net aboveground primary production was not reduced by clipping, but trampling and burning each decreased NAPP by approximately 35% (Turner 1987b).

COMBINED DISTURBANCES. Reductions in standing stocks were observed in response

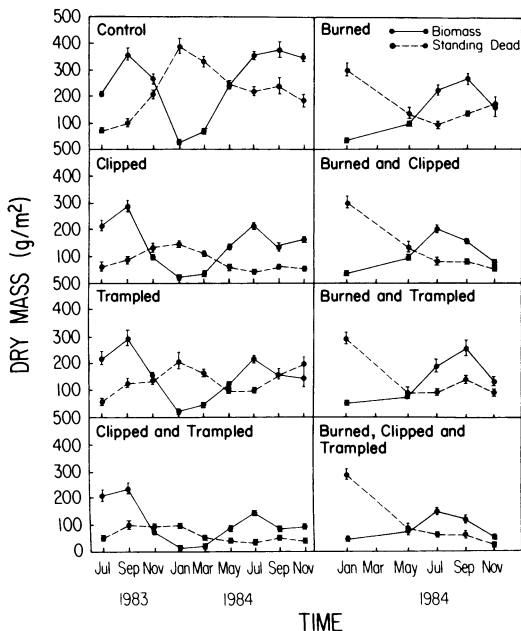


Fig. 1. Mean standing stock of aboveground *Spartina* by treatment (± 1 standard error, N = 2) (from Turner 1987b).

to the multiple disturbances (Fig. 1). The combination of clipping+trampling reduced peak biomass by 40% in 1983 and 70% in 1984; the combinations of burning+clipping and burning+trampling decreased peak biomass by 50% and 40%, respectively, during 1984. NAPP was reduced by all disturbance combinations compared with control plots (Turner 1987b).

TESTS FOR ADDITIVE RESPONSES TO COMBINED DISTURBANCES. When combined, clipping and trampling had additive effects on aboveground live and dead standing stocks of *Spartina* (Table 1). Predicted and observed standing stocks differed for live biomass only in September and November 1984 and for standing dead in May and July 1984. These data suggest that clipping and trampling affect *Spartina* biomass independently.

Burning and clipping had nonadditive effects on standing stocks of aboveground *Spartina* (Table 2). Plots that were burned and clipped had up to 53% more biomass and 300% more standing dead (in July 1984) than predicted if the combined effects were additive. Burning and trampling also usually had nonadditive effects (Table 3), al-

Table 1. Tests for nonadditive effects of clipping and trampling on aboveground *Spartina alterniflora*.

Date	Pre-dicted ^{a,b}	Ob-served ^a	Esti-mate ^c	SE of estimate ^c	Pr > t
Biomass					
Jul 83	60.6	49.9	0.077	0.085	0.373
Sep 83	57.2	56.1	0.014	0.084	0.870
Nov 83	18.3	17.2	-0.131	0.106	0.225
Jan 84	5.2	5.4	0.111	0.144	0.443
Mar 84	7.0	6.9	-0.007	0.116	0.952
May 84	16.9	23.6	-0.208	0.112	0.067
Jul 84	36.1	33.8	-0.048	0.084	0.564
Sep 84	24.0	29.9	-0.226	0.108	0.039
Nov 84	13.1	18.0	-0.281	0.114	0.016
Standing dead					
Jul 83	15.0	12.2	-0.079	0.163	0.630
Sep 83	27.6	25.9	0.102	0.115	0.376
Nov 83	17.2	23.0	-0.068	0.112	0.545
Jan 84	23.2	26.5	-0.222	0.112	0.051
Mar 84	16.5	13.5	0.053	0.114	0.638
May 84	6.4	11.8	-0.603	0.138	0.001
Jul 84	6.0	10.5	-0.642	0.118	0.001
Sep 84	9.9	12.2	-0.118	0.123	0.339
Nov 84	11.4	11.9	-0.197	0.121	0.107

^a Units are g·0.25 m⁻².

^b Standing stock if effects were additive (clipped+trampled/control); see Methods.

^c Units are log g·0.25 m⁻²; N = 2.

though aboveground standing dead exhibited an additive response in September and November of 1984. When responses were nonadditive, standing stocks were again greater than predicted. Observed biomass exceeded predicted by up to 94% (in September 1984) and standing dead exceeded predicted by up to 90% (in July 1984).

Comparisons of predicted and observed NAPP (Table 4) differed from comparisons of predicted and observed standing stocks. For two disturbance combinations (clipped+trampled and burned+clipped), observed primary production was less than predicted if the effects were additive (Table 4). This relationship appeared strongest for plots that were clipped and trampled. The combination of burning and trampling had additive effects on NAPP.

Discussion. The additive effect of clipping and trampling is intuitive when the disturbance mechanisms are considered. Trampling removed a constant proportion of the marsh surface from aboveground production. Clipping was applied uniformly across the study plot; thus, only the untram-

Table 2. Tests for nonadditive effects of burning and clipping on aboveground *Spartina alterniflora*.

Date	Pre-dicted ^{a,b}	Ob-served ^a	Esti-mate ^c	SE of estimate ^c	Pr > t
Biomass					
May 84	14.8	27.6	-0.588	0.112	0.001
Jul 84	35.4	54.1	-0.305	0.084	0.001
Sep 84	31.5	42.6	-0.348	0.108	0.002
Nov 84	13.9	23.4	-0.685	0.115	0.001
Standing dead					
May 84	9.0	36.9	-1.482	0.138	0.001
Jul 84	5.8	24.0	-1.403	0.118	0.001
Sep 84	10.2	24.1	-0.870	0.123	0.001
Nov 84	11.6	17.2	-0.518	0.121	0.001

^a Units are g·0.25 m⁻².

^b Standing stock if effects were additive (burned-clipped/control); see Methods.

^c Units are log g·0.25 m⁻²; N = 2.

pled portion of the plot was affected. This resulted in an additive relationship.

The nonadditive responses of *Spartina* standing stocks to disturbance combinations that included burning are more difficult to interpret. In burned plots, a morphological change was observed in the aboveground *Spartina*; regrowth following burning consisted of smaller plants with a higher stem density (personal observation). As a result, less plant biomass exceeded 15 cm in height, so relatively less biomass was affected by the clipping treatment. The reduction in standing stocks was thus less than expected. The mechanism for this growth response is not clear, and it was not observed on plots that were clipped only. A large nutrient pulse following burning was unlikely, due to the daily tides, and leaf nutrient concentrations did not differ between burned and unburned plots (Turner 1985). The nonadditive effects of burning and trampling may also be attributed to the change in plant morphology following burning. Plant growth at the edge of the trample holes was quite dense on the burned plots.

The estimation of nonadditive effects of multiple disturbances on vegetation may differ depending on the response studied. Functional ecological characteristics (e.g., NAPP) may respond differently to combined disturbances than structural characteristics (e.g., standing stocks). When predicted and observed NAPP were compared, results suggested that pairwise combina-

Table 3. Test for nonadditive effects of burning and trampling on aboveground *Spartina alterniflora*.

Date	Pre-dicted ^{a,b}	Ob-served ^a	Estimate ^c	SE of estimate ^c	Pr > t
Biomass					
May 84	13.4	19.9	-0.295	0.112	0.101
Jul 84	39.9	48.8	-0.221	0.084	0.009
Sep 84	33.9	65.8	-0.577	0.108	0.001
Nov 84	23.2	36.8	-0.754	0.115	0.001
Standing dead					
May 84	15.0	24.4	-0.459	0.138	0.001
Jul 84	13.1	24.9	-0.689	0.118	0.001
Sep 84	26.6	37.6	-0.143	0.123	0.246
Nov 84	37.1	26.0	0.032	0.121	0.795

^a Units are g·0.25 m⁻².

^b Standing stock if effects were additive (burned-trampled/control); see Methods.

^c Units are log g·0.25 m⁻²; N = 2.

tions of disturbances may have a greater impact than the sum of their separate effects. Because clipping alone did not significantly reduce NAPP compared with the control, the additive hypothesis predicts only a reduction due to trampling where the treatments were combined. The observed reductions, however, were greater. In contrast, burning and trampling each reduced NAPP separately but had less than additive effects when they were combined. The mechanism for these responses is not clear.

When disturbances are nonadditive, they may be greater or less than their expected sum. It is useful to distinguish this directionality, and appropriate terminology is common in other fields, including pharmacology, toxicology, and agriculture (e.g., Colby 1967; Tattersall *et al.* 1973; Akobundu *et al.* 1975; Morse 1978; Marking 1985).

Table 4. Predicted and observed net aboveground primary production of *Spartina alterniflora* for single and combined disturbances in 1984.

Treatment	Predicted ^{a,b}	Observed ^{a,c} ± 2 SE
Control	—	393 ± 44
Clipped	—	415 ± 4
Trampled	—	298 ± 84
Burned	—	267 ± 22
Clipped and trampled	314	211 ± 28
Burned and clipped	282	244 ± 34
Burned and trampled	228	172 ± 16

^a Units are g·m⁻².

^b NAPP if effects were additive; see Methods.

^c N = 2.

Effects that are greater than additive are termed synergistic, a term frequently used by ecologists. Effects that are less than additive are termed antagonistic; i.e., the disturbances have a negative interaction diminishing their combined impact. This distinction may be useful in ecological studies. In this study, nonadditive effects on *Spartina* standing stocks were antagonistic, whereas effects on NAPP appeared to be synergistic. Studies of the responses of a variety of structural and functional parameters to multiple disturbances might provide additional insights. For example, reproductive effort might be synergistically or antagonistically affected by multiple disturbances. In this study, inflorescences were suppressed with clipping (personal observation), and the interactive effects of disturbances on sexual and vegetative plant reproduction may vary.

Multiple disturbances occur in many ecological systems, and their combined effects may be not be easy to predict. For example, logging increases the susceptibility of trees to windthrow (Franklin and Forman 1987), drought may increase fire intensity in many ecosystems, and parasites and fire interact in forests (e.g., Knight 1987). Understanding and quantifying such interactions is necessary to predict vegetation dynamics in response to disturbances.

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