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Biomass and resource allocation of *Typha angustifolia* L. (Typhaceae): The effect of within and between year variations in salinity[1]

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ABSTRACT

WHIGHAM, D. F., T. E. JORDAN AND J. MIKLAS (Smithsonian Environmental Research Center, Box 28, Edgewater, MD 21037). Biomass and resource allocation of *Typha angustifolia* L. (Typhaceae): The effect of within and between year variations in salinity. Bull. Torrey Bot. Club 116: 364–370. 1989.—In a brackish wetland dominated by *Typha angustifolia,* we found similar aboveground and belowground production at three sites which had very different salinity regimes. There were, however, significant differences between the three areas in shoot density, height, and biomass. Density was greatest in the site with highest salinity while height and biomass were greatest at the site with lowest salinity. There were also differences in the distribution of belowground biomass with roots and rhizomes restricted to shallower depths at the site with highest salinity. Long-term study plots in one area have shown that interannual changes in salinity can result in an almost 75% difference in net aboveground biomass.

Key words: brackish wetland, *Typha angustifolia,* biomass allocation, salinity, aboveground biomass, belowground biomass, long-term study.

Salinity affects both the physiology (Donovan and Gallagher 1985) and distribution (Dawe and White 1986; Deschenes and Serodes 1985; Ewing 1986; Lieffers 1984; Roozen and Westhoff 1985; Shay and Shay 1983; Snow and Vince 1984) of wetland macrophytes and variations from the normal patterns of salinity often result in vegetation changes (Zedler 1983; Zedler and Beare 1986; Zedler *et al.* 1986). Vegetation changes also occur as a result of long-term changes in salinity (Brinson *et al.* 1985; Lieffers 1984; van Noordwijk-Puijk *et al.* 1979).

In contrast, many types of coastal brackish wetlands are exposed to seasonal and annual variations in salinity without any noticeable changes in vegetation. Brackish wetlands in the Rhode River subestuary of Chesapeake Bay, for example, are normally exposed to low salinity water in the winter and spring months and higher salinity in the summer and fall when freshwater runoff from the watershed is low. Despite large interannual variations in salinity, the species composition of brackish wetlands in the Rhode River, dominated by *Typha angustifolia,* has not noticeably changed since our studies began in 1979 (Jordan *et al.* 1983; Jordan and Correll 1985; Jordan and Whigham 1988). Salinity in the part of the subestuary where *T. angustifolia* dominates was generally lower than the long-term (1971–1988) annual pattern in the 1970's and higher in the 1980's (Fig. 1). There have also been differences among years, especially during the growing season months. In 1976 and 1980, weekly salinity values followed the long-term annual pattern. In 1985 and 1986 weekly salinity values increased earlier than usual while in others (1972 and 1978) it remained low for longer periods of time. What effects, if any, do the differences in salinity have on the wetland? This question is of interest because, while these wetlands are known to be very productive (Whigham *et al.* 1978), there is little information on how variation in salinity affects production from year to year and place to

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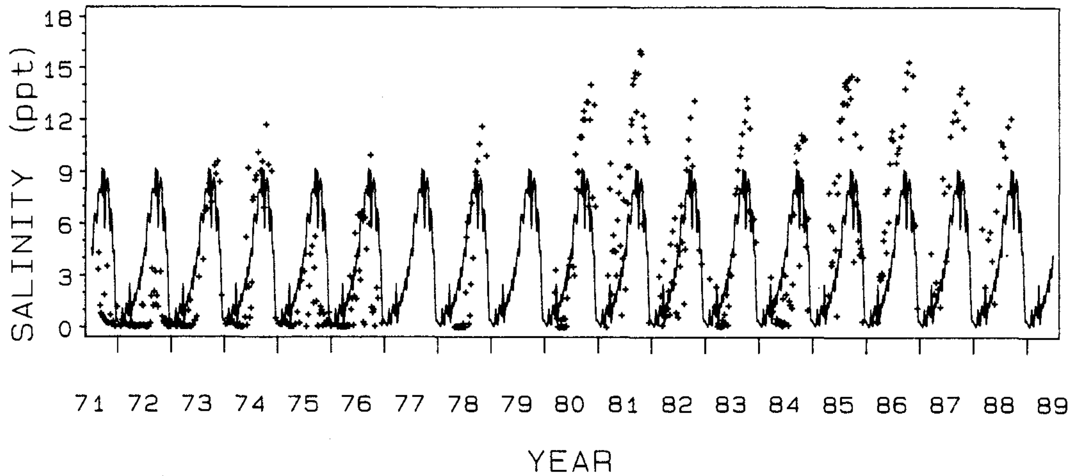

Fig. 1. Patterns of salinity in the low marsh portion of the Rhode River that is dominated by *Typha angustifolia*. The solid line is the same for each year and represents the long-term annual weekly pattern for the period 1971 to 1988. Crosses represent weekly values of composite samples for the same time period. The samples were taken from the tidal creek that flows through the wetland that was sampled during this study.

place within brackish wetlands. In this paper, we present data to demonstrate that variations in salinity can have a large influence on the dynamics of *Typha angustifolia* L. in a brackish wetland. We present two data sets: 1) a comparison of density, production, reproduction, and biomass allocation patterns for *Typha* for 1 year in areas of the wetland where salinities were different, 2) comparisons of 6 years of density, aboveground production, and reproduction data from permanent plots in one area within the wetland.

Materials and Methods. SITE DESCRIPTION. The Rhode River, a small subestuary of the Chesapeake Bay, is located a few kilometers south of Annapolis, Maryland. The study site was chosen because long-term water quality data were available for the portion of the subestuary where brackish wetlands are common and a distinct salinity gradient exists in the same area. The part of the subestuary considered in this paper is a tidal creek receiving runoff from a watershed of approximately 2286 ha (Jordan *et al.* 1986). The wetland dominated by *Typha angustifolia* covers approximately 15 ha. At the upstream border, it merges with forested freshwater wetlands (Whigham *et al.* 1986) and at the downstream end it blends with irregularly flooded brackish wetlands dominated by *Scirpus olneyi* Gray., *Spartina patens* (Aiton) Muhl, *Distichlis spicata* (L.) Greene and several other species characteristic of brackish high marshes in Chesapeake Bay (McCormick and Somes 1982). In addition to *Typha, Spartina cynosuroides* (L.) Roth. and *Scirpus olneyi* are also common.

We studied three areas in the wetland: an upstream area 200 m from a freshwater forested wetland, a downstream area 100 m from the ecotone with the brackish high marsh, and a middle area half way between.

SALINITY GRADIENT. The salinity of interstitial water was measured with a refractometer in the three areas in 1979. We sampled interstitial water which flowed into holes in the substrate that were created by removing material for determination of belowground biomass (procedures for biomass sampling described in the next section). Salinity in tidal water at high tide was measured weekly in the three areas between 1980 and 1988 with a Beckman RS5-3 salinometer. For comparison of the three areas in the 1980–1988 period, we present salinity data for weeks between Julian Day 110 (April 20) and Julian Day 190 (July 9). That time interval coincides with the period of active growth of *T. angustifolia* (D. F. Whigham unpublished phenological data).

COMPARISONS ALONG THE SALINITY GRADIENT. In 1979, we sampled vegetation in each area. An initial survey of the density of *Typha* was conducted by counting the

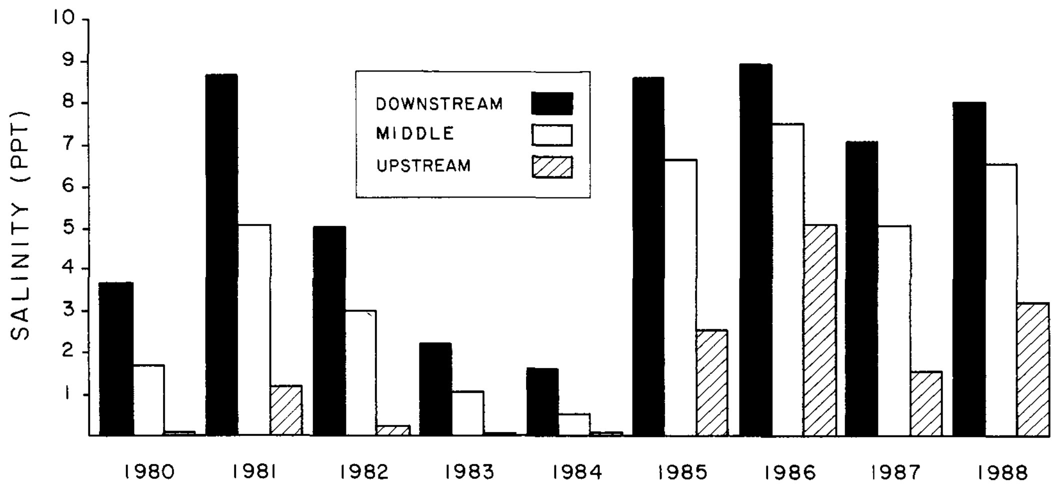

Fig. 2. Mean salinity between Julian days 110 and 190 for the tidal stream in the upstream, middle, and downstream areas for 1983–1988.

number of shoots in 50 randomly located quadrats (0.25 m^2) in each area. Between April and late July, we made four biomass harvests in each area but only report data from the July harvest since our objective is to compare peak aboveground standing crop. All aboveground and belowground biomass was harvested from four quadrats (0.25 m^2) in each area. Aboveground biomass was harvested first and the heights and diameters of all vegetative and reproductive shoots measured. The plants were then returned to the laboratory, dried at 60°C, and weighed. Because we could not separate belowground biomass for vegetative and reproductive shoots, aboveground biomass data was combined for the two types of shoots. Belowground biomass was sampled to a depth of 30 cm by removing the substrate as a block from each quadrat where the shoots had been harvested. The block was divided into 0–10-, 10–20-, and 20–30-cm depth intervals. The material from each depth interval was washed and all living roots and rhizomes (those which were turgid and white) were removed, dried at 60°C, and weighed. All substrate sampling was done at low tide.

COMPARISONS AMONG YEARS. Shoot height, shoot density, and the number of reproductive shoots were determined in two sets of long-term study plots in the middle area between 1983 and 1988. The two sets of plots were in different parts of the middle area where separate studies were being conducted (Jordan and Whigham 1988; Jordan *et al.* in press a). Biomass was estimated using the procedures described in detail in Jordan and Whigham (1988). Shoot density was determined in 2-m × 2-m plots which were subdivided into 1-m × 1-m subplots. The heights of the 3 tallest plants were measured in each of the subplots. A regression equation was then used to estimate biomass from the density and height data.

Results. COMPARISONS ALONG THE SALINITY GRADIENT. Interstitial salinity in 1979 was significantly ($P \leq 0.001$) higher (4.5 ± 0.3‰) at the downstream area, low-

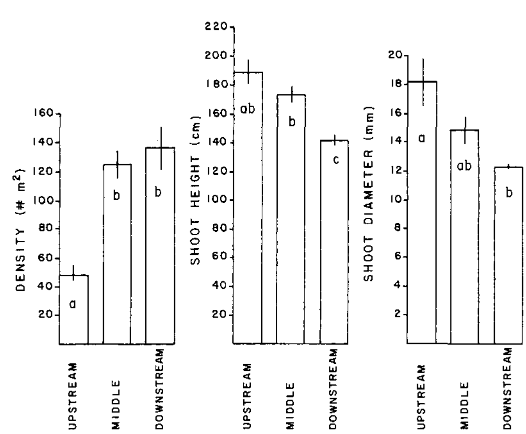

Fig. 3. Density (#/m^2), shoot height (cm), and shoot diameter (mm) of *Typha angustifolia* in the upstream, middle, and downstream areas in 1979. Values are means ± 1 standard error. Means that are not significantly different share the same superscript.

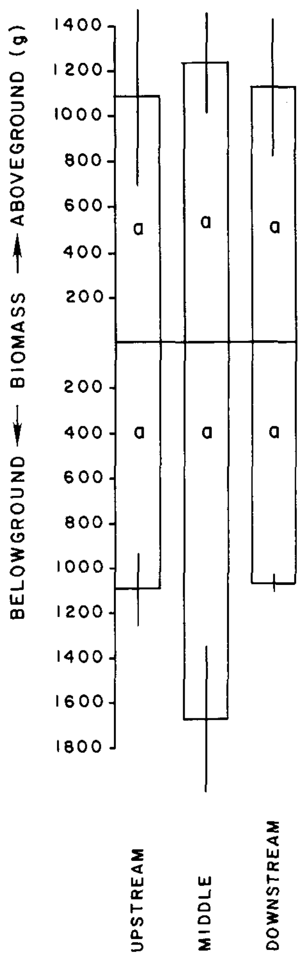

Fig. 4. Aboveground and belowground biomass expressed as g/m^2 for the upstream, middle, and downstream areas in 1979. All values are means ± 1 standard error and means which are not significantly different from each other share the same superscript.

est (1.0 ± 0.1‰) at the upstream area, and intermediate (2.0 ± 0.6‰) in the middle area in 1979. The same site relationships persisted for salinity in the tidal stream between 1980 and 1988 (Fig. 2).

In 1979, shoot density was greater ($P < 0.001$) in the downstream area but shoot diameter ($P \leq 0.0009$) and height ($P \leq 0.0035$) were greater in the upstream area (Fig. 3). The contrasting pattern in shoot density compared to shoot diameter and height resulted in similar amounts of aboveground and belowground biomass on an area basis (Fig. 4).

Only one flowering shoot (5.8%) was harvested in the upstream area, no flowering shoots were in the plots sampled in the middle area, and eight (33.0%) flowering shoots were in the plots in the downstream area.

There were no significant differences in the ratio of belowground to aboveground biomass but there were significant differences in the distribution of the belowground biomass. The greatest percentage of the rhizome and roots biomass occurred within the upper 10 cm at the downstream area (Fig. 5). There was an almost equal division of belowground biomass between the 0–10 and 10–20-cm depth in the upstream area and the middle area was intermediate.

COMPARISONS AMONG YEARS. As shown in Fig. 2, there have been clear differences between the three areas in the salinity of the tidal stream during the growing season and the differences have been most pronounced during years of high salinity. During the 6 years in which we have measured *Typha*, salinity between April and July has ranged from 0 to almost 9‰. There have been large interannual differences at all sites in some years (between 1984 and 1985) and large

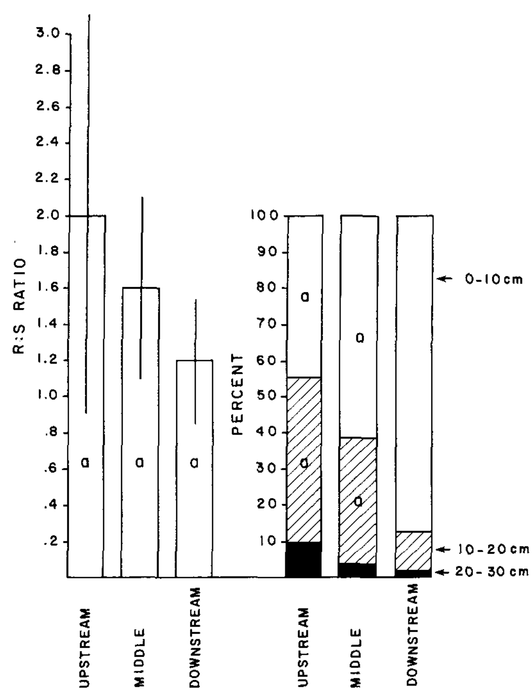

Fig. 5. Distribution of roots and rhizomes and belowground : aboveground ratios of *Typha angustifolia* in the upstream, middle, and downstream areas. Depth intervals are as indicated and the values are means of four samples for each area. Means that are not significantly different share the same superscript.

differences only at the upstream area between 1986 and 1987.

There were also interannual differences in growth and reproductive characteristics of *Typha* in the middle area during those same years (Fig. 6). Shoot density, height, and biomass in permanent plots measured between 1983 and 1985 were similar in the two low salinity years (1983–1984) but all decreased significantly ($P < 0.05$) in 1985 when salinity was high. The number of reproductive shoots in those plots also decreased in 1985. Differences among years for the plots measured between 1985 and 1988 were all significant ($P \leq 0.05$) except for 1985 and 1988 when the salinities were very similar. Density, height, and biomass were all high in 1987 when salinity was low. In 1985, we sampled both sets of permanent plots and biomass differed significantly ($P \leq 0.05$) between them.

Discussion. Salinity clearly influences the distribution of macrophytes in many types of wetlands (Adams 1963; Doumlele *et al.* 1985; Cahoon and Stevenson 1986; Ewing 1986; Roozen and Westhoff 1985; Semeniak 1983) and long-term monotonic changes in salinity result in dramatic changes in the vegetation (van Noordwijk-Puijk *et al.* 1979; Zedler *et al.* 1986). It is also clear that most species of brackish and saltwater wetlands grow better in freshwater (Ewing 1986; Phleger 1971; Zedler 1983). In contrast, there is very little information on the effects of seasonal and annual variations in salinity on specific vegetation types, although it is known that production of *Typha* spp. is affected negatively by increasing salinity (McMillan 1959). In hypersaline wetlands in southern California, Zedler (1983) found that a short-term reduction in soil salinity resulted in a 40% increase in the production of *Spartina foliosa* and a 160% increase for *Salicornia virginica.* Discharges of freshwater into the hypersaline wetlands resulted in the elimination of halophytes and establishment of *Typha.* Following the return of hypersaline conditions, production of *Typha* decreased but the clones have not been eliminated (Zedler and Beare 1986). Ewing (1986) studied vegetation characteristics along a salinity gradient in the Puget Sound in Washington. The productivity of *Scirpus validus, Eleocharis palustris,* and *Carex lyngbyei* was variable but was greatest in the fresher areas. Two other species (*Scirpus americanus* and *S. maritimus*) showed very little variation along the salinity gradient, as did *Typha* in our wetland. This suggests that some species are able to compensate for gradients in salinity. In our study, there were clear differences between areas in shoot density (both asexual and sexual shoots) and size but the differences were opposite in direction and the result was that there were no differences in aboveground or belowground biomass (Fig. 4). The reasons why shoot density was significantly higher in the two downstream areas are unclear but other studies in the same wetland have also shown that shoot density changes significantly as the oxygen concentration in overwintering *Typha* rhizomes is varied (Jordan and Whigham 1988).

The amounts of aboveground and belowground biomass measured in this study are within the wide range of values reported for other tidal wetlands (Whigham *et al.* 1978). The ratios of belowground to aboveground biomass were also within the range reported previously for brackish wetlands and for *Typha* (Whigham and Simpson 1978). This is the only study that we know of in which the vertical distribution of belowground biomass has been shown to vary along a salinity gradient even though there were no differences in total biomass (Fig. 4). Since *Typha angustifolia* is primarily a freshwater species (McMillan 1959), we expected that roots and rhizomes would have been more evenly distributed vertically in freshwater areas and restricted to the less saline part of the substrate in brackish areas. In our study, however, we found that roots and rhizomes in the brackish area were located closer to the surface where salinities were higher during the summer. We can only speculate that the upper part of the substrate in the downstream area is less saline at other times of the year, especially in the winter when freshwater inputs are higher.

The most striking result of sampling biomass in permanent plots has been the annual variations in net aboveground biomass and its relationship to salinity during the growing season (Fig. 6). There have been few studies of the affects that annual variations in salinity have on functional processes in brackish wetlands. During periods

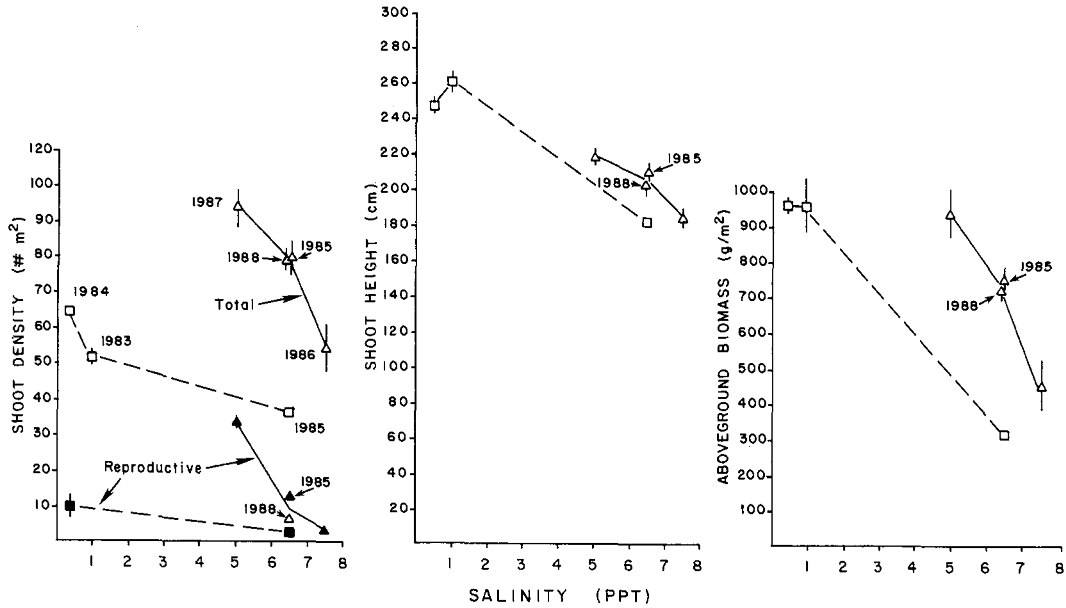

Fig. 6. Total shoot density and density of reproductive shoots, shoot height, and aboveground biomass for *Typha angustifolia* in two sets of plots in the middle area. Values for the plots measured between 1983 and 1985 (squares) are the average of 2 samples and the ranges are given. Values for plots measured between 1985 and 1988 (triangles) are means ± 1 standard error of 5 samples. All of the means are significantly different from each other except 1985 and 1988. The years associated with the data points are shown and they are in the same sequence in each part of the figure.

of brackish water intrusion into normally freshwater forested wetlands in North Carolina, leaf/litter production and radial growth of trees decreased (Brinson *et al.* 1985). Brinson *et al.* (1985) also measured higher concentrations of nitrogen in leaf litterfall during the year of brackish water intrusion and suggested that this was due to earlier senescence of leaves prior to the time when nutrients would normally be translocated from the leaves. We have found similar results (Fig. 6). In the long-term study plots, aboveground production decreased with increasing salinity. We also found that shoots had significantly higher concentrations of total Kjeldahl nitrogen during years of high salinity (Jordan *et al.* in press b). With the exception of the studies of Zedler in hypersaline wetlands in California (Zedler 1983; Zedler and Beare 1986; Zedler *et al.* 1986), our study is the only one that we know of which shows the significant impact that annual variations in salinity can have on biomass production in brackish wetlands. The 75% range in aboveground biomass production was as great as the differences in production among many different types of brackish wetlands (Whigham *et al.* 1978).

Is there any long-term effect of a series of years of either high or low freshwater input? Zedler's studies (Zedler 1983) suggest that wetlands which experience wide variations in salinity are resilient and will return to predisturbance conditions within a few years. Brinson *et al.* (1985) found that the forested system that he studied returned to predisturbance levels within 1 year. Our data (Fig. 6) also show significant responses from 1 year to the next but there is also a suggestion that consecutive years of higher salinity may have a cumulative effect on production. The salinity increase in the middle area between 1985 and 1986 was small (Fig. 2) yet the decreases in shoot height and biomass and increase in shoot density were large (Fig. 6). In 1985, we noticed that the shoots of *Typha* had almost completely senesced by early August. After that time, there was no net carbon gain but there would have been a large respiratory carbon demand by belowground rhizomes and roots because the substrate temperatures were still high (Jordan and Whigham 1988). The utilization of stored belowground organic matter following senescence in 1985 may have had a negative affect on growth early in the 1986 growing season. Growth during the remainder of the growing season would have also been low due to continued high salinity condition. High production rates in 1987 clearly demonstrate, however, that the effects of 2 years of high salinity can be reversed quickly and that these systems are very resilient.

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