Growth of the Marsh Elder *Iva frutescens* in Relation to Duration of Tidal Flooding

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ABSTRACT: *Iva frutescens* is a common shrub at the upland fringe of salt marshes throughout the East and Gulf Coasts of North America. Within a marsh, its location and relative size are governed largely by the degree of flooding by seawater. *Iva*'s wide distribution and restricted location within salt marshes may make it a useful indicator of overall conditions of the marshes. This work was designed to provide basic information on the age and growth of *I. frutescens*, especially as they relate to the degree of flooding that is needed in order to investigate *Iva*'s potential as an indicator. Cross-sections of older stems (living and standing dead) from salt marshes in Rhode Island, United States, were examined in order to age stems and estimate their growth rate from cumulative increase in woody tissue. Most stems were six yr old or less, suggesting that aboveground structures live for only a few years. Stem diameter correlated with growth rate and aboveground biomass. Elevation at the root zone was used to estimate the duration that plants were flooded, which was negatively correlated with stem diameter. The most robust plants came from sites that were flooded only up to 6–7% of the total time during the growing season. No plants were found in areas flooded more than 30% of the time.

Introduction

The shrub *Iva frutescens* ssp. *oraria* (Bartlett) R.C. Jackson (marsh elder) is widespread in North America, where it occurs in salt marshes from Nova Scotia to Texas (Crow and Hellquist 2000). Its relative tolerance to salinity and its relative intolerance to flooding by salt water combine to restrict its distribution primarily to a narrow zone at the upper reaches of salt marshes. Its wide latitudinal distribution, its narrow distribution within the marsh, and its near-ubiquitous presence in salt marshes make this species potentially useful for evaluating the effects of watershed activities on salt marsh condition. This work was designed to investigate that possibility, and was part of a larger effort in evaluating methods for determining the ecological integrity of salt marshes (Wigand et al. 2001).

The literature on *I. frutescens* refers primarily to its presence rather than to any detailed properties. One of the earliest of these references is from a single sentence published in 1871 to the effect that it grows in salt marshes in New York, United States (Anonymous 1871). In Mississippi, *I. frutescens* is a dominant species in a "definite shrub zone" on the border of saltwater marshes (Penfound and O'Neill 1938, p. 10). *Iva* is listed among the main components of one of the zonal communities in Louisiana salt marshes, which are "usually present where the average water level is one or more inch-

es below the surface" (Penfound and Hathaway 1938, p. 34). In this same Louisiana study *I. frutescens* is listed as a brackish water species with a soil salinity tolerance of 2.1–19.8‰.

Most of the few experimental studies to date have focused on *I. frutescens*' relative tolerance to salinity (Oosting 1945; Airall 1970; Bertness et al. 1992a; Young et al. 1994; Levine et al. 1998). Although it tolerates salinity better than other nearby shrub species, it does better when not flooded by salt water (Bertness et al. 1992b). This explains why it is generally limited to the upper reaches of salt marshes. Even so, *I. frutescens* can be among the most productive plants per unit area of marsh (Linthurst and Reimold 1978). It also can provide important refuge for small birds and mammals during high tides (Sibley 1955; Johnston 1957; Fisler 1961).

New England populations of *I. frutescens* grow at the landward edge of salt marshes. They often consist of a thin zone (a few meters wide), accompanied by occasional stunted individuals at slightly lower elevations than the seaward edge of the zone, along the borders of tidal creeks and on natural levees (Miller and Egler 1950; Bertness et al. 1992b). Because it is a perennial woody plant, old stems might make it possible to examine historical trends in the growth conditions from a given marsh using traditional dendrology methods (growth ring analysis). Little is known about the physiological ecology of this species, and very little information is known on the age structure of its

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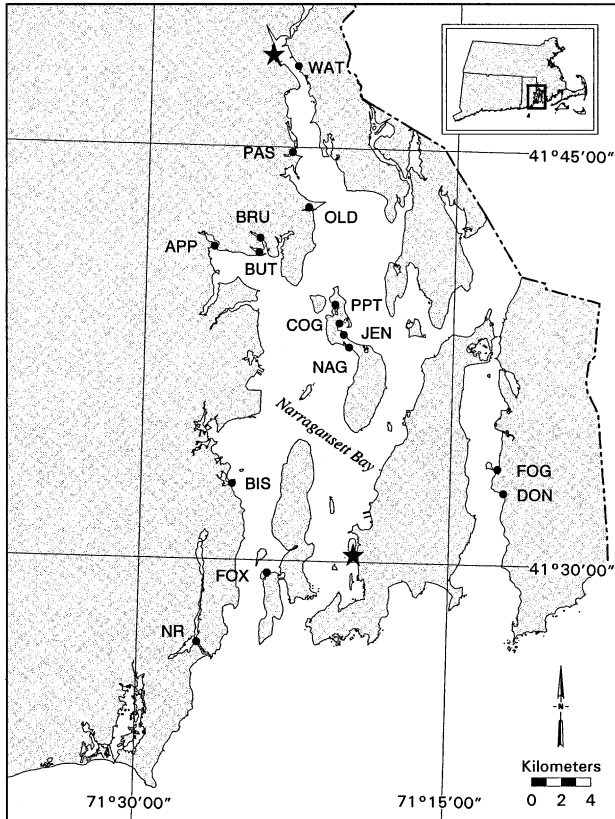
Fig. 1.   Map of the sampling locations in Rhode Island. Abbreviations are listed in Table 1. The star symbols mark the locations of the two tidal stations in Newport (southernmost) and Providence (northernmost), Rhode Island.
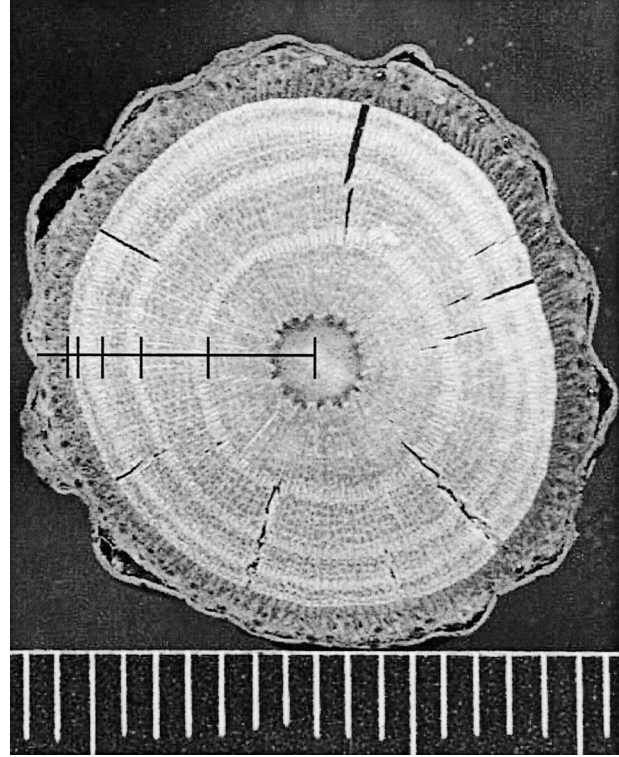

Fig. 2.   Stem cross section from *Iva frutescens* collected Winter 2000 in Rhode Island. Stem is five years old. An example of a measurement radius is shown. Each mark on the ruler scale is 1.0 mm.

populations or the speed at which its individuals grow. The immediate purpose of this work is to establish some basic information about the age and growth of *I. frutescens,* especially as they relate to the degree of flooding experienced by a given population. The resulting data add to the understanding of this species' natural history and lay the groundwork for using nondestructive techniques to monitor its productivity.

Materials and Methods

Stem Collection and Growth-ring Analysis

Plants were collected from 15 salt marshes in Rhode Island, selected to provide a variety of plant sizes (Fig. 1). At each site, samples 15–20 cm long were harvested from older stems (plants are multistemmed) of mature plants of *I. frutescens* L. ssp. *oraria* 10 cm above the soil surface. This helped assure that the oldest part of a given stem was sampled while avoiding the potential stem swelling near the soil surface at the transition between stem and root. Standing dead stems with the largest diameters that could be found were harvested at several sites. Segments from 334 live and 24 dead stems were accumulated. Most were collected in Winter 2000 (most recent growth ring represents 1999). Fifty more stems were collected in late Summer and Fall 2000.

Each stem segment for growth ring analysis was dried at 60°–70°C for at least 3 d. The lower ends were trimmed perpendicularly on a band saw and smoothed with a disk sander. The smoothed end (1 cm long) was cut from the segment. Each piece was digitally photographed alongside a ruler under a zoom microscope. Each cross-sectional image was analyzed with Image-Pro Plus 4.1 software from Media Cybermetrics. Three radii and three stem diameters were measured to the nearest 0.01 mm. Radii were measured from the pith center and the diameters through the visually identified center. The width of each successive ring was measured for each radius, and the cumulative area of wood produced each year was calculated from the resulting averages.

A typical cross-section of a live 5-yr-old stem from winter 2000 is shown in Fig. 2. The narrower, lighter rings represent early wood and the wider, darker rings late wood. This was confirmed by microscopically examining thin sections of young stems.
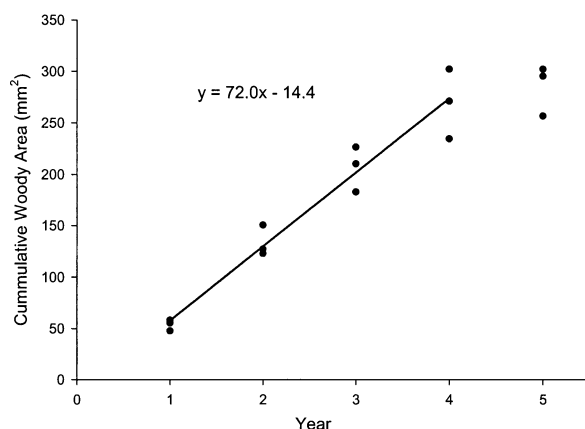
Fig. 3.   Example of a growth curve showing the cumulative area of wood with time. The slope of the line was used as a measure of the relative growth rate. The most recent ring (year 5 in this case) was omitted from the analysis.

A sharp transition is typical for woody stems between stoppage of growth in the fall and resumption in the spring. This occurred between the oldest (outer) portion of the darker areas and the youngest (inner) portion of the lighter areas. The more gradual transition from the youngest portion of a light ring and the oldest portion of darker areas indicates the gradual shift in growing conditions between spring and summer. Relative growth rates were estimated as the slope of the linear regression between age and cumulative woody cross-sectional area. The most recent year's wood in Fig. 2 consists of only a small ring of early wood. This ring was evident in many of the cross-sections from live stems and most of the sections from dead stems. Because the youngest ring often appeared to be incomplete, the most recent ring for each stem section was omitted from the growth rate calculation. An example of a regression is plotted in Fig. 3.

Standing Crop

Two measures of standing crop—stem length and stem dry weight—were compared with stem diameter. Using calipers, the diameters of fully developed stems from the field were measured to the nearest 0.1 mm at an internode region 10 cm above the soil surface. The lengths of these stems were measured to the nearest centimeter from the base of the stem to the tip of the main branch. Stems were cut to small lengths and dried (with their attached leaves) at 60°–70°C and were weighed to the nearest 0.1 g. The field stem diameters and dry weights from above were supplemented with data from greenhouse plants, including seedlings grown hydroponically at 15‰ for 6 wk and 4-mo-old plants rooted from apical stem cuttings. These plants had been cultured with commercial potting soil in 10×10 cm containers 30 cm tall setting in 10 cm of tap water. Diameters of seedlings were measured near the soil surface, and diameters of 4-mo-old plants were measured 10 cm above the surface.

Duration of Flooding Calculations

Elevation benchmarks were established in or near most of the salt marshes (Table 1). Each benchmark was normalized to the National Geodetic Vertical Datum of 1929 (NGVD29), and surveyed elevations referenced to those benchmarks.

TABLE 1. Salt marshes in Rhode Island from where *Iva frutescens* was collected. Those with no data did not have an elevation benchmark. All data refer to the seaward edge of the main *Iva* zone.

Location	Map Abbreviation	Surface Elevation (m above NGVD29)		Estimated Duration of Flooding at Root Depth (% of growing season)	
		Mean[a]	Range	Mean	Range
Apponaug Cove	APP	0.94 (7)	0.83–1.00	14.7	21.8–11.3
Bissel Cove	BIS	0.76 (11)	0.72–0.80	23.6	26.3–20.7
Brush Neck Cove	BRU	0.95 (1)	n/a	14.1	n/a
Buttonwoods Cove[b]	BUT	0.88 (12)	0.83–0.92	18.6	21.8–16.0
Coggeshall Cove	COG	–	–	–	–
Mary Donavon Marsh	DON	1.03 (8)	1.00–1.06	6.8	8.2–5.5
Fogland Beach	FOG	0.96 (11)	0.92–1.00	10.2	12.7–8.2
Fox Hill Cove	FOX	1.01 (12)	0.93–1.06	6.2	10.2–4.3
Jenny Creek	JEN	1.00 (17)	0.93–1.07	9.5	13.5–6.2
Nag Creek	NAG	–	–	–	–
Narrow River	NR	–	–	–	–
Old Mill Cove	OLD	0.90 (13)	0.80–1.05	17.3	23.7–8.9
Passeonkquist Cove	PAS	1.23 (8)	1.17–1.27	3.3	4.8–2.4
Providence Point	PPT	–	–	–	–
Watchamoket Cove	WAT	0.97 (6)	0.92–1.02	15.2	18.2–12.4

[a] Number in parenthesis is the number of measurements.

[b] Although there was a benchmark at Buttonwoods Cove (BUT), there is no data for that marsh in Fig. 7 because elevations and stems were not taken at the same location.
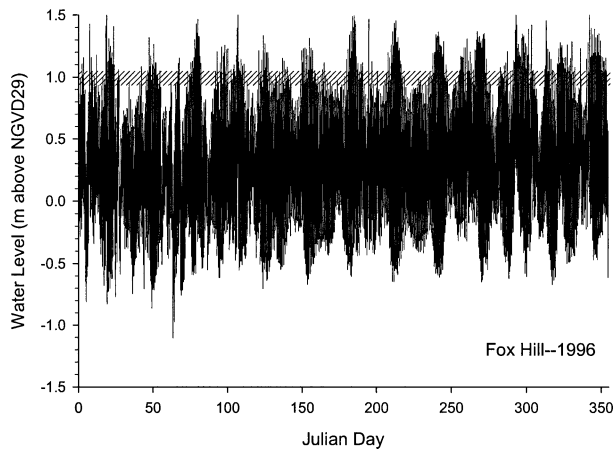
Fig. 4. Example of the hourly tidal data calculated for Fox Hill Cove in 1996. Elevations are relative to NGVD29 (approximately 15 cm lower than mean sea level at this site). The growing season was the beginning of April (day 92) through the end of October (day 305). The horizontal bar is the elevation of the main *Iva frutescens* zone.

Tidal information from the National Oceanic and Atmospheric Administration's (NOAA) tidal station No. 8452660, at Newport, Rhode Island, and station No. 8454000, in Providence, Rhode Island (star symbols in Fig. 1), was used to calculate the percent flooding at each site. Hourly tidal data relative to mean sea level for the Newport and Providence River stations for 1996–1999 were downloaded from the web site of NOAA's Center for Operational Oceanographic Products and Services (NOAA unpublished data), and also were normalized to NGVD29. The difference in tidal height between Newport and Providence, adjusted for each marsh's relative distance between the two permanent tidal stations, was added back to the Newport tidal data to estimate hourly tidal heights for the salt marshes that had an on-site benchmark. For example, Jenny Creek (JEN; Fig. 1) is four-tenths of the way up the bay, so four-tenths of the difference in tidal height between the two stations for each hour was added to the Newport value to estimate the tidal heights at the benchmark in this marsh. A sample of tidal heights at Fox Hill Cove (FOX in Fig. 1) during 1996 is shown in Fig. 4, with the elevation of its *Iva* zone shown for comparison. Similar data were generated for each of the 4 yr for each of the marshes.

Flooding durations were calculated for the mean elevation of the locations where stems of *I. frutescens* were collected, as well as along the seaward edge of the main *Iva* zone. Since the bulk of *Iva*'s roots lie in the top 5–10 cm of soil (Bertness et al. 1992b), the durations were calculated for 10 cm below the soil surface. The tidal height for each hour was compared to this reference point, and
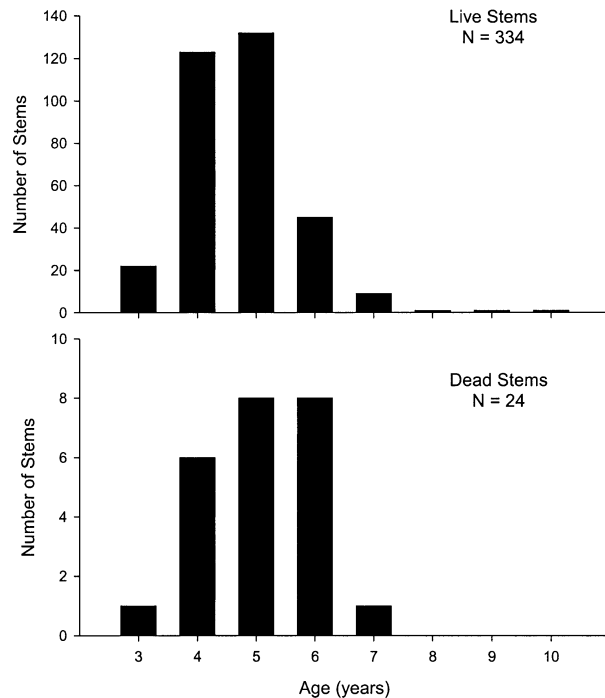

Fig. 5. Frequency distribution for age of live (top) and dead (bottom) stems of *Iva frutescens* collected from various salt marshes in Rhode Island, United States. An attempt was made to collect only the largest stems at each site.

the number of hours that the tidal height exceeded this reference was calculated. The total number of hours flooded between April and October each year (the primary growing season for *I. frutescens* in Rhode Island) was determined and expressed as a percentage of the total period.

Results

Most of the 334 live and 24 dead stems from Rhode Island were 4–6 yr old (Fig. 5). Three were older than 7 yr (8, 9, and 10 yr old). The age distribution was similar at all sites so the data were combined into one figure. Growth rate was positively correlated with total stem diameter for live stems older than 3 yr old (Fig. 6). Stem diameter and plant height were closely related, as were stem diameter and aboveground biomass of that stem (Fig. 6). This held for 6-wk-old seedlings grown at 15‰, 4-mo-old mature plants grown in freshwater, and plants from the field that ranged in age from 4 to 6 yr and exposed to salinities of 23–31‰.

The average diameter of older stems correlated negatively with duration of flooding during the growing season (Fig. 7). The largest plants were found in areas that are less flooded ($<7\%$); while plants flooded much more than 20% of the time were stunted. Areas flooded more than 30% of the time were devoid of *I. frutescens* (as shown by linear

transects from the upland edge of the marsh to the cove; data not shown). The mean surface elevation among plants at the seaward edge of the *Iva* zone ranged from 0.76–1.23 m above NGVD29, representing flooding of 23.6–3.3% at the root depth (Table 1). The overall average elevation of this edge was 0.97 m above NGVD29. The mean flooding at this transitional edge was 12.7%. Measurements of elevation on a few transects through the *Iva* zone (one or two in each of the benchmark marshes) showed that the average elevation of the main area of the *Iva* zone (robust plants) was 1.05 m.

Discussion

The strong correlation between basal diameter of stems and their growth rate came about because the ages of most mature stems were within a couple of years. Larger diameter stems generally had wider growth rings, not more rings. The close correlation between the diameter of a stem and its aboveground dry weight is to be expected because diameter was related to relative growth rate. That these relationships hold for stems from small seedlings to mature flowering plants will make it easy to estimate biomass for this species in the future, and will make it possible to rapidly and nondestructively follow growth rates and calculate biomass production in the field. Rapid techniques are important since large numbers of replicates may be needed for determining statistical significance among marshes (Thursby et al. 2002). A nondestructive technique is particularly important, since *I. frutescens* frequently represents a small area of the total marsh, making nondestructive methods important for preserving the standing stock.

Our observations of the link between flooding and diameter of mature stems further quantified earlier observations from Rumstick Cove, Rhode Island, where the most robust *I. frutescens* plants within its zone were found at the higher elevations (Bertness et al. 1992b). The close correlations between diameter, length, and aboveground biomass of stems meant that the plants were more robust when they were flooded less (at the higher elevations). The largest *I. frutescens* occurred in areas where roots were estimated to be submerged <7% of the time. The longer roots were submerged, the smaller the plants were. A change of only a few cms in elevation made a major difference in flooding and therefore in robustness of plants. This is consistent with the observations from Bertness et al. (1992b) that an increase of only 10 cm within the *Iva*'s zone correlated with more robust plants.

Flooding influences soil salinity and the availability of oxygen to roots. *Iva* can tolerate full seawater but, like many salt marsh plants, grows best in freshwater. This effect has been confirmed in
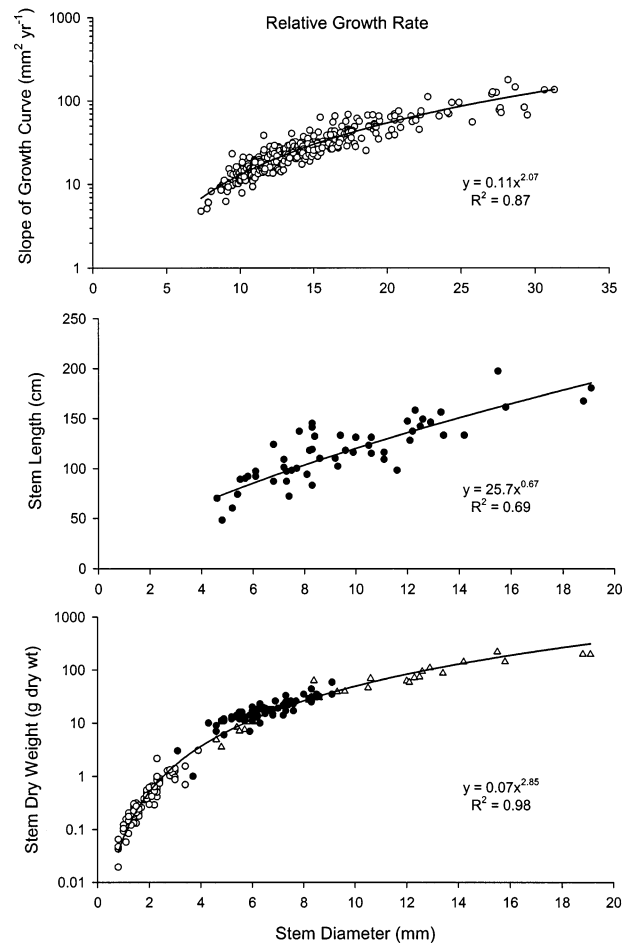

Fig. 6. Relationship between stem diameter (c. 10 cm from base of plant) and relative growth rate for stems 3 years old and older of *Iva frutescens* collected from various salt marshes in Rhode Island; stem length; and stem dry weight. For the latter open circles are from greenhouse seedlings (diameter measured at 1–2 cm above soil surface), filled circles from greenhouse mature plants, and open triangles from mature plants from the field. The solid line in each plot represents the nonlinear line of best fit and was determined using Microsoft Excel 2000.

greenhouse studies, where plants tolerated waterlogging by freshwater very well, but not by seawater (Bertness et al. 1992a). Although we did not measure soil salinity, Bertness and Yeh (1994) found lower salinity values in the upper reaches of *Iva* zones (less frequent flooding) in another Rhode Island salt marsh. In spite of *I. frutescens*' sensitivity to salinity, which keeps it from moving too far into the lower elevations of the high marsh, it tolerates salinity better than other nearby shrubs such as *Myrica cerifera* (bayberry) and *Baccharis halimifolia* (groundsel tree) (Young et al. 1994). The slight saltwater flooding tolerated by *I. frutescens* appears to give it an edge over its potential upland competitors within its narrow zone.
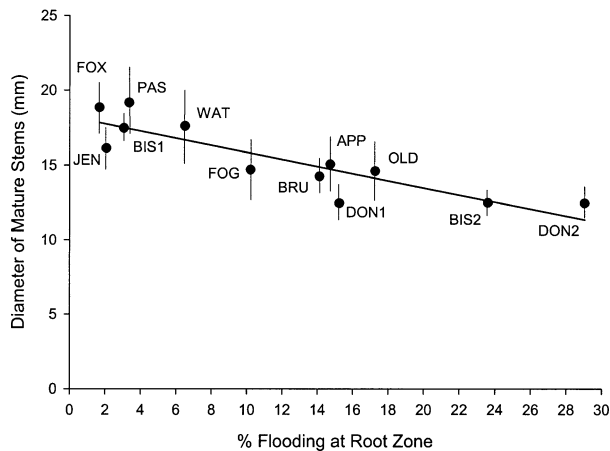
Fig. 7.   Relationship between mean stem diameter for older stems of *Iva frutescens* and the duration of flooding (as percent of growing season) at the root zone (10 cm below soil surface). Percent flooding values are based on elevation measurements made near the same location that the stem samples were taken. The labels are the same as those in Table 1. Labels followed by a number 1 or 2 are from different locations within the same marsh. Vertical bars are ± 2 SE. The means are of 10 stems except for Fox Hill Cove (FOX) and Jenny Creek (JEN) (n = 30) and Mary Donavon Marsh-1 (DON1) (n = 20); (p < 0.01).

While the general location of *I. frutescens* appears to be controlled by tolerance to salinity, and its landward border is likely limited by competition with less salt-tolerant shrubs and other vegetation, its seaward border may be controlled more by tidal flooding (Bertness et al. 1992b). Elevation, through its control of tidal inundation frequency (Bockelmann et al. 2002), is a primary factor determining the general distribution of plant species within a marsh (Adams 1963), and this is certainly true for *I. frutescens*. This species was not present at elevations corresponding to flooding durations of 30% or higher. There are many local factors that regulate the fine-tuning of its distribution. Soil aeration is one such factor for *I. frutescens* (Bertness et al. 1992b), as it is for other salt marsh plants (Reed 1947; Armstrong et al. 1985). The oxygen in soils near the seaward border of *I. frutescens* is often increased by *J. gerardi* (black rush), a frequently dominant plant on the terrestrial border of the high marsh (Bertness and Ellison 1987) whose upland limit often overlaps with the seaward border of *I. frutescens* (Bertness and Hacker 1994). *Juncus gerardi* can increase the oxygen in soils through leakage from the aerenchyma tissue in its roots and thereby improve the environment for *I. frutescens* and allow it to colonize lower elevations (to tolerate higher degrees of flooding) than it might otherwise (Bertness and Hacker 1994; Hacker and Bertness 1995). We have shown that the duration of flooding at the seaward boundary of

the *Iva* zone in many Rhode Island marshes can vary by as much as 15% within a single marsh (e.g., Table 1; Old Mill Cove [OLD]) and 20% between marshes. Some of these marshes do not have the typical presence of *J. gerardi* mixed within the seaward boundary of *I. frutescens*. For example, at Apponaug (APP) and Buttonwoods (BUT) Coves the plant zone immediately adjacent to the seaward edge of the *I. frutescens* is the low marsh plant *Spartina alterniflora*.

Marshes with less flooding of the seaward edge of the *Iva* zone also have a narrower range of flooding duration along that boundary. These marshes include Mary Donavon Marsh (DON), Fogland Beach (FOG), Fox Hill Cove (FOX), Jenny Creek (JEN), and Passeonkquist Cove (PAS) (Table 1). They have well-developed high marsh areas (dominated by *Spartina patens* seaward and commonly containing *J. gerardi* on the terrestrial side) and generally lower sand and higher peat content high-marsh soils (Wigand unpublished data). The marshes with greater duration of flooding at the *Iva* transition zone (APP, Bissel [BIS], Brush Neck [BRU], BUT, OLD, and Watchamoket Coves [WAT]) have little or no high marsh and much more sand content in the soil. For example, APP has as much as 92% sand and the *Iva* zone at our station in OLD is on a sand spit near the entrance of the cove. The soils in the more-flooded marshes would likely reoxygenate more quickly than those with more peat and less sand. From this and previous work, it is clear that the survival and growth of *I. frutescens* at lower elevations within a marsh are regulated by physical factors. The duration of flooding at which this species can survive is dependent, at least in part, on the local soil conditions. The rate of soil reaearation after a flooding event may be the main factor setting the lower boundary for this species. This is not new for salt marshes, since Reed (1947) listed soil drainage as one of the main factors (along with inundation and salinity) in setting the lower periphery for salt marsh species (although he did not include *I. frutescens*).

Besides soil aeration, nitrogen is an additional factor that may contribute to an increase in flood tolerance exhibited by some *I. frutescens* in Rhode Island. A positive interaction of *J. gerardi* on *I. frutescens* has been attributed to increased soil oxygenation (as detailed above) and prevention of salinity increases due to evaporation from the soil surface at low tide (Bertness and Hacker 1994; Hacker and Bertness 1995). Nitrogen fertilization can compensate for negative effects from removal of *J. gerardi* adjacent to *I. frutescens* (Levine et al. 1998). This effect of nitrogen is presumed to be through an increase ability to create the necessary

compounds for osmoregulation (Levine et al. 1998). Most of the marshes in this study that have increased flooding tolerance are also in the upper region of Narragansett Bay, which has higher residential development and presumed higher levels of nitrogen available to the plants in those marshes (McKinney et al. 2001; Wigand et al. 2001). In a previous study also conducted in a series of marshes in Rhode Island the degree of marsh border developed was positively correlated with direct measurements of plant nitrogen availability (Bertness et al. 2002). It is possible that the same mechanism that allows *I. frutescens* to tolerate higher salinity may also allow it to tolerate longer exposures to a given salinity.

Even though growth rings showed that most of the stems in this study were 4–6 yr old, plants were probably much older, since new stems are produced adventitiously each year from the rootstock. It is difficult to know the exact age of a particular plant. Observations in another salt marsh in Rhode Island indicated that most plants live at least 10 yr (Hacker and Bertness 1995). Although growth rings of *I. frutescens* plants from a salt marsh in New Jersey yielded a maximum age of 4 yr (Shisler et al. 1978), those plants had probably not reached their maximum possible age because they had come from recently colonized dredge material. The relatively short life of this shrub's stems means that we will not be able to use growth rings to infer historical trends in growing conditions for a single marsh, although such analyses can be used to compare stations within and among marshes.

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SOURCES OF UNPUBLISHED MATERIALS

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