

Article (refereed)

Moffett, Kevan B.; **Robinson, David A.**; Gorelick, Steven M.. 2010 Relationship of salt marsh vegetation zonation to spatial patterns in soil moisture, salinity and topography. *Ecosystems*, 13. 1287-1302. [10.1007/s10021-010-9385-7](https://doi.org/10.1007/s10021-010-9385-7)

© Springer Science+Business Media 2010

This version available <http://nora.nerc.ac.uk/8699/>

NERC has developed NORA to enable users to access research outputs wholly or partially funded by NERC. Copyright and other rights for material on this site are retained by the authors and/or other rights owners. Users should read the terms and conditions of use of this material at <http://nora.nerc.ac.uk/policies.html#access>

This document is the author's final manuscript version of the journal article, incorporating any revisions agreed during the peer review process. Some differences between this and the publisher's version remain. You are advised to consult the publisher's version if you wish to cite from this article.

The original publication is available at www.springerlink.com

Contact CEH NORA team at
noraceh@ceh.ac.uk

Relationship of salt marsh vegetation zonation to spatial patterns in soil moisture, salinity and topography

Journal:	<i>Ecosystems</i>
Manuscript ID:	draft
Types:	Original Article
Date Submitted by the Author:	
Complete List of Authors:	Moffett, Kevan; Stanford University, Environmental Earth System Science Robinson, David; University of the West Indies, Food Production Gorelick, Steven; Stanford University, Environmental Earth System Science
Key Words:	pattern, salt marsh, vegetation, zonation, edaphic, wetland, geophysics, ECa, Q-DEMI

1
2
3
4
5
6
7
8
9
10
11
12
13

**Relationship of salt marsh vegetation zonation to
spatial patterns in soil moisture, salinity and topography**

14 Kevan B. Moffett^{1,*}, David A. Robinson^{2,†}, and Steven M. Gorelick¹

15
16
17
18
19 ¹*Dept. of Environmental Earth System Science, Stanford University, Stanford, CA 94305 USA*

20
21 ²*Dept. of Geophysics, Stanford University, Stanford, CA 94305 USA*
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47

48 **Author Contributions:** DAR, SMG, and KBM conceived of and designed the study. DAR and KBM
49 performed field work and processed the data. KBM and SMG developed the analytical methodology.
50
51 KBM analyzed the data and wrote the article.
52
53

54 * Corresponding author. E-mail: moffett@stanford.edu. Fax: 650-725-0958.

55
56
57 † Present address: Dept. of Food Production, University of the West Indies, St. Augustine, Trinidad and Tobago
58
59
60

1 ABSTRACT

2
3
4
5
6 An intertidal San Francisco Bay salt marsh was used to study the spatial relationships between
7
8 biotic and abiotic ecosystem components: specifically, between vegetation patterns and
9
10 hydrologic and edaphic variables. Multiple abiotic variables were represented by six metrics:
11
12 elevation, distance to major tidal channels and to the nearest channel of any size, edaphic
13
14 conditions during dry and wet circumstances, and the magnitude of tidally-induced changes in
15
16 soil saturation and salinity. A new approach, quantitative differential electromagnetic induction
17
18 (Q-DEMI), was developed to obtain the last metric. The approach takes the difference in soil
19
20 induction from dry to wet conditions and converts that information to quantitative maps of
21
22 tidally-induced changes in root zone soil water content and salinity. The result is a spatially
23
24 exhaustive map of edaphic changes throughout the ecosystem. Spatially-distributed data on the
25
26 six metrics were used to explore two hypotheses. 1) Multiple abiotic variables relevant to
27
28 vegetation zonation each exhibit different, uncorrelated, spatial patterns throughout an intertidal
29
30 salt marsh ecosystem. 2) Vegetation zones and habitats of individual plant species are uniquely
31
32 characterized by different combinations of key metrics. The first hypothesis was supported by
33
34 observed, uncorrelated spatial variability in the metrics. The second hypothesis was supported by
35
36 binary logistic regression models that identified key vegetation zone and species habitat
37
38 characteristics from among the six metrics. Based on results from 108 models, the Q-DEMI map
39
40 of saturation and salinity change was the most useful metric for distinguishing different
41
42 vegetation zones and species habitats in the salt marsh.
43
44
45
46
47
48
49
50

**51
52
53 KEYWORDS**

54
55 pattern, salt marsh, vegetation, zonation, edaphic, wetland, geophysics, ECa, Q-DEMI
56
57
58
59
60

1 INTRODUCTION

2 The segregation of a few dominant plant species into distinctive zones is characteristic of
3 intertidal salt marshes. Each zone comprises a distinctive macrophyte assemblage and may also
4 uniquely sustain other species of concern. For example, stands of native *Spartina foliosa* densely
5 dissected by tidal channels San Francisco Bay support endangered *Rallus longirostris obsoletus*
6 (California Clapper Rails), but endangered *Reithrodontomys raviventris* (Salt Marsh Harvest
7 Mice) favor largely monospecific and undissected *Salicornia virginica* flats (USFW 2008). The
8 nature and causes of this ecologically important vegetation zonation have been studied for
9 decades with gradient analyses and paired plot, mesocosm, or transplant studies. Such studies
10 have determined that the causes of salt marsh vegetation zonation are both physical, determined
11 in part by variability in soil (edaphic) and tidal conditions (Pennings and others 2005), and
12 biological, the result of interspecific resource competition and biological response to periodic
13 disturbance (Bertness and others 1992; Emery and others 2001; Pennings and Callaway 1992),
14 even as the specific patterns and species vary regionally (Peterson and others 2008).

15 At the ecosystem scale, it remains a challenge to explain salt marsh vegetation patterning
16 despite knowledge of specific zonation mechanisms at the plant scale. Characterization of the
17 spatial variability of vegetation within salt marsh ecosystems has thus far relied heavily on
18 metrics of relative landscape position such as elevation and distance to tidal channels; however,
19 these geographic metrics, alone, have been insufficient predictors of salt-marsh vegetation zones
20 (Zedler and others 1999, Silvestri and others 2005). Although remote sensing has been used to
21 map spatial patterns of tidal channels (e.g., Marani and others 2006) and marsh surface
22 elevations (e.g., Sadro and others 2007) in relation to salt marsh vegetation, such maps are highly
23 nonspecific, failing to distinguish unique and consistent salt marsh vegetation habitat

Salt marsh spatial patterns and zonation

Moffett, Robinson, Gorelick

1
2
3 24 characteristics. Probabilistic models based on geographic metrics (e.g., Sanderson and others,
4
5 25 2001) fare somewhat better, but the fraction of marsh vegetation cover predicted correctly is
6
7
8 26 greatly skewed by very high or very low coverage by a given species. Part of the difficulty in
9
10
11 27 such analyses is that geographic metrics are only rough proxies for the combined effects of many
12
13 28 physical, chemical, and biological variables that contribute to salt marsh zonation.

14
15 29 In this study we explored two hypotheses about the spatial nature of multiple zonation-
16
17 30 relevant variables and their relationship to salt marsh vegetation distribution. First, we
18
19
20 31 hypothesized that different variables, such as tidal flood duration and direction, root zone soil
21
22 32 water content, and soil salinity, may each exhibit different spatial patterns in a salt marsh. The
23
24 33 patterns of such variables may have different characteristic spatial scales and gradients oriented
25
26
27 34 in opposing directions. Second, each plant species or zone may correlate with different
28
29 35 combinations of variables. For example, one species might grow among dry soil conditions or
30
31 36 high soil salinity, but not both; another species might not grow among dry or salty edaphic
32
33
34 37 conditions. Also, due to interspecific interactions, a zone dominated by one species may not be
35
36 38 characterized by the same variables as the total habitat range of the species. Prior to this study,
37
38
39 39 such concepts had not been tested in a *spatially-distributed manner* throughout a salt marsh; we
40
41 40 investigated these hypotheses on the basis of extensive data sets spanning the full range of
42
43
44 41 conditions within an intertidal salt marsh ecosystem.

45
46 42 We examined the first hypothesis by comparing the spatial patterns of six zonation-
47
48 43 relevant metrics: elevation, distance to major tidal channels and to the nearest channel of any
49
50 44 size, the soil saturation/salinity state during dry and wet marsh conditions, and the difference in
51
52
53 45 this edaphic state between conditions. The first three metrics are geographic measures of
54
55
56 46 landscape position and proxies for hydrologic processes relevant to salt marsh vegetation
57
58
59
60

Salt marsh spatial patterns and zonation

Moffett, Robinson, Gorelick

1
2
3 47 zonation. Elevation is commonly employed to represent the effects of flood/exposure duration
4
5 48 and surface water ponding. A location's distance to the nearest tidal channel represents the likely
6
7
8 49 direction of tidal flooding and groundwater drainage and directional tidal energy effects (e.g.,
9
10
11 50 sediment deposition). This study uniquely considered both distances to primary tidal channels,
12
13 51 typically identified from aerial imagery, and distances to small (~0.1 – 0.5 cm wide, rarely
14
15 52 mapped) surface drainage pathways hidden beneath the vegetation that we term microtributaries.

17 53 The remaining three metrics reflected soil properties under different hydrologic
18
19
20 54 conditions (dry and wet marsh soils) and the magnitude of change between conditions. The soil
21
22 55 properties considered, soil saturation, salinity, and texture, are known to contribute to salt marsh
23
24 56 zonation (Silvestri and others 2005) but previously could only be measured at points, prohibiting
25
26
27 57 extensive repeat sampling and marsh-wide analysis. Geophysical electromagnetic induction
28
29 58 (EMI) imaging of bulk apparent soil electrical conductivity (ECa) captures the combined state of
30
31
32 59 soil saturation, salinity, and texture in one ECa number (Friedman 2005, Rhoades and others
33
34 60 1999) and can be surveyed quickly over a large area. EMI has been used to investigate patterns
35
36
37 61 in soil properties (e.g., Lesch and others 2005, Robinson and others 2009) but its potential to
38
39 62 provide new insight into ecosystem patterning is only beginning to be explored (Stroh and others
40
41 63 2001, Robinson and others 2008). Prior to this study the method had not been tested in an
42
43
44 64 environment with as extremely high soil water, salt, and clay contents as in salt marshes. To
45
46 65 further the applicability of EMI to salt marsh vegetation analysis, we developed a method to
47
48 66 filter out the effects of the soil clay content on the ECa data and leverage the information on
49
50
51 67 changes in soil saturation and salinity from sequential EMI surveys. Our approach was to
52
53 68 subtract the data from two EMI surveys (differential or time-lapse EMI; Lesch and others 2005,
54
55 69 Robinson and others 2009) and then convert the ECa difference values (Δ ECa) to quantitative

Salt marsh spatial patterns and zonation

Moffett, Robinson, Gorelick

1
2
3 70 estimates of soil water content and salinity change using Archie's Law (Quantitative Differential
4
5 71 EMI, or Q-DEMI). Our Q-DEMI methodology quantified tidally-induced saturation and salinity
6
7
8 72 changes in the salt marsh root zone and enabled assessment of their spatial relationship to
9
10 73 vegetation zonation throughout a marsh in unprecedented detail.

11
12
13 74 To explore the second hypothesis, that each salt marsh plant species might bear a
14
15 75 different relationship to a suite of relevant variables, we sought to isolate distinguishing
16
17 76 characteristics of each of the major vegetation zones and individual species habitats composing
18
19 77 the salt marsh ecosystem. We used logistic regression modeling to assess the correlation between
20
21 78 vegetation patterns and the six geographic and edaphic metrics. The geophysical data on salt
22
23 79 marsh edaphic conditions provided greater insight into the underlying abiotic characteristics of
24
25 80 the vegetation patterns than was gained from the geographic metrics alone. In particular, spatial
26
27 81 variability in tidally-induced changes in soil water content and salinity, reflected in the Q-DEMI
28
29 82 ΔE_{Ca} metric, were the most effective means of distinguishing vegetation zones and habitats.

30
31
32 83 Multiple variables combine to support ecosystem structures, functions, habitat
33
34 84 heterogeneity, integrity, and supply of ecosystem services of salt marshes (Turner and Chapin
35
36 85 2005, Peterson and others 2008), but these variables are seldom analyzed in a spatially-
37
38 86 distributed manner. With this study we aimed to better understand how the effects of multiple
39
40 87 abiotic variables combine into something more than the sum of the parts, a spatially-variable
41
42 88 abiotic template upon which salt marsh vegetation patterns and biotic interactions are expressed.
43
44 89 A system-level perspective that integrates both abiotic and biotic variables may help inform the
45
46 90 maintenance and restoration of coastal wetlands, a matter of increasing interest worldwide amid
47
48 91 concerns of sea level rise, increased storm activity, and coastal development pressure (Peterson
49
50 92 and others 2008).

93 MATERIALS AND METHODS

94 Field Site and Hydrology

95 The study site was a 0.9 ha intertidal salt marsh in southern San Francisco Bay, within the
96 Palo Alto Baylands Nature Preserve (37°27'54" N, 122°6'58" W). The geological and botanical
97 history of the surrounding Santa Clara Valley were described by Cooper (1926) and the geology
98 underlying the Palo Alto Baylands by Hamlin (1983). The history and character of the marsh
99 were similar to that described by Hinde (1954) for the adjacent marsh to the south. The
100 underlying site stratigraphy consisted of 3-5 meters of fine estuarine mud, predominantly
101 montmorillonite clay, overlying a saline aquifer system (Hamlin 1983).

102 Vegetation Mapping

103 Plant species at the site were: *Spartina foliosa*, *Salicornia virginica* (*S. depressa*),
104 *Distichlis spicata*, *Jaumea carnosa*, *Grindelia stricta*, *Frankenia salina*, *Salsola soda*, and
105 *Atriplex prostrata* (see USDA (2009) for synonymous species names). The habitat occupied by
106 each species was mapped by: marking the boundaries of assemblages distinguished by the
107 presence/absence of each of the species, digitizing these polygonal boundaries using streaming
108 GPS, and identifying the relative abundance of each species within each polygon. This method
109 was similar to that of Zedler and others (1999) for San Diego Bay marshes, but with greater
110 emphasis on identifying the locations of assemblage boundaries. Surveys of species' percent
111 cover within 1-m² quadrats verified assemblage composition at 69 locations. The 57/134
112 assemblage polygons verified by one or more quadrats accounted for 81% of the marsh area.

113 Vegetation zones were classified by the species of greatest (dominant) cover fraction in
114 each assemblage polygon. The quadrat surveys confirmed that this was a sufficient means of
115 identifying vegetation zones since assemblage composition within each zone defined in this

1
2
3 116 manner was consistent. In addition to the spatial distribution of major vegetation zones, in this
4
5 117 study we were interested in the full range of conditions among which each plant species grew.
6
7
8 118 We refer to a plant species' habitat as all the areas the species occupied regardless of cover
9
10 119 density. In our vegetation discrimination analysis we assessed the salient characteristics of zones
11
12 120 and species habitats separately and compared the results.

121 **Mapping Edaphic Conditions**

122 A logical precursor to understanding salt marsh vegetation distribution is a three-
123 dimensional description of root zone edaphic conditions throughout the ecosystem, but obtaining
124 spatially-extensive data on relevant physical and chemical soil properties has been intractable
125 with point-sampling methods. The combination of heterogeneous soil water content, salinity, and
126 clay fraction was captured in this study by maps of bulk soil electrical conductivity (ECa). The
127 ECa data were obtained on two separate days by repeatedly traversing the field site carrying a
128 streaming EMI instrument (DUALEM-1S, Dualem, Inc., Milton, ON, Canada) and GPS, logged
129 concurrently. Sequential traverses were separated to account for the ~4 m² EMI measurement
130 support area. We estimated the vertical soil interval represented by the ECa data was 0-0.40 m
131 depth (see online supplement), approximately the depth of the salt marsh root zone. We post-
132 processed ~5000 ECa measurements per survey (Robinson and others 2008) and corrected for
133 effects of soil temperature (Reedy and Scanlon 2003) to produce kriged ECa maps at 2-m
134 resolution. Successive measurements of ECa at test locations agreed to within 0.01 dS/m, which
135 we take to be the ECa uncertainty, though the EMI instrument accuracy was 0.001 dS/m.

136 The two EMI surveys were timed to capture different hydrologic conditions. The first
137 survey occurred just prior to the neap-spring tidal transition, when the marsh had not been
138 flooded in eight days (Nov. 19, 2007); we refer to these as data from "dry" marsh conditions.

Salt marsh spatial patterns and zonation

Moffett, Robinson, Gorelick

1
2
3 139 The second survey was partially into the next spring tide cycle, immediately following a flood
4
5 140 tide (Dec. 7); we refer to these as data from “wet” marsh conditions. We use the terms “dry” and
6
7
8 141 “wet” as qualitatively convenient reminders of antecedent tidal conditions although both
9
10 142 circumstances represent very moist soils (>80% saturation). Both survey times were near mid-
11
12 143 day and no rain occurred while the marsh surface was exposed during the study period.

144 The field site experiences mixed semi-diurnal tides and a semi-arid Mediterranean
145 climate with winter precipitation (~39 cm/yr). The marsh plain is above mean high water and is
146 flooded by the higher high tide on $\frac{2}{3}$ - $\frac{3}{4}$ of days during each spring-neap cycle. To verify
147 ambient hydrologic conditions, we monitored groundwater and tidal conditions at the site by
148 logging pressure and temperature every 10 minutes at the bed of the two primary tidal channels
149 and in 43 wells and piezometers installed 0.5 to 1.0 m into the marsh substrate. We monitored
150 hydraulic heads in the root zone with 23 tensiometer pairs spanning 10-15 and 20-25 cm depths.
151 Tensiometer data were collected manually during the geophysical surveys.

152 Empirical relationships have shown ECa to increase with increasing soil clay content,
153 water content (θ), or solution electrical conductivity (ECw) (e.g., Rhoades and others, 1999),
154 though not for as high values as occur in salt marshes. We conducted laboratory analyses to
155 establish the specific relationships between ECa and salt marsh soil properties. Twenty-three soil
156 sampling locations were strategically chosen using the ECa data from the first survey and
157 response-surface directed sampling (Corwin and Lesch 2005, Lesch 2005). After collecting ECa
158 data at each location, soil cores (2.5 cm diameter) were collected manually from 0-30cm and 30-
159 60cm depth. The 0-30 cm depth interval was chosen to correspond roughly to the EMI signal
160 depth, enabling correlation with ECa survey data. The 30-60 cm deep samples were used in
161 parameterizing the Q-DEMI methodology, discussed below. The cores were immediately sealed

1
2
3 162 in plastic bags and promptly weighed in the laboratory. Samples were air-dried for 11-28 days,
4
5 163 homogenized subsamples weighed, oven-dried at 105°C for at least 12 hours and re-weighed,
6
7
8 164 and core water fractions and bulk densities calculated. Duplicate homogenized subsamples were
9
10 165 analyzed for soil paste extract electrical conductivity (ECe) and soil texture (University of Idaho
11
12 166 Pedology Laboratory standard procedures). Pore water samples extracted adjacent to the coring
13
14
15 167 locations from 30 cm depth using a suction lysimeter (“sipper”, $\sim \leq 5$ kPa suction) were analyzed
16
17 168 in the laboratory for pore water electrical conductivity (ECw).

19 169 **Quantitative Differential EMI Methodology**

20
21
22 170 Each geophysical survey provided a snapshot of the combination of water, salt, and clay
23
24 171 conditions throughout the salt marsh at one point in time. We developed a method to transform
25
26 172 the difference in ECa between dry and wet tidal conditions into spatially-distributed, quantitative
27
28 173 estimates of changes in root zone soil water content and salinity. The premise of the Q-DEMI
29
30 174 method was that a change in the ECa value of a location was due to changing soil water content
31
32 175 and salinity while clay content remained constant. In our Q-DEMI analysis, we subtracted the
33
34 176 later “wet” ECa data from the earlier “dry” ECa data, simulating a case of increasing soil
35
36 177 moisture ($\Delta ECa = ECa_{dry} - ECa_{wet}$). We then determined the nature of the edaphic change,
37
38 178 whether caused by changing soil water content or by changing soil salinity, from the sign of
39
40 179 ΔECa . An observed increase in ECa between dry and wet conditions ($-\Delta ECa$) indicated an
41
42 180 increase in soil water content: an increase in salt content could not explain the change in these
43
44 181 areas because tidal waters were known *a priori* to be less saline (33.4 dS/m) than the marsh pore
45
46 182 waters ($ECw \approx 57.2$ dS/m) to which they were added in order to wet-up the marsh. In contrast,
47
48 183 an observed decrease in ECa ($+\Delta ECa$) indicated a decrease in pore water salinity: under
49
50 184 conditions of increasing tidal water availability, water content would remain constant or increase
51
52
53
54
55
56
57
58
59
60

Salt marsh spatial patterns and zonation

1
2
3 185 and so could not explain the ECa change in these areas. Because saturation and salinity changes
4
5 186 could occur simultaneously with opposing effects, the Q-DEMI calculations represent the
6
7
8 187 conservative case in which all ECa change is ascribed to the dominant process, identified by the
9
10 188 sign of ΔECa .

11
12
13 189 Quantifying saturation and salinity changes was accomplished using Archie's Law in our
14
15 190 Q-DEMI methodology. Archie's Law is a well-studied geophysical relationship between ECa
16
17 191 and: pore water conductivity (EC_w), a formation factor (f) related to porosity, the soil saturation
18
19 192 (S), and the soil mineral surface conductivity due to adsorbed ionic charge (σ_s) (Kirsch 2006).

$$20 \quad 192 \quad ECa = EC_w \cdot f \cdot S^2 + \sigma_s \quad (Eqn. 1)$$

21
22
23
24
25 194 The mineral surface conductivity (σ_s) is important in soils with large clay fractions, such as in
26
27 195 our salt marsh, but has not been tabulated for salt marsh clay soils. We estimated f and σ_s using a
28
29 196 simple linear regression between ECa and pore water conductivity (EC_w) for saturated samples
30
31 197 ($S = 1$). The samples used for this regression were from 30-60 cm depth since these samples were
32
33 198 known to be from the saturated zone below the water table. The resulting f and σ_s parameter
34
35 199 estimates compared favorably with estimates from more complicated methods (see online
36
37 200 supplement). These parameters permitted Q-DEMI calculation of changes in saturation, due to
38
39 201 aerated pore space being filled by tidal waters, and changes in salinity, due to flushing of salt
40
41 202 marsh soils, using variations on Archie's Law.

42
43
44
45
46 203 In the saturation-change dominated ($-\Delta ECa$) areas of the marsh we solved Archie's Law
47
48 204 (Eqn. 1) for the net soil water content change required to account for the observed increase in
49
50 205 ECa between dry and wet marsh conditions. To reduce one excess degree of freedom in the
51
52 206 calculation we assumed that initially aerated pore space in the soil was completely filled by the
53
54 207 flood tide, leading to a minimum estimate of soil saturation change since the effect of any
55
56
57
58
59
60

trapped air would have reduced the magnitude of ΔECa . The formula we derived to calculate saturation change (ΔS) is shown below (Eqn. 2). The parameters are the: formation factor (f), mineral surface conductivity (σ_s), tidal flood water electrical conductivity (EC_{tide}), and ECa during wet (ECa_{wet}) and dry (ECa_{dry}) conditions.

$$\Delta S = \frac{-(\sigma_s - ECa_{wet} - f \cdot EC_{tide}) - \sqrt{(\sigma_s - ECa_{wet} - f \cdot EC_{tide})^2 - 4 \cdot (f \cdot EC_{tide}) \cdot (ECa_{wet} - ECa_{dry})}}{2 \cdot (f \cdot EC_{tide})} \quad (\text{Eqn. 2})$$

The real solution to Eqn. 2 using a positive discriminant root yielded unrealistic ΔS values greater-than one, so was discarded.

In the salinity-change dominated ($+\Delta ECa$) areas of the marsh we solved Archie's Law (Eqn. 1) for the pore water electrical conductivity (ECw) under dry and wet marsh conditions. We then used the seawater equation of state to convert each ECw value to a salinity value. Subtracting the salinity values yielded the change in salinity required to account for the observed decrease in ECa between dry and wet marsh conditions. To reduce one excess degree of freedom in the calculation we assumed that these areas of the marsh remained water-saturated, leading to a minimum estimate of salinity change since the effect of any concurrent increase in soil water content would have reduced the magnitude of ΔECa . (Field observations suggested that these areas of the marsh did remain saturated throughout dry and wet marsh conditions.)

In addition to the two maps of ECa , from dry and wet marsh conditions, the map of saturation and salinity changes produced by the Q-DEMI methodology provided a third spatially-distributed metric of salt marsh root zone characteristics against which to compare salt marsh vegetation zonation.

Mapping Marsh Geometry

Geometric measures of spatial context within the ecosystem have traditionally been employed as indicators of salt marsh ecosystem structure and spatially-variable intertidal

Salt marsh spatial patterns and zonation

1
2
3 231 hydrologic effects. The most common such geographic, or “landscape position” (Zedler and
4
5 232 others 1999), metrics are elevation and distance-to-channel. We mapped these metrics at the
6
7
8 233 same high resolution as our edaphic data sets. We represented marsh plain topography by a 2-m
9
10 234 horizontal resolution kriged map of 742 marsh plain surface elevations surveyed using a total
11
12 235 station, verified against LIDAR data. Major tidal channels are typically identified from aerial
13
14 236 imagery, but we could find no precedent for mapping the small, connected surficial drainage
15
16 237 pathways hidden under the vegetation canopy (“microtributaries”). We identified the banks of
17
18 238 major tidal channels and microtributaries by traversing them with a streaming GPS (20-cm post-
19
20 239 processed horizontal accuracy). Two distance-to-channel metrics were calculated as the shortest
21
22 240 straight-line distances from the center of each elevation grid cell to: 1) the nearest of the two
23
24 241 primary tidal channels (bounding and bisecting the study area, Figure 1); 2) the nearest channel
25
26 242 of any size.

Statistical Vegetation Differentiation

27
28 244 To contrast the utility of the six metrics described above in differentiating vegetation
29
30 245 zones and plant species habitats, we employed binary logistic regression (BLR) models (SPSS
31
32 246 2009). A logistic regression is analogous to a linear regression but with a categorical, instead of
33
34 247 continuous, dependent variable. By comparing the vegetation at each location in the marsh to the
35
36 248 collocated values of the six metrics and repeating this for all marsh locations, the BLR method
37
38 249 built models of those combinations of the six metrics that best distinguished the selected
39
40 250 vegetation zone or habitat type. BLR models were assessed at the 95% confidence level.

41
42 251 We tested 108 BLR models, including univariate and multivariate analyses for each
43
44 252 vegetation zone and species habitat. In the univariate cases we assessed whether any of the six
45
46 253 metrics, alone, could correctly differentiate the marsh areas inside and outside each of the six
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3 254 major vegetation zones (6 metrics x 6 zones = 36 zone models). We also tested whether any of
4
5 255 the six metrics, alone, could correctly differentiate the marsh areas occupied or not occupied by
6
7
8 256 each species, regardless of its cover density (6 metrics x 6 species = 36 habitat models). These 76
9
10 257 models served to test the univariate predictive capacity of each of the six metrics in relation to
11
12 258 vegetation patterning at our site. For these models, the two-fold null hypothesis in each case was
13
14
15 259 either 100% or 0% cover by the selected zone or species.

16
17 260 In the multivariate analyses, we built forward-conditional BLR models for each
18
19 261 vegetation zone and species habitat. This approach tested whether a combination of multiple
20
21 262 metrics could better identify the distinguishing characteristics of each zone and habitat than a
22
23 263 single metric. We tested three metric combinations: 1) the three geographic metrics, 2) the three
24
25 264 edaphic metrics, 3) all six metrics, for total of 36 multivariate models (3 combinations x (6 zones
26
27 265 + 6 habitats) = 36 models). The forward-conditional BLR method selected only those metrics
28
29 266 that significantly contributed to the zone or habitat prediction at the 95% confidence level. For
30
31 267 these models, the two-fold null hypothesis in each case was either 100% or 0% cover by the
32
33 268 selected zone or species. The results of the BLR models revealed the key characteristics
34
35 269 distinguishing each habitat envelope and zone at our site.

36 37 38 39 40 41 270 **RESULTS**

42 43 271 **Vegetation Patterns and Marsh Geometry**

44
45 272 The spatial distribution of vegetation zones at the site is shown in Figure 1a, with zones
46
47 273 labeled by the genus of the dominant species. Quadrat surveys verified that species identified as
48
49 274 zone dominants occupied a majority ($59\% \pm 16\%$) of the zone's cover. Zones dominated by the
50
51 275 succulent *Salicornia* (28% of total marsh area) and the grasses *Spartina* (19%) and *Distichlis*
52
53 276 (47%) were most prominent at the site, with smaller areas dominated by *Jaumea* (4%),
54
55
56
57
58
59
60

Salt marsh spatial patterns and zonation

1
2
3 277 *Frankenia* (1%), and *Grindelia* (2%). *Salsola* and *Atriplex* individuals were present in only a few
4
5 278 locations. The thick black outlines in Figure 1a highlight the three major vegetation zones,
6
7
8 279 dominated by *Spartina*, *Distichlis*, and *Salicornia*. Zone assemblage compositions are illustrated
9
10 280 by maps of relative cover density for each species (see appendix Figure A1), which were used to
11
12 281 assess the total habitat occupied by each species.

15 282 The elevation ranges ($\mu \pm 1\sigma$ m above mean sea level) spanned by the species were not
16
17 283 distinct: *Distichlis*, 1.04 ± 0.04 ; *Salicornia*, 1.03 ± 0.05 ; *Spartina*, 1.00 ± 0.06 ; *Jaumea*, $1.03 \pm$
18
19 284 0.05 ; *Frankenia*, 1.03 ± 0.03 ; *Grindelia*, 1.04 ± 0.03 . Overlap between the elevation ranges of
20
21 285 key species is common in salt marshes despite their characteristically distinct vegetation zonation
22
23 286 (Silvestri and others 2005, Sadro and others 2007). The average marsh plain elevation from the
24
25 287 kriged topographic data was 1.02 ± 0.06 m above mean sea level (m aMSL) and ranged from
26
27 288 0.61 to 1.32 m. The seeming visual correlation between areas of slightly lower elevation and the
28
29 289 southern, *Spartina*-dominated zone (Figure 1b) was not statistically supported because those
30
31 290 same elevations elsewhere in the marsh were dominated by different species. Employed in
32
33 291 univariate BLR models, elevation failed to justify rejecting the null hypothesis for any of the
34
35 292 vegetation zones or species habitats at our site.

41 293 Qualitative assessment of marsh locations' distance to primary tidal channels showed the
42
43 294 major zones dominated by *Spartina*, *Distichlis*, and *Salicornia* to each occur at any distance from
44
45 295 the major tidal channels that bound and bisect the marsh (Figure 2a). The *Spartina*-dominated
46
47 296 zone appeared to coincide with a region of dense microtributaries (Figure 2b), yet neither
48
49 297 distance-to-channel metric warranted rejecting the univariate BLR models' null hypothesis for
50
51 298 any of the vegetation zones or species habitats.

299 Edaphic Conditions and Vegetation

1
2
3 300 The spatial structure of edaphic conditions throughout the marsh, and the magnitude of
4
5 301 ECa values reflecting these conditions, remained consistent between the dry (Figure 3a) and wet
6
7 302 (Figure 3b) surveys. Mean ECa values for the two surveys were 13.37 and 13.71 dS/m,
8
9 303 respectively (2.05 dS/m standard deviations; correlation coefficient $r = 0.83$). Tensiometer data
10
11 304 confirmed that the root zone was drier during the first, “dry” geophysical survey than during the
12
13 305 second, “wet” survey. Tides rapidly and uniformly covered the marsh to a depth of 0.5 m during
14
15 306 spring tide flooding events between the surveys. The specific relationships between ECa values
16
17 307 and edaphic conditions (soil solution and paste extract conductivities and water and clay
18
19 308 contents) determined for this salt marsh are presented in the appendix.

20 309 The configuration of vegetation zones (Figure 1a) did not resemble the spatial pattern of
21
22 310 edaphic conditions (Figure 3). Instead, interior marsh areas that exhibited persistent high soil
23
24 311 water content and/or salinity (high ECa) appeared coincident with major zone boundaries. A
25
26 312 phenomenon of stressful edaphic conditions and major zone boundaries occurring in the same
27
28 313 location was described for *Spartina* and *Salicornia* in northern San Francisco Bay salt marshes
29
30 314 by Mahall and Park (1976a) but had not been illustrated in two dimensions; our result is
31
32 315 consistent with this explanation of ecotone locations. Though not consistently correlated with
33
34 316 any vegetation zone or elevation, the edaphic variability in the marsh was significantly related to
35
36 317 the hydrologic processes represented by the distance-to-channel metrics ($r = 0.36$ to 0.54). Low
37
38 318 soil saturation and/or salinity (low ECa) occurred close to tidal channels and more stressful
39
40 319 edaphic conditions (high ECa) occurred further from the channels. Neither ECa data set provided
41
42 320 information sufficient to reject the null hypothesis of the univariate BLR models.

43
44 321 The spatial pattern of tidally-induced changes in edaphic conditions revealed by
45
46 322 subtracting the wet and dry ECa surveys (Δ ECa, Figure 4a) was more heterogeneous than the
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Salt marsh spatial patterns and zonation

Moffett, Robinson, Gorelick

1
2
3 323 spatial variability in static edaphic conditions (Figure 3). The pattern of change was not altered
4
5 324 by the Q-DEMI calculations, which converted ΔECa values to soil saturation and salinity change
6
7 325 quantities (Figure 4b). The conversion was made using values of $f = 0.223$ and $\sigma_s = 2.479$ dS/m.
8
9 326 The average estimated saturation change in the fluid-exchange dominated areas of the marsh
10
11 327 (blue in Figure 4b) was 6.2 ± 5.5 % ($\mu \pm 1\sigma$). The average estimated salt loss from the salt-
12
13 328 exchange dominated areas of the marsh (red in Figure 4b) was 0.77 ± 0.64 kg/m². The large
14
15 329 standard deviations of these average results were due to highly heterogeneous soil aeration and
16
17 330 flushing throughout the marsh. Despite the Q-DEMI methodology producing conservative
18
19 331 estimates of the magnitude of edaphic change, we emphasize that the methodology permits
20
21 332 mapping the magnitude of salt and water exchange in a spatially-distributed way throughout an
22
23 333 ecosystem for the first time.
24
25
26
27
28

29 334 Spatial patterns of saturation and salinity change did not qualitatively resemble
30
31 335 vegetation zonation (Figures 1a, 4b), yet BLR models based on ΔECa were able to partially
32
33 336 describe the zones dominated by every species except *Distichlis*. For the *Salicornia*-, *Spartina*-,
34
35 337 *Jaumea*-, *Frankenia*-, and *Grindelia*-dominated zones, the BLR models correctly distinguished
36
37 338 22-44 % of the area inside each zone and 63-67% of the area outside each zone. Though short of
38
39 339 the ideal prediction (100% correct both inside and outside each zone), these results using the
40
41 340 ΔECa metric were a substantial improvement over the null hypothesis returned by the models
42
43 341 based on the other five metrics.
44
45
46
47

48 342 ΔECa BLR models were more successful at distinguishing between marsh areas occupied
49
50 343 and not occupied by each of the six plant species, regardless of cover density (appendix Figure
51
52 344 A1). ΔECa BLR habitat models correctly identified 64% of the observed *Distichlis* and
53
54 345 *Salicornia* occurrences and 37% and 44% of observed absences, respectively. ΔECa BLR
55
56
57
58
59
60

Salt marsh spatial patterns and zonation

Moffett, Robinson, Gorelick

1
2
3 346 models for *Spartina* and *Jaumea* habitat correctly predicted 70% and 73% of the observed
4
5 347 occurrences and 41% and 46% of observed absences, respectively. Δ ECa BLR models for
6
7
8 348 *Frankenia* and *Grindelia* were less successful at correctly predicting occurrences of these species
9
10 349 (28% and 23%, respectively) but more successful at correctly predicting absences (63% and
11
12 350 60%, respectively). For all six species, the Δ ECa BLR habitat models justified rejecting the null
13
14
15 351 hypotheses (95% confidence).

16
17 352 The patterns in edaphic conditions and geographic metrics of salt marsh structure support
18
19
20 353 our two hypotheses regarding the spatial nature of zonation-relevant variables and their
21
22 354 relationship to salt marsh vegetation distribution. 1) Multiple metrics relevant to salt marsh
23
24 355 vegetation zonation each exhibit different patterns. These patterns are characterized by different
25
26 356 spatial scales and degrees of spatial heterogeneity. 2) Alone, only the Δ ECa metric provided
27
28 357 information useful in indentifying vegetation zones and species habitats. The relation of the
29
30 358 Δ ECa metric to vegetation differed depending on the species considered and whether the species
31
32 359 was considered alone or as a zone-dominant.

360 Multivariate Vegetation Zone and Habitat Discrimination

361 We hypothesized that a combination of multiple metrics might better discriminate salt
362 marsh vegetation zones and individual species habitats than univariate models. The metric
363 combinations we tested using forward-conditional BLR models were: 1) the three geographic
364 metrics, 2) the three edaphic metrics, and 3) all six metrics. Salient results are presented here;
365 complete BLR model results are provided in the online supplement.

366 Except in the case of the *Distichlis*-dominated zone, none of the multivariate models
367 identified vegetation zones or habitats significantly better than the univariate Δ ECa BLR models.
368 For the *Distichlis*-dominated zone, a BLR model including all three geographic metrics correctly

Salt marsh spatial patterns and zonation

1
2
3 369 predicted 45% of the marsh area within the zone and 72% of the area outside the zone, compared
4
5
6 370 to the null hypothesis returned by the univariate ΔECa BLR model. This result suggests that
7
8 371 *Distichlis* may be reliant on the hydrologic marsh processes implicit in the elevation and
9
10 372 distance-to-channel metrics to maintain a dominant cover fraction. In contrast, the dominance of
11
12 373 the other five major species at the site may be related to the magnitude of temporal variation in
13
14 374 root zone soil water content and soil salinity, represented by the ΔECa metric. For example,
15
16 375 ΔECa was the *only* significant predictor of the marsh areas that *Jaumea* occupied, whether it was
17
18 376 the dominant cover fraction or not, even when the other five metrics were made available to the
19
20 377 forward-conditional model. However, a BLR model based on ΔECa correctly predicted 73% of
21
22 378 *Jaumea* occurrences in the salt marsh but only 32% of *Jaumea*-dominated zones. The difference
23
24 379 between the zone and habitat models suggest that the tidally-induced changes in root zone water
25
26 380 and salt content represented by the ΔECa metric may affect the growth and interspecific
27
28 381 interactions of a species within a vegetation assemblage differently than the growth and survival
29
30 382 of individual plants of that species throughout the marsh.

DISCUSSION**Vegetation Zonation**

31
32
33
34
35
36 383
37
38 384
39
40
41 385 Our use of geophysical EMI technology was motivated by the inherent spatial limitations
42
43 386 of transect- and plot-based methods of investigating *in situ* salt marsh vegetation patterning.
44
45
46 387 Logistic regression models based on extensive two-dimensional data identified major
47
48 388 characteristics that distinguished the vegetation zones and species habitats at our site. The detail
49
50 389 of our regression models, based on over 2000 data points, makes it striking that some zones and
51
52 390 species habitats were uniquely identified by a combination of multiple variables (e.g., *Distichlis*)
53
54
55 391 but others were best identified by a single variable (e.g., *Jaumea*). It is also significant that there
56
57
58
59
60

Salt marsh spatial patterns and zonation

Moffett, Robinson, Gorelick

1
2
3 392 was a large difference in the ability of the models to describe the key characteristics of the total
4
5 393 habitat envelope of a species *versus* the zone for which it provided the dominant cover class.
6
7
8 394 Existing theory suggests that the survival of individual salt marsh plants may be strongly affected
9
10 395 by environmental conditions but that the growth rate and relative cover of a species may be more
11
12 396 strongly affected by interspecific interactions with its neighbors (e.g., Emery and others, 2001).
13
14
15 397 This hypothesis seems to be supported by the greater success with which our regression models,
16
17 398 based on metrics of abiotic ecosystem variability, were able to identify characteristic individual
18
19 399 species habitats compared to vegetation zones.

400 Tide-induced Edaphic Change

20
21
22
23
24 401 The most striking result of the vegetation discrimination analysis was the utility of the
25
26 402 ΔECa metric, alone, in identifying vegetation zones and species habitats. The Q-DEMI method
27
28 403 and soil core analyses showed that ΔECa represented the amount of water and salt exchanged
29
30 404 from the root zone (Figure 4b) between two points in time. The data from this study could not
31
32 405 definitively separate, however, whether observed changes in edaphic conditions were due
33
34 406 entirely to intervening tidal flooding, or due to a combination of physical and biological effects.
35
36 407 The lack of correlation between ΔECa and either elevation or distance-to-channel argues against
37
38 408 the hydrologic processes implied by the elevation and distance-to-channel metrics as the
39
40 409 dominant determinants of spatial patterns in edaphic change.

41
42
43
44
45 410 The phenomenon of large, broadly distributed decreases in soil salinity, identified in this
46
47 411 study by decreases in ECa between dry and wet marsh conditions, has not previously been
48
49 412 reported and the precise cause is unknown. Potential mechanisms for what was apparently rapid
50
51 413 flood tide-induced salt removal from the salt marsh root zone include: diffusion, leaching, or
52
53 414 dissolution of salt from the surface; plant salt uptake; or dilution by convective mixing in soil
54
55
56
57
58
59
60

1
2
3 415 macropores. On average, the 0.77 kg/m^2 of salt loss from the salt-exchange dominated areas of
4
5
6 416 the marsh constituted approximately 15% of the salt contained in the root zone pore water fluids.
7
8 417 Were dilution the only mechanism in operation, a salinity decrease of this magnitude would have
9
10 418 required approximately 70% of the root zone pore water to be replaced by the less salty tidal
11
12 419 waters, on average across the marsh. Salt uptake by vegetation would reduce the amount of pore
13
14 420 water turn-over required to match the geophysical observations.

17 421 **Plant – Soil Interactions**

18
19
20 422 Qualitative comparison of tide-induced edaphic change and vegetation zonation (Figures
21
22 423 1a, 4b) suggests that the greatest density of areas experiencing large saturation increases due to
23
24 424 tidal flooding occurred in the *Spartina*-dominated zone, the greatest density of areas
25
26 425 experiencing salt loss occurred in the *Salicornia*-dominated zone, and changes of intermediate
27
28 426 magnitude prevailed in the *Distichlis*-dominated zone. We hypothesize that these spatial
29
30 427 coincidences may be related to three different ecosystem engineering effects enabled by the
31
32 428 different physiologies and morphologies of these three species.

33
34
35
36 429 First, enhanced sediment deposition within, and enhanced erosion around, *Spartina*
37
38 430 clusters has been reported at low marsh elevations (Temmerman and others 2007, van Hulzen
39
40 431 and others 2007). This mechanism may also explain the great density of microtributaries in the
41
42 432 *Spartina*-dominated zone (Figure 2) at our high-elevation marsh site. Because *Spartina* is more
43
44 433 productive in low-salinity conditions than *Salicornia* and *Distichlis* (Bertness and others 1992,
45
46 434 Mahall and Park 1976b), it may remain dominant precisely where surrounding microtributaries
47
48 435 enhance pore water drainage and flushing. This hypothesis is supported by experimental
49
50 436 manipulations of marsh hydrology (Balling and Resh 1983, Wiegert and others 1983).
51
52
53
54
55
56
57
58
59
60

1
2
3 437 Second, *Salicornia* is one of the most salt-tolerant halophytes, producing more biomass
4
5
6 438 than *Spartina* and *Distichlis* at high salinities and water contents, but less at low salinities
7
8 439 (Pearcy and Ustin 1984). We hypothesize that efficient root salt exclusion and water use by
9
10 440 *Salicornia* (Mahall and Park 1976b) may locally maintain a saturated and salty root zone,
11
12 441 enhancing *Salicornia* competitiveness.

13
14
15 442 Third, the matted morphology of *Distichlis* may decrease surface water velocities and so
16
17 443 inhibit erosion of microtributaries (and so *Spartina*-dominance) in areas of low salinity favorable
18
19 444 for both grasses (Bertness and others 1992). *Distichlis*, like *Salicornia*, is quite effective at
20
21 445 excluding ions at the root membrane (Marcum and others 2007), and so may persist in areas of
22
23 446 intermediate salinity, where it is often found nearly co-dominant with *Salicornia* at our site. A
24
25 447 lack of known disturbance at our study site in at least 30 years argues against disturbance as an
26
27 448 explanation for the distribution of *Distichlis* at the site; furthermore, both *Distichlis* and
28
29 449 *Salicornia* are very effective at recovering from disturbance in northern California salt marshes,
30
31 450 neither necessarily competitively displacing the other (Allison, 1995).

32 451 CONCLUSION

33
34
35
36
37 452 This study explored the spatial relationships between salt marsh vegetation patterns and
38
39 453 six zonation-related metrics. The metrics were based on geographic and edaphic data: elevation,
40
41 454 distance to major tidal channels and to the nearest channel of any size, the soil saturation/salinity
42
43 455 state during dry and wet marsh conditions, and the difference in this edaphic state between
44
45 456 conditions. The metrics, mapped at high resolution throughout a salt marsh ecosystem, exhibited
46
47 457 very different spatial patterns. Among the six metrics, information on tide-induced edaphic
48
49 458 change was most useful in discriminating salt marsh vegetation zones and individual species
50
51 459 habitats. Unexpectedly poor spatial correlation between edaphic conditions and proxies for
52
53
54
55
56
57
58
59
60

Salt marsh spatial patterns and zonation

1
2
3 460 hydrologic forcing suggest, instead, the potential importance of plant-soil relations in spatial
4
5 461 patterns of tide-induced edaphic change.
6
7

8 462 The results of this study supported two hypotheses relating the spatial patterns of salt
9
10 463 marsh vegetation and abiotic variables. The hypotheses extend classic concepts of niche breadth
11
12 464 and overlap (Colwell and Futuyma 1971) into three spatial dimensions. First, the influence of
13
14 465 each resource used by, and stressor endured by, salt marsh vegetation may be spatially variable.
15
16 466 These spatial patterns are combined implicitly in nature by superposition and may exhibit
17
18 467 emergent patterns and properties that are more than the sum of the contributing variables.
19
20 468 Second, multiple contributing variables may affect the distribution of interacting species
21
22 469 assemblages differently than the distribution of individuals. Multivariate relationships between
23
24 470 abiotic and biotic ecosystem patterns are difficult to assess without high-resolution spatially-
25
26 471 distributed data at the ecosystem-scale. Geophysical methods such as EMI and Q-DEMI provide
27
28 472 means to obtain high-resolution, spatially-distributed data on root zone soil properties that have
29
30 473 previously been prohibitively difficult to obtain. In this study, such edaphic data was more useful
31
32 474 in characterizing salt marsh vegetation zones and habitats than traditional geographic metrics
33
34 475 such as elevation and distance-to-channel.
35
36
37
38
39

40
41 476 The challenge of predicting the vegetation distribution of intertidal salt marsh ecosystems
42
43 477 persists. Despite functional similarity between different salt marsh species around the world,
44
45 478 regional and latitudinal differences so far prohibit development of a universally-applicable,
46
47 479 mechanistic, zonation model (Farina and others, 2009; Pennings and others 2003). Even if such a
48
49 480 model were possible, its accuracy would necessarily vary from site to site. Some of the most
50
51 481 pressing questions regarding salt marsh vegetation zonation, such as the expected response of a
52
53 482 marsh to restoration efforts or to an invasive species, must be answered on a site-by-site basis
54
55
56
57
58
59
60

1
2
3 483 and may require probabilistic, not deterministic, answers. Three-dimensional mapping, EMI
4
5 484 geophysics, and the Q-DEMI methodology can provide a cost-effective, rapid, and repeatable
6
7
8 485 means to statistically characterize a salt marsh site. The resulting spatial and temporal patterns
9
10 486 can then be used as a foundation upon which to interpret or predict vegetation distributions and
11
12 487 biotic interactions based on existing region- and species-specific knowledge. Linking plot-scale
13
14 488 studies of plant-soil relations and interspecific interactions to marsh-scale studies of spatial
15
16 489 variability such as this one may provide the most promising means to fill the gap between the
17
18 490 general principles and site-specific needs of salt marsh vegetation zonation science.
19
20

21 22 491 **ACKNOWLEDGMENTS**

23
24 492 This work was supported by National Science Foundation grant EAR-0634709 to Stanford
25
26 493 University. Any opinions, findings, and conclusions or recommendations expressed in this
27
28 494 material are those of the authors and do not necessarily reflect the views of the National Science
29
30 495 Foundation. We thank the City of Palo Alto Baylands Nature Preserve and K. Brauman, M.
31
32 496 Cardiff, S. Giddings, E. Hult, K. Knee, I. Lebron, and K. Tufano for field assistance.
33
34

35 36 497 **LITERATURE CITED**

37
38 498 Allison SK. 1995. Recovery from small-scale anthropogenic disturbances by northern California
39
40 499 salt marsh plant assemblages. *Ecological Applications* 5(3): 693-702.
41
42 500 Balling SS, Resh VH. 1983. The influence of mosquito-control recirculation ditches on plant
43
44 501 biomass, production and composition in two San Francisco Bay salt marshes. *Estuarine Coastal*
45
46 502 *and Shelf Science* 16: 151-161.
47
48 503 Bertness MD, Gough L, Shumway SW. 1992. Salt tolerances and the distribution of fugitive salt
49
50 504 marsh plants. *Ecology* 73: 1842-1851.
51
52
53
54
55
56
57
58
59
60

Salt marsh spatial patterns and zonation

Moffett, Robinson, Gorelick

- 1
2
3 505 Colwell RK, Futuyma DJ. 1971. On the measurement of niche breadth and overlap. *Ecology*
4
5 506 52(4): 567-576.
6
7
8 507 Cooper WS. 1926. Vegetational development upon alluvial fans in the vicinity of Palo Alto,
9
10 508 California. *Ecology* 6: 325-473.
11
12 509 Corwin DL, Lesch SM. 2005. Applications of apparent soil electrical conductivity in precision
13
14 510 agriculture. *Computers and Electronics in Agriculture* 46: 103-133.
15
16
17 511 Emery NC, Ewanchuk PJ, Bertness MD. 2001. Competition and salt-marsh plant zonation: stress
18
19 512 tolerators may be dominant competitors. *Ecology* 82: 2471-2485.
20
21
22 513 Farina JM, Silliman BR, Bertness MD. 2009. Can conservation biologists rely on established
23
24 514 community structure rules to manage novel systems? ... Not in salt marshes. *Ecological*
25
26 515 *Applications* 19(2): 413-422.
27
28
29 516 Friedman S P. 2005. Soil properties influencing apparent electrical conductivity: a review.
30
31 517 *Computers and Electronics in Agriculture* 46: 45-47.
32
33
34 518 Hamlin SN. 1983: Injection of treated wastewater for ground-water recharge in the Palo Alto
35
36 519 Baylands, California: Hydraulic and chemical interactions -- preliminary report. U.S.
37
38 520 Geological Survey Water-Resources Investigation Report 82-4121.
39
40
41 521 Hinde HP. 1954. The vertical distribution of salt marsh phanerogams in relation to tide levels.
42
43 522 *Ecological Monographs* 24: 209-225.
44
45
46 523 Kirsch R. 2006. Petrophysical properties of permeable and low-permeable rocks. Kirsch R,
47
48 524 editor. *Groundwater Geophysics*. New York: Springer.
49
50
51 525 Lesch SM. 2005. Sensor directed response surface sampling designs for characterizing variation
52
53 526 in soil properties. *Computers and Electronics in Agriculture* 46: 153-179.
54
55
56
57
58
59
60

Salt marsh spatial patterns and zonation

Moffett, Robinson, Gorelick

- 1
2
3 527 Mahall BE, Park RB. 1976a. The ecotone between *Spartina foliosa* trin. and *Salicornia virginica*
4
5 528 I. in salt marshes of northern San Francisco Bay: I. biomass and production. *Journal of Ecology*
6
7 529 64: 421-433.
8
9
10 530 Mahall BE, Park RB. 1976b. The ecotone between *Spartina foliosa* trin. and *Salicornia virginica*
11
12 531 I. in salt marshes of northern San Francisco Bay: II. soil water and salinity. *Journal of Ecology*
13
14 532 64: 793-809.
15
16
17 533 Marani M, Silvestri S, Belluco E, Ursino N, Comerlati A, Tosatto O, Putti M. 2006. Spatial
18
19 534 organization and ecohydrological interactions in oxygen-limited vegetation ecosystems. *Water*
20
21 535 *Resources Research* 42: W06D06.
22
23
24 536 Marcum KB, Yensen NP, Leake JE. 2007. Genotypic variation in salinity tolerance of *Distichlis*
25
26 537 *spicata* turf ecotypes. *Australian Journal of Experimental Agriculture* 47: 1506-11.
27
28
29 538 Percy RW, Ustin SL. 1984. Effects of salinity on growth and photosynthesis of three California
30
31 539 tidal marsh species. *Oecologia* 62: 68-73.
32
33
34 540 Pennings SC, Callaway RM. 1992. Salt marsh plant zonation: the relative importance of
35
36 541 competition and physical factors. *Ecology* 73: 681-690.
37
38
39 542 Pennings SC, Grant M-B, Bertness MD. 2005. Plant zonation in low-latitude salt marshes:
40
41 543 disentangling the roles of flooding, salinity and competition. *Journal of Ecology* 93: 159-167.
42
43
44 544 Pennings SC, Selig ER, Houser LT, Bertness MD. 2003. Geographic variation in positive and
45
46 545 negative interactions among salt marsh plants. *Ecology* 84(6): 1527-1538.
47
48
49 546 Peterson CH, Able KW, DeJong CF, Piehler MF, Simenstad CA, Zedler JB. 2008. Practical
50
51 547 proxies for tidal marsh ecosystem services: application to injury and restoration. *Advances in*
52
53 548 *Marine Biology* 54: 221-266.
54
55
56
57
58
59
60

Salt marsh spatial patterns and zonation

Moffett, Robinson, Gorelick

- 1
2
3 549 Reedy RC, Scanlon BR. 2003. Soil water content monitoring using electromagnetic induction.
4
5 550 Journal of Geotechnical Geoenvironmental Engineering 129: 1028-1039.
6
7
8 551 Rhoades JD, Chanduvi F, Lesch S. 1999. Soil salinity assessment: methods and interpretation of
9
10 552 electrical conductivity measurements. Irrigation and Drainage Paper 57, FAO, Rome, Italy.
11
12 553 Robinson DA, Abdu H, Jones SB, Seyfried M, Lebron I, Knight R. 2008. Eco-geophysical
13
14 554 imaging of watershed-scale soil patterns links with plant community spatial patterns. Vadose
15
16 555 Zone Journal 7(4): 1132-1138.
17
18 556 Robinson DA, Lebron I, Kocar B, Phan K, Sampson M, Crook N, Fendorf F. 2009. Time-lapse
19
20 557 geophysical imaging of soil moisture dynamics in tropical deltaic soils: an aid to interpreting
21
22 558 hydrological and geochemical processes. Water Resources Research 45: W00D32.
23
24 559 Sadro S, Gastil-Buhl M, Melack J. 2007. Characterizing patterns of plant distribution in a
25
26 560 southern California salt marsh using remotely sensed topographic and hyperspectral data and
27
28 561 local tidal fluctuations. Remote Sensing of the Environment 110: 226-239.
29
30 562 Sanderson EW, Foin TC, Ustin SL. 2001. A simple empirical model of salt marsh plant spatial
31
32 563 distributions with respect to a tidal channel network. Ecological Modeling 139: 293-307.
33
34 564 Silvestri S, Defina A, Marani M. 2005. Tidal regime, salinity and salt marsh plant zonation.
35
36 565 Estuarine Coastal and Shelf Science 62: 119-130.
37
38 566 SPSS. 2009. PASW Statistics 17. Chicago, IL: SPSS Inc.
39
40 567 Stroh JC, Archer S, Doolittle JA, Wilding L. 2001. Detection of edaphic discontinuities with
41
42 568 ground-penetrating radar and electromagnetic induction. Landscape Ecology 16: 377-390.
43
44 569 Temmerman S, Bouma TJ, van de Koppel J, van der Wal D, De Vries MB, Herman PMJ. 2007.
45
46 570 Vegetation causes channel erosion in a tidal landscape. Geology 35: 631-634.
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Salt marsh spatial patterns and zonation

Moffett, Robinson, Gorelick

- 1
2
3 571 Turner MG, Chapin FS III. 2005. Causes and consequences of spatial heterogeneity in ecosystem
4
5 572 function. Lovett GM, Jones CG, Turner MG, Weathers KC, editors. Ecosystem Function in
6
7 573 Heterogeneous Landscapes. New York: Springer.
8
9 574 USDA. 2009. Plants Database. U.S. Department of Agriculture, Natural Resources Conservation
10
11 575 Service. <<http://plants.usda.gov/index.html>>
12
13 576 USFW. 2008. Species Account: California Clapper Rail. Species Account: Salt Marsh Harvest
14
15 577 Mouse. U.S. Fish and Wildlife Service, Sacramento Office.
16
17 578 <http://www.fws.gov/sacramento/es/animal_spp_acct/>
18
19 579 van Hulzen JB, van Soelen J, Bouma TJ. 2007. Morphological variation and habitat modification
20
21 580 are strongly correlated for the autogenic ecosystem engineer *Spartina anglica* (common
22
23 581 cordgrass). *Estuaries and Coasts* 30: 3-11.
24
25 582 Wiegert RG, Chalmers AG, Randerson PF. 1983. Productivity gradients in salt marshes: the
26
27 583 response of *Spartina alterniflora* to experimentally manipulated soil water movement. *Oikos*
28
29 584 41(1): 1-6.
30
31 585 Zedler JB, Callaway JC, Desmond JS, Vivian-Smith G, Williams GD, Sullivan G, Brewster AE,
32
33 586 Bradshaw BK. 1999. Californian salt-marsh vegetation: an improved model of spatial pattern.
34
35 587 *Ecosystems* 2: 19-35.

APPENDIX**Vegetation Habitat Distribution Maps**

(Figure A1 and caption.)

Relating ECa to Salt Marsh Soil Properties

52
53 592 Despite the extreme environment, correlations between our ECa and soil core data
54
55 593 showed that salt marsh ECa measurements can be interpreted in terms of three key edaphic

Salt marsh spatial patterns and zonation

Moffett, Robinson, Gorelick

1
2
3 594 properties: water content, salt content, and clay content. Variability in ECa values was
4
5
6 595 significantly related to variability in each of these edaphic properties ($p < 0.005$, Table A1). At
7
8 596 our site the EMI signal was dominated by the total salt content of the soil (as measured by the
9
10 597 soil paste extract conductivity, ECe) but the soil water (θ) and clay contents also contributed. The
11
12 598 clay content throughout the marsh was remarkably uniform and so did not figure significantly in
13
14 599 our analysis. See the online supplement for comparison of our salt marsh relationships with prior
15
16 600 published relationships at lower water, salt, or clay contents. In brief, we conclude that the salt
17
18 601 marsh ECa – ECe and ECa – θ relationships scale as in other environments but that the soil pore
19
20 602 solution conductivity (ECw) and soil clay content of intertidal salt marshes have unique effects
21
22
23
24 603 on EMI signals.
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

604 FIGURE AND TABLE CAPTIONS

605 Figure 1. a) Major vegetation zones, classified by the species of greatest cover fraction. b) Site
606 topography, units: meters above mean sea level.

607 Figure 2. a) Shortest distance to one of the main tidal channels, shown in light blue bounding and
608 bisecting the marsh site. b) Shortest distance to the nearest channel of any size,
609 including microtributaries shown in dark blue.

610 Figure 3. Root zone bulk soil electrical conductivity (ECa) from (a) dry and (b) wet marsh
611 conditions. Dark blue lines are channel and microtributary banks, black lines depict
612 major vegetation zone boundaries.

613 Figure 4. a) Edaphic change between dry and wet marsh conditions, represented by the change in
614 bulk soil electrical conductivity (ΔECa , dS/m). b) Result of Q-DEMI conversion of
615 ΔECa to changes in root zone saturation (%) or salinity (kg/m^3) between dry and wet
616 marsh conditions. Blue areas were dominated by net saturation increase between dry
617 and wet conditions, red areas were dominated by net salinity decrease. Dark blue lines
618 are channel and microtributary banks, black lines depict major vegetation zone
619 boundaries.

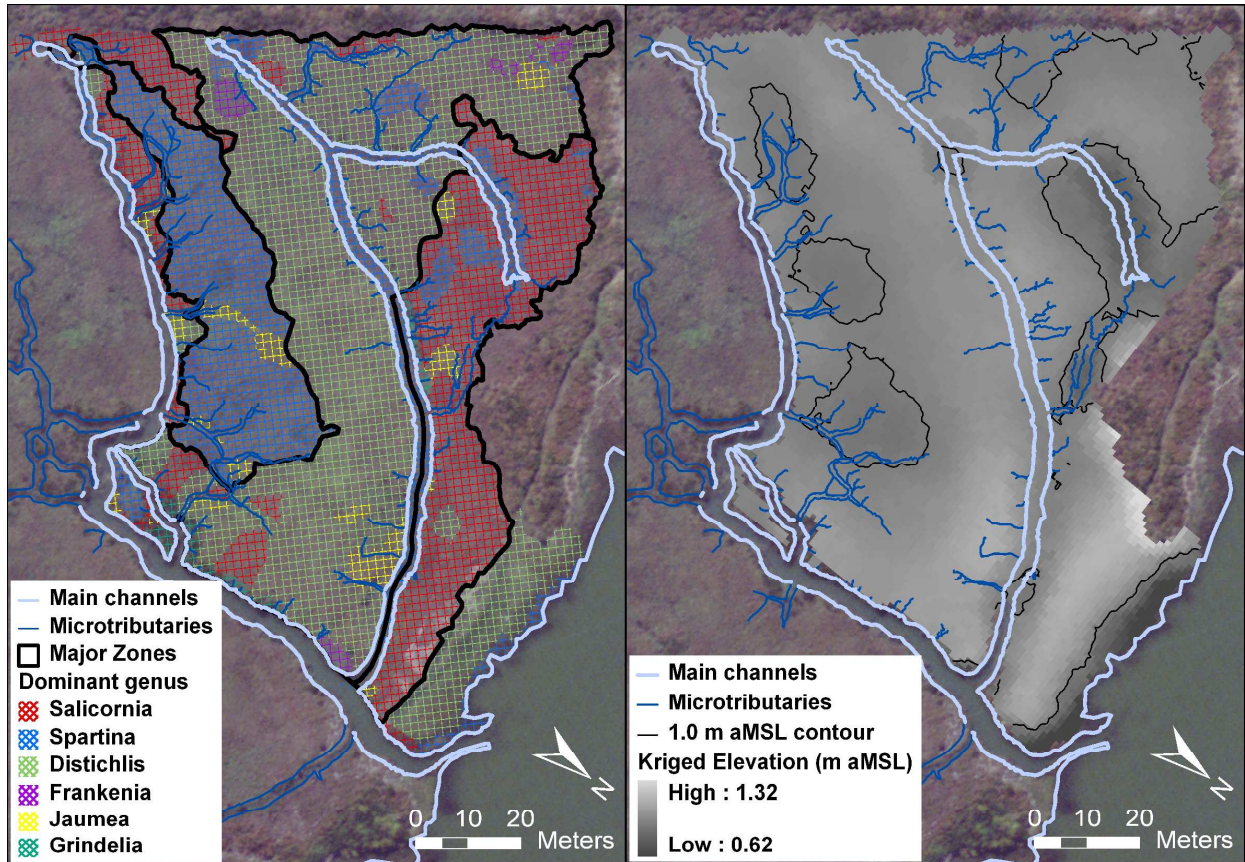
620 Figure A1. Relative cover fraction of each major plant species at the site: primary cover,
621 secondary cover, tertiary cover, present as minor cover. Clockwise from lower left:
622 *Distichlis spicata*, *Salicornia virginica* (*S. depressa*), *Spartina foliosa*, *Grindelia*
623 *stricta*, *Frankenia salina*, *Jaumea carnosa*.

624 Table A1. Relation of ECa data to soil properties.

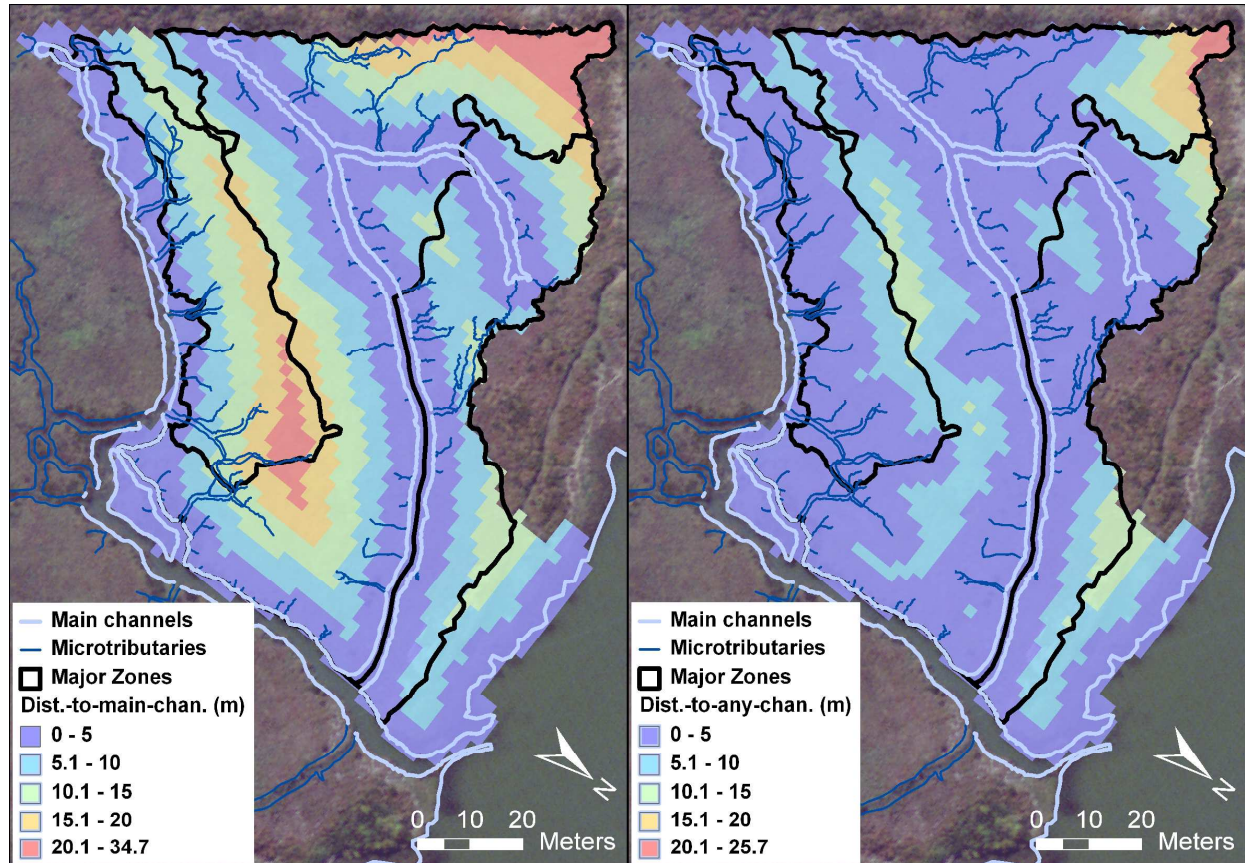
Salt marsh spatial patterns and zonation

625 FIGURES

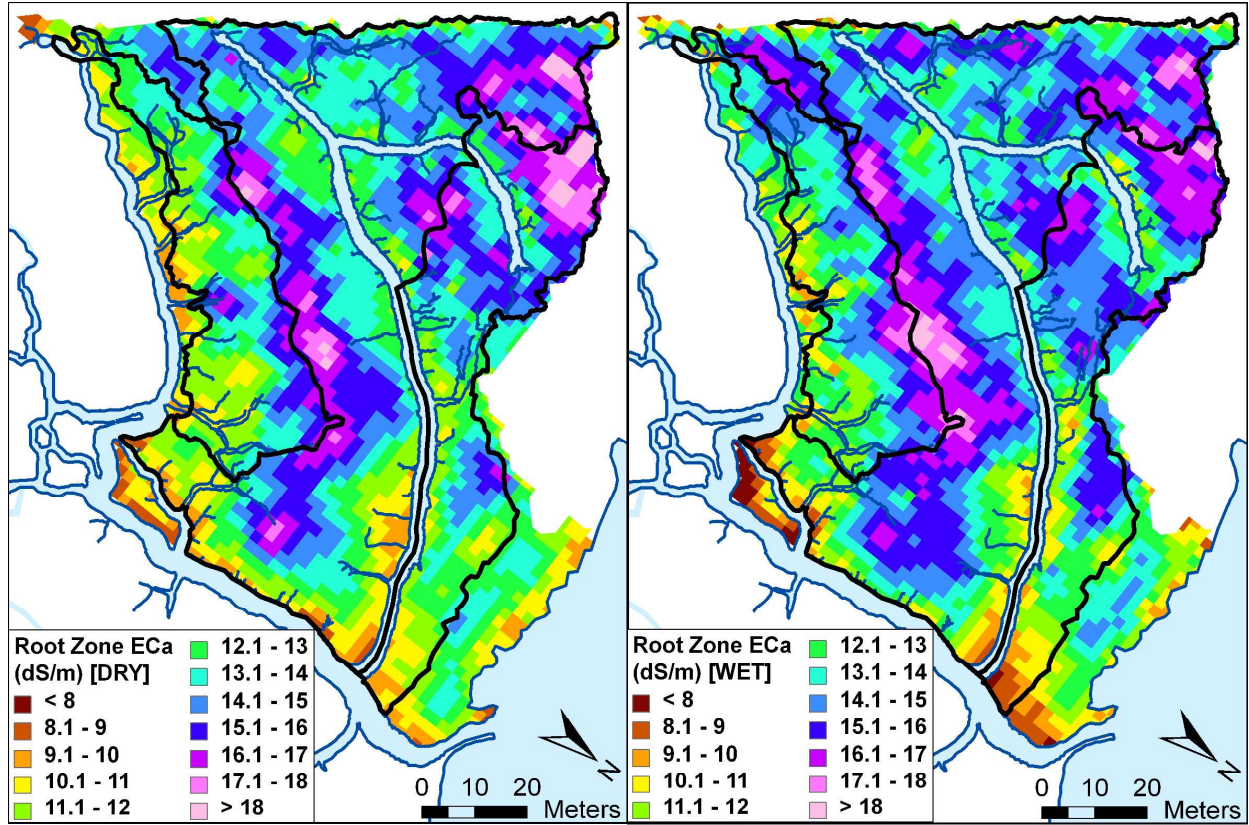
626 Figure 1a, 1b.



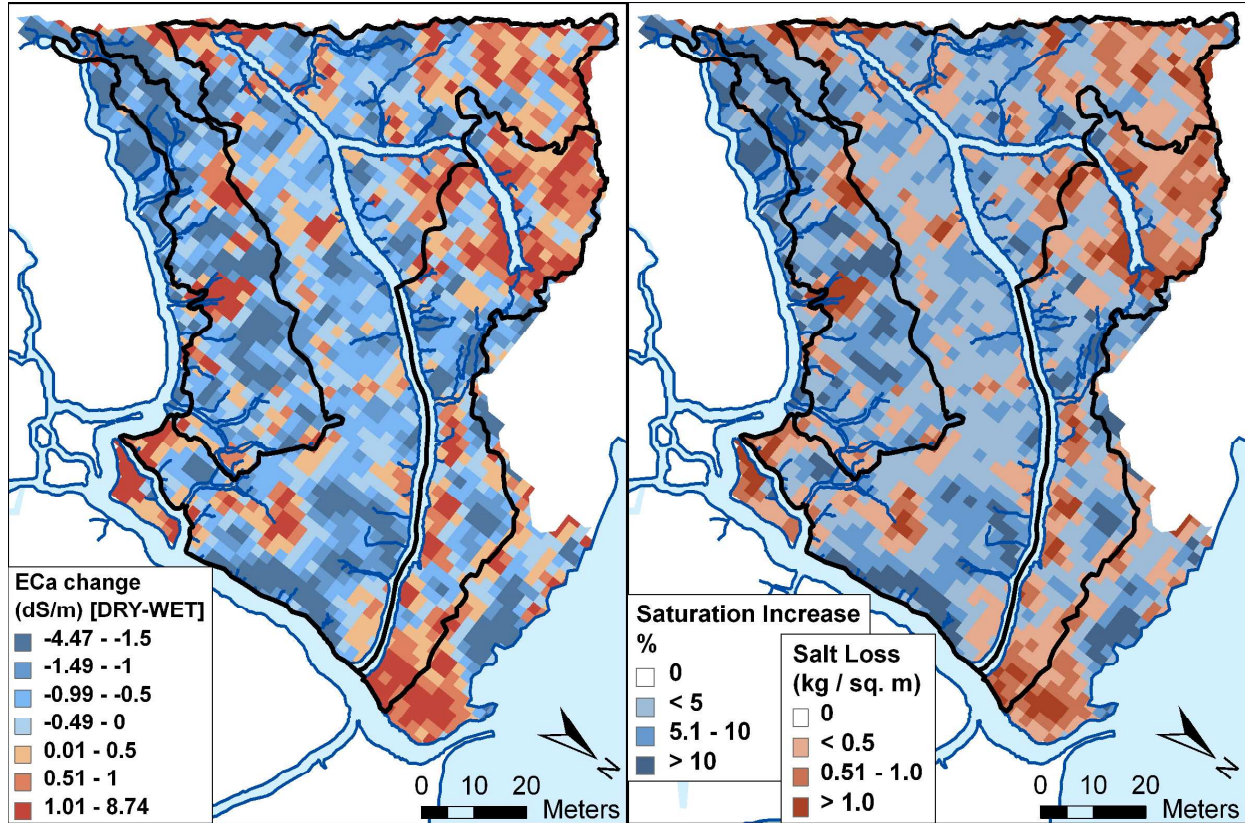
627 Figure 2a, 2b.



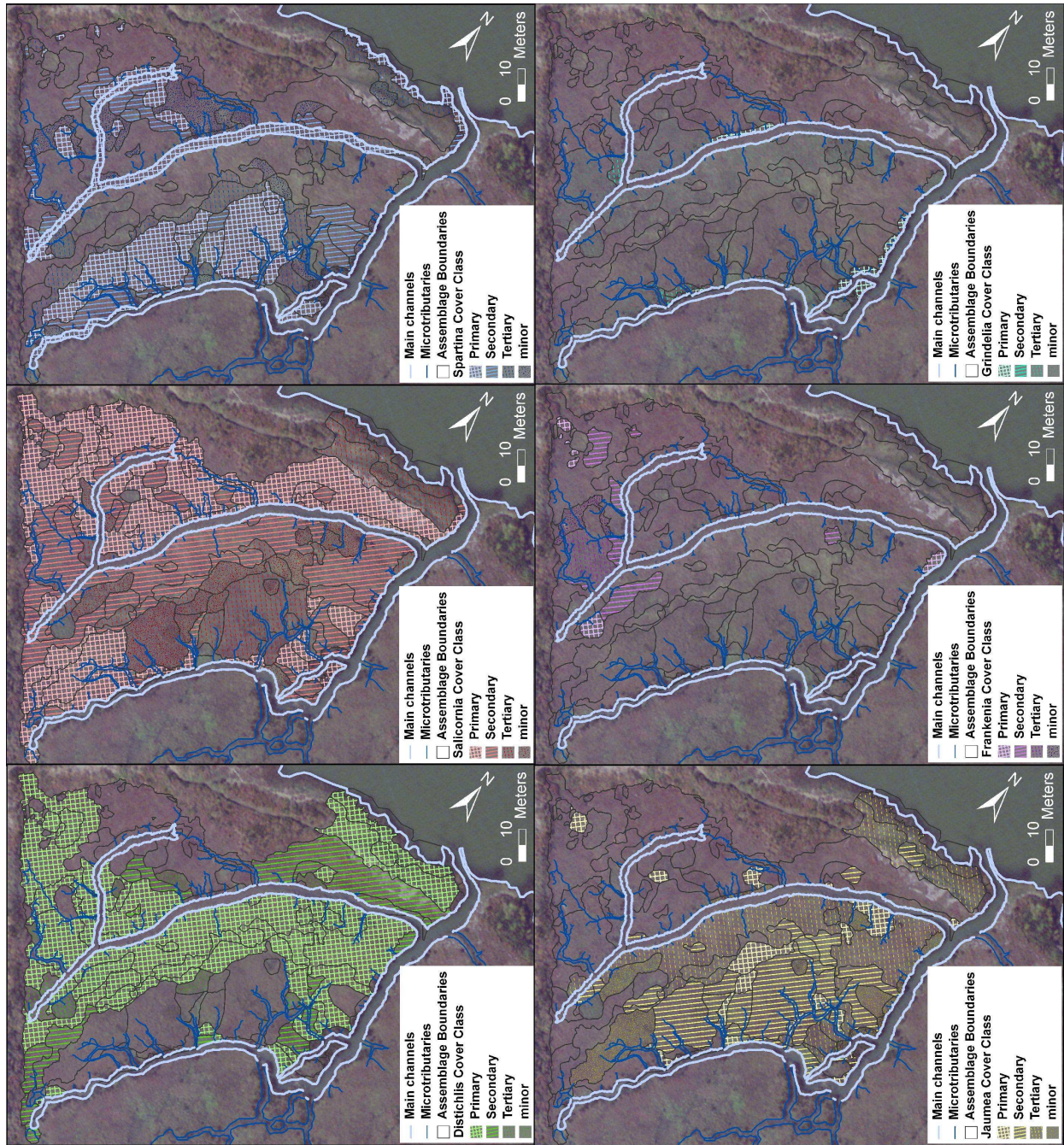
628 Figure 3a, 3b.



629 Figure 4a, 4b.



630 Figure A1.



631

Table A1. Relation of ECa Data to Soil Properties			
Property	Sample Statistics		Correlation with ECa
	Mean	Standard Deviation	
Soil Paste Extract Electrical Conductivity ⁱ (ECe, dS/m)	68.9	15.0	0.67
Soil Pore Water Electrical Conductivity ⁱⁱ (ECw, dS/m)	57.2	7.0	0.53
Soil Volumetric Water Content ⁱ (θ)	0.83	0.15	0.43
Soil Clay Content ⁱ (%)	61.8	9.4	0.51
Soil Temperature ⁱⁱⁱ (dry conditions, °C)	13.98	0.54	--
Soil Temperature ⁱⁱⁱ (wet conditions, °C)	11.56	0.41	--
Tide Water Electrical Conductivity (EC _t , dS/m)	33.4	--	--
ⁱ N = 23, ⁱⁱ N = 17, ⁱⁱⁱ N = 14			

632