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INFLUENCE OF BIOTIC AND ABIOTIC FACTORS ON ANNUAL ABOVEGROUND BIOMASS OF AN INTERMEDIATE COASTAL MARSH

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Abstract: Annual production of vegetation is an important indicator of various ecosystem processes in coastal marshes; many factors, both biotic and abiotic, can influence production of aboveground biomass. Using a 14-year data set, we evaluated the relative influence of 38 biotic and abiotic factors on annual aboveground biomass of an intermediate coastal marsh on the upper Gulf Coast of Texas. We used visual obstruction (VO) measurements as a surrogate variable in a prediction model to estimate available aboveground biomass in the marsh. Available biomass was greatest (3.34 kg/m^2) when sampling site was flooded. Plant growth form, type of animal present, and composition of the ground cover influenced biomass of the marsh. Presence of insects was related to biomass (regression beta weight = 0.28), uniquely accounting for 7.6% of the incremental variance in biomass. The presence of moderate amounts of litter was also related to available biomass (beta weight = 0.86). Soil capping had little or no influence on aboveground biomass. Implementing standard protocols for long-term vegetation monitoring can be cost and time intensive. Our results suggest quantitative measurement of VO and qualitative observation of few variables (standing water, insects, and litter) measured annually can yield a reasonable assessment of aboveground biomass of intermediate coastal marshes.

Key Words: aboveground biomass, growth form, insects, intermediate coastal marsh, litter, soil capping, visual obstruction (VO) measurement

INTRODUCTION

Many biotic and abiotic factors can alter the structure and function of wetland plant communities by influencing the extant community composition, growth, nutrient acquisition, and productivity. Evaluating the relative influence of factors that affect production of aboveground biomass in coastal wetlands is important for wetland ecologists and managers because macrophytes are the main source of organic matter that supports various trophic structures in these systems (Teal 1962, Odum and Heald 1975). For example, canopy structure and distribution of herbaceous species in tidal freshwater swamps are primarily determined by the flooding regime (Rheinhardt 1992). Increased levels of sedimentation and flooding have been shown to reduce seedling emergence in freshwater wetlands (Peterson and Baldwin 2004). Bhattacharjee et al. (2007) reported that extended flooding or drought can both act as disturbance leading to changed vegetation structure over time in coastal marshes.

Although studies have been conducted on the productivity of coastal marshes (White et al. 1978, Hopkinson et al. 1980, Roman and Daiber 1984, Baldwin and Mendelsshon 1998), the relative influence of many abiotic and biotic factors that may influence aboveground biomass of these marshes are unknown. Studies have emphasized the effects of salinity (Mendelssohn and McKee 1987, Blits and Gallagher 1991, van Diggelen 1991, Marcum and Murdoch 1992, Broome et al. 1995, Baldwin and Mendelssohn 1998), soil moisture (Haukos and Smith 2006), or hydrologic regime (van der Valk and Davis 1978, Parker and Leck 1985, Leck 1989, Casanova and Brock 2000, Peterson and Baldwin 2004) on production of wetland plant communities. Changes in vegetation community composition due to altered hydroperiod and intrusion by saltwater have also been reported by Chabreck and Linscombe (1982) and Visser et al. (2002). In intermediate coastal marsh (salinity 0.5–3.5 ppt), elevation gradient and drainage patterns often influence soil salinity and aeration, which are considered to be among the

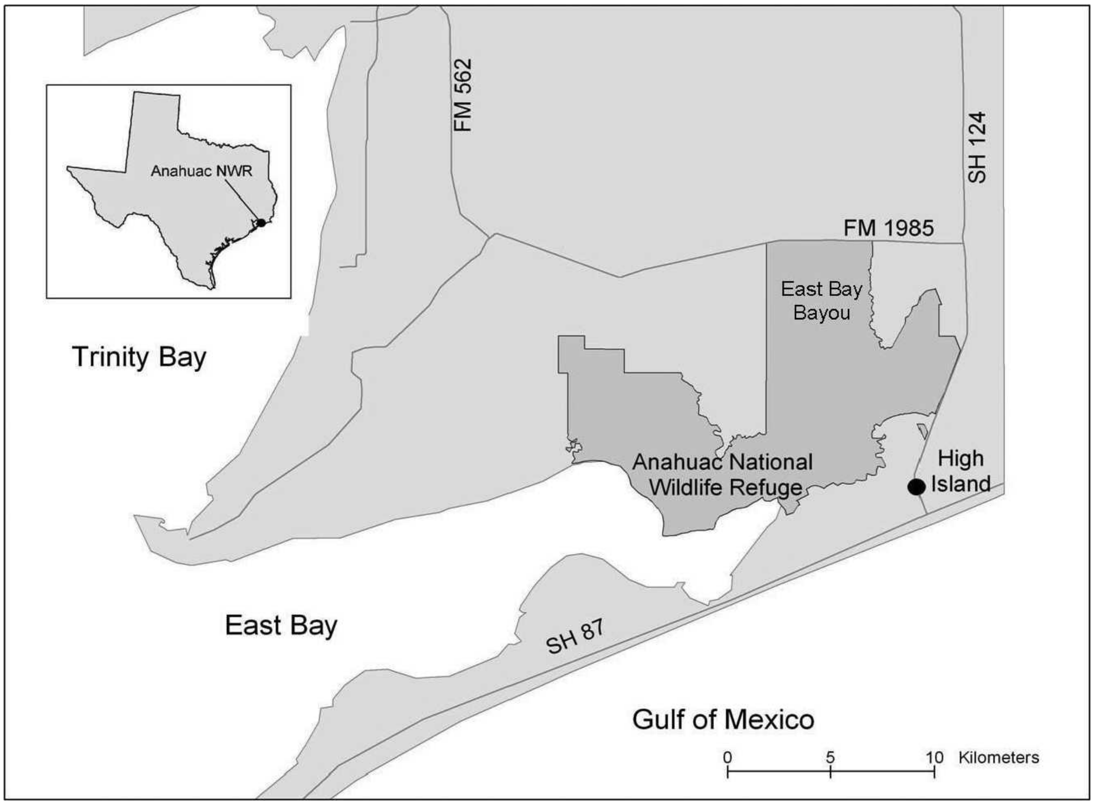

Figure 1. Location of the Anahuac National Wildlife Refuge, Anahuac, Texas, showing the East Bay Bayou study area.

most important abiotic factors regulating production of vegetation biomass (Ungar 1998). However, simultaneous examination of multiple variables potentially affecting annual aboveground biomass of vegetation in coastal marsh is lacking.

We evaluated the relative influence of 38 environmental factors on aboveground biomass of an intermediate coastal marsh over a 14-year period. Our objective was to determine the potential influence of groups of biotic (e.g., canopy cover, plant age, plant type, type of animal present) and abiotic (e.g., soil capping, type of groundcover, salinity) factors on biomass of intermediate coastal marsh. An intricate knowledge of available biomass of a marsh has theoretical and applied values. For example, aboveground biomass is often used as a surrogate measure of habitat conditions for wildlife and to calculate fuel load to determine prescribed fire behavior. Further, management of livestock grazing is also driven by the amount of available biomass (Whitbeck and Grace 2006).

METHODS

Study Site

Our study was conducted in the East Bay Bayou Marsh Unit (29°37′19.58″N, 94°25′45.45″E) of Anahuac National Wildlife Refuge, Chambers County, Texas (Figure 1). This upper Texas Gulf Coast Unit was 1137 ha in size and comprised of 458 ha of intermediate marsh, 373 ha of brackish marsh, 271 ha of nonsaline grassland and prairie wetland, and 35 ha of freshwater marsh (United States Fish and Wildlife Service, unpublished data).

East Bay Bayou was primarily an intermediate marsh; however, both salinity level and water depth varied depending on prevailing winds, tides, and amount of freshwater inflow due to precipitation and drought. It is a structurally managed marsh with a goal of maintaining water salinities of no greater than 5 ppt throughout most of the unit. Mean annual salinity during our vegetation sampling from 1989–2002 ranged from 0 to 6 ppt, varying mostly due to rainfall events or storm surges. The area has a humid subtropical climate, with mean monthly precipitation ranging from 7 to 16 cm, an average annual precipitation of 137 cm, and mean air temperature of 20°C, ranging from 10 to 33°C (NOAA, NCDS, Texas 1971–2000).

Vegetation in the East Bay Bayou Unit included grasses (e.g., *Distichilis spicata* [L.] Greene., *Paspalum* spp., *Spartina patens* [Ait.] Muhl.), sedges (*Cyperus* spp., *Eleocharis* spp.), rushes (*Scirpus olneyi* Gray, *Juncus roemerianus* Scheele), and cattail

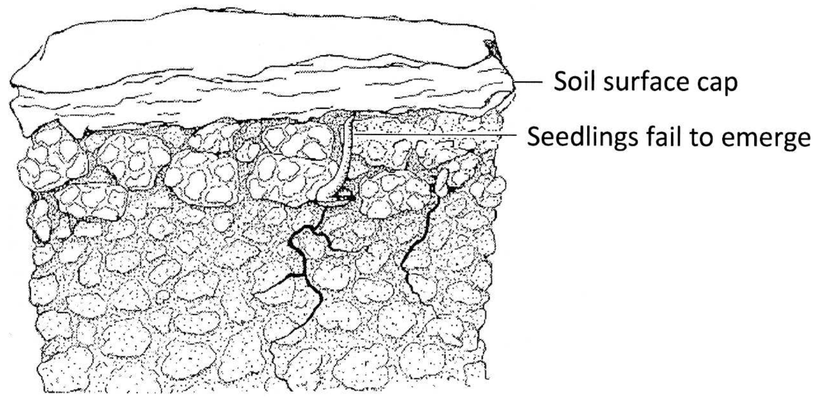

Figure 2. Soil capping as a result of rainfall, water waves, animal trampling, etc., showing the surface cap. Once dry and hardened, it can prevent seedling emergence. Redrawn from Batey (1988).

(*Typha domingensis* Pers.) (United States Fish and Wildlife Service, unpublished data), which is typical for intermediate marsh habitats found in mesohaline and oligohaline marshes (Stutzenbaker 1999).

Vegetation Sampling

We sampled vegetation annually for 14 years (1989 to 2002). Data were collected during late summer of each year (August–September; typically the driest time of year). Vegetation was sampled along five transects of varying length (150–175 m). The first transect was assigned randomly each year, and the remaining four transects were placed in a stratified fashion to sample the entire area of intermediate marsh. Each transect was divided into 50 equidistant points at which vegetation was sampled.

At each sampling point, we assigned soil surface cover into one of five categories: bare ground (soil exposed), litter-1 (a single ground layer consisting of leaves, roots, stems, sticks, dung produced within the previous year), litter-2 (decomposing layers that are gradually getting incorporated in the soil), water (standing water), or basal cover (actual area of the soil surface covered by the crowns or stems of plants). In a circular plot (0.28 m^2) surrounding each sampling point, we recorded the degree of soil capping. Capping was defined as the ''crust'' formed on top of the soil layer due to rain impact, animal trampling, waves, and other forces that compress the soil (Figure 2). During this process, finer particles of silt and clay detach from aggregates move short distances into the soil, which blocks pores and reduces infiltration of both air and water through the soil surface. Following extended drying or during drought, a dense surface crust can form a rigid cap that resists or prevents seedling penetration. We categorized degrees of soil capping into mature (long rested soil with dark appearance, salt-crust present, and presence of algae), young or immature (cap had been broken earlier but had resealed), recent (cap due to a recent rainfall, usually very thin), broken (resulting from recent animal impact or drying of the ground following flooding), and covered (cap condition could not be determined due to litter cover). Within the same circular plot, we also recorded the presence of insects, other invertebrates, and animals (or signs of animal use). Salinity of any standing water present was measured (ppt).

We categorized vegetation type as grass, sedge, forb, tree, brush, rush, or cattail. We measured vegetation cover of each plant type as a percent of the total plot area. Percent vegetation cover was further grouped into cool or warm season species. We categorized plant type within each circular plot based on their growth stage (young, mature, decadent, or resprout) and growth form (either normal, with good tillering, seed production, and lack of old growth stems and parts, or overrested, with herbaceous plants that were older and grew parallel to the ground or bushes that were stout and short with little outside branching and often with several dead branches).

At each plot, a visual obstruction (VO) measurement was taken. We used a 2-m PVC pipe marked in black and white 10-cm bands and 5-cm increments, similar in design to that used by Robel et al. (1970). The pole had a 4-m nylon cord attached used to determine sighting distance. Observers would read the number of the lowest band not obstructed by vegetation to record a height-density index. To estimate aboveground biomass of the marsh, we used VO measurements as surrogates of plant biomass (Whitbeck and Grace 2006). Using VO measurements and biomass as reported by Whitbeck and Grace (2006) for East Bay Bayou, we developed a regression model to estimate annual aboveground biomass (kg/m^2) (Biomass = −0.177 + 0.057 * VO, r^2 = 0.69, P = 0.005, n = 9). The use of VO measurement to predict biomass has been used widely as an effective and nondestructive means to estimate annual production (Vermier and Gillen 2001, Whitbeck and Grace 2006), and the effectiveness and ease of estimation makes VO measurements useful for wildlife managers to estimate biomass as a means of assessing habitat condition.

Data Analysis

We used a two-factor analysis of variance to test for differences in productivity among years and between sampling periods with or without standing water. We used multivariate linear regression (PROC GLM, SAS 9.1, 2003), with discrete variables treated as dummy variables (*sensu* Kutner et al. 2004), to examine relationships between year-end biomass and variables within eight categories: 1) canopy cover, 2) plant growth stage, 3) plant growth form, 4) plant type, 5) animal presence, 6) ground cover, 7) soil capping, and 8) other factors (consisting of water salinity, percent annuals, percent cool season and warm season plants). Variables that appeared less than three times in the 14-year data set were not included in analyses. Data from1993 were eliminated from biomass analysis as VO measurements were missing.

We also present standardized multiple regression coefficients (beta weights) and uniqueness indices to determine the relative importance of the variables in predicting marsh productivity (O'Rourke et al. 2005). The uniqueness index of a variable is the percent variance explained beyond the variance accounted for by other predictor variables. Uniqueness was calculated using the formula: $U = R^2_{full} - R^2_{reduced}$ where U = uniqueness index for the predictor variable, R^2_{full} = the value of R^2 obtained for the full multiple regression equation containing all the variables in each category, and $R^2_{reduced}$ = the value of R^2 obtained for the multiple regression equation containing all the variables except the variable of interest within each category. To determine if the unique contribution of a variable was statistically significant we carried out a full model-reduced model F-test using the formula:

$$F = \frac{(R^2_{full} - R^2_{reduced})/(K_{full} - K_{reduced})}{(1 - R^2_{full})/(N - K_{full} - 1)}$$

where, K is the number of predictor variables and N is the total number of observations.

RESULTS

Aboveground vegetation biomass of the marsh was dependent on the presence or absence of standing water at time of sampling (late summer), with biomass being greater ($F_{1,48}$ = 5.42, P = 0.02) during periods that had standing water than those when water was not present (3.34 kg/m^2, SE = 0.41 and 2.59 kg/m^2, SE = 0.34, respectively). There was no interaction among years and water presence-absence ($F_{11,48}$ = 0.80, P = 0.64). Aboveground biomass of the marsh differed among the 13 years ($F_{12,48}$ = 2.06, P = 0.04), with 1999 and 2000 having the greatest productivity (approx. 5 kg/m^2) and 1989, 1998, and 2002 having the lowest aboveground marsh biomass (< 2 kg/m^2; Figure 3).

Among the eight categories of variables tested, only variables within the categories of ground cover, growth, and animal type influenced vegetation biomass (Table 1). Variables within categories of canopy, age, plant type, soil cap and others (salinity, annuals, density, and cool and warm season plants) did not influence biomass.

The full-model–reduced-model F-test was significant ($F_{calculated\ 1,73}$ = 5.26, P = 0.02) for normal growth form with a beta weight of 0.33 and uniqueness index of 6.97% (i.e., additional variance in productivity explained by 'normal growth form', beyond that accounted for by other growth form factors) for marsh aboveground biomass (Table 1). Within the category of ground cover (bare ground, cover by water, litter-1, litter-2, and basal plant cover), only litter-1 (beta weight = 0.86) and litter-2 (beta weight = 0.72) were related to aboveground biomass (Table 1). Litter-1 uniquely accounted for 11% of the variation in productivity (Table 1). Within the animal presence category, only insect occurrence influenced productivity (beta weight = 0.29, Table 1). Insect presence accounted for 7.67% of the variance in biomass. Ground cover (bare ground, cover by water, litter-1, litter-2, and basal plant cover) was related to aboveground biomass ($F_{5,67}$ = 2.33, P = 0.05), but only litter-1 (beta weight = 0.86) and litter-2 (beta weight = 0.72) were related to aboveground biomass (Table 1). Litter-1 uniquely accounted for 11% of the variation in productivity (Table 1).

DISCUSSION

The presence or absence of water in the marsh at the time of sampling was an important factor influencing available aboveground biomass in intermediate marsh. Greater biomass during years of standing water during late summer can directly be

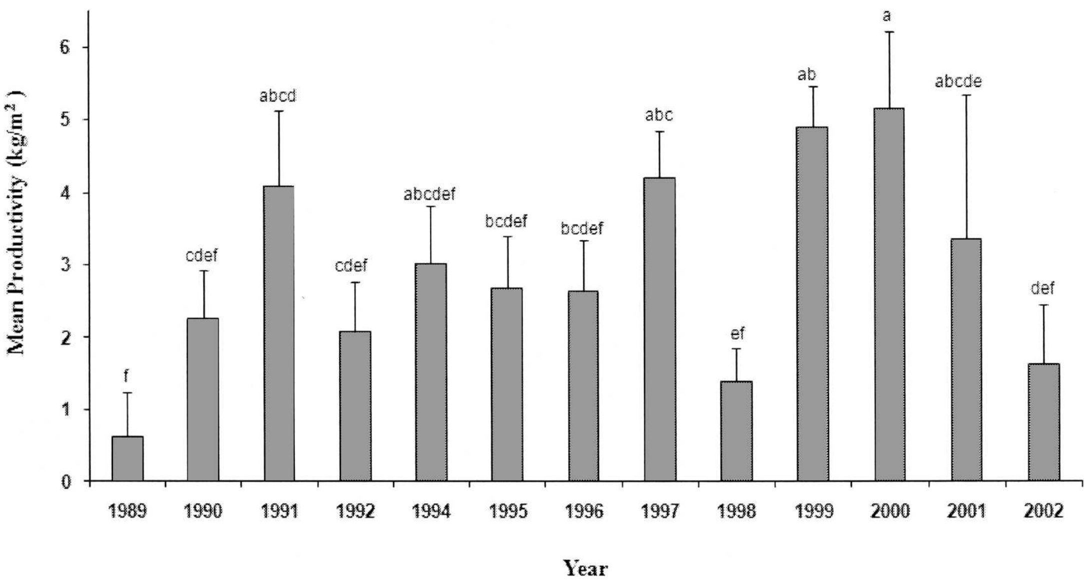

Figure 3. Mean biomass (kg/m^2) of vegetation samples conducted annually from 1989 to 2002, in an intermediate coastal marsh at East Bay Bayou, Anahuac National Wildlife Refuge, Texas. Year 1993 was not used due to loss of data. Years represented by the same lowercase letter were not different ($P > 0.05$). Bars represent standard errors.

attributed to the favorable growing conditions for plants adapted to marsh hydrology. Water stress (i.e., drought) in wetland plants has been known to reduce overall biomass (Froend and McComb 1994, Hudon et al. 2000, Wilcox 2004). Haukos and Smith (2006) reported that under slight water stress, some wetland plants redistributed resources by increasing seed production against vegetative development. Further, results of a recent study by Touchette et al. (2007) on drought tolerance in wetland plants, suggest that drought periods as short as 14 days are sufficient to reduce productivity significantly. Thus, in our study, water stress might have led to reduced morphological development and altered resource allocation in the marsh plant community during years with no standing water.

Year-end biomass of the marsh was related to plant growth form, type of animal present, and composition of the ground cover. Biomass was greatest in areas where plants exhibited a normal pattern of growth (abundant seed production, good tillering, or branching, and absence of any old or

Table 1. Different environmental categories and their corresponding factors[1] that were used to predict aboveground vegetation biomass in an intermediate coastal marsh at East Bay Bayou, Anahuac National Wildlife Refuge, Texas from 1989–2002.

Category	Variable(s)	t	P	Standardized Parameter Estimates (beta weights)	Uniqueness Index[†]	F-value For Unique Contribution
Growth form	Normal	2.29	0.02	0.339	6.97	5.26 *
	Overrested	1.87	0.06	0.296	4.60	3.48
Animal type	Insects	2.42	0.018	0.278	7.67	5.84 *
	Birds	−1.03	0.308	−0.134	1.38	1.05
	Small animals	−0.14	0.888	−0.019	0.02	0.01
	Large animals	−1.19	0.240	−0.136	1.85	1.41
Ground cover	Bare	−0.86	0.395	−0.097	0.93	0.73
	Litter-1	2.94	0.005	0.861	11.01	8.67 *
	Litter-2	2.50	0.015	0.727	7.97	6.28 *
	Water	0.12	0.902	0.016	0.02	0.02
	Basal cover	−1.45	0.151	−0.182	2.67	2.10

[1] Only categories that were influential ($P < 0.05$) in predicting biomass are presented in the table.
[†] Uniqueness index is the percent variance in productivity explained by an individual variable above and beyond other variables within a category.
* Significant unique contribution (F- test) at $F_{critical,1,73} = 3.97$, $P < 0.05$.

dead branches). Typically, brush exhibited stout appearance and often had several dead branches contributing little towards VO measurement. Similarly, overgrazed plots were characterized by grasses that were short and had more lateral than vertical branches; any associated shrubs had a heavily hedged appearance. These structural characteristics were associated with low VO measurements and indicative of reduced levels of available biomass.

Ground cover had a direct influence on available aboveground biomass of the marsh. Bare ground reflected lack of vegetation, whereas increased ground cover by litter resulted in greater productivity, including cover by litter being gradually incorporated in the soil (litter-2), which is an indicator of nutrient recycling. Litter cover is an important component in determining soil moisture, seed germination, and plant productivity as it increases the amount of organic nutrients available to the plants. Litter is one of the most important sources of nitrogen for plants, in turn contributing to primary production (Berendse 1990).

Salinity of the standing water was less important than originally thought based on several previous studies (Blits and Gallagher 1991, Broome et al. 1995, Baldwin and Mendelssohn 1998) in determining marsh productivity. Perhaps the gradient of salinity recorded in our study (1–6 ppt) was not sufficient to affect production.

Our results suggest that consecutive years of flooding followed by periods of drought will lead to the accumulation of litter and organic matter as drought-intolerant plants die (Sargeant et al. 1993). Alternating dry and wet conditions also expedites the breakdown and decomposition of organic matter, which results in higher productivity of the marsh (Baldwin and Mendelssohn 1998). Extremes of hydrologic conditions will also ameliorate seedling emergence or resprouts through cracks in the soil cap (commonly observed as soil dries out following a wet period). Thus, in managing marshes for greater productivity, periodic cycles of flood and dry conditions will promote plants with normal growth forms while overrested and decadent vegetation die due to extremes of hydrological conditions.

Managing coastal marshes for greater productivity is highly desirable for managing healthy wildlife populations, especially wintering ducks and geese. For example, non-maritime habitats along the Gulf Coast of Mexico contain some of the most important shorebird habitats in North America (Withers 2002). Management of these habitats often includes prescribed burning, which may not be possible due to smoke regulations and other practical and political impediments in some areas, making effective habitat management for shorebirds and other wildlife more difficult. In such areas, it may be possible to maximize available aboveground biomass for wildlife habitat by controlling water levels and managed livestock grazing. In most coastal public management areas, water-control structures are present to regulate water levels and associated salinities in the marsh. Our recommendations are also supported by a study (Moran et al. 2008) showing that managed grazing can increases floristic diversity in wetlands in addition to controlled hydrological regimes. However, this relationship is non-linear and can lead to the formation of rosette-plant forms, influencing overall productivity.

In this study, from a wide range of environmental variables considered, only a few variables were found to be indicative of increased available aboveground biomass of intermediate coastal marshes. Managers can use VO readings to estimate standing biomass, and, additionally, they can qualitatively assess condition of units of intermediate coastal marsh by recording the presence of surface water, relative abundance of insects, and depth of litter. Further, to maximize availability of aboveground biomass, management of intermediate coastal marsh should strive to maintain a normal growth form (good tillering, seed production, and lack of old growth stems and parts) through water, prescribed fire, and managed grazing to avoid the vegetation from becoming overrested, which will result in a reduction of available biomass.

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