Salt Marsh Secrets

Who uncovered them and how?

By Joy B. Zedler

An e-book about southern California coastal wetlands for readers who want to learn while exploring

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This e-book records favorite stories about salt marsh secrets that my collaborators and I uncovered while studying southern California coastal wetlands, from the 1970s to date. In 1986, we became the Pacific Estuarine Research Lab.

Please download the files as they appear online and enjoy learning what we learned…and more. You'll meet many "detectives," and you'll be able to appreciate how they learned so much--undeterred by mud and flood. Learn while exploring the salt marshes near you!

Each chapter (1-21) is being posted at the TRNERR as a separate file (PDF).
Chapter numbers precede page numbers (for chapter 1: 1.1...1.14).
Layout by Emily L. Rosenthal. Photos by the author or as noted.

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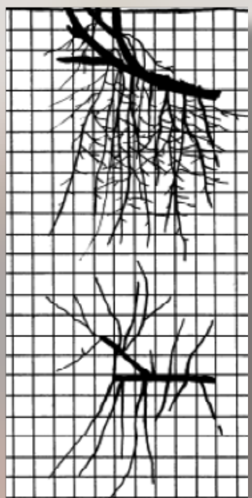
Water and salt explain a lot about salt marshes

"Salt marsh" is a good name for a place that is often flooded with seawater. But seawater influences a lot of coastal habitat that is not salt marsh—especially rocky shores and sandy beaches. So what's unique about salt marshes? It's about particle sizes! Salt marshes develop on substrates with fine particles (silt and clay), not sand or pebbles or cobbles. And salt marsh plants have to tolerate both the flooding and the salt.

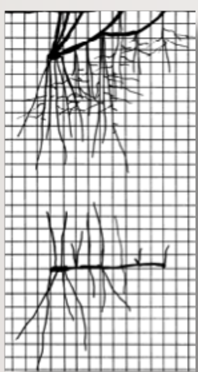
How hydrophytes deal with water

Hydrophytes are water-adapted plants that have lots of air tissue. Living in a marsh requires roots that can anchor the plants in waterlogged, anaerobic (anoxic, without oxygen) mud. But a root can only grow as deep as its oxygen supply can keep cells alive.

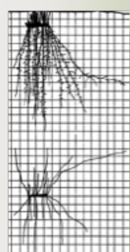
Salt marsh plant roots appear below, first in a side profile, and below in a top-down view (from Purer 1942). Three species on the left have rhizomes (belowground stems) with attached roots; two on the right have carrot-like tap roots with radiating roots (along the radii).



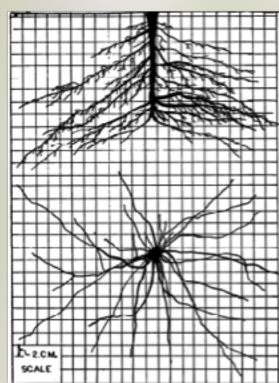
Cordgrass, grid = 3 cm



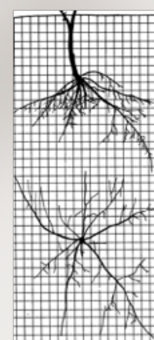
Perennial pickleweed, grid = 2 cm



Love grass, grid = 1 cm



Sea lavender, grid = 2 cm



Sea blite, grid = 1 cm

• Calculation: How deep and how widespread were the root systems of the above species? Hint: The scale changes, so multiply the grid by scale and by the number of grid lines.

• It's hard to know how well each image represents each species. How would you obtain representative samples to quantify root depth and spread? I don't recommend digging in the salt marsh (that requires a permit); however, a research project might involve growing plants from seed (after obtaining a seed collection permit from the manager). Try creating "pots" like small "ant farms" (glass plates enclosing a narrow slice of soil) to make the roots spread in a flat plane. As the roots grow next to the glass, you could measure their depths.

• If you water each pot to a different depth, you can see if roots grow into the saturated soil. Think about all the things you would need to do to make sure that the only variable is water depth. Hint: same soil, same planting dates, same lighting….etc. It's not easy being a scientist, but it's exciting to uncover secrets!

Two more problems with inundation (being covered with water) are the reduced light that reaches leaves and the leaf's loss of access to carbon dioxide, which is needed for photosynthesis (trapping energy). And when the soil is wet, the bacteria and roots use up the oxygen that is left from the last low tide "aeration" event. So, for roots to grow, oxygen has to move from the leaves to the roots by moving through the moist aerenchyma (air tissue). Plants that have lots of aerenchyma can live in wet soil.

Hydrophytes have not revealed all there is to know about coping with anaerobic conditions. Secrets remain to be uncovered for both halophytes (salt-tolerant plants) and glycophytes (non-salt tolerant plants)! Would you like to uncover secrets about how marsh plants cope with water and salt? Would you call them halophytic hydrophytes or hydrophytic halophytes? These descriptive names are intended to help with communication, but do they? I'll avoid them by talking about salt first, using just the term, halophyte.

How halophytes deal with salt

Salt is a problem, even for halophytes because too much salt in the soil reduces the ability of roots to take up water, and too much salt in the plant can cause sodium toxicity (damage to plant enzymes that catalyze important reactions in plant cells).

Halophytes harbor many secrets about how their seeds, seedlings, and maturing plant tissues cope with salt. Maybe some of you will explore these amazing adaptations further. Some halophytes exclude salts at the root surfaces, taking in the H_2O without the NaCl. Some plants take up the salts (which are potentially toxic) and excrete them. Some of the salt crystals might simply be from a drop of seawater evaporating from the surface of a leaf, but the presence of lots of salt crystals indicates excretion. Tiny salt glands on the leaf surface are responsible. More secrets await discovery about how halophytes cope with high salinity. Some animals have salt glands, too (see Belding's Savannah sparrow, below).

Wilted sunflower (hydrogold.com/jgp/images)

Salt marsh plants either exclude the salts from entering the roots or tolerate the toxicity of salt. Not many plants can do that, and not many plants are found in both kinds of marshes. Halophytes tolerate salt; glycophytes do not.

So here's a puzzle—why can't halophytes thrive in freshwater marshes? My hypothesis (what I think is true) is that halophytes have been selected for salt tolerance, not tall stems. They use up some energy dealing with salt, so they can't grow as robust and tall as glycophytes in freshwater marshes. So, they lose out to competitors (species with similar needs).

And why can't freshwater marsh plants thrive in salt marshes? That's easier—glycophytes cannot tolerate salt. Sodium (the Na part of sodium chloride, NaCl) poisons their enzymes and the salty soil draws water out of the plant roots. That is the opposite of what glycophytes need.

In tidal marshes, seawater alternately floods and drains the marsh, with the daily rise and fall of tides. Salt and tides are inter-related. Where there is tidal influence every day, seawater can maintain a near-constant water salinity at about 35 parts per thousand (3.5%). On a hot day, the seawater warms up while it covers the salt marsh, and as the tide recedes ("ebbs" or flows out), water evaporates and salt is left behind. Sometimes you can see a white crust on the soil and on plants and on debris.

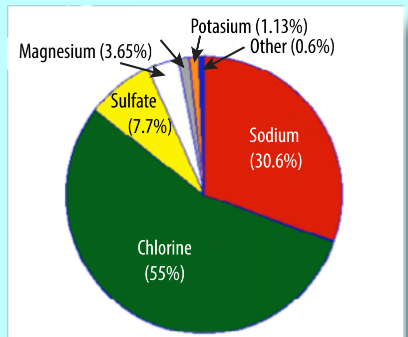
Simple demonstrations you can try at home:

• Taste how salty the ocean is (but don't drink more than a drop or two): Mix 3.5% salt water (using table salt, which is NaCl) by adding 3.5 teaspoons of table salt to 100 teaspoons of water. Rather than count 100 teaspoons, calculate how many cups of water that would be: 1 cup has 16 tablespoons, and each tablespoon holds 3 teaspoons. So 1 cup has 48 teaspoons; 2 cups have 99 teaspoons, so about 2 cups of water with 3.5 teaspoons of salt have about the same salinity as the ocean. Or, use the metric system (so much easier), either using volume or mass: Add 3.5 ml salt to 100 ml of water, or add 3.5 g salt to 100 g of water. Taste only a drop…..it's too salty to drink. Yuck!

• Another experiment: Take a cup of the 3.5% salt water and dilute it with another cup of freshwater in a pint jar. Taste a drop—is 1.75% salt still too salty. Yes! Don't taste more than a couple of drops. Then take the jar with 1.75% salt and discard a cup, replacing it with freshwater. Now you have 0.87% salt. Taste a drop—is it still too salty? Probably. One more dilution will bring it down to 0.43% salt.

• Use an eye dropper to put 5 drops of each solution in separate jar lids, arranged to compare low to high salinity, and put the lids in the sun to evaporate the H_2O. Did you recover salt crystals in proportion to the amounts the solutions contained?

• If you're interested in germinating seeds, compare the number of lettuce or radish seeds that germinate when watered with the lower 1-2 salt concentrations. Lettuce seeds are a good "indicator," because they germinate quickly. A simple set-up is to use plastic jar lids (if you don't have access to petri dishes). Pam Beare invented the following routine for germinating cattails seeds (chapter eleven): Cut a square of styrofoam from a meat tray, place it in the bottom of the jar lid, add a piece of paper towel that hangs over the edge of the styrofoam, and count out 25 seeds for each container. Over the next 4 weeks, watch for germination. Do you see decreasing numbers of seeds with increasing concentrations of salt? Do you think that salt prevents upland weeds from invading salt marshes? I do, and our research agreed for many weeds (more information in chapter six).



Salts in Seawater

(from The Ocean Health Team)

• Seawater has 3.4 to 3.5% salt, on average.

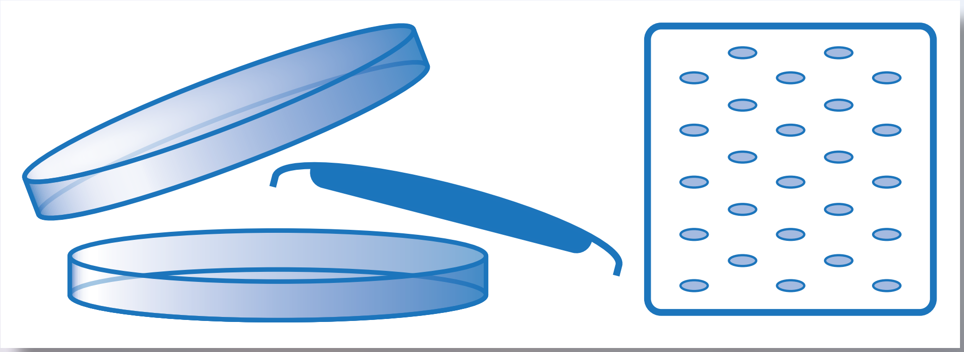
• Salt usually refers to sodium chloride (NaCl) but, while seawater is mostly water (H_2O) and NaCl, it also includes magnesium, sulfate, calcium, potassium, inorganic carbon (as in carbon dioxide and carbonates), bromine, borostrontium and fluoride.

• Saline generally means salty, but when compared to less salty water, there are three descriptive classes: freshwater has 0 to 0.5% salt; brackish water has 0.5 to 3% salt; and saline water has more than 3% salt.

• Hyposaline refers to low-salinity water that is less salty than saline.

• Hypersaline refer to high-salinity water that is more salty than 3.5% salt.

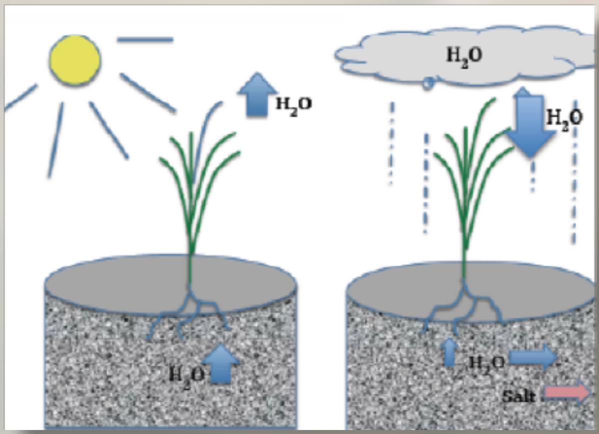
• Salinity means the level of salt in a solution.



Left: Side view of petri dish. Right: Top view with 25 seeds plated onto wet paper.

The above activities demonstrate that salt is soluble, that salt is recoverable upon evaporation of the water, and that even low concentrations of salt taste salty. Salt water isn't safe to drink, just as it is not good for garden plants (not for seeds or seedlings or adult plants).

In the tidal marsh soil, salt becomes concentrated when plant roots take up water (H_2O) and leave the NaCl and other salts behind. Upslope toward the high marsh, soil salinity is increasingly variable. High marsh soil becomes more saline with evaporation, but less saline with dilution during a rainstorm at low tide. The cordgrass soil salinity is usually around 4.0 to 4.5% (40 to 45 parts per thousand), while the high marsh soil can range from nearly fresh to several times as salty as the ocean. I admire plants that can tolerate such variation.



Most of the water moves upward, except at low tide during heavy rainfall, when salt is leached out of the soil.

It is amazing that roots can take up water from salty soil. One trick is to accumulate certain chemicals in the roots so that the water will flow in; we call them osmo-regulators (e.g., glycine-betaines, prolines and mannitol). Without the ability to take up water from saline soil, roots would lose water, shrivel and die.

A second trick is to keep salt from being taken up along with the soil water. This trick involves salt exclusion by root cells. This is not an easy task, because cells have to pump sodium out while still letting in calcium, magnesium, potassium and other useful cations (positively charged ions, like Ca^{++}).

A third trick is for the halophyte to allow the salt in and sequester (store) it where it can't cause mischief. Hiding places include vacuoles (bags of liquid) within cells where the NaCl can't contact delicate cell components (chloroplasts that photosynthesize; and mitochondria that respire).

A fourth trick is to let salt in and pump it out through specialized salt glands. Look on the lower surfaces of leaves of alkali heath, salt grass, cordgrass, and sea lavender. Where you see lots of salt crystals over the leaf, they were probably excreted as salt solutions that then dried to form crystals.

• Salt hairs sequester (store) salt where it doesn't harm the plant. Hairs can actually benefit plants by reflecting sunlight and reducing leaf temperatures on hot days: Inspect the hairs on matscale (*Atriplex watsonii).*

• Succulent stems and leaves store water; the idea is to dilute the salt: Pickleweeds are good examples of succulent stems. Salt wort leaves seem to accumulate salt; then the plant drop the leaves as a way of disposing excess salt.

• Leaves fold up to reduce water loss. This is a common characteristic of grasses: Compare leaves of salt grass where they are wet and where they are much drier.

Animals have to deal with excess salt, too, and their adaptations deserve more research. Birds can't always avoid drinking or eating salt. The water and foods that Belding's Savannah sparrows consume contain salt, so these birds need some way to dispose of excess salt. Ornithologists (people who study birds) have learned that Savannah sparrows have salt glands (like some plants have). Our state-endangered Belding's Savannah sparrows (photo by Abby Powell) can live year-round in the salt marsh by excreting excess salt through their nares (nose cavities).

What would you expect to happen to the estuary's water salinity when rain falls during high tide? A small, local rainfall event won't change the salinity of a large body of seawater, so I would not expect rainfall during a high tide to have much effect on the salt marsh. Why? Because there would be lots of ocean water present inside the estuary at high tide. But, what if the rainfall event is large and the storm extends over much of the watershed**?** Then, the estuary water and the marsh will be diluted by fresh floodwater, not just local rainfall.

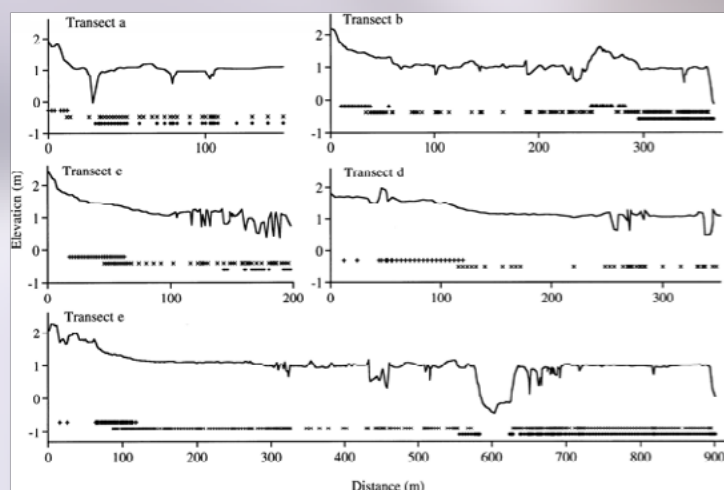
(Modified from trw.sdsu.edu/images/trw_graphic.jpg)

Besides inundation and salinity, what else influences plant distributions?

The Californian Biographic Region extends from Point Conception near Santa Barbara south along the Baja California Peninsula. We had to visit Mexico to explore the least disturbed marshes and to characterize salt marsh plant distributions fully. Our 848 sampling plots and elevations across Volcano Marsh showed that the salt marsh canopy only looks flat and smooth. The marsh is not homogeneous (uniform), however--not at the macro- or microtopographic scale. In chapter eight, I discuss how microtopography affects plants and animals. Here, I describe some effects of macrotopography.

TIDAL SUBSIDIES. Volcano Marsh has several large tidal channels, which show as big dips in the cross-sections of its intertidal topography. When we summarized our data, we realized that cordgrass was not only restricted to low elevations but also to areas next to a channel or bay. Restriction to low elevation indicates inundation tolerance, while restriction to a tidal channel or bay indicates that it also requires more than average tidal mixing. Near channels and bays, there is greater influx (movement in) of oxygen into the soil and efflux (movement out) of accumulated wastes. Atlantic Coast ecologists have called this mixing a "tidal subsidy." The tides subsidize (add something extra to) marsh productivity.

Cordgrass occurred only at the bayward margins of Volcano Marsh, even though "suitable" elevations were present further inland. Additional sampling in the Sweetwater Marsh of San Diego Bay revealed a similar pattern (Zedler et al. 1999).



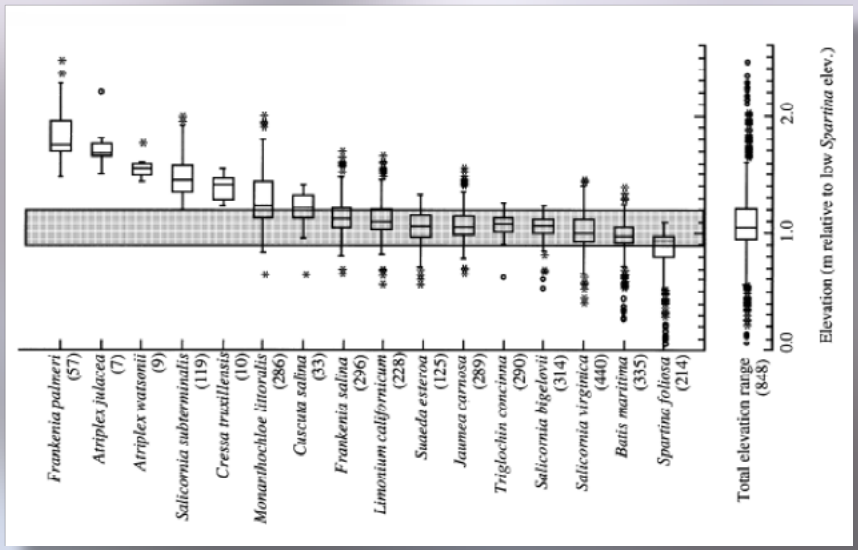
Below each transect are symbols for occurrences of glasswort (top row: ++++), perennial pickleweed (middle row, xxxx), and cordgrass (bottom row: ••••).

There were more secrets about the influence of tidal creeks: While most species occurred primarily within the marsh plain (a 30-cm elevation range), four species tended to "avoid" the lower 10 cm of the marsh plain except within 1 m of a tidal creek. These were alkali heath, sea lavender, sea blite, and annual pickleweed. Species richness (number per 0.25 m^2) was, on average, 0.6 species greater at the margins of tidal creeks. We hypothesized that the soil near creeks drained better during low tide and reduced the stress of anaerobic conditions (= tidal mixing = tidal subsidy).

In other words, nearness to tidal creeks interacted with elevation. Well-drained creek margins were less often waterlogged than soils of interior flats and pools. At the creek edge, we hypothesized that the soil had more air and oxygen, and roots were less stressed.

This kind of pattern had been studied for cordgrass in Atlantic Coast salt marshes. Later, I talk about studies that claimed the difference was genetic (a supergrass along creek edges), while other authors said it was environmental. The latter authors transplanted creekside plants inland and inland plants to the creek edge. Next year, when the short plants grew tall and the tall plants were shorter, the researchers knew that genetics were not controlling height. The debate was about "nature versus nurture" and it continued for many years, because, like many debates, there was evidence for both sides. Nature is complex. Patterns don't always have the same causes.

ELEVATION AND DIVERSITY. The Marsh plain is pretty flat but it is not "plain" by being ordinary. Instead, it is complex in response to tidal channels, creeks, and rivulets, all organized into networks that spread out the incoming tide water and re-collect the outflowing tide water. In the graph below, we considered the 30-cm elevation range (shaded) to be the marsh plain. Above is the high marsh; below is cordgrass. Read more about diversity in chapter ten.



The eight species most common on the Volcano Marsh plain and their frequency (% occurrences in 0.25-m² plots) were

Annual pickleweed (63%),

Perennial pickleweed (62%),

Arrow weed (58%),

Salt wort (52%),

Salt marsh daisy (48%),

Alkali heath (44%),

Sea lavender (35%), and

Sea blite (18%).

We spent several days sampling 848 plots at Volcano Marsh. On the marsh plain, 90% of our plots included 3 or more species, with an average of 4.38 species (±0.08 standard error; see next page).

• What do the average and standard error tell us? Average (= mean) values are simply the total divided by the number of values in a sample. If I sample 5 plots and find that they have 1, 2, 3, 4, & 5 species, the data range from 1 to 5, and the average = 15/5 = 3.

• What's the standard error? A measure of variability in the data. The standard error for the above data is 0.71. If all 5 plots had 3 species (3, 3, 3, 3, 3), the mean would still be 3, but there would be zero variability (S.E. = 0.00) — a rare situation in ecological data! If the plots have 1, 1, 3, 5, & 5 species, the average is still 3 but the variation is quite high, because two plots are well below the average, and two are well above it. The S.E. in this case = 0.89.

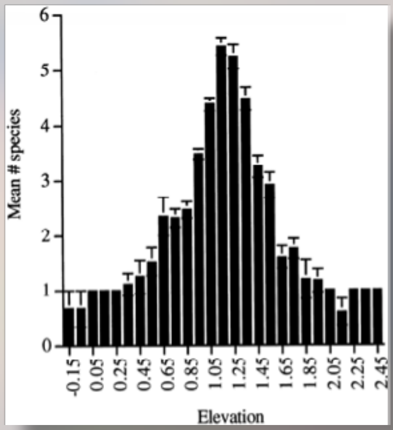
• For large samples with many data, like those in the histogram below, the number of times you encounter 1s, 2s, 3s, etc. of form a "bell-shaped curve" (or histogram). For these data, the mean at the top of the bell = 4.38, and the S.E. is low (0.08) relative to the mean.

• Take home message: when an author reports only the average of some data, be sure to ask "yeah, but what about the standard error?" And when the S.E. sounds large, you might also ask, "so what was the range in the data, and were there any outliers. Have fun with statistics!

Plots at the lowest elevations had the fewest species, especially plots with cordgrass. That's no surprise—Edith Purer noted that in 1942. But we quantified the differences and found a bell-shaped distribution:

This histogram shows the average number of species found within 0.25-m^2 plots at each 10-cm elevation class. Why do you think the intermediate elevations had the most species per plot? Why do you think the average species richness is so low (fewer than 6 per plot)?

On this graph, the marsh-plain elevations = midpoints of 10-cm classes, relative to the lower limit of cordgrass (our "benchmark" because there were no markers for actual elevation). The marsh plain classes were 0.95–1.15 m above the reference point; high marsh was 1.25–2.05; upland was >2.05.



Species richness x Elevation

SECRET COMPLICATIONS. With hundreds of plots and elevation measures, we were able to update Purer's idea that salinity and elevation determine salt marsh plant occurrences. Our new model is that: Elevation is a very useful, *but incomplete*, indicator of environmental conditions. Landscape position and tidal creek topography are important additional variables. Proximity (nearness) to creek edge appears to affect species distributions by altering soil moisture, nutrient supply, and removal of wastes (such as excess salt on leaves and soil). Tidal creeks add heterogeneity (roughness, bumps and mounds) to the relatively flat topography.

Are there more secrets to learn about which plants occur where and why? Yes there are! Read on…..

Why are some salt marshes dominated by just one species, perennial pickleweed?

Perennial pickleweed dominates Los Peñasquitos Lagoon and Mugu Lagoon. Both marshes have a history of being nontidal for prolonged periods of time. If the salt marsh you visit most often appears to support more perennial pickleweed than any other plant, you might suspect that the marsh has a history of reduced tidal influence.

When lots of sand moves alongshore, it can block the estuary or lagoon mouth. When that happens, the saline water and soils evaporate water and become hypersaline. The superior ability of perennial pickleweed to grow in hypersaline, nontidal conditions is part of the reason that this plant species is so widespread and often dominant. I think that it can survive nontidal conditions by producing deep roots where tides do not keep the soil waterlogged. I saw this in 1984 when Tijuana Estuary was nontidal for 8 months. Perhaps perennial pickleweed gained an advantage by taking up less-salty water deep in the soil (groundwater). Once the pickleweed becomes dominant, it tends to remain dominant. More work is needed to uncover its secret ability to dominant the lagoons that are not always open to tidal flushing.

A scientific benefit of monotypic pickleweed is that you can study this dominant species without interference from other species.

(Mugu Lagoon; Aerial Photography of So. CA, Ventura County region)

Dr. Chris Onuf uncovered the secrets of perennial pickleweed growth in Mugu Lagoon by putting tags on branches in his research plots and measuring and re-measuring and re-measuring month after month!

The marsh at Mugu Lagoon is dominated by perennial pickleweed near the water's edge and further inland, although eight other halophytes co-occur with pickleweed further from the water's edge.


Chris uncovered all of these secrets at Mugu Lagoon:

• Perennial pickleweed grows year-round both belowground and aboveground, but its branches grow most robustly in summer. Perennial pickleweed produced new branches in every month except January. At times, Chris found new branches even while plants were declining in total biomass.

• A fourth of the annual production occurred after peak biomass. This was news! Most productivity studies compared biomass harvested at the low point (often March) through peak biomass (Aug.- Sept.). By sampling only between the low and peak biomass periods, he would have estimated just 80 $g/m^2/yr$.

• Perennial pickleweed annual productivity was relatively low; it averaged only 240 g dry weight/m^2/year. That is about a fourth what we measured for cordgrass in Tijuana Estuary.

• Despite low annual productivity, pickleweed provides an evergreen canopy all year long, while cordgrass stems and leaves die to the ground in October and don't resprout till spring.

• Pickleweed did not establish seedlings at Mugu Lagoon, even though it produced many seeds. In Chris's many visits (and with his sharp observation skills), he would have seen any that appeared in his study plots. As you will read in a later chapter, we only saw masses of pickleweed seedlings in excavated restoration sites. Most of the time, it reproduces vegetatively, via rhizomes.

• The marsh plain had very patchy plant cover.

Chris explained the low productivity of pickleweed and low plant cover by considering materials washed in with the tides. Debris that flowed into the marsh sometimes settled on vegetation and remained long enough to shade or abrade (wear away) living plants (Onuf 1980). Chris characterized pickleweed productivity as uniform over time but patchy over space.

I think perennial pickleweed grows until it becomes top heavy, then tide water or winds break the tallest branches. I once saw a plant at Goleta Slough that grew next to a chain-link fence. It was about 2 meters (6 feet) tall, thanks to its unnatural "crutch." And at Tijuana Estuary, it grows taller where it can lean on a sturdy shrub near the upland. Without such crutches, it remains short.


Cathi Bonin revealed another of perennial pickleweed's secrets: Perennial pickleweed is not superior in very many attributes (read more in chapter ten). In fact, the ability to grow tall is a key trait that allows this plant to become dominant in so many salt marshes. While other perennials die to the soil surface, this one retains its aboveground stems, adding branches year after year. OK, some branches fall off, because they're rather brittle. How might losing some branches be adaptive?

So, who will test the hypothesis that perennial pickleweed height has mechanical limits on height? Maybe normal cell mortality causes the taller branches to break off. Maybe herbivores munch the youngest juiciest branch tips. After all, even people eat perennial pickleweed. Of course, it's called "sea asparagus" or "samphire" on restaurant menus.

Note of caution—don't collect plants in salt marsh reserves and don't taste plants in the field. Germs can be present in the inflowing runoff and blowing dust.

EPISODIC EVENTS: My colleagues, Drs. John Callaway and Gary Sullivan, and I learned a lot by trying to establish native plants in two restoration projects within Tijuana Estuary (read more in chapter eighteen). The first and most basic lesson was that a species can't necessary establish where it thrives as an adult. How can that be? It can be true if the conditions that favor establishment are episodic (unusual events) and not recurring during your project!

Episodic means happening suddenly and occasionally. In southern CA, for example, the Pacific Decadal Oscillation is a climate phenomenon that operates over periods of 20-30 years, then swings back to an alternative pattern for 20-30 years, like a pendulum. Our attempts to plant marshes took place during the stormy decades, and major storms were always a possibility--either floods from the watershed, with days of freshwater inflows from the upstream watershed, or sea storms, involving strong winds and dune overwash during high tide. High seawater anomalies were sometimes 30 cm higher than predicted tides. Those were exciting events.

This photo shows Tijuana River mouth in a non-flood condition; on the right (obviously) is the flooded condition.

A secret impact of major storms was revealed in 1984. When Tijuana Estuary closed to tidal influence that April, the salt marsh lost much of its plant and animal diversity. Perennial pickleweed became dominant, even where a dozen plant species had previously shared resources.

The years of flooding began in 1978 and continued intermittently for over 20 years. The salt marsh did not fully recover from the 1984 nontidal drought, in part because floods brought in enough sediment to elevate the salt marsh plain. A higher, drier plain gave pickleweed a big advantage. But do not despair; that sediment will be needed in the future (Think about sediment accumulation as an essential way for a salt marsh to keep up with rising sea level; and read chapter eight).

In the salt marsh, another kind of extreme event—major freshwater flooding--allows cordgrass to establish from seed. Ever wonder how plants spread from one estuary to another? One way is for plant fragments to wash out of one river mouth and float alongshore into another estuary. Another way is by seeds getting stuck to the feet and feathers of waterfowl. Perhaps a wind blows seeds long distances during ferocious storms.

Regardless of how cordgrass made its way into Tijuana Estuary, it was there in abundance from the earliest record (Purer 1942). Strangely, it never seemed to produce many seedlings. Instead, it would expand as a clone through vegetative reproduction (sending out new "tillers"). Recall that a clone is a group of individuals that were produced vegetatively from a parent. All that parent's offspring have the same genetic make-up as the parent. Why might that be a problem in the very long term?

A tiller is a young grass stem that sprouts vegetatively from a parent's stem. The rhizome is an underground stem. Other plants (like love grass) have aboveground stems that run along the soil surface ("runners"). Along a trail you sometimes see them running for a meter or more. Once they the substrate is suitable, the runner produces roots. And with new resources from those roots, they are all set to "run" further. Why don't all plants do this? I don't know, but I do know there are many strategies that lead to the "desired outcome," which is to survive and reproduce.

Ecologists have used military terms to describe two extremes of clonal expansion—phalanx and guerilla. Who says plants are dull? They battle one another for territory, in rhizome-to-rhizome combat. If a lot of rhizomes grow a short distance and produce a sharp boundary, like a wall of marching soldiers, it's called a "phalanx." If a few rhizomes grow long distances before popping up in enemy territory to infiltrate the stronghold….you've got it; that's a guerilla tactic.

Cordgrass can produce new stems both in guerilla and phalanx forms. The sharpest boundary I ever saw was at Volcano Marsh in San Quintin Bay. The sharp edge could have been caused by something underground besides an overly ambitious rhizome. Perhaps there was a buried ledge of ancient lava. I can also imagine a tangle of dead eelgrass burying the edge of the clone and halting cordgrass growth along a straight line. A deposit of wrack (floating debris) could have broken up and floated away sometime before my visit. I never had the opportunity to test that or other potential causes of sharp vs. gradual edges, which could include genetic differences. Are there more hypotheses about clonal expansion? I'm not fond of schemes that classify plant traits into two or three alternatives. Upon a closer look, you might find intermediate examples.

So far, I've described vegetation patterns from place to place (spatial variation). But the salt marsh is also variable from year-to-year. One year, to my surprise, cordgrass produced hundreds of seedlings in the tidal mudflats (former sewage lagoons) at Tijuana Estuary. The same year, small clones of cordgrass expanded to form larger clones. It was after a big flood event, suggesting that lowered salinity stimulates both seed germination and seedling establishment. No one had planned a study, but coincidences like more reproduction during flooding are hard to ignore. I marked many of the clones with stakes and began measuring clone diameters, repeating those measures in following years. Voila! They expanded more rapidly during the flood year (Zedler 1986). A decade later, we learned how and why it happened. Read on….

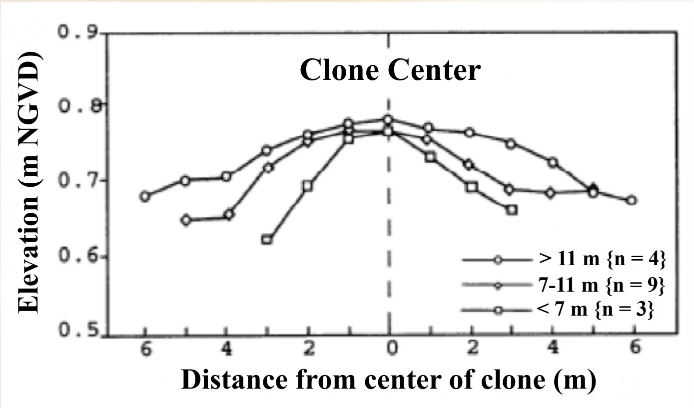
The heavy winter storms of 1993 during El Nino Southern Oscillation (ENSO) brought in sufficient sediment to allow clones of cordgrass to establish in a large 16-acre (6.5-ha) mudflat in northern Tijuana Estuary. In 1997, we counted >80 new clones (see map in chapter eight). How about the seedlings?

Kristen Ward decided to study how cordgrass establishes from seedlings. How could she measure plants on a soft squishy mudflat, where you can sink into the mud above your knees? Her secret? Use a canoe!

Kristen hypothesized that the clones, once established, would increase sedimentation by slowing the flow of water at the very small scale. With slower flow of sediment-laden water, the clay and silt particles would settle out among the plant stems. This would be a positive feedback (that is, sedimentation → plant establishment → sedimentation). Kristen measured 4.0–12.7 cm of sediment accretion during the 1997–1998 ENSO flooding, In the non-flood year, 1998-9, sediments accreted only 1 cm/yr.

The clones that grew from seedlings had dome-shaped mounds, suggesting higher sediment retention rates within the older stems in the middle of the clones than at the younger edges.

Elevation data are meters above NGVD = the national geodetic vertical datum, which is the mean sea level in 1929. Because sea level changes, coastal scientists use a specific reference year, often 1929.



Here are average elevations in October 1998, moving outward from the centers of small, medium, and large clones.

The dome shape is also consistent with a positive feedback (more sedimentation → more robust cordgrass → greater ability to accrete sediment→ more sedimentation). Another secret uncovered.

SUMMARY. Plants grow almost everywhere on earth, in sizes, shapes, and functions that suit their local environment. It is much easier to document where they grow than to learn why. In salt marshes, salt and deep water (leading to waterlogged soil) are key stresses. Mechanisms for dealing with NaCl include avoiding, sequestering, and excreting salt, but more needs to be known about which plants use each strategy. Mechanisms for tolerating deep water are to grow tall, like cordgrass, and to have large air spaces in the leaves, stems and roots so all living cells have access to oxygen. Recall that oxygen is a by-product of photosynthesis, but it certainly is not a waste product in anaerobic (anoxic) soil.