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Citation	Albert, D. A., Cox, D. T., Lemein, T., & Yoon, H. D. (2013). Characterization of Schoenoplectus pungens in a Great Lakes coastal wetland and a Pacific Northwestern estuary. Wetlands, 33(3), 445-458. doi:10.1007/s13157-013-0402-4
DOI	10.1007/s13157-013-0402-4
Publisher	Springer
Version	Accepted Manuscript
Terms of Use	http://cdss.library.oregonstate.edu/sa-termsofuse

WETLANDS

Characterization of Schoenoplectus pungens in a Great Lakes coastal wetland and a Pacific Northwestern estuary

--Manuscript Draft--

Manuscript Number:	WELA706R2
Full Title:	Characterization of Schoenoplectus pungens in a Great Lakes coastal wetland and a Pacific Northwestern estuary
Article Type:	Article
Keywords:	Bulrushes, Great Lakes coastal wetlands, Pacific Northwestern estuaries, biomass, aerenchyma, Young's modulus of elasticity
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Abstract:	This study seeks to identify key components of structure and growth habit of Schoenoplectus pungens (bulrush) that allow it to thrive in severe environments. Schoenoplectus pungens, an emergent herbaceous plant growing in shallow, high-energy freshwater and brackish coastal wetlands, occurs throughout North America and several continents. We observe the plant in ecologically distinctive Laurentian Great Lakes and Pacific Northwestern estuaries. Plant populations were characterized in terms of above-ground and below-ground biomass, stem density, diameter, height, and flexibility. Plants grown in flooded planters for research were compared with populations in their natural environments. The modulus of elasticity was found to be similar for planter- and wild-grown plants from fresh and brackish waters. Aerenchyma tissue, important for conducting oxygen to roots, increased with flooding and possibly reduced stem flexibility. Stem diameter and height increased as water depths or flooding increased, while below-ground biomass decreased. Soils ranging from course gravels to clays supported S. pungens. Most regeneration occurs as sprouts from rhizomes, not seedlings. Below-ground biomass accounted for a greater proportion of total biomass than above-ground biomass in most zones. This study collected large below-ground biomass samples that allowed for more effective evaluation of root and rhizome structure than traditional small samples.
Response to Reviewers:	Response to reviewer 2-10-2013 Following is a summary of the changes made in response to the latest reviewer comments: Abstract: The suggested sentence was incorporated into the abstract, although shortened to meet publisher's abstract text limit. Suggested sentence in introduction add, although incorporated into another similar sentence to avoid redundancy. Page 4. The suggested sentence was incorporated. Page 12. We added the suggested figure (3b) for Tillamook. Addition of this figure

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	required adding more detail to the paragraph on Nearshore Bathymetry on page 6, as well as two sentences within Structure on page 7, a sentence within Reproduction on page 8, and Stem density on page 9. Page 14 and beyond: Citations were expanded to reference Tables more often as suggested. Page 15 (mid). A sentence was added concerning wild-driven sentence, now at beginning of page 16. On the same page, the discussion of snow geese predation on plants was modified to reflect information from a local waterfowl expert, who clarified that migratory routes exclude Oregon coast. Page 23. Added suggested sentence on aerenchyma. Page 24. The third paragraph of Summary was reworded at suggestion of reviewer. Table 2: Zeros were added to p values where missing. Figures 2 and 3: The incorrect versions of figures 2 and 3 were supplied in revision. Non-serif version attached in final version. The legend of figure 3 was expanded to address the addition of figure 3b. All of the detailed corrections in the text by reviewer were also reviewed and made.

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Introduction

This study focuses on the characterization of *Schoenoplectus pungens* (Vahl) Palla (common threesquare bulrush), a species recognized as important for occupying high energy, flooded coastal environments in the Great Lakes (GL) and within brackish tidal waters of estuaries and deltas of the Pacific Northwest (PNW) and the Gulf of Mexico. We sought to identify the key components of the species' structure and growth habit that allow it and similar species to thrive in such extreme environments. *Schoenoplectus pungens* is recognized in the PNW as an early colonizer of estuary sites with high wave energy, tidal fluctuations, and unstable accreting sediments (Eilers 1975; Jefferson 1975). The services provided by coastal wetlands, such as those dominated by *S. pungens*, include wave-energy reduction and erosion control, sediment and nutrient accumulation, and habitat functions that support commercial and sport fish, shellfish, and waterfowl, as well as overall biological diversity (Jude et al. 2005; Zedler and Kercher 2005). This study is part of a larger program to evaluate wave attenuation and sediment retention by *S. pungens*, initiated with the purpose of quantifying these important services in coastal wetlands. In this publication we compare characteristics of *S. pungens* plants from both freshwater and marine environments to assess how consistent the species' growth is under a range of site conditions. Important growth and morphological characteristics potentially affecting wave attenuation and sediment retention include stem diameter, height, and flexibility, as well as the density of stems, below-ground biomass, and above-ground biomass. All of these factors are measured by plant zone as described below. Soils and bathymetry provide the broad framework for understanding the energy dynamics and size of the wetlands and their zones.

General Plant Description and Distribution

Schoenoplectus pungens is an emergent herbaceous plant that grows in shallow freshwater and brackish habitats throughout North America, including inland and coastal estuarine sites, and in Mexico, the West Indies, South America, Europe, Australia, and New Zealand (Ball et al. 2003). *Schoenoplectus pungens* is a long-lived perennial that reproduces both clonally and sexually. The above-ground plant consists of a single upright stem triangular in cross-section, with basal leaves either well-developed or absent (Fig. 1). The below-ground plant consists of a rhizome that produces one or more vertical stems annually, coarse anchoring roots that can penetrate downward into underlying consolidated sediments, and fine roots that are concentrated close to the rhizome or in surface sediments. Anchoring and fine roots are most abundant near the stem base, and the remainder of the rhizome has few roots.

Study Sites and Landscape Context

Schoenoplectus pungens was studied at several sites along the GL shoreline in Michigan and along Oregon's Pacific coastline, with quantitative sampling focused at Cecil Bay, MI on Lake Michigan and within the estuary at Tillamook Bay, OR on the Pacific coastline (Fig. 2). Distinctively different coastal landscapes of the GL and the PNW are important for understanding differences in vegetation zonation and structure and they provide a perspective on the species' adaptability to diverse habitats. Most large bays on the Great Lakes are underlain by flat-lying limestone and dolomite bedrock, and the slopes of these bays are gentle, resulting in the creation of broad, shallow wetlands with *S. pungens* beds up to 400 meters wide, but with little protection from storm waves. In contrast, Tillamook and most other PNW estuaries are protected from the direct force of ocean storms by sand spits or barrier islands. For the remainder of this paper, we will refer to the sites as Cecil Bay and Tillamook.

Schoenoplectus pungens is potentially an important plant for wetland restoration due to its ability to thrive in both brackish and freshwater ecosystems. While freshwater characterizes GL coastal wetlands, estuarine wetlands in the PNW are brackish, with salinity as high as 30 ppt, as are its habitats on the Gulf of Mexico, the Atlantic coast, and many other of its habitats world-wide. In the PNW, *S. pungens* typically grows in monocultural stands, but it often co-occurs with *Carex lyngbyei* Hornemann (Lyngbye's sedge), which grows slightly upslope. The characteristic flora of PNW salt marshes is limited to approximately 30 vascular plant species and several marine algae, many of which have adaptations for surviving in brackish conditions, with species in the regularly flooded lower salt marsh most tolerant of high salinity (Jefferson 1975). In contrast, many more plant species survive in freshwater wetlands, and Cecil Bay supports more than one hundred vascular plant species (Brian Scholtens, unpublished data). Among the most common species co-occurring in the high-energy open marshes with *S. pungens* are *Schoenoplectus acutus* (Bigelow) A. & D. Löve (hardstem bulrush) and *Eleocharis palustris* Roem. & Schult. (spike-rush).

Water-level fluctuations differ greatly between the two sites. Water levels in the GL can fluctuate over a meter from year to year, resulting in major plant community changes (Gathman et al. 2006; Wilcox and Nichols 2008), as well as altered bottom sediments, nutrient availability, and plant structure. At Cecil Bay, the 100 plus plant species recorded during extended low-water conditions were preceded by a low of ten species when the entire wetland was flooded for four successive years (Barbour et al. 1975). Nutrient availability fluctuates greatly in GL coastal wetlands due to multi-year fluctuations in water level (Cronk and Fennessey 2001), and this in part drives rapid changes in vascular plant diversity.

Short-term fluctuations within a single growing season or day have less influence on plant structure, although major storms can alter vegetation dramatically (Harris et al. 1981). More sediment in GL coastal wetlands is moved by waves in high-water than in low-water years, resulting in increased accretion of sand and gravel into coastal beach ridges, while silts and clays are deposited off shore regardless of water levels (Dorr and Eschman 1981).

In contrast, major year-to-year water-level variability does not characterize PNW estuaries, but instead, tidal cycles result in twice-daily inundation and dewatering of coastal wetlands and mud flats (Hutchinson 1982). Plants growing in estuaries receive daily influxes of fine sediments carried by the tides, into which *S. pungens* and other marsh plants extend roots, resulting in sediment accretion (Jefferson 1973). Winter storms result in increased sediment movement (Cahoon et al. 1996; Komar et al. 2004), but documentation of impact on estuary vegetation is lacking. Salt water, introduced into estuaries with each tide cycle, also alters vegetation size and distribution (Deschênes and Sérodes 1985).

Methods

Nearshore Bathymetry

Bathymetric profiles were drawn at Cecil Bay (Fig. 3a) and Tillamook (Fig. 3b) using a dumpy level and stadia rod. In this article, we use the terms upper, mid, and lower marsh; at Cecil Bay, the term upper marsh (shore) was used for the highest elevations just below a large beach ridge at the upper extent of standing water during storms (10 m along transect), mid marsh was intermediate in elevation near the edge of water during 2008 and 2009 (100 m along transect), and lower marsh was the outer extent of vegetation in deep water (130 m along transect). In Tillamook's tidal marsh, there was no distinct beach ridge, although there was a distinct slope break, which was located 5 to 15 m from the irregular upland bluff edge along the stretch of

shoreline where vegetation was sampled. Vegetation sampling was conducted within the upper, mid, and lower marsh zones. The upper marsh sample was located within a meter above the slope break (5 to 15 m from the bluff), where flooding occurred only briefly during most high tides. The mid marsh sample was located midway between the upper marsh sample and the lower marsh sample (17 to 23 m from the bluff), and the lower marsh sample was located within a meter of the outer edge of the vegetation (25 to 32 m from the bluff), where flooding was deepest and occurred during every high tide. For both Cecil Bay and Tillamook, the upper marsh boundary was relatively discrete, with a rapid change in elevation and drier conditions, while the boundary between mid and lower marsh was more gradual.

Soils

The soils at Cecil Bay were characterized along transects from the edge of the shoreline dune to 10 m beyond the outer edge of the bulrush beds. Six soil samples were taken at 10, 25, 100, 130, and 150 m along transects. Soil textural analysis was conducted on bulk samples collected with a 10-cm-diameter auger at 25-cm depth increments from the surface into the underlying parent till. At Tillamook, less intensive sampling was conducted to characterize soil texture and depth, with one set of soil samples taken at 5, 17, and 32 m along a transect within a protected inner estuary site and at 16, 53, and 88 m along a second transect at a higher-energy site near the mouth of the estuary. At each Tillamook sampling point, bulk soil samples were taken with an auger from 0 to 10 cm below the surface and from between 20 and 30 cm depth. For both sites, the proportion of sand, silt, and clay in samples was determined using the hydrometer method (Day 1965). The Cecil Bay sand fraction was further broken into very course, course, medium, fine, and very fine sand (Soil Survey Staff 1975) and the dark, organic-rich Tillamook soils had organic content

determined by dry ignition (Allison 1965). The details of textural analysis are not presented but are discussed generally in the Results and Discussion section that follows.

Plant Structure, Reproduction, and Biomass

Structure

At Cecil Bay, plant samples were collected in July 2009 along a transect parallel to the elevational gradient, with samples at 10, 100, and 130 m. At each of these distances, six randomly located samples were taken for stem height and three for above-ground and below-ground biomass. Twelve additional biomass samples were collected in August 2011 and 2012 at 10 m and 100 m, and seven additional samples at 130 m. At Tillamook, three sets of samples were collected in the upper marsh (5 to 15 m), mid marsh (17 to 23 m), and lower marsh (25 to 32 m) along transects perpendicular to the slope, with above-ground biomass collected in November 2011 and July 2012, and below-ground samples collected in mid-March 2011. Three sets of additional biomass samples were collected in October 2012 in the upper and lower marsh zones, while storm damage precluded above-ground biomass collections in the mid marsh.

Reproduction

The study compared *S. pungens* sexual reproduction from seed and asexual reproduction from rhizomes. Searches were conducted for plants recently established from seed in 2008 and 2009 at Cecil Bay and in 2010 at Tillamook. In 2008, rhizomes were dug from the sediment within six randomly located quadrats 10, 100, and 130 m along the elevation transect, and it was noted if the plant had sprouted from seed during the last five years. In 2009, further searches for seedlings were conducted in three quadrats at Cecil Bay at 10, 25, 100, and 130 m and at

Tillamook in the upper (5 to 15 m), mid (17 to 23 m), and lower marsh (25 to 32 m) along transects.

Above-ground biomass sampling

Stem heights were measured in the upper, mid, and lower zones. Five to six replicate samples were taken for Cecil Bay and five for Tillamook within 0.25 m^2 sampling frames constructed from pvc tubing. For each sample, 25 stems were cut at ground level, heights measured, and oven-dried at 75° C. The total number of stems within sampling frames was counted, and above-ground biomass was computed from the weight of the 25 collected stems.

Below-ground biomass sampling.

Bulrush rhizomes and roots were harvested in 0.25 m^2 (0.5 m x 0.5m) or 0.09 m^2 (0.3 m x 0.3 m) sampling frames at Cecil Bay, and in 0.09 m^2 (0.3 m x 0.3 m) or 0.04 m^2 (0.2 m x 0.2 m) frames at Tillamook. The initial large sample frames at Cecil Bay were reduced in size to facilitate collection of more samples and to speed sample processing. Stem counts and biomass were standardized to 1.0 m^2. The standard depth of root and rhizome samples was 30 cm, but sampling occasionally extended to 45 cm when there was deeper rooting.

Blocks of sediment containing rhizomes and roots were cut with straight-bladed shovels, and most soil was washed from the sample on site, with further washing in the laboratory. Root and rhizome samples were collected on a 0.67-cm wire-mesh screen. Further analyses included separating roots from rhizomes, measuring total rhizome length, measuring rhizome internode length, and drying and weighing of all root and rhizome classes. Mean rhizome length and spatial orientation were computed to assist in understanding changes in plant growth over time. Rhizomes and fine roots were dried at 75° C until weights stabilized.

Stem density

Stem density was measured for 0.25 m^2 plots along transects parallel to wetland slope at Cecil Bay and Tillamook. For Cecil Bay, stem density measurements were based on averaged values from five to six sampling points at 10, 25, 100, and 130 m along the transect, examined in late July and early August 2009, while at Tillamook, five points was examined in the upper (5 to 15 m), mid (17 to 23 m), and lower marsh (25 to 32 m) along transects on July 6, 2012.

Stem Flexibility

Stem flexibility is an important factor for the attenuation of waves by vegetation (Kobayashi et al. 1993; Mendez et al 1999; Feagin et al. 2010; Riffe et al. 2011) and is defined in terms of the modulus of elasticity, *E*. The modulus of elasticity (or Young's Modulus) is a common parameter used to define bending capacity of materials and is defined as $E = \sigma/\varepsilon$ where σ is the stress and ε the strain. Using Euler beam theory, *E* can be determined for a cantilever beam of length *L* with uniform cross-section,

$$E = \frac{Pa^2(3L - a)}{6dI} \quad (1)$$

where *P* is the load applied at a distance *a* from the fixed end, δ is the deflection measured at the free end, and *I* is the moment of inertia. For a beam with circular cross-section, the moment of inertia is $I = (\pi r^4)/4$, where *r* is the radius.

The modulus of elasticity was estimated and plotted for four groups of specimens as a function of stem diameter. Group 1 plants were measured at Tillamook in 2009, Group 2 plants were measured later in 2009 at the same estuary to check method repeatability, Group 3 plants were collected from Tillamook and grown in a fresh water outdoor facility at Oregon State University, and Group 4 plants were measured at Cecil Bay in 2010.

To measure *E* for plants in the Tillamook estuary, a simple tool was devised using a carpenters level, square, and metric ruler fastened to a long wooden pole such that the square was at right angles to the pole and could be made level with the ground. Individual *S. pungens* stems were harvested below the mudline, cleaned of silt, diameter measured, and then carefully attached to the square using velcro straps without crushing the stem. In trials where cells were damaged, stems were rejected from analyses. After securing the specimen, it was trimmed to a length L = 14.0 cm. A known weight was added at a distance a = 10.0 cm from the fixed end, and the deflection d was measured at the free end. For smaller stems 4 to 6 mm in diameter, the load was increased in 1-2 gram increments (by 4 to 6 grams for stems larger than 10 mm in diameter), yielding deflections of 2 to 20 mm for the specimens tested. *E* was estimated for each specimen following Eq 1 and plotted as a function of stem diameter.

Aerenchyma tissue- large specialized cells for gas conductance in flooded environments

Aerenchyma was examined in *S. pungens* stem cross-sections, with two stems collected from Tillamook's upper marsh and two from the lower marsh during late May 2011. Stem cross-sections were fixed in paraformaldehyde, dehydrated in a graded alcohol series, embedded with glycol methacrylate plastic, and then sectioned to 4-6 microns on a rotary microtome. Sections were stained and mounted on glass slides, viewed with a Leica Labolux microscope at 40x magnification, and digital images were created with a MOTICAM 1000 camera. CellProfiler software was used to quantify aerenchyma tissue in digital images. Examinations of aerenchyma from Cecil Bay were done with a Keyence digital dissecting scope and camera.

Statistical Analyses

Statistical analyses were conducted in MATLAB and JMP. Paired *t*-tests were conducted for comparison of *S. pungens* stem heights, where sample distributions approached normality. For comparisons of total, above-ground, and below-ground biomass within sites, as well as stem density and diameter, Wilcoxon's rank sum tests were used due to small sample size and lack of normality.

Results and Discussion

Nearshore Bathymetry

Major differences in slope distinguish Cecil Bay from Tillamook, and more generally, GL bays from PNW estuaries. The slopes of many large GL bays ranges from 0.25 to 0.60 percent, and Cecil Bay had a slope between 0.55 and 0.60 percent within the 130-m-wide bulrush zone of the marsh (Fig. 3a). In contrast, the Tillamook estuary transects had steeper slopes ranging from 1.3 to 4.3 percent and narrow bulrush beds 30 to 90 m wide (Fig. 3b). Tillamook's protected inner *S. pungens* bed grew adjacent to a bedrock upland, and slopes transitioned from 6% near the upland edge to 4% in the regularly flooded portions of the 30-m-wide marsh. A second Tillamook transect at the base of a steep dune had a relatively stable 1.3% slope across the entire 90-meter wide marsh. In comparision, *S. pungens* beds growing on the deltas of the Fraser and Nooksack Rivers, two large PNW estuaries, had gentler slopes in the range of 0.2 to 0.3% (Disraeli and Fonda 1979; Hutchinson 1982). The deltas within the Tillamook estuary also support beds of *S. pungens*, but the bathymetry of the *S. pungens* beds on the delta were not measured, although slopes appeared similar to those at the dune site (1.3%). Several other *S. pungens* beds observed within the estuaries of Oregon and Washington were at the margins of sand spits or uplands, and these were characterized by steep slopes and relatively narrow emergent vegetation zones.

In summary, *S. pungens* beds occupy a range of slopes from 0.2 to 6%, with the steepest slopes observed in steep-sided PNW estuaries. The steeper-sloped estuaries are characterized by narrow vegetation beds, often considerably less than 100 m wide, while those growing on gently sloping lacustrine plains of the GL or on PNW deltas can be hundreds of meters wide.

Soils

Soils at Cecil Bay were characterized along transects and summarized in Figure 3a. A veneer of sand of variable depth covered underlying silt-loam to clay-loam till along the entire vegetated marsh. *Schoenoplectus pungens* grew in an average 22 cm of gravelly sand in the upper marsh (sampled at 10 m), in 5 to 15 cm sand in the mid marsh (at 100 m), and in 4 cm sand in the continually flooded lower marsh (at 130 m). The 15-cm-deep sand in mid marsh was where a small beach ridge formed during the 1999-2011 low-water conditions. The surface sands along the entire 130 m of vegetated marsh consisted largely of medium-sized sand grains, reflecting the grain-size distribution of the underlying till (lead author's unpublished data). The limited accumulation of 15 cm of sand over twelve years underscores both reduced erosion rates in the *S. pungens* beds and the fine texture of the parent till, which provides relatively small amounts of sand for beach ridge formation.

At Tillamook, upper marsh soils were sands underlain by gravel, both derived from the erosion of upland bluffs. These soils rapidly transitioned to organic-rich loamy sand and sandy loam in mid marsh, and organic-rich silt loams in the lower marsh (Fig. 3b). Near the higher-energy mouth of the Tillamook estuary, sands similar to those of the nearby dunes on the Bayocean Spit characterized the entire marsh. Much coarser sands characterized the sediments at

the five river mouths along the eastern shore of Tillamook Bay, where *S. pungens* occupied the lower delta margins. These course sands entered the bay from the nearby mountainous uplands.

Our investigations demonstrated that soil sediment size was not a major limiting factor for *S. pungens* growth. The plant was observed rooting in sediments ranging from course gravels and sands to dense clays, allowing it to stabilize sediments across a broad range of high-energy lacustrine and estuarine environments, and increasing the potential of the plant for use in restoration.

At Cecil Bay, where wave energy was greater, sediment texture and accumulation was determined largely by wave action, especially during storm events. In the Tillamook estuary, low-energy tidal currents deposited fine organic and mineral soil particles daily. In both GL and PNW wetlands, the role of *S. pungens* in soil stabilization could readily be observed in the unstable sediment beyond the vegetation or where vegetation had been removed by landowners.

Cecil Bay and Tillamook upper marsh sediments were similar: coarser sands and gravels containing abundant *S. pungens* fine roots and rhizomes highly resistant to wave and current erosion. In contrast, sediments in mid and lower marsh differed greatly between these sites. Cecil Bay's mid- and lower-marsh sediments were highly compacted tills capped with a thin veneer of sand and gravel. The underlying till provided stable habitat for *S. pungens*, the compact till containing deep roots and rhizomes protected by a surface lag of erosion-reducing course gravel. In contrast, Tillamook's mid- and lower-marsh sediments ranged from loose erodible sands to silt loams, neither as stable for plant growth as Cecil Bay's dense tills.

Plant structure, reproduction, and biomass

Reproduction – the predominance of asexual reproduction

Our study found that almost all reproduction and expansion in *S. pungens* beds at both sites occurred through rhizome growth, not from seedling establishment. In our 2008 and 2009 studies at Cecil Bay, less than 1% of plants examined were identified as seedlings that had established during the previous three to five years, even though there had been a nine-year period of low water conditions optimal for seedling establishment. No seed-origin plants were noted in the Tillamook below-ground samples collected in 2011. These findings agree with results of a reproduction study in the lower St. Lawrence River estuary (Giroux and Bédard 1988), where large amounts of seed were observed, but plant establishment from seed was low, and establishment occurred only on the upper marsh edge. Summary of biomass and structural data below is based primarily on mature, asexually reproducing plants.

Total biomass comparisons between marsh zones

The upper marsh zone at Tillamook contained roughly four times more biomass than the mid or lower marsh (Table 1), both statistically different (Table 2). There was no statistically significant difference between the biomass of the mid and lower marsh zones. Earlier estuary studies on the Fraser River in British Columbia and the Nooksack River in Washington (Disraeli and Fonda 1979; Karagatzides and Hutchinson 1991) found similar results. Total biomass differences between Cecil Bay's zones were not significant (Table 2). Cecil Bay's upper marsh had less than a quarter of the biomass found in the upper marsh at Tillamook, a statistically significant difference. Total biomass of Cecil Bay's mid and lower marsh zones did not differ statistically from Tillamook. Discussions will therefore focus on above-ground and below-ground biomass.

Below-ground biomass comparisons between marsh zones

In our study, below-ground biomass accounted for a high proportion of total biomass in the upper marsh, 90% at Tillamook and 94% at Cecil Bay (Table 1). At Tillamook, a statistically

greater amount of below-ground biomass was concentrated along the upper edge of the marsh than in the mid marsh or the lower marsh (Tables 1 and 2), with a decrease in biomass toward the deeper, lower marsh. At Cecil Bay, there was a similar, statistically significant decrease in below-ground biomass between the upper and lower marsh zones (Tables 1 and 2), while below-ground biomass in the mid marsh was variable and not statistically different from its neighboring zones.

The large amount of below-ground biomass in the upper marsh at Tillamook appeared to be the result of greater accumulations of coarse sediment, due largely to erosion from upslope and the responding vertical growth of *S. pungens* rhizomes up into these accreting sediments. This dense root mat was up to 30 cm thick and accounted for up to 30% of the soil volume; the remaining volume was sand tightly trapped among the rhizomes and roots. Such dense mats resist storm waves and reduce soil erosion during the late winter and spring months. In contrast, roots and rhizomes accounted for less than 5% of surface soil volume in the lower marsh, while the remaining 95 to 98% is loose organic-rich silt, which is much less resistant to erosion.

Difference in erosion resistance between upper and lower marsh sediments was demonstrated during sample processing. Two hours or more were needed to separate upper marsh roots and soil with a high-pressure water hose, while a similar block of lower-marsh sediment and vegetation took only five to ten minutes (lead author's personal observations).

In contrast to Tillamook, Cecil Bay's upper marsh receives most of its sediment from storm waves, and that sediment has been in short supply at upper elevations in recent low-water years. There was no evidence of wind-driven sediments in recent low-water years. Accretion of Cecil Bay sediments is cyclic, dependant on high-water conditions to renew sediment availability.

Intense feeding by migratory waterfowl, especially snow geese (*Chen caerulescens* Linnaeus), is an important factor that accounts for reduced *S. pungens* rhizome biomass in estuaries of the Canadian PNW (Karagatzides and Hutchinson 1991), the Gulf of Mexico (Miller et al. 2005), and eastern Canada (Giroux and Bédard 1987, 1988). In Canada, grubbing by snow geese resulted in up to 60 percent loss of net below-ground productivity along the St. Lawrence River. However, only low levels of waterfowl feeding on bulrush rhizomes has been observed by the authors within the Tillamook estuary during November of 2011 and 2012 and waterfowl grubbing does not appear to be responsible for reduced rhizome density in the lower marsh zone. Snow geese are uncommon in the Tillamook estuary and the more common Canada geese (*Branta canadensis* Linnaeus) do not grub rhizomes (OR Department of Fish and Wildlife waterfowl biologist, Brandon Reishus). Waterfowl grazing on *S. pungens* rhizomes is likely of little consequence at Cecil Bay and other GL bays because of the protective gravel lag that covers much of the wetland surfaces.

Above-ground biomass comparisons between marsh zones

Above-ground biomass was consistently less than 20% of the below-ground biomass at both sites, except in Cecil Bay's permanently flooded lower marsh (Table 1). At Tillamook, the only statistically significant difference in above-ground biomass was between the mid and lower zones, with less biomass in the mid marsh (Table 2). While there is little above-ground biomass difference between the zones, the actual density of stems in the upper marsh is much greater. The ecological significance of this difference will be discussed under the stem density section. In contrast, Cecil Bay's lower marsh had significantly greater amounts of above-ground biomass than either the upper marsh or mid marsh (Tables 1 and 2). No statistically significant difference was found between above-ground biomass of the mid and lower marsh zones.

The above-ground biomass of Tillamook's upper marsh was three times greater than that of Cecil Bay's (Table 1), a statistically significant difference (Table 2). The biomass difference was largely due to the much greater stem density at Tillamook (Table 3), as both sites had similarly short stem heights (Table 3). Intermediate amounts of stem biomass characterized the mid marsh of both sites, and large amounts of biomass grew in both lower marsh zones (Table 1).

The ratio of above-ground to below-ground biomass

A low ratio of above- to below-ground biomass characterizes most emergent species able to survive in high wave-energy environments. While wave energy is absorbed by thin, flexible stems, the extensive root system protects from sediment erosion. As a perennial, below-ground biomass accumulates each year for *S. pungens*, while above-ground biomass decomposes or is partially reabsorbed into the rhizomes (Cronk and Fennessey 2001). Cecil Bay's high above-ground biomass in the lower marsh appears to be a response to permanent flooding during the growing season, which caused increased vertical growth and diameter growth in the form of aerenchyma production, both recognized responses in plants flooded during the growing season (Cronk and Fennessey 2001).

Above-ground stem density comparisons between marsh zones

Stem densities were statistically greater (1174 stems/m^2) in Tillamook's upper marsh, with three times the number of stems as in the mid or lower marsh (Tables 2 and 3). Stem densities were similar for mid and lower marshes. Greater stem density in the upper marsh was consistent with Karagatzides and Hutchinson's (1991) results in the Fraser River estuary. Stem densities were less in Tillamook's lower marsh than in the Fraser River. Giroux and Bédard (1988) linked low stem density in the lower marsh to a combination of greater stem mortality due to wave damage, reduced oxygen availability, and more severe herbivory by waterfowl. Even though Tillamook's

stem density was high in the upper marsh (Table 3), the above-ground biomass (Table 1) was similar to that of the mid and lower marsh because of the short, thin stems (Table 3) growing in the upper marsh.

In contrast to Tillamook's upper marsh, Cecil Bay's upper marsh had the lowest density of stems observed, 69 stems/m^2, significantly less than the 130 stem/m^2 in the lower marsh (Tables 2 and 3). High stem density characterized all of Cecil Bay's lower marsh except the extreme outer margin, where storm waves resulted in increased stem breakage. Stem densities were neither statistically different between Cecil Bay's upper and mid marsh nor its mid and lower marsh (Tables 2 and 3).

Low stem densities in Cecil Bay's upper marsh may have reflected strong competition for nutrients and moisture from other plants growing in this relatively dry zone. In 2012, nineteen other herbs and two shrubs grew in the upper marsh, forming a several-centimeter thick mat of dense, fine roots above the roots of *S. pungens* (lead author personal observations). Giroux and Bédard (1988) hypothesized that low *S. pungens* stem numbers and heights in the St. Lawrence River's upper marsh resulted from competition with other emergent and meadow plants. High stem densities in Cecil Bay's lower marsh probably resulted in part from reduced competition.

Stem densities of the equivalent marsh zones of Tillamook and Cecil Bay were statistically different in all zones (Table 2), with Tillamook consistently having greater density of stems (Tables 3). The cause of higher stem densities in the estuary was unclear but may have resulted from a daily addition of sediment and nutrients with each tide.

The *S. pungens* planters grown for wave-energy experiments had mean stem densities of 1219, 1000, and 635 stems/m^2 , most similar to the stem density of the upper Tillamook zone (1174 stems/m^2), from where they had been harvested a year earlier. Their stem height and

diameter were also similar to *S. pungens* from the upper marsh zone, resulting in accurate portrayal of Tillamook's upper marsh wave-energy reduction by *S. pungens* in our subsequent experiments. The high stem densities within the planters likely means that *S. pungens* influence on wave-energy reduction might be overestimated for Cecil Bay's less dense marsh zones.

Stem height comparisons between marsh zones

Average stem heights were greatest in the lower Tillamook and Cecil Bay marsh zones (Table 3). At Tillamook, stems were nearly twice as tall in both the mid and lower marsh as the stems in the upper marsh, and there was little stem height difference between these two more regularly flooded zones (Tables 2 and 3). The contrast between zones was even greater at Cecil Bay where all zones differed statistically from each other, and the lower marsh stems were nearly three times taller than those of the upper marsh (Tables 2 and 3). Statistical comparisons between equivalent zones of the two sites found all three zones statistically different, with taller plants in the upper and mid zones at Tillamook, and taller plants in the lower zone at Cecil Bay. Competition from other herbs and shrubs likely reduced plant height in Cecil Bay's upper and mid zones, while continual inundation increased *S. pungens* height and reduced competition in Cecil Bay's lower zone.

Tall stem heights in the lower marsh zone were in contrast to earlier estuary studies in the PNW (Karagatzides and Hutchinson 1991) or northeast Atlantic (Giroux and Bédard 1988), where stems were shorter in the lower, more regularly flooded zone. Karagatzides and Hutchinson hypothesized that reduced growth resulted from estuarine water turbidity, thermal shock, inhibited oxygen availability due to anoxic substrate, and the typical patina of fine sediment on emergent vegetation as factors that reduce growth in the lower estuary. Tillamook's

waters were not turbid, but the other growth-limiting factors identified by Karagatzides and Hutchinson also characterize the estuary water and substrate.

A contrasting view is that tall stem height is consistent with a plant's physiological needs in flooded environments, where increasing above-water height results in both increased photosynthetic potential and potential for oxygen transfer to the roots, critical for maintaining plant metabolism (Cronk and Fennessey 2001). This is especially important in GL coastal wetlands, where entire marshes may be continually flooded for several years during high-water periods. GL plant-height data collected in 1997, a high-water year in lakes Huron and Michigan, demonstrated a pattern of plant height increasing proportionally to water depth, with plants averaging 1.81 m tall in meter deep lower marsh, while plants growing in shallower 0.66 m deep upper marsh averaged only 1.35 m (D. Albert, unpublished data). The 1.18 m tall plants at depths of 0.50 m at Cecil Bay in 2009 were consistent with these 1997 findings.

The short stem height in the drier upper marsh at both Tillamook and Cecil Bay appeared consistent with results seen on the Nooksack River delta in northern Washington (Disraeli and Fonda 1979) and on the St. Lawrence estuary (Giroux and Bédard 1988) where competition was strong from other plant species for water, nutrients, and root space. Strong competition from other emergent and meadow plants characterized the upper marsh at Cecil Bay, but at Tillamook, there was little competition from other vascular plants, *S. pungens* clones appeared to compete with each other for nutrients, moisture, and root space in the dense turf.

Stem diameter comparisons between marsh zones

Stem diameter increased from upper to mid and lower marsh for both sites (Table 3). At Tillamook, stem diameters in the lower marsh were statistically different from those of the mid and upper, but the stem diameters of the upper and mid zones were not statistically different

(Table 2). Stem diameters were statistically different from each other in all Cecil Bay zones, with stems increasing in diameter from upper to mid and lower marsh (Tables 2 and 3). Stem diameters differed between Tillamook and Cecil Bay by marsh zone as well, with the diameters of Tillamook stems consistently and statistically larger than from those from Cecil Bay (Tables 2 and 3). Our study also found stem flexibility greater for smaller diameter stems than for the larger diameter stems of the lower marsh, which may make narrow upper marsh stems less vulnerable to storm-wave breakage.

Another PNW study found that increased stem diameter in the lower marsh was correlated with anoxic conditions and increased amount of aerenchyma (Ewing 1986**)**, which is consistent with our results at both sites. Discussions of aerenchyma tissue follow.

Below-ground plant structure provides insights into environmental differences within marsh zones

Traditionally, below-ground biomass researchers have collected circular plugs ten centimeters (0.008 m^2) or smaller in diameter (Disraeli and Fonda 1979; Giroux and Bédard 1988; Karagatzides and Hutchinson 1991), limiting the observation of below-ground plant structure. In this study, roots and rhizomes were collected in relatively large blocks ranging from 0.04 m^2 (20 cm x 20 cm) to 0.25 m^2 (50 cm x 50 cm), which allowed for evaluation of the structure of *S. pungens* relevant for plant survival and habitat modification in each marsh zone.

Measurement of rhizome segments demonstrated that annual growth differs with water depth and sediment characteristics. Rhizomes growing in deep water (lower marsh) were typically large in diameter, widely spaced, and had long internodes (Fig. 4). In contrast, shorter, smaller diameter, vertically oriented rhizomes were predominant in the upper marsh zone (Fig. 5). Stark structural differences were observed in rhizome internode lengths between the upper

and lower marshes, both at Tillamook and Cecil Bay (Fig. 6). In permanently flooded lower marshes, widely spaced rhizomes had internodes as long as 22 cm, averaging greater than 5.9 cm. In contrast, rhizome segments in the upper marsh zone averaged 3.7 cm or less, with a prevalence of rhizome segments less than 2 cm long (Fig. 6). At both Cecil Bay and Tillamook, there were four to five times as many rhizome segments in the dry upper marsh as in the wetter lower marsh, and most of these segments were short. Similar structural changes have been observed in seagrass (*Posidonia oceanic* (L.) Delile) beds in the Mediterranean Sea (Molenaar et al. 2000), where long horizontal internodes were associated with early colonization of habitat and short vertical rhizome internodes were associated with denser, older beds.

Another factor contributing to shorter *S. pungens* rhizomes in Cecil Bay's upper marsh was establishment and growth of competing plant species tolerant of the dry conditions between 1999 and present, as noted in recent wetland studies along Lake Huron (Gathman et al. 2006; Wilcox and Nichols 2008). Of the numerous plant species growing in Cecil Bay's upper marsh in low-water years, most produced shallow, dense roots that grew above the earlier established *S. pungens* roots and rhizomes, resulting in competition for light, nutrients, and moisture.

The short and long rhizomes allowed *S. pungens* to provide different functions in ecologically distinct portions of the marsh. In the lower marsh, low density rhizomes and roots began stabilization of marsh sediments and wave energy reduction. In the upper marsh, high density of rhizomes and roots strongly held sediment in a highly erosive environment, while the dense beds of flexible stems reduced wave energy and erosion, and accumulated additional sediment. The plasticity of *S. pungens*' structure accounts for its importance in the heterogeneous nearshore and deltaic environment of both the GL and PNW coastal wetlands.

Stem flexibility – importance for withstanding wave and current energy

The modulus of elasticity, *E*, was estimated and plotted as a function of stem diameter for four groups of specimens at Tillamook and Cecil Bay. For the population of stems with D < 8.0 mm, the average stem diameter was D = 5.7 mm, with a standard deviation of 1.3 mm, and the corresponding average modulus of elasticity was E = 73 MPa (±27 MPa) (Fig. 7). For stems D > 8.0 mm, the average stem diameter was D = 12.1 mm (±2.1mm), and the average modulus of elasticity was *E* = 27 MPa (±7 MPa). The scatter in modulus of elasticity values, particularly for smaller stems, could be attributed to several factors, including plant health, consistency of the cross section, and measurement error. We suspected that the major source of error, especially for smaller stems, was in measuring the stem diameter, which was raised to the fourth power in Eq 1. Careful selection of healthy plants, immediate testing after harvest, and consistently similar stem cross sections ruled out these factors as major sources of data scatter.

The data (Fig. 7) clearly show a trend toward decreasing *E* with increasing stem diameter, an unexpected result since for a homogenous material such as metal or plastic, *E* would be constant with respect to *D*. Our observation that flexibility was lower (larger *E*) in the smaller diameter stems of the upper marsh than in the larger diameter stems of the lower marsh may be the result of greater amounts of aerenchyma tissue (Fig. 8) in the lower, wetter portions of the marsh. Aerenchyma of *S. pungens* growing in the lower marsh is created by the breaking down of cell walls (Seliskar 1990), which could explain reduced mechanical strength of plants growing in deeper water, where there are more enlarged aerenchyma cells. It is important to note that the stems from Tillamook, Cecil Bay, and the plant beds all have similar E values for equivalent diameter stems, indicating that the stem response to wave energy is similar for both freshwater Great lakes and brackish PNW populations of *S. pungens*.

Aerenchyma- specialized cells for gas conductance in flooded environments

Cross sections of *S. pungens* stems were made to compare the relative amount of aerenchyma in upper marsh plants and more regularly flooded lower marsh plants (Fig. 8). Our results, although based on a small sample size, showed 50% aerenchyma in stems from the flooded lower marsh versus 30% aerenchyma in stems from the drier upper marsh. These findings were in agreement with tests conducted by Kawase and Whitmoyer (1980) and Seliskar (1988; 1990), who demonstrated that, while all *S. pungens* stems contained aerenchyma, there was a much higher percentage of aerenchyma tissue in stems that were either regularly flooded by tides or kept permanently flooded. Physiologically, more aerenchyma would be advantageous with greater flooding to allow greater air transport to the rhizomes. At Tillamook, where our plants were collected, upper marsh plants were completely exposed to air roughly one third more hours throughout the growing season than those in the lower marsh, which were flooded both more hours per day and to a greater depth.

Seliskar (1990) identified aerenchyma in *S. pungens* as lysigenous aerenchyma, created by break down of cell walls due to high levels of ethylene production by plants in flooded, anaerobic environments. However, our study found that stem cross-sections from a dry beach ridge at Cecil Bay, where plants were well above the water table, also had abundant aerenchyma cells. This may indicate that aerenchyma is part of the normal cell structure in *S. pungens*, and that flooding results in formation of additional lysigenous aerenchyma.

Summary

The ability of *S. pungens* to colonize and survive in high energy, flooded coastal environments in the GL and within brackish tidal estuaries of the PNW is the result of several plant characteristics. The concentration of biomass below ground allows *S. pungens* to stabilize sediments and withstand wave erosion. Dense rooting and vertical rhizome growth increase resistance to wave

erosion in the high-energy upper marsh, while long rhizome internodes in deeper water or in areas with less plant competition allow the plant to expand its habitat and facilitate additional sediment accumulation and wave attenuation.

Reproduction from seed accounted for less than one percent of *S. pungens* stems at both sites. The predominance of asexual reproduction by rhizomes allows for continual expansion of the plant even when conditions are not optimal for seed germination and juvenile plant survival.

Stem flexibility, combined with low stem biomass, allows *S. pungens* to withstand high wave energy without being physically damaged. In deep water, stem flexibility is reduced by increased aerenchyma formation. Increases of gas-conducting aerenchyma tissues and stem growth in flooded conditions allow *S. pungens* to thrive to greater depths in coastal waters, but at the expense of reduced mechanical strength during storms.

In open, high-energy coastal environments, *S. pungens* is able to thrive in either permanently flooded or saturated conditions, as seen in GL coastal wetlands, or in tidal ecosystems with daily cycles of inundation and drying. It also grows across a broad gradient of soils, from coarse rock, cobble, or sand to fine silt, clay, and organic soils.

The ability of *S. pungens* to survive across such a broad gradient of salinity, sediment, and wave- and current-derived energy conditions make it a strong candidate for use in restoration of high-energy coastal habitats. Low reproductive success from seed in natural environments indicates that restoration using *S. pungens* would require planting rhizomes or plants.

Acknowledgments

This research was supported by the National Science Foundation under Grant No. CMMI-0828549. The authors gratefully acknowledge the work of Lukas Bell-Dereske and Lindsey Croghan, both supported by NSF REU supplements, and David Tolle supported by an RET

supplement to conduct preliminary field work, Clair Thomas for assistance on Tillamook bathymetry, and Kathy Cook, who processed bulrush thin sections. Dan Cox gratefully acknowledges support by the Japan Society for the Promotion of Science and his hosts at the Disaster Prevention Research Institute of Kyoto University during manuscript preparation. Kerri Bridges, Munki Kim, Sean Kim, Hayden Ausland, Sean Laguna, and Heather Smith assisted in stem height and diameter measurements. Shane Lishawa, Doug Wilcox, and a anonymous reviewer provided insightful review. Students in the Great Lakes coastal wetland class at the University of Michigan Biological Station assisted with collection of biomass data at Cecil Bay.

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Figure captions

Fig. 1 *Schoenoplectus pungens*, a long-lived clone-forming plant with a triangular stem and poorly developed leaves, has a well-developed rhizome with large numbers of fine surface roots and many fewer large-diameter deep anchoring roots

Fig. 2 Study sites at (a) Cecil Bay, MI on northern Lake Michigan and (b) Tillamook Bay, OR

Fig. 3 (a) Bathymetric transect at Cecil Bay, northern Lake Michigan. The transect begins on a beach ridge formed during 1986 and 1997 high water levels and continues 180 m into the bay. Water levels have remained low since 1999. Marsh vegetation ends at 130 m. A thin veneer of

sand covers the entire transect and is relatively thick near the 2009 shoreline. Closed triangles represent points of vegetation and sediment sampling. Open triangles represent elevation sampling points. (b) Bathymetric transect from the protected inner estuary at Tillamook Bay, separated from the Pacific Ocean by the Bayocean Spit. The transect begins at the base of a wave-cut bluff and continues 40 m into the bay. Marsh vegetation ends at 32.5 m. Open triangles represent elevation and sediment sampling points, while closed triangles represent vegetation sampling points. Coarse sand over cobbles and gravel eroded from the nearby headlands are the characteristic soil of the upper marsh, while wave- and tide-deposited organic-rich fine sand over silt characterizes the mid marsh and organic-rich silt characterizes the lower marsh.

Fig. 4 *Schoenoplectus pungens* rhizomes growing in lower marsh on fine-textured till (30 cm x 30 cm area). Rhizome density is similar to the 130 m point along the transect shown in Fig. 3

Fig. 5 *Schoenoplectus pungens* rhizomes growth in upper marsh. Large diameter, horizontal rhizomes (bottom of photo) formed when plants expanded into open sediments. As sandy sediments accreted, rhizome growth becomes dense and vertical. Vertical extent of rhizomes in photo is 13 cm

Fig. 6 *Schoenoplectus pungens* average rhizome internode lengths from the upper and lower marsh zones of Cecil Bay and Tillamook. The number of internodes of each length is plotted for upper and lower marsh zones. Upper marshes are characterized by many very short internodes and few long internodes, while rhizome segments from the lower marsh zones are often as long as 20 cm

Fig. 7 Modulus of elasticity *E* as a function of stem diameter *D* observed for *Schoenoplectus pungens* from Tillamook estuary and Cecil Bay. Measured *in situ* in 2009 (solid circle), in 2010 (open circle), laboratory samples grown in fresh water (star), and Cecil Bay in 2010 (plus sign).

Fig. 8 Cross-section of *Schoenoplectus pungens* stems (scale = 1mm). Large, open aerenchyma cells, important for transportation of oxygen from the stem to roots and rhizomes, are present in all bulrush stems, even those in the relatively dry upper marsh (a). Stems in the deep lower marsh (b) contain higher amounts of aerenchyma tissue, formed as ethylene breaks down cell walls

Table captions

Table 1 Above- and below-ground biomass of *Schoenoplectus pungens* collected in sampling plots at Cecil Bay, MI and Tillamook, OR

Table 2 Statistical comparisons of biomass and stem parameters of *Schoenoplectus pungens* samples from Cecil Bay, MI and Tillamook, OR. Wilcoxon's Rank Sum analyses were utilized on total biomass, below-ground biomass, above-ground biomass, stem density, and stem diameter due to small sample sizes. Students' *t* tests were utilized on stem height data due to larger sample sizes. Within-site comparisons of variables at Tillamook and Cecil Bay were conducted between the upper, mid, and lower marsh zones. Across-site comparisons of Tillamook and Cecil Bay were between the same marsh zones at each site

Table 3 Stem density, height, and diameter of *Schoenoplectus pungens* collected in sampling plots at Cecil Bay, MI and Tillamook, OR

line figure

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Table 1

	Total Biomass (g/m^2)			Above-ground Biomass (g/m^2)			Below-ground Biomass (g/m^2)		
	N	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.
Tillamook									
Upper	6	4303.3	1591.5	6	410.5	263.7	6	3892.8	1389.2
Mid	3	1098.4	316.9	3	212.4	16.0	3	886.0	302.8
Lower	6	1056.1	344.6	6	433.7	140.3	6	622.4	269.1
Cecil Bay									
Upper	15	2088.9	1123.2	15	135.5	83.4	15	1953.4	1093.8
Mid	15	2182.8	1851.5	15	250.2	324.8	15	1932.6	1780.1
Lower	10	1496.6	767.4	10	490.5	266.3	10	1006.1	583.1

table
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Table 2

	Tillamook Bay			Cecil Bay			Tillamook-Cecil Comparisons			
Total biomass	χ^2	**d.f.**	***p***	χ^2	**d.f.**	***p***		χ^2	**d.f.**	***p***
Upper-Mid	5.40	1	**0.0201**	0.12	1	0.7244	Upper	7.01	1	**0.0081**
Upper-Lower	8.31	1	**0.0039**	1.11	1	0.2919	Mid	0.59	1	0.4413
Mid-Lower	0.07	1	0.7963	0.15	1	0.6978	Lower	1.99	1	0.1585
Below-ground biomass	χ^2	**d.f.**	***p***	χ^2	**d.f.**	***p***		χ^2	**d.f.**	***p***
Upper-Mid	5.40	1	**0.0201**	0.65	1	0.4186	Upper	7.01	1	**0.0081**
Upper-Lower	8.31	1	**0.0039**	5.69	1	**0.0171**	Mid	1.01	1	0.3139
Mid-Lower	2.40	1	0.1213	1.49	1	0.2223	Lower	1.69	1	0.1931
Above-ground biomass	χ^2	**d.f.**	***p***	χ^2	**d.f.**	***p***		χ^2	**d.f.**	***p***
Upper-Mid	0.60	1	0.4386	0.65	1	0.4186	Upper	8.30	1	**0.0040**
Upper-Lower	0.10	1	0.7488	10.71	1	**0.0011**	Mid	3.82	1	0.0506
Mid-Lower	5.40	1	**0.0201**	4.68	1	**0.0305**	Lower	0.58	1	0.4477
Stem density	χ^2	**d.f.**	***p***	χ^2	**d.f.**	***p***		χ^2	**d.f.**	***p***
Upper-Mid	6.82	1	**0.0090**	0.78	1	0.3768	Upper	7.50	1	**0.0062**
Upper-Lower	6.82	1	**0.0090**	3.69	1	0.0547	Mid	7.53	1	**0.0061**
Mid-Lower	0.27	1	0.6015	2.14	1	0.1432	Lower	6.82	1	**0.0090**
Stem diameter	χ^2	**d.f.**	***p***	χ^2	**d.f.**	***p***		χ^2	**d.f.**	***p***
Upper-Mid	3.49	1	0.0619	10.39	1	**0.0013**	Upper	16.36	1	**<0.0001**
Upper-Lower	14.17	1	**0.0002**	15.56	1	**<0.0001**	Mid	4.68	1	**0.0305**
Mid-Lower	3.86	1	**0.0494**	13.91	1	**0.0002**	Lower	8.28	1	**0.0040**
Stem height	***t***	**d.f.**	***p***	***t***	**d.f.**	***p***	***t***		**d.f.**	***p***
Upper-Mid	22.70	242	**<0.0001**	10.88	226	**<0.0001**	Upper	9.28	276	**<0.0001**
Upper-Lower	20.59	227	**<0.0001**	38.07	303	**<0.0001**	Mid	15.56	267	**<0.0001**
Mid-Lower	0.01	242	0.4971	22.55	294	**<0.0001**	Lower	8.39	275	**<0.0001**

table
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Table 3

	Stem density (#/m^2)			Stem height (cm)			Stem diameter (mm)		
	N	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.
Tillamook									
Upper	5	1173.6	289.4	125	54.4	13.7	10	5.4	0.97
Mid	5	348.0	84.8	125	97.2	15.9	10	7.0	2.83
Lower	5	333.6	52.4	125	97.2	18.7	10	9.1	1.45
Cecil Bay									
Upper	6	68.7	44.1	153	40.1	12.0	10	3.2	0.42
Mid	6	91.3	43.0	144	61.7	20.7	10	4.7	1.06
Lower	5	130.4	38.1	152	118.2	22.3	10	7.4	0.84

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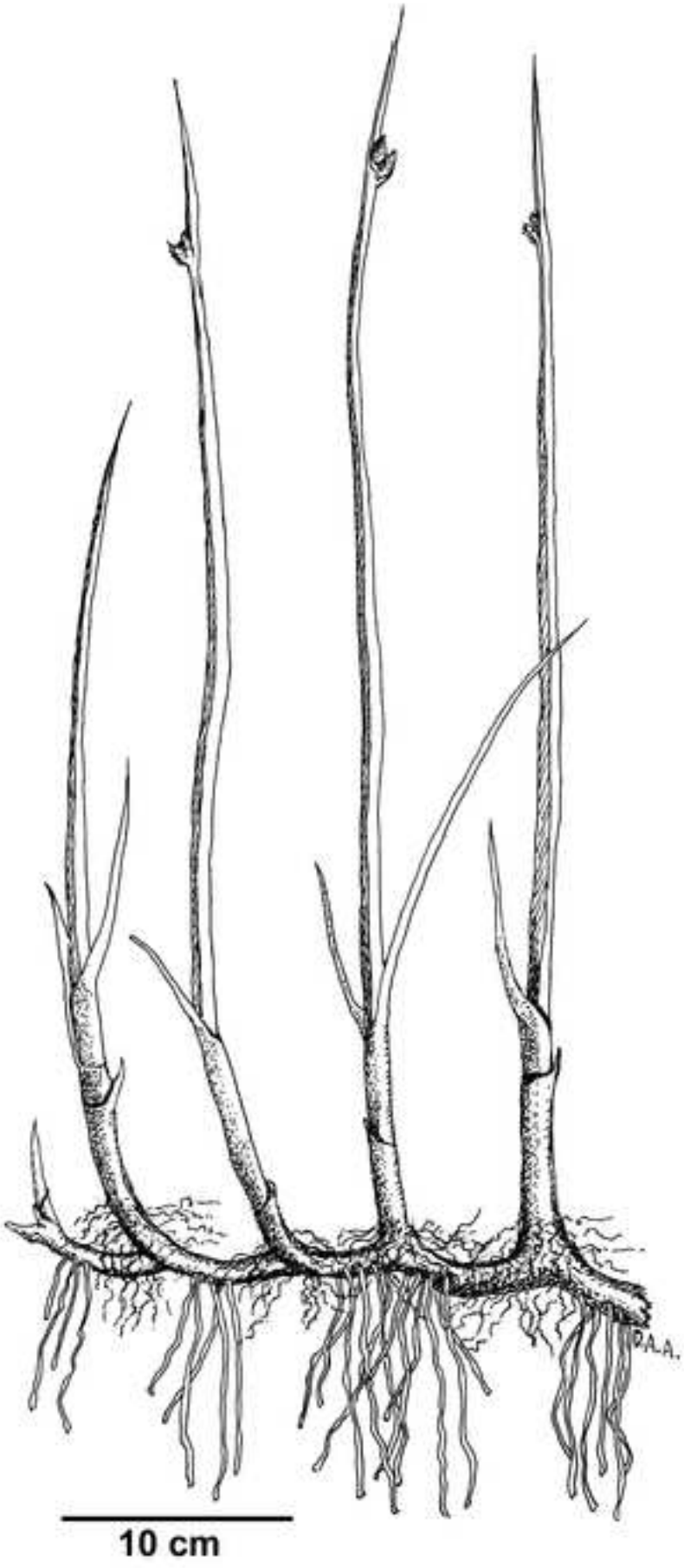

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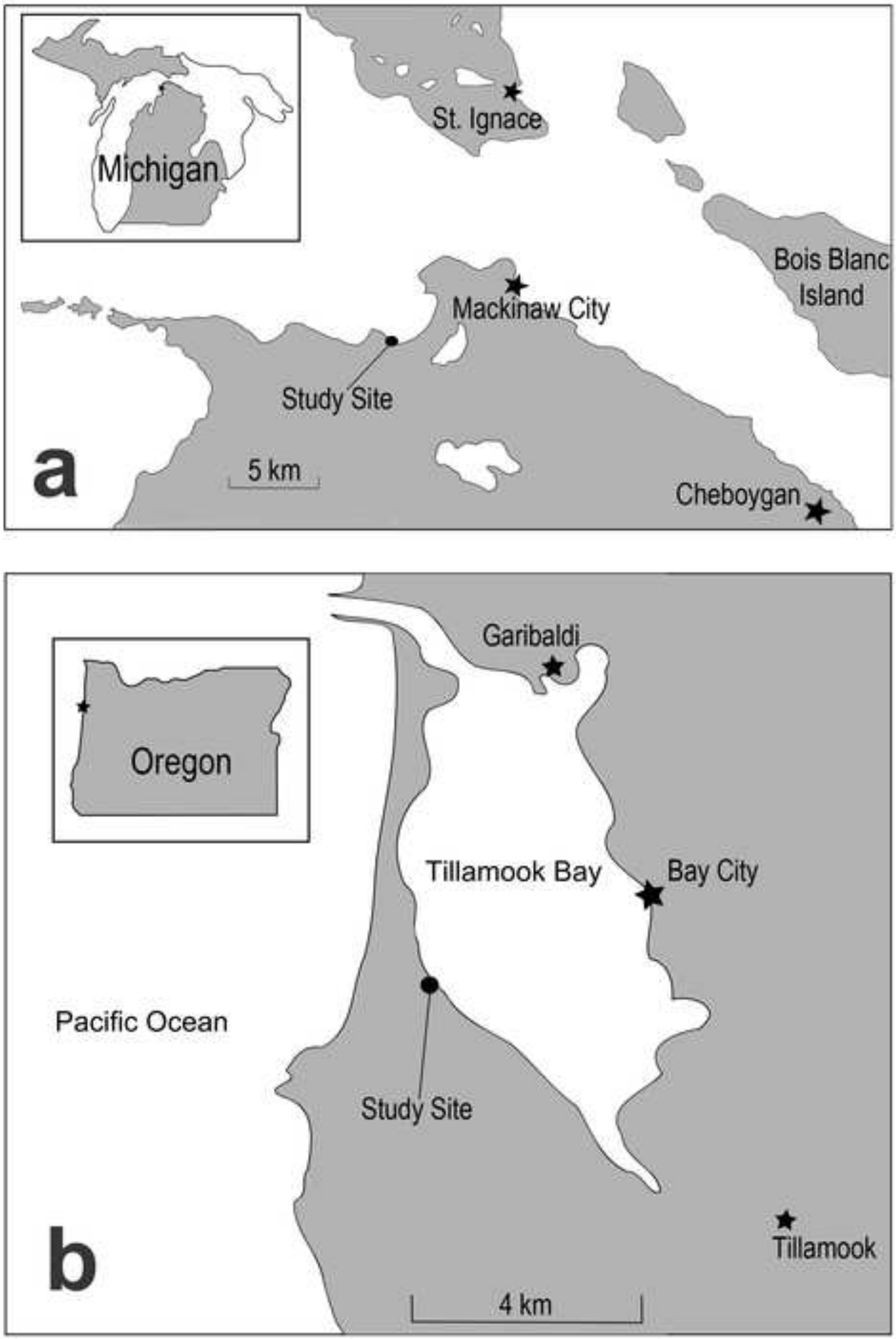

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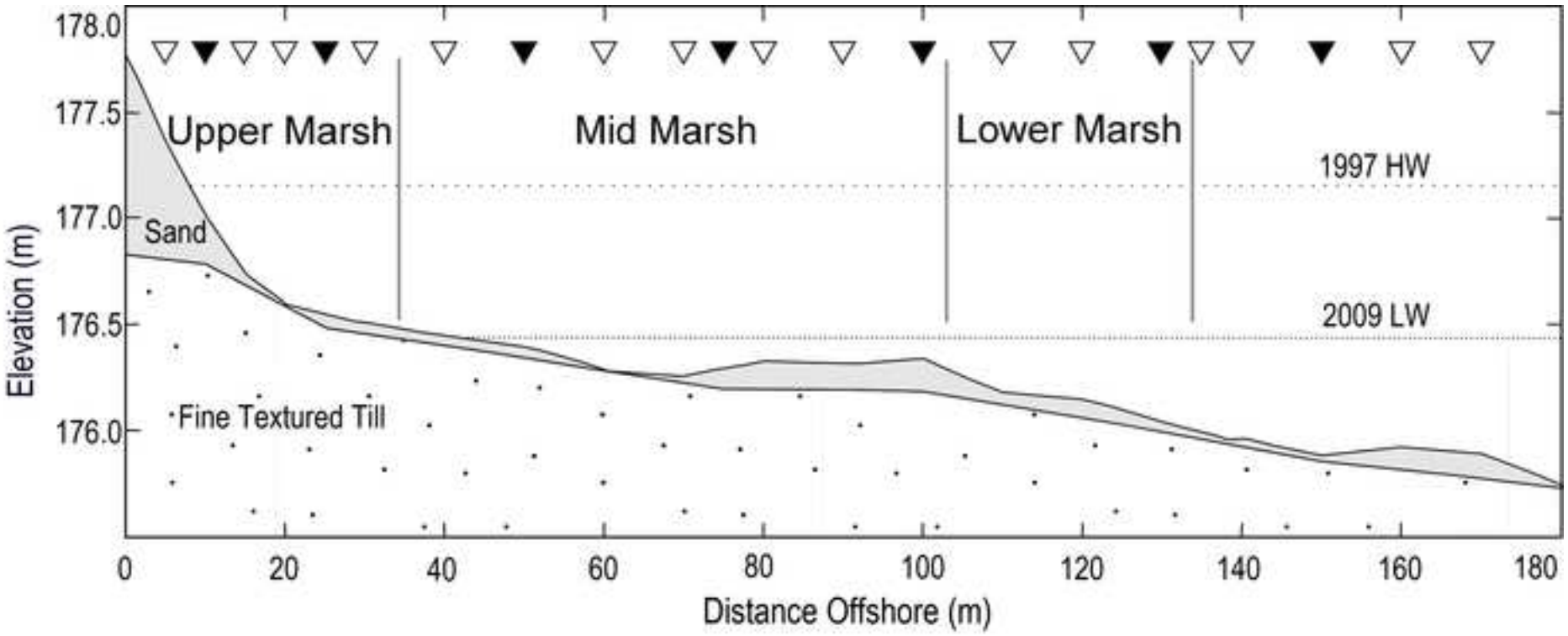

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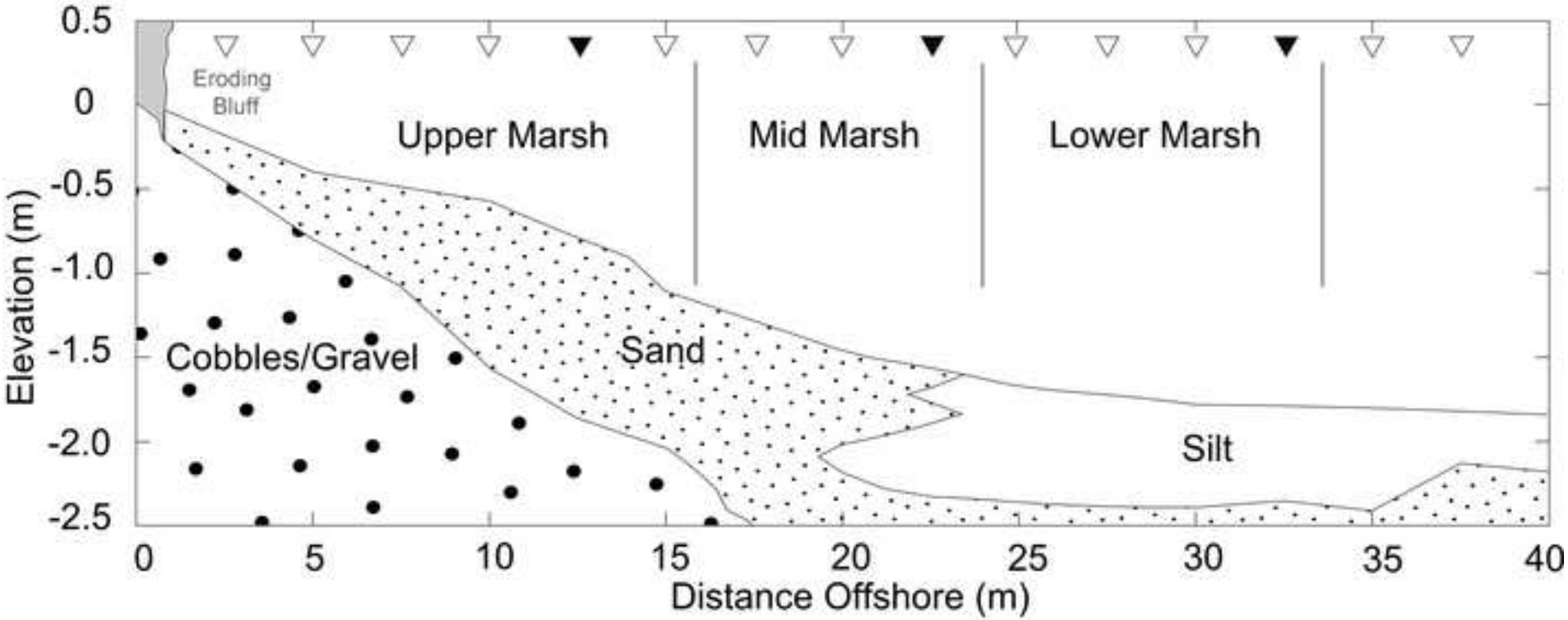

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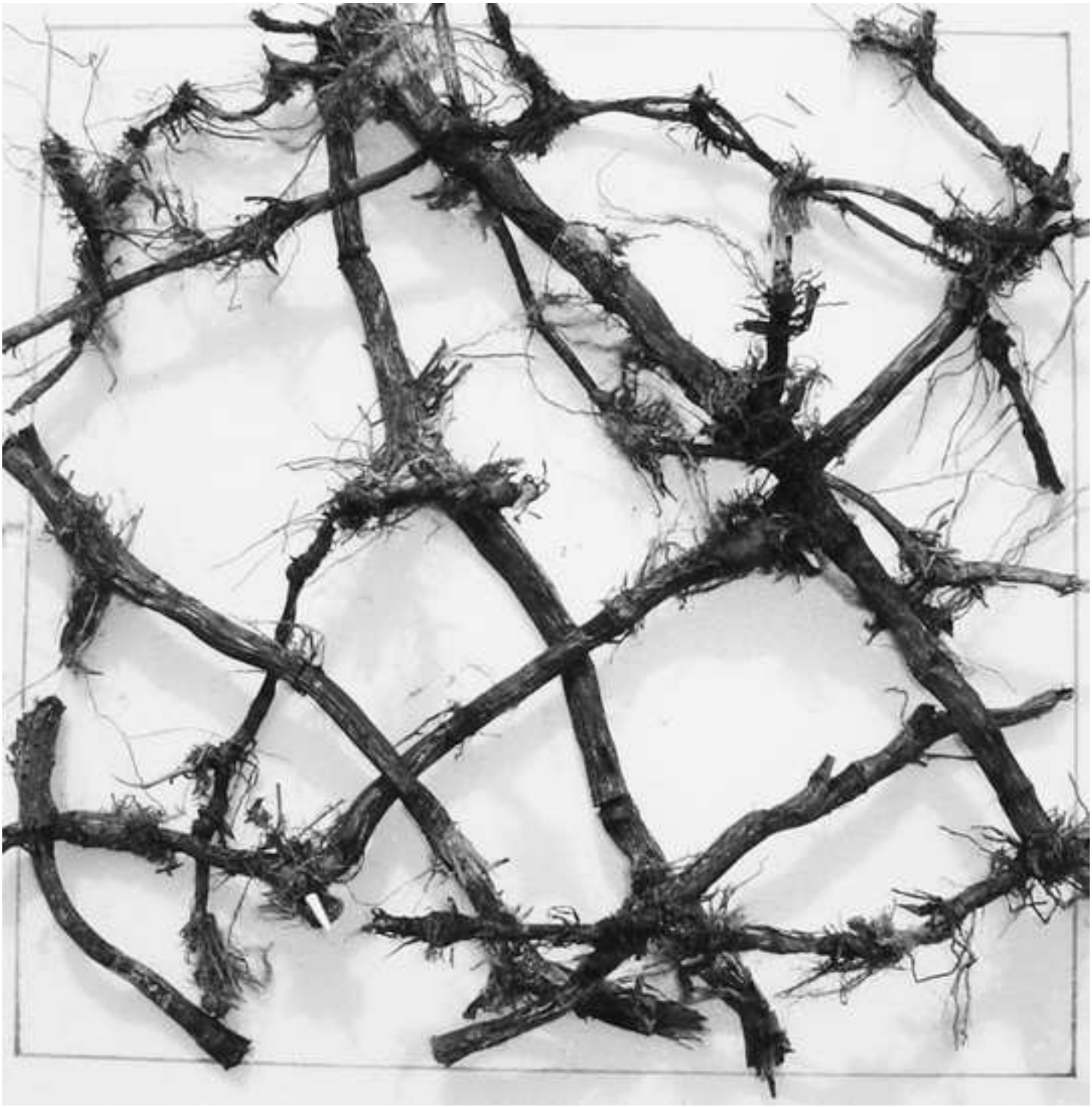

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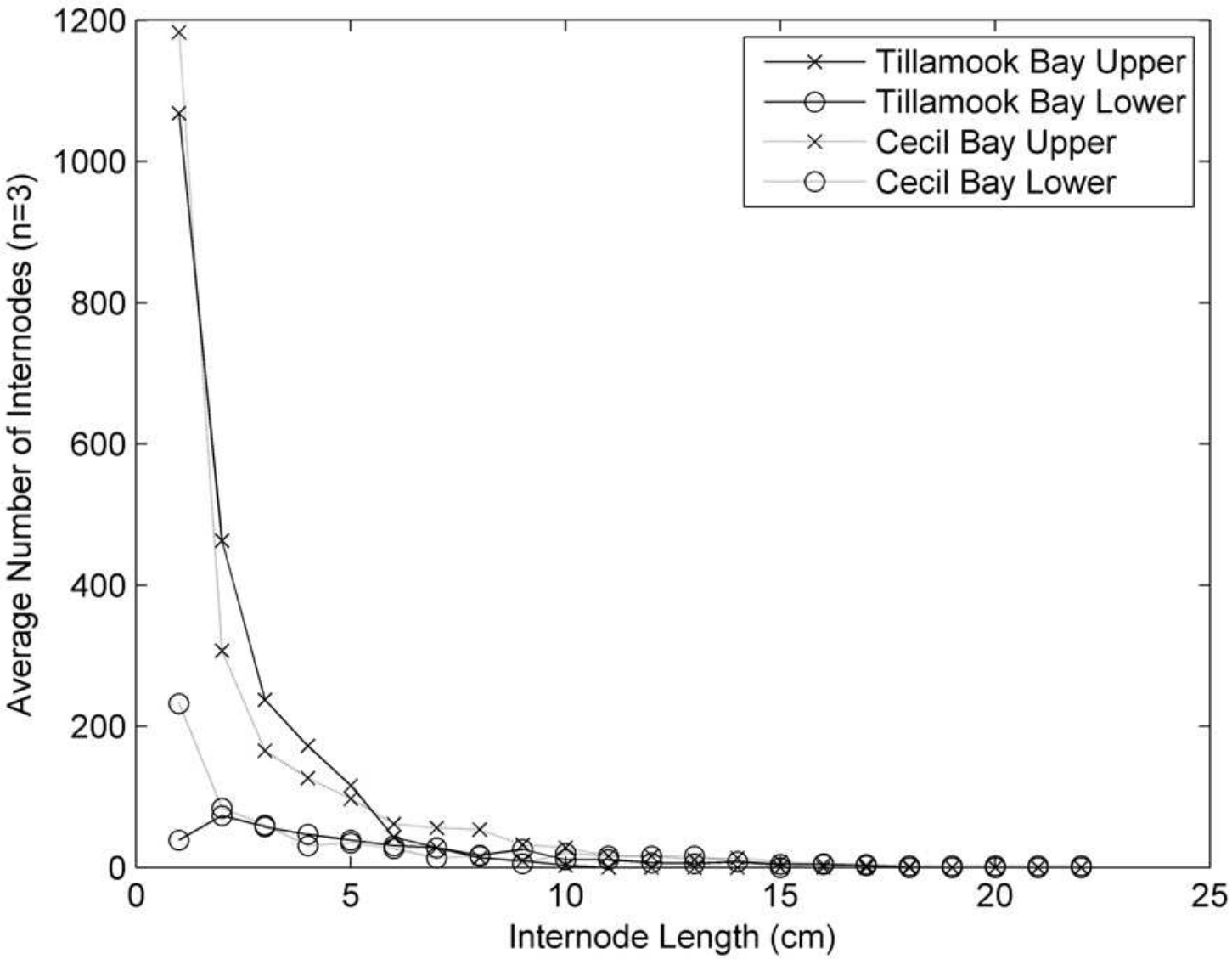

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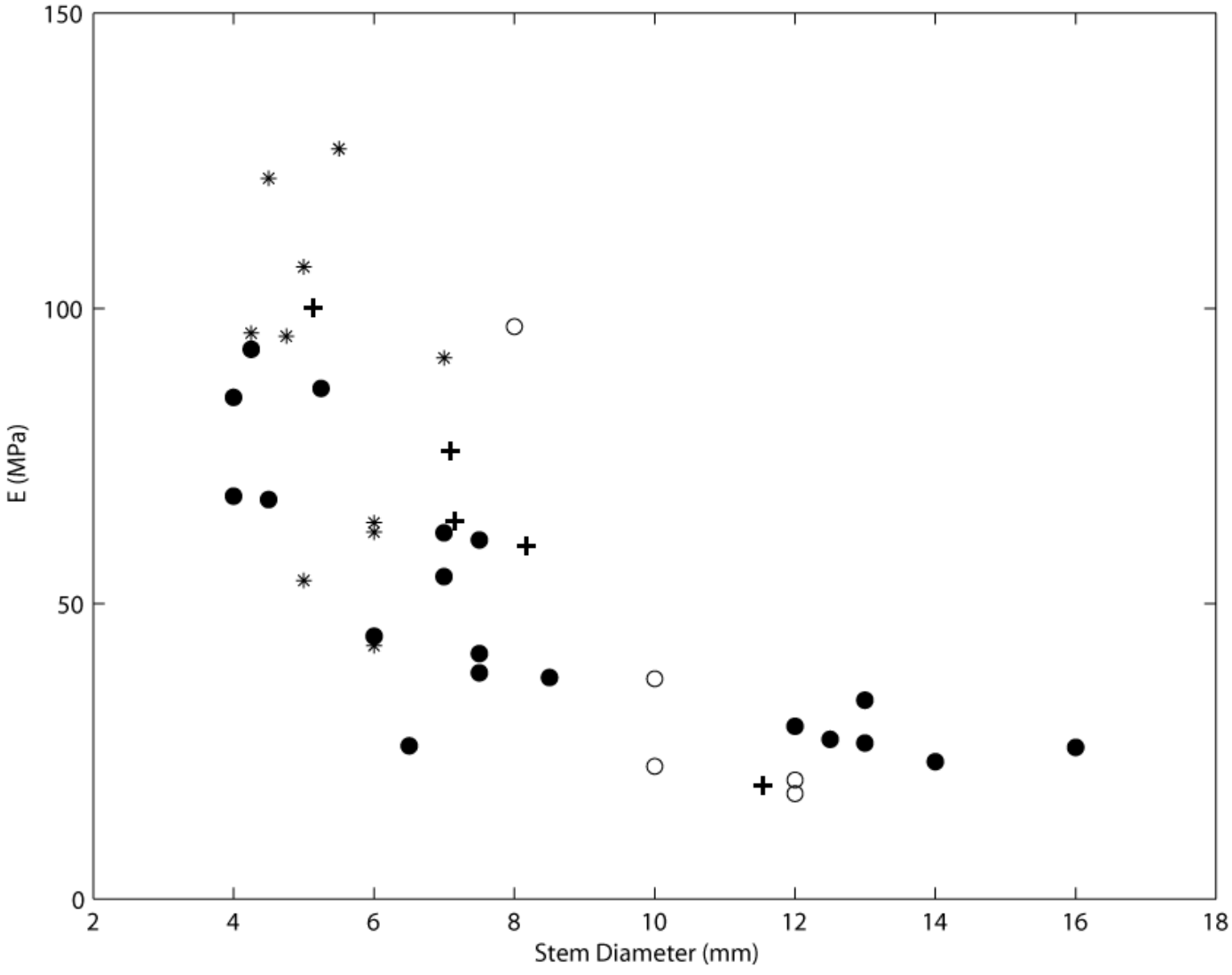

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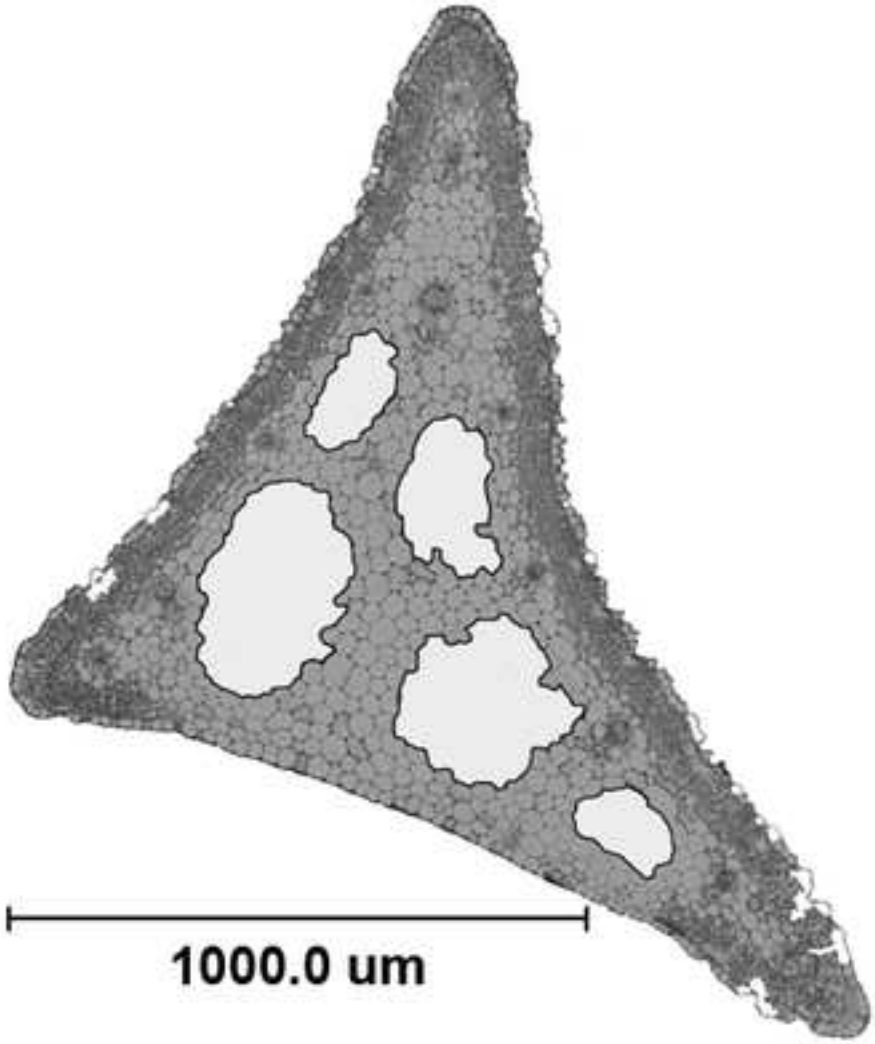

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