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Large Woody Debris Influences Vegetation Zonation in an Oligohaline Tidal Marsh

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ABSTRACT: The amount of large woody debris (LWD) in Pacific Northwest estuaries has declined dramatically since Euro-American settlement in the mid 19th century. Little is known about the ecological significance of estuarine LWD. This ignorance impairs protection and restoration of habitat critical to threatened Chinook salmon (*Oncorhynchus tshawytscha*), as well as other fish and wildlife. This study investigates whether LWD affects the distribution of estuarine shrubs, particularly nitrogen-fixing *Myrica gale* L. (sweetgale), which dominates the tidal shrub community of the Skagit River estuary, Washington, U.S.A. LWD, *M. gale*, and other shrubs were surveyed along line transects in an oligohaline tidal marsh and in abandoned agricultural land whose dikes failed more than 50 years ago and which has reverted to marsh. The results demonstrate a strong association between LWD and *M. gale*. *M. gale* was very rare on LWD < 30 cm in diameter, increasingly more common for LWD between 30 and 75 cm, and always present on LWD ≥ 75 cm. The marsh surface was generally 45 cm below mean higher high water (MHHW), suggesting LWD benefits *M. gale* by providing a growth platform at an elevation near MHHW and reducing flooding stress. The largest and most abundant tree in the marsh, *Picea sitchensis*, averaged only 35.8 cm in diameter, which suggests LWD recruitment from upstream sources is necessary to sustain *M. gale* populations in the geomorphologically dynamic Skagit marsh. By affecting the distribution and abundance of *M. gale* in the estuary, LWD may indirectly affect nitrogen dynamics in the marsh and secondary production of detritivores and herbivores.

Introduction

Large woody debris (LWD) likely plays a variety of ecological roles in Pacific Northwest estuaries, such as input to detrital food webs, shelter for fish from high current velocities and predators, egg attachment sites for some fish, e.g., *Clupea pallasi* (Pacific herring), perches for birds, and colonization sites for woody vegetation, e.g., *Picea sitchensis* (Bong.) Carr. (Sitka spruce; Maser and Sedell 1994). There have been few empirical studies to confirm or further characterize hypothesized ecological functions of estuarine LWD. This contrasts with the abundant literature on LWD in riverine (reviewed in Maser and Sedell 1994; Bilby and Bisson 1998) and terrestrial systems (e.g., Harmon et al. 1986).

Landscape management since the mid 1800s has dramatically reduced LWD volume and size in coastal systems of the Pacific Northwest and other regions (Maser and Sedell 1994; Collins et al. 2001; MacNally et al. 2002). LWD in the Nehalem estuary, Oregon, has declined in number by 50% and in volume by 60% since 1939 (Maser and Sedell 1994). The ecological function of estuarine LWD must be better understood to gage what function has been lost by estuarine LWD declines. Estuarine habitat restoration for threatened Chinook salmon (*Oncorhynchus tshawytscha*) and other fish and wildlife will be incomplete without a better understanding of the role of LWD. Management of riparian and coastal shorelines that are likely sources of estuarine LWD might be improved if there was evidence of the importance of LWD subsidies (e.g., Polis et al. 1997) to estuarine ecosystems.

This study aims to determine whether LWD plays a role in the establishment of shrubs, particularly *Myrica gale* L., in the Skagit Delta tidal marshes (Washington, U.S.A.). This study focused mostly on *M. gale*, because it was the most abundant shrub in the tidal marsh, often forming large, dense, nearly impassable, 2-m high, monospecific thickets. *M. gale* is a nitrogen-fixing plant (Schwintzer 1979), so strong dependence of *M. gale* on LWD would suggest indirect LWD effects on marsh nitrogen dynamics.

The hypothesis motivating this paper is that flooding stress limits the ability of *M. gale* and other shrubs to colonize the tidally flooded marsh surface (e.g., Bertness et al. 1992), but LWD provides elevated surfaces that allow *M. gale* and other shrubs to colonize lower marsh elevations than otherwise possible. LWD provides nurse logs (e.g., Duncan 1993; Santiago 2000) and a regeneration niche (Grubb 1977; Seabloom et al. 1998) for *M. gale* and other shrubs in the Skagit tidal marsh. Reduced flooding stress at higher marsh elevations should similarly reduce the association between shrubs and LWD. This paper characterizes this hypothesized spatial pattern of shrub dependence on estuarine LWD. It also characterizes the size of LWD colonized by estuarine shrubs on the presumption

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that some logs could be too small to elevate seedlings above a critical flooding threshold. This study contrasts shrub and LWD abundance between natural marsh and farmland abandoned 50 years ago, now reverted to marsh. The abandoned farmland is partially enclosed by dikes breached in past floods. The breached dikes allow tidal inundation and development of marsh vegetation within the dikes, but impair LWD recruitment. The contrast between diked and undiked marsh is considered a natural experiment in this study. Marsh within the abandoned dikes represented the experimental treatment (removal of LWD and marsh vegetation during historical conversion to agriculture), while adjacent natural marsh was considered the undisturbed control. The passage of more than 50 years since dike breaching was assumed sufficient time for reestablishment of *M. gale* and other shrubs in the experimental area; *M. gale* shoots reach adult size within five years (Schwintzer 1983).

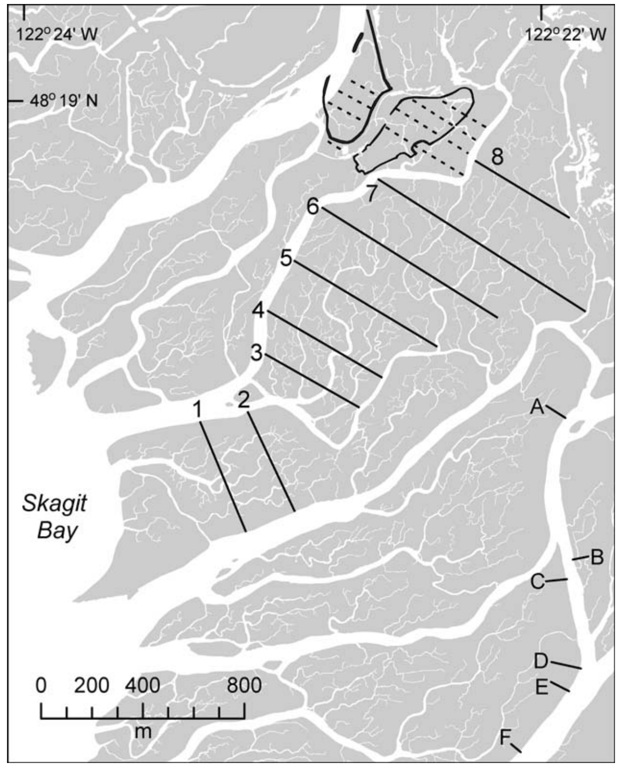

Fig. 1. The three study areas. Transects 1–8 are in the reference marsh of the South Fork Skagit Delta (straight solid lines). The natural experiment sites are shown relative to breached dikes (curved solid lines, digitized from 1956 photos and overlain on the 2,000 marsh to illustrate the degree of river erosion). Treatment and control transects (straight dashed lines) are within and outside the breached dikes, respectively. Marsh profiles A-F describe shrub distribution relative to natural distributary levees.

Methods

Site Description

The Skagit is the largest river draining into Puget Sound. With a watershed of about 8030 km^2, it drains the Cascade Mountains of northwestern Washington State and southern British Columbia. More than 90% of the 32,670-ha delta has been isolated from riverine and tidal influence by dikes and converted to agriculture and other uses (Collins and Montgomery 2001). Most of the remaining undiked wetlands are at the outlet of the South Fork Skagit River distributary. The South Fork marsh is oligohaline, even at its most bayward extent, with soil porewater salinity ranging from 0 to 7 psu.

The study took place in two distinct areas in the South Fork marsh. The first was tidal marsh extending from sandflats in Skagit Bay to diked agricultural lands about 2 km from the bay, hereafter called the reference marsh because it serves this role for several restoration projects. The second area was the natural experiment: tidal marsh nearly surrounded by abandoned dikes (Fig. 1). Aerial photos from 1956 show the dikes covered with vegetation, breached in several places, and enclosing marsh vegetation rather than pasture or row crops. Nearby dikes protecting active farmland were completely bare of vegetation, i.e., well maintained. Aerial photos of the same area from 1941 show bare, intact dikes and farmland. The dikes were likely breached during the 1951 flood, the third largest on record, and the property abandoned more than 50 years ago. This area was considered a natural experiment in comparison to adjacent undiked marsh, because LWD and marsh vegetation were removed when the site was converted to agricultural use. After abandonment, revegetation would have occurred in an area depauperate of LWD compared to adjacent natural marsh.

Vegetation Mapping

Tidal shrub vegetation patches (as small as 2.5 m diameter) were mapped by digitizing infrared orthophotos (15-cm pixel resolution) in a geographic information system (GIS, ArcView 3.2a). Photo interpretations were extensively groundtruthed. Two types of shrub vegetation were identifiable: monospecific patches of *M. gale* and mixed-species patches of shrubs with occasional trees. These were easily distinguished from emergent vegetation dominated by *Carex lyngbyei* Hornem. (sedge), *Typha angustifolia* L. (cattail), and *Schoenoplectus tabernaemontani* (K.C. Gmel.) Palla (softstem bulrush), each with a distinct photosignature.

Sampling Methodology

GIS was used to overlay eight reference marsh sampling transects (T_1-T_8) on the infrared orthophotos of the South Fork delta (Fig. 1). Transects were perpendicular to the delta elevation gradient, spaced at 215-m intervals, and ranged in length from 426 to 823 m, with a total length of 4423 m. T_8 was farthest from the bay. Similar transects were laid out in the natural experiment. There were two separate remnant-dike experimental areas. The first was adjacent (proximal) to Freshwater Slough, the principal distributary of the South Fork Skagit River. The second was distal to the distributary. The control marsh was outside of, and adjacent to, the remnant dikes. Total transect length was 500 and 732 m in the proximal and distal experimental marshes, respectively, and 674 m in the control marsh. Real-time kinetic global positioning surveying (RTK-GPS) measured elevation (NGVD29, 2 cm vertical and horizontal accuracy) at 10-m intervals along each reference, experimental, and control marsh transect.

Transects were located in the field using laminated 1:600-scale infrared orthophotos. They were traversed using a compass and landmarks visible in the photos, such as tidal channels, vegetation patches, and LWD. Total transect length was estimated using GIS. The length of transect intersecting shrub canopy and LWD was measured in the field using a stadia rod. Data consisted of the proportions of a transect intersecting the canopy of various shrub species growing on soil, the canopy of various shrub species growing on LWD, soil without shrub cover, and LWD without shrub cover. Some LWD was buried or highly decomposed, so shrubs were classified as growing on LWD only when LWD was clearly identifiable. The amount of shrub canopy associated with LWD was conservatively estimated, especially for the higher transects where small tidal channels often partially exposed shallowly buried LWD underlying dense thickets of *M. gale*. LWD diameter was measured at the midpoint of the logs.

Six short marsh profiles (A-F) were surveyed to characterize tidal shrub distribution relative to natural distributary levees formed by flood-deposited sediments (Fig. 1). Profiles were delineated with a tape measure oriented perpendicularly to a large distributary and ranged from 45 to 120 m in length. Transect elevations were surveyed with a laser level at 1-m intervals for the shorter profiles and 2-m intervals for the longer profiles. Elevations were measured relative to the NGVD29 datum, approximated from lidar data for the area (15 cm vertical and 3 m horizontal accuracy) and corrected for vegetation cover (Hood 2007). Vegetation patch boundaries were noted along the profile transects at a resolution of 1 m.

Statistical Analysis

Paired sample *t*-tests, linear regression, and one-way analysis of variance (ANOVA) were done with SYSTAT10 software (SPSS, Inc., Chicago, Illinois). ANOVA was followed by Tukey's HSD test for post hoc comparisons. Where appropriate, a nonparametric ANOVA (Kruskal-Wallis [K-W]) test was applied, followed by nonparametric comparison of a control to other groups (Zar 1999). A two-way unbalanced factorial ANOVA (assuming treatment interaction) was used to compare LWD diameter between *M. gale* colonized versus uncolonized logs, while also testing for possible transect effects. Only significant effects are reported. For all tests, the criterion for statistical significance was $p < 0.05$.

Results

Estuarine Shrubs in the Skagit Delta

Tidal shrub habitat is currently limited to 190 ha in the Skagit Delta, mostly in the South Fork area. This contrasts with a much wider distribution prior to Euro-American settlement when tidal shrub habitat likely amounted to 3780 ha (Collins 2000; Collins and Montgomery 2001; Fig. 2). Historical tidal shrub habitat was well landward of current dikes, so all losses were to agricultural development. Remnant tidal shrub habitat in the Skagit Delta amounts to only 5% of the historical estimate.

Two shrub-associated photo signatures were distinguished in the orthophotos. Ground-truthing associated one with monospecific thickets of *M. gale*, the other with mixed-species shrub vegetation, including *Salix* spp. (willows), *Lonicera involucrata* (Rich.) Banks (black twinberry), *Rosa nutkana* Presl. (Nootka rose), *Spiraea douglasii* Hook. (hardhack), *Rubus spectabilis* Pursh (salmonberry), *Gaultheria shallon* Pursh (salal), *Alnus rubra* Bong. (red alder), *Crataegus douglasii* Lindl. (hawthorn), *P. sitchensis* (Sitka spruce), and occasional *M. gale*. Mixed-species shrub vegetation was generally associated with natural levees of current or historical large river distributaries, while *M. gale* was more evenly dispersed through the marsh plain (Figs. 3 and 4; see Hood 2006 for distributary history). Mixed-species shrub vegetation amounted to 6.1% of the South Fork tidal marsh area, while monospecific *M. gale* thickets comprised 6.2% of the area.

Reference Marsh Transect Surveys

Mean transect elevation in the reference marsh increased from T_1 to T_3, plateaued from T_3 to T_7, and increased again from T_7 to T_8 (Fig. 5). *M. gale* was not present on T_1-T_2, but it steadily increased in

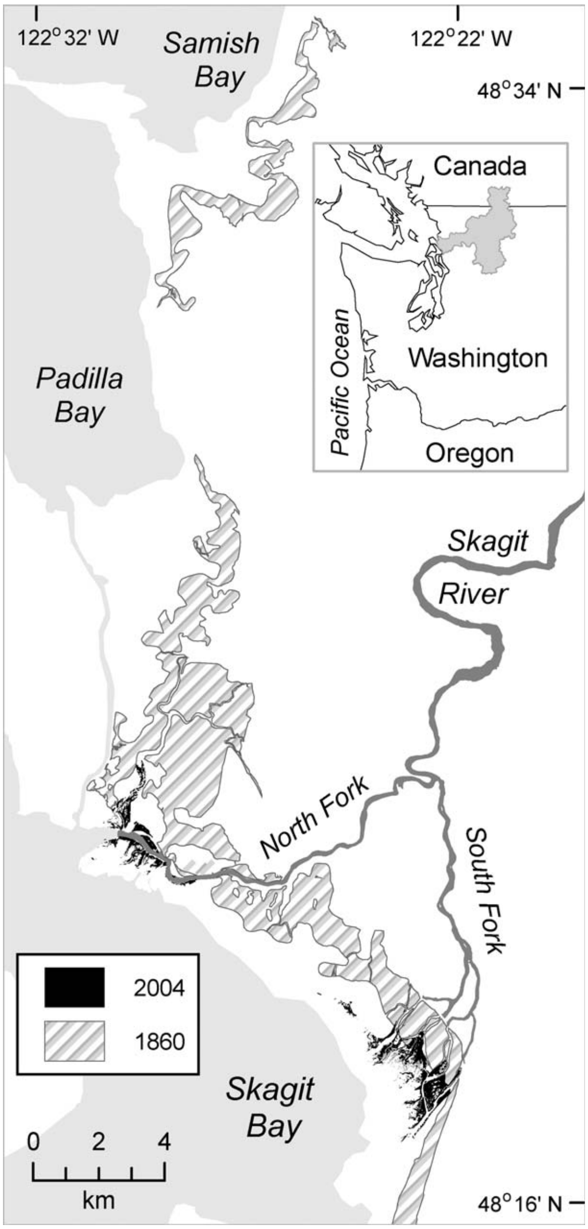

Fig. 2. Comparison of the extent of tidal shrub habitat between 1860 and 2004. The 1860 reconstruction is from archival survey notes and maps (Collins 2000; Collins and Montgomery 2001). Area seaward of the tidal shrub habitat was tidal emergent marsh in 1860; area landward consisted of a variety of floodplain wetland habitats. The 2004 data was digitized from high resolution (15-cm pixel) infrared orthophotos and ground-truthed. The insert shows the location of the Skagit watershed (gray).

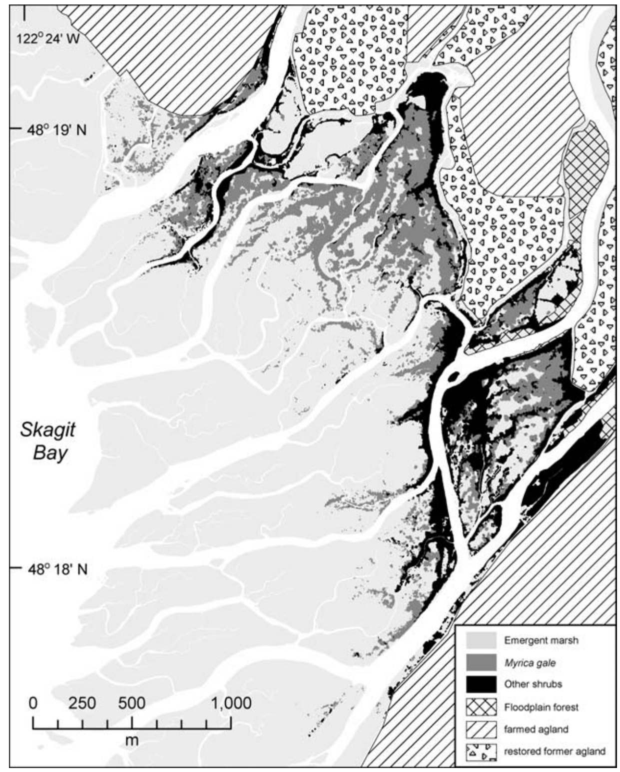

Fig. 3. Distribution of *Myrica gale* and mixed-species shrub vegetation in the South Fork tidal marsh. Mixed-species shrubs are associated with the natural levees of large river distributaries, while *M. gale* is more evenly distributed through the marsh interior.

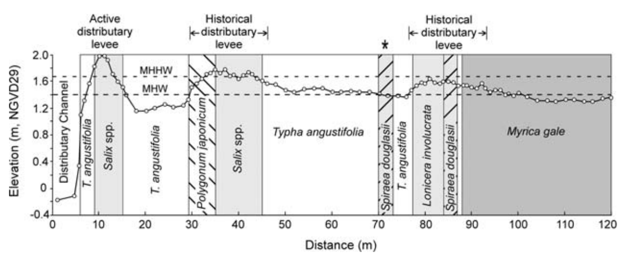

Fig. 4. A representative marsh profile (D in Fig. 1), oriented perpendicular to a large river distributary, illustrating the distribution of various shrub species relative to active and historical natural distributary levees (berms are formed by flood-deposited sediments). Shrub vegetation zones are shaded, emergent vegetation zones are unshaded. An asterisk denotes vegetation growing entirely on LWD. Note that *Myrica gale* is growing at a relatively low elevation, comparable to *Typha angustifolia*. The *M. gale* thicket continued unbroken for many more tens of meters into the marsh. The dashed horizontal lines are for visual reference; MHHW = mean higher high water, MHW = mean high water.

canopy cover from 0.3% of T_3 to more than 50% of T_7, before declining to about 40% of T_8. The remaining portions of the transects intersected primarily *T. angustifolia* and *C. lyngbyei*. Other shrub species were uncommon until T_8, when *L. involucrata* and *Salix* each began to amount to more than 5% of the transect cover. High proportions of LWD were colonized by *M. gale* from T_5 to T_8, while other shrubs and trees colonized significantly lesser proportions of available LWD in the estuarine marsh. Not until T_8 did any other shrub compare to *M. gale* in abundance on LWD.

The observed proportion of *M. gale* growing on LWD on each transect was compared to a null model of *M. gale* having no substrate preference for germination and growth. The expected distribution of *M. gale* on LWD and soil under the null model would be equal to the observed distribution of the two substrates on the transects. No LWD was found on T_1, only 0.5% of T_2 intercepted LWD, and from T_3 to T_6 LWD increased from 1.2% to more than 4% of the transects, before declining to 1.5% of T_8 (Fig. 5). No *M. gale* was found on the first two transects, but on T_3 and T_4 all *M. gale* was growing on LWD. For T_5-T_8, the observed proportion of *M. gale* growing on LWD steadily declined from more than 70% to less than 6% as transect distance from the bay increased. In every case, observed proportions of *M. gale* growing on LWD were much greater than the null expectations (paired $t = 3.184$, df = 5, $p < 0.05$). *M. gale* is clearly associated with LWD throughout the tidal marsh, but differences between observed and expected proportions of *M. gale* on LWD declined linearly as transect distance from the bay increased ($r^2 = -0.94$, $F_{1,4} = 74.84$, $p < 0.001$). The low abundance of LWD on T_7 and T_8 compared to T_4-T_6 may be due to LWD burial by accumulating sediments. Small tidal channels in this area frequently exposed LWD buried by only a thin layer of sediment. Little LWD accumulates in T_1-T_3, probably because at these low elevations it is easily mobilized by high tides and storms.

Mean LWD midpoint diameter generally increased moving landward from the bay ($r^2 = -0.62$, $F_{1,6} = 8.05$, $p < 0.05$), but LWD colonized by *M. gale* consistently averaged 50–60 cm midpoint diameter for T_3-T_8 and was twice the size of uncolonized LWD (Fig. 5; $F_{1,133} = 37.935$, $p < 0.001$). LWD of 55 cm midpoint diameter on a marsh surface of elevation 1.25 m NGVD29 provides growth substrate for *M. gale* at an elevation of 1.80 m NGVD29, about 12 cm above mean higher high water (MHHW). With the exception of *Salix* spp., *R. nutkana*, and *L. involucrata*, all other tidal shrubs and trees grew on LWD that was considerably larger than the LWD supporting *M. gale* ($F_{5,\ 116} = 7.034$, $p < 0.001$; Fig. 6). All woody species grew on LWD that averaged at least 50 cm midpoint diameter. Most grew on LWD of at least 80 cm midpoint diameter. A sample of 37 *P.*

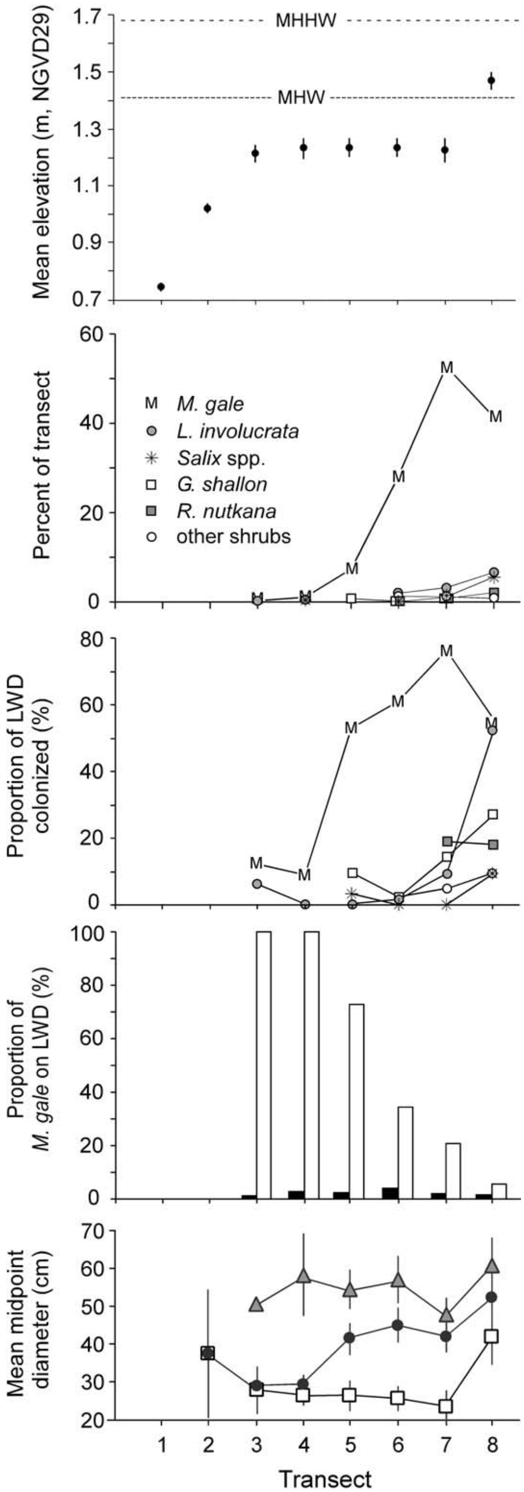

Fig. 5. First panel: Mean elevations of reference marsh transects. Error bars are 1 standard error. MHW = mean high water, MHHW = mean higher high water. Mean low water is −1.0 m. Second panel: Proportion of each transect intersecting various shrub species. Third panel: Proportion of large woody debris (LWD) colonized by various shrub species. The legend is the same as in the second panel. Fourth panel: Observed (gray ← bars) versus expected (black bars) proportion of *Myrica gale* on LWD. Expected values are the proportion of each transect intersecting LWD. Fifth panel: Mean midpoint diameter of bare LWD (open squares), *M. gale*-colonized LWD (gray triangles), and all LWD (solid circles). Error bars are 1 standard error.

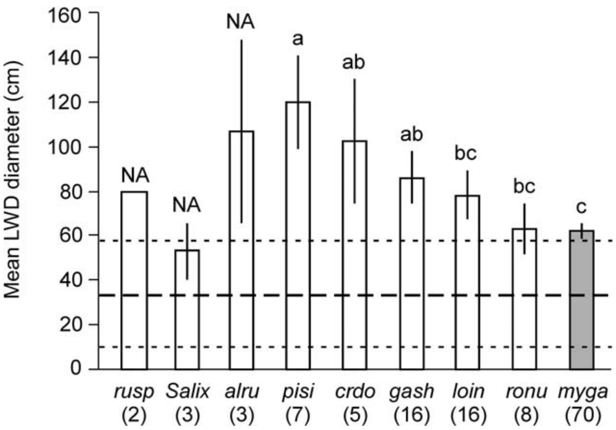

Fig. 6. Mean midpoint diameter of large woody debris (LWD) colonized by various shrubs and trees. Data represent T_3-T_8, collectively. Error bars are 1 standard error. Sample sizes, in parentheses, follow the species names. *rusp* = *Rubus spectabilis*, *Salix* = *Salix* spp., *alru* = *Alnus rubra*, *pisi* = *Picea sitchensis*, *crdo* = *Crataegus douglasii*, *gash* = *Gaultheria shallon*, *loin* = *Lonicera involucrata*, *ronu* = *Rosa nutkana*, *myga* = *Myrica gale*. Statistically indistinguishable means are labeled with the same lower case letter; NA = not analyzed, due to very small sample size. Mean diameter at breast height of *Picea sitchensis* growing in the tidal marshes (dashed horizontal line) ± 2 standard deviations (dotted horizontal lines) is shown for comparison. The small size of *Picea* suggests large LWD is allochthonous.

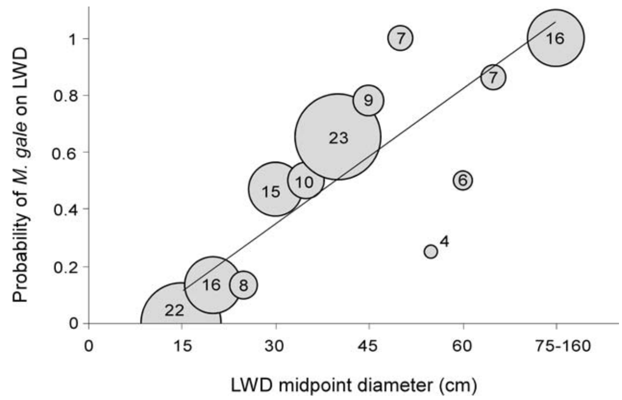

Fig. 7. Probability of encountering *Myrica gale* on large woody debris (LWD) of given size classes. Data represent T_3-T_8, collectively. Bubble label and diameter represent LWD sample size in a given size class. The regression line was fitted by weighting each data point by its sample size ($y = 0.016x - 0.123$, $r^2 = 0.76$, $p < 0.001$).

sitchensis, which is the largest and most abundant tree in the marsh, had a mean diameter at breast height (DBH) of only 35.8 cm and a maximum of 73 cm.

To examine the relationship between LWD size and probability of *M. gale* colonization, data were pooled across transects for sample sizes within LWD size classes to be sufficiently large. Five of the six transects containing *M. gale* were at similar elevations, so interaction between elevation and LWD size on *M. gale* colonization of LWD was unlikely. Every log 15 cm in diameter or smaller was bare, while every log 75 cm in diameter or greater was colonized by *M. gale*. In between, the likelihood of finding *M. gale* on a log increased steadily with log size (Fig. 7).

Natural Experiment

The mean elevation of the control marsh was 1.20 m NGVD29 ($n = 26$; SE = 0.05). The mean elevation of the distal experimental marsh was 1.23 m ($n = 34$; SE = 0.02) and the proximal experimental marsh (exclusive of the natural levee) was 1.28 m ($n = 23$; SE = 0.03). The natural levee adjacent to the river had a mean elevation of 1.62 m ($n = 11$; SE = 0.05). Except for the natural river levee, elevations of the experimental and control marshes were similar to those of reference marshes T_3-T_7.

Remnant dikes bordering the natural experiment were overgrown by shrubs and trees. Random 40-m line-intercept transects characterized dike-top vegetation, three on dikes 90–130 cm higher than the adjacent marsh and two on dikes 40–70 cm higher. The higher dikes were entirely covered by eight shrub and tree species, and *M. gale* was absent. The lower dikes were 60% covered by four shrub species, including *M. gale*. A 200-m transect along the 34-cm high natural levee separating the proximal experimental site from a major river distributary was 65% covered by five shrub species, including *M. gale*.

The experimental marshes, bounded by abandoned dikes and the natural river levee, were dominated by monospecific expanses of *C. lyngbyei* and *T. angustifolia*. *M. gale* intercepted only 0.4% of the transect lengths in the distal experimental marsh and 6.7% in the proximal marsh. *M. gale* intercepted 42.3% of the transect lengths in the control marsh (K-W test statistic = 9.87, $p < 0.01$; $Q' = 2.51$ for control versus proximal experimental marsh, $p < 0.05$; $Q' = 2.72$ for control versus distal experimental marsh, $p < 0.05$), which was comparable to the abundance of *M. gale* on T_7 and T_8 in the reference marsh.

LWD intersected 2.8% of the control marsh transect lengths, comparable to reference marsh transects T_3-T_8, which were at similar elevations and where LWD intersected 2.4% ± 0.5% of the transects. Only 0.1% of the transects intersected LWD in the proximal experimental marsh, while only 0.2% did so in the distal experimental marsh. LWD was 18 times more abundant in the control marsh than the experimental marshes (K-W test statistic = 7.94, $p < 0.05$; $Q' = 2.27$ for control versus proximal experimental marsh, $p < 0.05$; Q'

= 2.43 for control versus distal experimental marsh, $p < 0.05$). LWD averaged 75.9 cm midpoint diameter in the control marsh (n = 27), while in the distal experimental marsh LWD averaged 23.3 cm midpoint diameter (n = 3), and none were colonized by *M. gale*. In the proximal experimental marsh, the single piece of LWD encountered had a midpoint diameter of 60 cm and was colonized by *M. gale*.

Discussion

Lower limits of salt marsh vegetation zones are set primarily by tolerance to physical stress, while upper limits are set by competition (Snow and Vince 1984; Bertness 1991; Pennings and Callaway 1992; Pennings and Moore 2001). The lower limit of the shrub zone in tidal oligohaline marshes is usually near or above MHHW (Bertness et al. 1992; Thursby and Abdelrhman 2004). *M. gale* distribution in the Skagit Delta is consistent with this theory of intertidal zonation, particularly if one accounts for the role of LWD in modifying physical constraints on *M. gale* distribution. At low intertidal elevations (T_1 and T_2, more than 70 cm below MHHW), LWD is rare and unstable (easily moved by tides and storms), so *M. gale* is absent. At intermediate elevations (T_3-T_7, about 45 cm below MHHW), LWD is relatively common and of sufficient size to elevate colonizing *M. gale* near or above MHHW. At higher elevations (T_8, about 20 cm below MHHW), *M. gale* begins to become displaced by other shrub and tree species on LWD. *L. involucrata*, *Salix* spp., *A. rubra*, and other woody species are often taller than *M. gale* and shade it out at higher elevations (*M. gale* is shade-intolerant; Skene et al. 2000). Other shrubs and trees are apparently less tolerant to tidal inundation than *M. gale* and require larger LWD and higher marsh elevations to sustain themselves. Vegetation patterns on natural distributary levees and abandoned dikes support this interpretation, with the additional consideration that natural levees are generally composed of sandier soils and likely have better drainage. Elevation differences between the marsh plain and shrub-dominated dike and levee tops were comparable to the midpoint diameter of shrub-colonized LWD. Smaller LWD (mean = 55 cm midpoint diameter) and shorter dikes and levees (34–70 cm above the marsh plain) supported significant cover of *M. gale*, while larger LWD (80–120 cm midpoint diameter) and taller dikes (90–130 cm above the marsh plain) supported taller shrubs and trees.

Clear patterns of *M. gale* abundance (increasing from T_1 to T_8 in the reference marsh) and LWD abundance (increasing from T_1 to T_6), proportions of LWD colonized by *M. gale* (increasing from T_4 to T_7), proportions of *M. gale* colonizing LWD (decreasing from T_4 to T_8), and LWD size (increasing from T_3 to T_8) are not evident when these parameters are plotted against transect elevation, because T_3-T_7 have the same mean elevation. This suggests marsh surface elevation alone is not responsible for observed *M. gale* distribution patterns. Marsh age, reflected by transect distance from the bay, may play a role. This suggests *M. gale* distribution in tidal marshes is dependent on the rates of sediment accumulation to raise marsh elevations sufficiently to trap LWD, LWD recruitment to the marsh, *M. gale* germination and growth on LWD, and clonal expansion of *M. gale* (Skene et al. 2000) to adjacent marsh surfaces during sediment accumulation and burial of LWD. From the perspective of marsh community succession, LWD appears to function as a habitat island (regeneration niche) that can be colonized by pioneering individuals of *M. gale*. LWD islands elevate *M. gale* seedlings and reduce the frequency and extent of inundation. Once established on LWD, *M. gale* spreads by clonal growth from LWD platforms to the adjacent accreting marsh surface and forms dense thickets. With further increases in marsh elevation, other woody species are capable of colonizing and competing with *M. gale*.

Because LWD affects the distribution and abundance of *M. gale*, a nitrogen fixing plant, it may also indirectly affect nitrogen dynamics in the Skagit marshes. Herbivores and detritivores generally prefer high nitrogen content foods, so the high leaf and stem nitrogen content of *M. gale* (Schwintzer 1983) may contribute to increased secondary production in the marsh. Chironomid larvae were twice as abundant on decomposing *M. gale* leaves in a Michigan stream as on leaves of four other woody species (Maloney and Lamberti 1995). *M. gale* also affects *Castor canadensis* (beaver) distribution and activity in the tidal marsh. Beaver eat *M. gale* leaves and twigs, build lodges in *M. gale* thickets, and use *M. gale* stems to construct small dams in tidal channels (Hood personal observation). Beaver activity is not evident in the shrubless emergent vegetation zone. LWD indirectly affects several oligohaline marsh ecosystem processes through its effect on tidal shrub distribution.

LWD in Estuarine and Terrestrial Systems

In terrestrial systems LWD occupies 1.5% to 20.2% of the forest floor (mean = 8.0%, n = 32; Smith 1955; Thompson 1980; MacMillan 1981; Graham and Cromack 1982; Christy and Mack 1984; Harman et al. 1986; Spies et al. 1988; Hofgaard 1993; Lusk 1995; McGee and Birmingham 1997; Santiago 2000; Zielonka and Piatek 2001; Lusk and Kelly 2003). LWD in the Skagit marshes ranged from 1.5% to 4.2% of the higher elevation transects (mean = 2.6%, n = 5), comparable to the lower third of the terrestrial data set with a range of 1.5% to 4.5% (mean = 2.7%, n = 11). The small size and paucity of trees in the Skagit marshes relative to the larger size and abundance of LWD, suggest that LWD is delivered to the marshes primarily through riparian and coastal erosion mediated by floods, storms, and tides. The mobility of estuarine LWD likely affects its suitability as nurse logs. The larger the LWD, the less likely it is to be rolled by tides and waves and crush colonizing seedlings and shrubs. The size-dependent probability of LWD colonization by *M. gale* is likely due to greater elevation above MHHW and greater platform stability with increasing diameter.

While nurse logs clearly ameliorate flooding stress for colonizing shrubs and trees in tidal and freshwater wetlands (Duncan 1993; Santiago 2000), other nurse log benefits have been found in terrestrial systems, including reduced competition from other vegetation, reduced browsing, reduced moisture stress as a result of higher water-holding capacity, earlier snowmelt and longer growing season, reduced infection by pathogenic fungi, specific mycorrhizal communities, higher seed input by rodents, less seedling smothering by litter, greater nutrient availability, and warmer microhabitat (Harmon et al. 1986; Goodman and Lancaster 1990; Brang et al. 2003; Lusk and Kelly 2003; O'Hanlon-Manners and Kotaneu 2004). Many of these additional benefits may also be relevant to estuarine nurse logs. Nurse logs provide an important regeneration niche for many terrestrial trees and are critical to sustaining species diversity in many forests (Grubb 1977; Lusk 1995; McGee and Birmingham 1997; Santiago 2000). In the Skagit marshes, nurse logs likewise appear to increase estuarine species and habitat diversity by facilitating the germination and growth of *M. gale* and other tidal shrubs and trees (Fig. 8).

Fig. 8. A large woody debris (LWD) island supporting *Gaultheria shallon and some Lonicera involucrata, Alnus rubra, Crataegus douglasii*, and *Myrica gale*. The stadia rod is 1.7 m tall. Another large LWD island is in the right background. Emergent marsh vegetation in the foreground includes *Carex lyngbyei* (short, dark) and *Typha angustifolia* (tall, light, senescent stems).

Habitat Restoration and Management

Currently, *M. gale* and other shrubs are rarely found in estuaries in Oregon, Washington, and southern British Columbia (personal observation). Most estuaries in this area have been modified by urban and agricultural development since 1860, including dam, dike, and jetty construction; channel armoring, dredging, and snag removal; and clearing and draining (Bortleson et al. 1980). Historical (ca. 1860) Puget Sound data indicate tidal shrub habitat comprised 33% of the Skagit Delta estuarine wetlands, 35% in the Stillaguamish Delta, and 70% in the Snohomish Delta (Collins and Montgomery 2001). Today, tidal shrub habitat has almost completely disappeared in the Stillaguamish and Snohomish estuaries, while only 5% of the historical estimate remains in the Skagit. Other Pacific Northwest estuaries where *M. gale* has been documented and where similar zonation has been observed (*C. lyngbyei* in the lower intertidal zone, *M. gale* in the adjacent higher intertidal zone, other shrubs and *P. sitchensis* at the terrestrial border), include the Fraser Delta, British Columbia (North and Teversham 1984), Bella Coola Delta, British Columbia (McAvoy 1931), Campbell River Delta, British Columbia (Bell and Thompson 1977), Somass Delta, British Columbia (Morris and Leaney 1980), and Copper River Delta, Alaska (Thilenius 1990).

Estuarine habitat restoration in the Pacific Northwest is gaining momentum due to the listing of estuary-dependent Puget Sound Chinook salmon as a threatened species (U.S. Federal Register 1999). Diked farmlands in several Puget Sound deltas have recently been returned to tidal and riverine influence by breaching or removing dikes. While reestablishing native estuarine emergent vegetation is a typical restoration goal, little thought is given to restoring tidal shrub vegetation because little is known due to its current rarity. The possible ecological importance of tidal shrub habitat restoration has not been examined. Extensive loss of tidal shrub habitat suggests greater consideration should be given to its restoration where conditions are appropriate (e.g., oligohaline marshes of large river deltas).

The natural experiment shows merely breaching dikes is insufficient to restore tidal shrub vegetation. Within the remnant dikes of the experimental area LWD was 1/18th as abundant as in the control marsh and vegetation contrasted with the control marsh, i.e., *T. angustifolia* dominated rather than *M. gale*. The presence of *M. gale* on natural levees and on the only piece of large LWD encountered within the experimental area indicates sufficient time has elapsed in the experimental area for *M. gale* to flourish, provided there is suitable substrate. The paucity of both LWD and shrub vegetation in the experimental site, compared to their relative abundance in the control and references sites, is consistent with the hypothesis that LWD provides critical nurse log function for tidal shrub vegetation, especially *M. gale*. Limited LWD recruitment to the experimental area over the past 50 years could be due to limited LWD supply from upstream sources and obstructed access from the remnant dikes. Tidal shrub habitat restoration will likely require dike breaching or removal, and propagation of *M. gale* or other shrubs and trees on supplemented LWD or small mounds to initiate shrub community development.

Some areas of the Skagit marshes have been eroded by distributary meandering and widening, while localized progradation has created other relatively young areas (Hood 2004, 2006). In this dynamic environment, sustainability of estuarine *M. gale* habitat will depend on LWD recruitment to the estuary. Bereft of LWD, new marsh will not develop significant *M. gale* coverage. On-site LWD recruitment from senescing *P. sitchensis* (by far the most abundant tree in the marsh) is an insignificant source of nurse logs for *M. gale* and other estuarine shrubs and trees. *P. sitchensis* rarely grows to a sufficient size in the estuary to provide large LWD. Thirty-seven *P. sitchensis* sampled in the modern reference marsh had a mean DBH of 36 cm, while historical (1866–1877) mean tree DBH in the Skagit tidal shrub zone was 38 cm (n = 45; Collins 2000). LWD large enough to support tidal shrubs must come from sources outside the marsh, i.e., upstream riparian zones. LWD recruitment to rivers is currently very low compared to historical conditions, because lowland riparian zones have been deforested, and because levees constrain river meandering (Maser and Sedell 1994; Collins et al. 2001; see also MacNally et al. 2002).

M. gale dependence on estuarine LWD suggests upstream riparian management can affect LWD subsidies to estuaries with potentially cascading effects on estuarine ecology, particularly community structure and nitrogen dynamics (because *M. gale* is a nitrogen-fixing shrub). Long-term estuarine habitat management should include upstream riparian zone management to allow LWD recruitment to the estuary to sustain LWD-dependent estuarine ecosystem structures and processes. While this paper has focused on Pacific Northwest river deltas, the results may be applicable throughout the coastal range of *M. gale*, including eastern Canada, northeastern USA, northern Europe and Scandinavia, eastern Russia, and Japan.

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