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.

PDF name and brief description:

Testing theory related to restoration

Using theory to restore salt marsh vegetation

Ecological theory helps practitioners plant restoration sites by predicting what to plant where. In the newly-excavated Model Marsh (photo in early 2000, below), cordgrass was planted at elevations predicted to be appropriate for this low-marsh halophyte. The prediction was correct.

Theory was not sufficient to predict how densely the ramets of cordgrass needed to be planted, however. Thus, we recommended an adaptive restoration approach, involving a large field experiment with plots to compare denser and less-dense plantings. After a few years, it was difficult to distinguish the outcomes. Thus, the restoration effort advanced theory by indicating that initial planting density was less important to growth than other factors, such as planting time. Theory helped restoration and adaptive restoration advanced theory.

Theory could not predict the delayed start date, which forced plantings to occur when tidal amplitudes were narrow. Theory did explain outcomes of planting halophyte seedlings, however. Plants in tight clusters had higher survivorship than those spread apart. Science helped the practice of ecological restoration, while restoration experiments improved the science of restoration ecology.

Pure and applied science

If you pursue studies in science, eventually you will encounter the terms applied and pure (a.k.a. basic) science. People seem to love having two alternatives or clear choices, whether they are real or not. We call them "dichotomies." Are we more comfortable in a world with strong contrasts? Are we uncomfortable considering gradients or spectra, instead of discrete conditions? Even in the field of ecosystem restoration, some authors draw lines between science and practice. I am not among them.

After 50 years "in the restoration arena," I find it hard to make clear distinctions between science and practical applications. I'm not always sure when I'm acting as a scientist or when I'm applying science as a practitioner. Mostly, I do both….or try to, as a strong advocate of "learning while restoring." At Tijuana Estuary, my collaborators and I planted the Tidal Linkage salt marsh while testing the importance of diversity to ecosystem function.

Nearly all our research projects and papers have included some test of a hypothesis about how a salt marsh is organized or how it functions, while at the same time suggesting how to restore a site. We offered recommendations for management. In restoration, it's not clear when basic science becomes applied science or vice versa. Adaptive restoration is a combination of testing and applying ideas. The science informs the practice while the practice informs the science!

The lines between basic and applied research are blurry, and I don't see the need to separate them into discrete boxes. Science is about inquiry and testing and revising one's thinking as data and knowledge accumulate. Traditional ecological knowledge develops along similar lines, with practitioners trying new ways of restoring damaged land or repeating old ways and verifying their effectiveness. Over time, practitioners know more and understand more and can make more informed decisions.

Our research on how to restore salt marshes tested practical management methods, while testing theories about limiting factors (light and nutrients), competitive interactions, alternative states, dispersal, diversity-ecosystem function, plant dominance, and topographic heterogeneity.

Testing theory of light limitation

While measuring epibenthic algal productivity (chapter two), a reasonable hypothesis developed: The open canopy. with high light reaching the soil, allowed the algae to be highly productive (photo on right). By comparison, epibenthic algal mats in Georgia, under tall dense cordgrass canopies, were likely limited by low light (see my comparison chart in the Preface of this e-book).

How could we test the light-limitation theory?

Enter Dr. Mary Kentula: In 1984, Mary was looking for a postdoctoral opportunity in San Diego after working on eelgrass ecology along the Oregon shore for her doctoral dissertation. She was eager to try something new. We were a good team, and the Mission Bay salt marsh was a good research site. Our idea was to test the hypothesis that cordgrass canopies allow ample light to reach the epibenthic algae, and that more shade would reduce growth.

Changes in three measures of algal growth were planned for the field study: algal mat biomass, chlorophyll a (chl_a) and primary productivity. Mary also decided to test effects of light intensity, which could be controlled in a lab setting. She ordered materials to make clear plastic chambers, based on a design she had used in her PhD research (like those in chapter two), and set out to measure productivity in the salt marsh.

How would you vary light levels in a stand of cordgrass? Mary wanted to create shade treatments by removing some stems with tall leaves and also add shade where needed for each treatment. Some researchers build frames with window screen to shade plants, but Mary had a much better idea. She could re-use the leaves she harvested from reduced-shade plots, tie the stems to short stakes and "plant" the stakes in shaded plots! It worked; the leaves remained in place and upright, and they shaded the algal mats.

RESULTS: Algal mats could tell the difference between 100% sunlight and reduced light (10, 25, or 50%) caused by an increase in canopy cover. They produced more biomass and chl_a with more light. Differences in productivity and chl_a were more apparent in the summer experiment than during winter. Were there confounding variables? Probably, given herbivores, animal feces, bioturbation, etc. Could she clarify that light alone could cause similar reductions in productivity? Yes; please continue….

In the lab, Mary varied light levels exactly, ranging from low to high (1x, 2x, 4x, and 6x). Results: Productivity increased up to 4x then leveled off. The algal mats seemed light-saturated at 4x. Something else must have become limiting to photosynthesis.

Mary also explored the algae that made up the epibenthic mats. She brought samples of the mats into the lab and used a microscope to tally presence of algal groups in subsamples.

Harry Phinney of Oregon State University helped Mary identify these three groups:

diatoms (including *Gyrossigma obliquum,* which lives in tubes that it secretes),

greens (*Enteromorpha, Cladophora, Rhizoclonium*) and

bluegreens = cyanobacteria (*Microcoleus lybgbyaceus, Oscillatoria lutea, Nodularia* sp.).

Armed with information on algal identity, Mary noticed that the greens, especially *Enteromorpha,* were dominant in winter when soil temperatures were low, while bluegreens were dominant in summer when the soil was ~10ºC warmer. When Mary compared productivity of green versus bluegreen algae given average summer and winter temperatures, she uncovered a secret....

RESULTS: Given winter temperatures and high light, green and bluegreen algae were equally productive (maximum level measured as oxygen release to chamber water). However, given summer temperatures, the pattern differed. The bluegreen algae (cyanobacteria) produced almost 30% more than the green algae. The greens weren't much more productive with summer versus winter temperatures. This result suggested the bluegreen algae are adapted to take advantage of the bright summer sun that reaches the soil through the open cordgrass canopy, especially during daytime low tides.

While Mary was busy testing how shade lowers algal productivity, I agreed to help the Environmental Protection Agency (EPA) develop a national Wetland Research Plan. Writing a national research plan was a new experience for me, and Mary made huge contributions to the effort. When EPA approved the Plan, the EPA lab in Corvallis, OR, advertised for a person to implement it, and Mary was the top candidate. Her career traces back to Mission Bay salt marsh.

Testing theory of nitrogen limitation

The factor that limits plant growth is usually something that is in short supply relative to the plant's needs. Resources that are plentiful don't usually limit growth or cause competition among species. For example, people rarely compete for oxygen. The air is about 19% oxygen, which is abundant relative to our needs (thanks to plants, by the way).

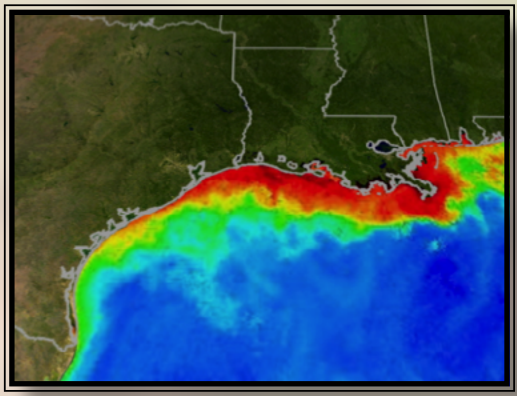
Plants often compete for nutrients, but which one? Nutrient-limitation theory says that phosphorus (P) or nitrogen (N) is usually in short supply relative to the species' needs. Plants don't need a lot of P, but P can be limiting where there is not much available. Plants need lots more N, for enzymes and proteins and compounds that help the plants take up water from a salty solution. Cyanobacteria can fix N to make it available, but at the same time, bacteria in wet anoxic soils are usually busy getting rid of nitrates via denitrification. If denitrifying bacteria are removing nitrates from the salt marsh faster than cyanobacteria are fixing N from the air and supplying it to the soil, that's another reason why N could become limiting.

Elsewhere, ecologists had long debated whether nutrients were limiting plant growth in coastal waters. Was phosphorus or nitrogen the limiting nutrient? P was being blamed for algal blooms in freshwater lakes, while nitrogen was considered the culprit for coastal algal blooms.

Aerial view of an algal bloom in Lake Erie

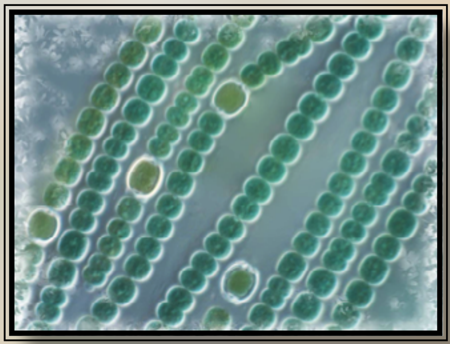
(from cover of IJC 2012).

(d32ogoqmya1dw8.cloudfront.net)



P was blamed for lake eutrophication, because it was present in detergents that were carried in wastewater that flowed toward nearby lakes. At the same time, coastal scientists noticed that "dead zones" were developing at the mouths of large rivers, such as the Mississippi River outflow into the Gulf of Mexico (red area on map). There, algae grew so dense that they clouded the surface water and shaded deeper water, where dying and decaying phytoplankton consumed oxygen and caused fish kills.

Nutrient-limitation theory emerged: Inland lake phytoplankton are limited by the supply of P, but if they fix their own N, nitrogen doesn't limit the bluegreens till they use up all the N in the lake.



(www.algae.su)

Some bluegreens (cyanobacteria) do fix their own N in enlarged cells (heterocysts; photo of *Anabaena*). With their own supply of N fixed from N_2 in the air, the bluegreen algae with heterocysts can keep growing until they run out of P.

In contrast, algae cannot "fix" P when the supply is depleted. But coastal waters receive ample supplies of P from large watersheds. Because most coastal plankton are not N-fixers, N becomes limiting. Adding N renews growth; adding P does not.

Nutrient-limitation theory focused on lakes where wastewater inflows were causing bluegreen algal blooms. Because such blooms were sometimes toxic to wildlife, livestock, and even people, it is understandable that lakes received more attention than wetlands, including salt marshes. [Note that new research shows that some non-N-fixing bluegreens respond to N addition, and some produce deadly toxins when they "bloom."]. At Tijuana Estuary, intermittent sewage spills from the City of Tijuana flowed north in the Tijuana River, and into estuary channels. During an inflowing tide, nutrient rich wastewater would back up and spread out over the salt marsh.

In San Diego Bay, however, there were no raw sewage spilles. We re-tested theory that N limits cordgrass growth as part of our research to help CalTrans figure out why the cordgrass grew too short in constructed salt marshes. In the process of monitoring cordgrass to see if it would satisfy nesting criteria for the clapper rails (see chapter three), we asked: Is N was the limiting factor. It was. Not only did N limit cordgrass height growth in the short term (Boyer and Zedler 1998, Boyer et al. 2000) it also did in the long term (see test of alternative state theory, below).

Tests of competition

It is relatively easy to discover that two species compete, by showing that one expands when the other is removed, and vice versa. It is harder to learn what they are competing for. If you have a sibling, do you compete most for good grades, your parents' attention, space in your room, who sits in which chair, or who gets the TV remote control? Maybe all of those motives drive you to compete. If there were a dozen empty chairs all the same, there would be little reason to insist on any single chair, other than to pick a fight.

Plants can't think and they don't have motives and they don't pick fights, but they do respond to limiting factors. When essential resources are limiting, one competitor will compete with another, and the stronger competitor will win, at least untill conditions change to favor the other.

Perennial pickleweed and cordgrass usually occur at higher and lower intertidal elevations, respectively, but they overlap at their boundaries (lower limit of pickleweed and upper limit of cordgrass). Do they compete? If so, does their interaction change in relation to water levels?

Ted Griswold decided to test the importance of water depth in favoring one species over the other in field plots and in both mesocosms (meter-square impoundments) and microcosms (15-cm diameter tubes). He wanted to know if the competitive outcome depended on the depth to the water table.

In the field, Ted could remove pickleweed and watch for cordgrass to grow more biomass, but he could not control the water table. In meso- and microcosms, he could control the water table and assess conditions that favored each of the species. Based on their occurrences in the field, cordgrass should tolerate lower elevations with wetter soil, right? But which species was the superior competitor when they were grown together?

In the field, Ted found that cordgrass produced far more stems where pickleweed was removed. Cordgrass expanded steadily from April through October without pickleweed, but remained near-constant in density where pickleweed was not removed. Voila! Competition was indicated. But how did it operate?

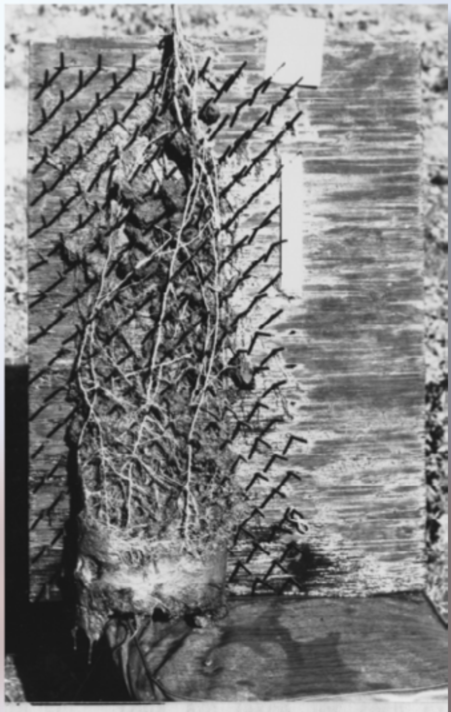
The next two experiments showed that the species differ in their tolerance of standing water and that the reason is different patterns of root growth. The mesocosm experiment was actually two tests in tandem, because the 1985 set-up had low plant density; their roots did not overlap; and it wasn't clear that the two species were given a chance to compete. So Ted repeated the test in 1986-87 with higher-density plantings. As predicted, cordgrass grew well in wet soil, and pickleweed grew well in higher, drier soil. Biomass of both cordgrass and pickleweed was highly variable, and the results did not clearly show that the species were competing for light or space or other resources.

Today, if we still had the biomass that Ted collected, we might be able to remove some confounding factors and show how competition was operating. It would help to know the ash (salt) content of the dry shoots. I've been accused of being a packrat for storing biomass from experiments, but I did not hang onto bags of dry plant harvests for 26 yrs.

Still, I can speculate: First, based on Chris Onuf's study at Mugu Lagoon, our measures of biomass were biased toward pickleweed, which produced and accumulated biomass over ~2 years, while cordgrass died to the ground and accumulated biomass during just 1 year. Second, through Gary Sullivan's greenhouse study, we learned to compare species using ash-free dry weights, and that pickleweed biomass was probably heavier due to higher salt content.

So it goes with research—we learn from every investigation!

Moving to the microcosm experiment, Ted devised a clever way to wash the roots from the soil without disrupting their depth distribution. He pushed the root and soil mass onto a board with a grid of >100 upright spikes (yikes!). The spikes held the roots in place. Then he washed away the soil with a hose to reveal the secret root distribution. First, cordgrass did not survive in the tall tube, >70 cm from the water level, and it produced very few roots in tubes that were ~45 cm from the water level. In the 25-cm tubes, however, it grew roots at all depths and especially near the water level and especially where pickleweed was not added to its tube. In contrast, pickleweed grew well at all levels above the water. These results clearly show differential effects of standing water—too much water limits pickleweed, and too little limits cordgrass. The mechanism is differential root growth.

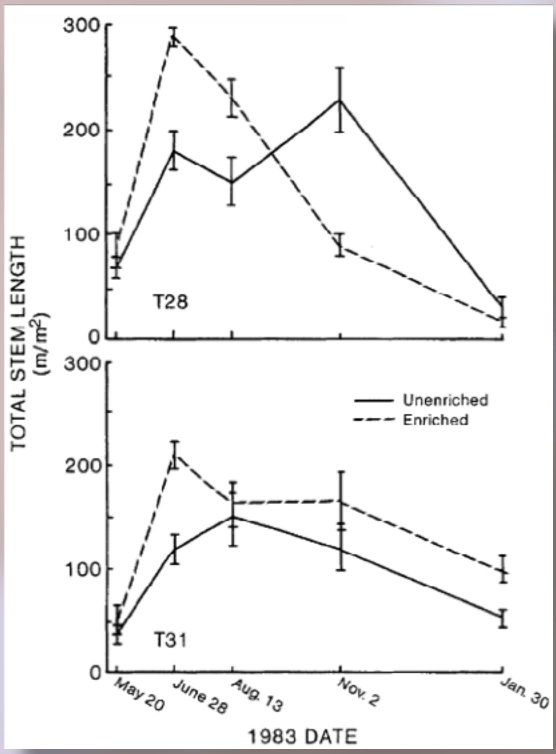


Testing competition for nitrogen

If nitrogen is scarce, plants won't grow well, and removing a competitor will allow the remaining plant to grow more. Likewise, adding nitrogen will increase growth more for the species that is the better competitor under the conditions at the experimental site.

Jordan Covin asked how N-rich sewage might affect cordgrass, perennial pickleweed, and their interactions. If N was the limiting nutrient for one of the two species, would that species expand following sewage spills? How would sewage spills affect habitat for clapper rails, which prefer cordgrass and Belding's Savannah sparrows, which prefer perennial pickleweed? And if a sewage treatment plant were ever built, should the nutrient-rich treated wastewater be released to Tijuana River, upstream of the salt marsh?

Jordan noted that most of the papers published about salt marshes and nutrients were from the Atlantic Coast, which was a hotbed of salt marsh ecology. In 1982, when Jordan began his work, the latest words on coastal wetlands were that nutrients, and N in particular, definitely contribute to variations in salt marsh productivity. What about Pacific Coast marshes?



(from Covin and Zedler 1988)

Jordan's first question was: Does N limit salt marsh plant growth? In April 1983, Jordan added urea fertilizer (45% N and no P) to cordgrass plots (3x3 m) in the north arm of Tijuana Estuary salt marsh. The adjacent 3x3-m cordgrass plots had no urea addition. Then, Jordan waited for the plants to grow, planning to collect soils and measure stem number and heights in smaller, 0.1-m subplots. Counting stems and measuring heights were nondestructive ways to assess plant responses. He could repeat them frequently without damaging his experiment.

In August, Jordan harvested the biomass in all plots to make sure he had a complete accounting for plant growth. The measures of height and stem numbers are useful additions to biomass data, but biomass is the "universal currency" for growth responses. Destructive sampling might not be allowed today. Nondestructive measures of "total stem length" are much preferred when working in habitat that is critical for endangered birds.

In August, cordgrass was taller, had more N in its leaves, and produced about 40% more biomass where N had been added. Voila! The vegetation was N-limited But there was also a big surprise—many of the fertilized cordgrass stems died after an initial growth phase, and a new species of fly (*Incertella* sp.) appeared to be the culprit. Its larvae were very abundant where leaves were high in N, following fertilization. That makes sense—N-rich plant tissue makes great food for herbivores. It was quite a surprise to learn that our pesky fly was a new, not-yet-named species!

Jordan's second question was: How does N addition affect the interaction between cordgrass and perennial pickleweed? His second experiment used plots along the boundary of the cordgrass, where both species were present. He subdivided each plot and removed the aboveground biomass of cordgrass from 1/3 of each plot, left cordgrass and perennial pickleweed together in the middle, and removed aboveground biomass of perennial pickleweed from the other 1/3 of each plot. Then he added urea to half of the plots. Roots of both species were left intact.

Where cordgrass and perennial pickleweed were both present, cordgrass did not respond to N addition. Cordgrass was able to increase its growth only where Jordan had removed perennial pickleweed. Pickleweed, however, increased its growth whether or not cordgrass was removed. Voila again! Pickleweed was competing with cordgrass. N addition increased pickleweed's competitive ability.

Both Ted Griswold's and Jordan Covin's data support Purer's 1942 hypothesis (modified as in chapter one) that the landward limit of cordgrass can be explained by competition, while the seaward limit of pickleweed is related to physical conditions, such as inundation.

Also, Jordan cautioned that longer-term responses to N addition need to be known before we can recommend how to handle treated wastewater.

Final outcome? The US built a wastewater treatment plant at the US-Mexico border (left side of photo). It collects wastewater up to 25 MGD (million gallons/day), treats it, and transports it to the ocean via an underground pipe (9 feet in diameter) that is buried deep under the salt marsh. The treated wastewater is then discharged offshore…..except when the wastewater system is overflows following heavy rainfall.

(upload.wikimedia.org)

Further tests of competition, water and nitrogen

Competition and nutrient limitation vary in time and space. Plants interact along a range of environmental stresses, so two species might facilitate each other under some circumstances and compete under others.

The stress-gradient hypothesis acquired a name when researchers began debating the role of competition as environmental conditions shift from benign to stressful. Sound familiar? Recall Purer's 1942 idea (in modern terms) that competition limits species where conditions are benign and physical factors limit species where conditions are stressful. The stress-gradient hypothesis is hardly new.

As part of her dissertation research, Hem Morzaria-Luna decided to test this part of competition theory, because few researchers had tested how and where competition limits species' growth. Rigorous experimentation was needed. But tests of complex hypotheses require many decisions. First, Hem had to decide which environmental factor would represent "stress," which resource might alter that stress, and which species should represent competitors? Hem focused on water depth as the key physical stress, nitrogen as a resource that might alter inundation stress, and perennial pickleweed and arrow grass as the potential competitors.

Hem stated two hypotheses as:

> H1: Competitive responses between perennial pickleweed and arrow grass would differ with N addition and inundation. Arrow grass would withstand higher water levels and lower N.
>
> H2: Arrow grass would gain advantage with longer interaction time (allowing greater root growth and N sequestration).

Next, Hem made several choices: 3 water levels, each ± N addition, for 6-month-old plants, and in three separate experiments. She established short (4-month) and long (1-yr) experiments in a greenhouse plus a 1-yr field experiment at the Model Marsh. In the field, she couldn't control water evels, but she could plant the species at lower and higher elevation. Because the results of experiments depend partly on how experiments are implemented, a smart, ambitious researcher hedges bets with multiple experiments.

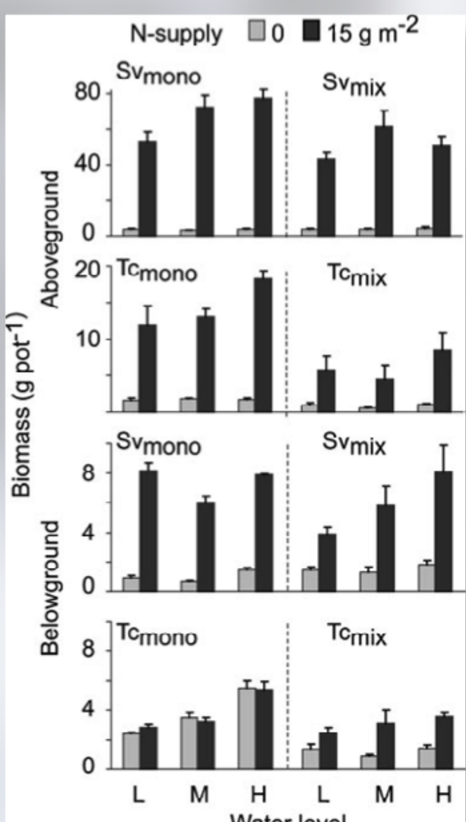
Researchers debate how to test for competition.

• One approach is to focus on one species and then add a potential competitor; this is called an additive design (Let's focus on A, with constant density = 12 plants, ± 6 plants of B). Control pots would have 12 plants, and competition pots, 18.

• Another approach is to hold total plant density constant ± a competitor, called a substitutive design. Control pots would have 12 plants of A, and competition pots would have 6 plants of B and 6 plants of A. In both designs, A is expected to grow better without B (likewise for B ± A). Some researchers conduct both additive and substitutive designs to avoid criticism and strengthen results.

Beginning in 2001, Hem grew perennial pickleweed and arrow grass from seed for 6 months, then transplanted them in pots (22 cm diameter x 22 cm tall) with monocultures (6 plants) and mixtures (12 plants) in three additive experiments. Her greenhouse set-up involved buckets (11.5 liters [L]), each bucket with 3 pots holding the pickleweed monoculture, the arrow grass monoculture, and the mixture. Her water-level treatments mimicked different degrees of tidal flushing. Maximum and minimum water depths varied over 2-week periods, with daily variation in water level. How did she do that? By using tubing to connect buckets to seawater tanks (large trash bins) in a recirculating system, she created three water-level treatments by adding low, medium and high volumes of seawater.

The greenhouse experiments were amazing! Hem mixed the saltwater solution, pumped it to the appropriate buckets, allowed it to drain on schedule, and replaced water lost to evaporation that would increase salinity. Plants were grown in pots for 6 months, then pots were move to large buckets for water-level control.



After tending the first experiment for 4 months, Hem harvested the shoots and roots, dried and weighed the biomass, and analyzed the data. The files of results filled gigabites, but the graph below is a nice summary. All data are grams per pot after 4 months (note the different scales for the y axes). To comprehend the complex outcome, start by comparing the monocultures for perennial pickleweed (Sv_{mono}) and arrow grass (Tc_{mono}). Looking at the gray bars (no N added), note that arrow grass produced a lot more belowground biomass than pickleweed.

Now, comparing gray and black bars, note that productivity was much higher with N addition, except for arrow grass grown alone (Tc_{mono}). This made sense, because another experiment had shown that arrow grass accumulates N in its roots (Sullivan et al. 2007). If it was able to collect N from poor soil, adding N made no difference. Even so, pickleweed reduced its growth in mixed pots (Tc_{mix}).

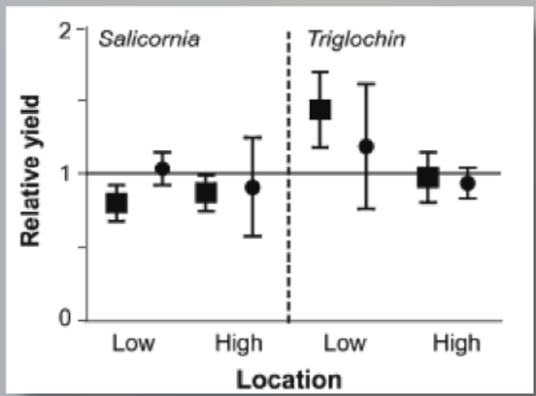
Was water level a stress? There was some evidence for water stress in the second (12-month) experiment. In other cases, the high-water treatment was not high long enough to stress roots or shoots very much. The 12-month outcome (additional graph in Morzaria-Luna and Zedler 2014) suggested reduced growth of pickleweed in high-water treatments, but the response was weak. Perhaps the one-time initial N treatment outweighed an effect of water level. In 4 months, interactions shifted with stress, but N-limitation was more of a stress than Hem's water level treatments.

Arrow grass responded to pickleweed by shifting resources belowground. Its behavior (allocation) changed; it developed a higher ratio of roots:shoots. This is an example of plasticity. As we saw with pickleweed (Bonin and Zedler 2008), plasticity can contribute to co-dominance. Perhaps this is how a low-productive, N-conserving species like arrow grass co-exists with perennial pickleweed.

When the two species grew together without N added, pickleweed benefited by having arrow grass nearby. We call this facilitation, and, as you may recall from chapter eight, Hem showed that arrow grass labeled with ^{15}N shared its ^{15}N with the soil and the adjacent pickleweed! She revealed a short-term facilitation and a mechanism to explain it.

Before getting too excited, note that the 12-month experiment did not indicate facilitation. The two species were competitors across the stress levels provided. Also, in the field experiment, there were no shifts in species interactions with varied N-supply or water level (elevation).

The field results are graphed as relative yield = RY = total biomass grown together relative to grown alone (dividing Sv_{mix} by Sv_{mono} and Tc_{mix} by Tc_{mono}). In this graph, each symbol indicates the RY from a low or high location; squares had N added, and circles did not. Data are averages $\pm$S.E. The horizontal reference line (RY = 1.0) indicates equal biomass with or without a competitor. Where RY > 1, a species grew more with the competitor; where RY < 1, a species grew less with the competitor. The strongest pattern is the RY > 1 for arrow grass. Arrow grass outcompeted pickleweed at low elevation +N.

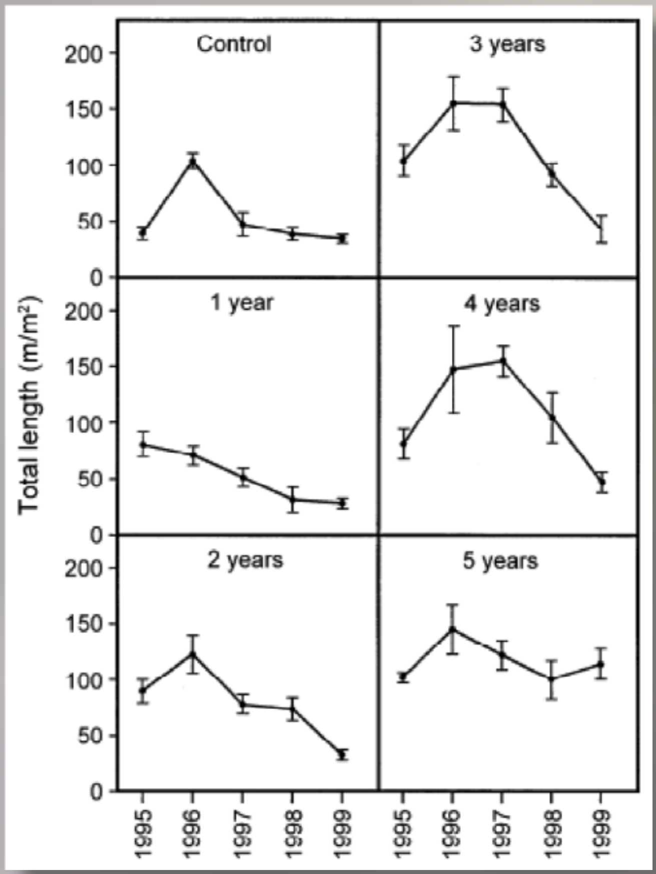


Overall, the concept Hem addressed was complex, and even three amazing experiments could not fully explore changes in competitive interactions across all stress levels. Nature varies many factors simultaneously, sometimes gradually and sometimes suddenly, sometimes predictably (like tide levels) and sometimes unpredictably (rainfall or storm surges).

Experimentalists can only grow a couple of species under a few conditions for a short time . It is not surprising that results from greenhouse and field experiments are not identical. Still, our understanding improved. Here's what we concluded: "The complexity of species' responses to the multiple resource and non-resource stress gradients found in estuarine systems is not fully explained by the original formulation of the stress-gradient hypothesis nor the….synthesis model, which predicts that facilitation is more prevalent at moderate stress levels when resource-based stress is present." You guessed it: More research is needed.

A test of alternative state theory

Our five-year nitrogen-addition experiment in Sweetwater Marsh tested theory on alternative states. Australians borrowed this theory from physics, to answer a common question in restoration: Once an ecosystem shifts from one condition (state) to another, how easily can the shift be reversed? Or does the ecosystem cross a threshold that prevents recovery? This theory goes by other names, such as regime shifts, tipping points (a sudden change when a threshold is crossed) and hysteresis (a lag in response of an ecosystem due to past conditions).



In our case, we asked: Can short cordgrass in N-poor soil be made to grow tall by adding N over a longer time period? We knew that short-term additions of N produced tall plants and ample roots systems. We set up a longer experiment that would increase the effort to build N-rich soil to meet the requirement that tall cordgrass must be self-sustaining.

We reasoned that organic matter would accumulate every year, eventually providing a sustainable supply of N for tall cordgrass. Our experiment had 30 field plots in short cordgrass, and we followed each for 5 years. Treatments were 0, 1, 2, 3, 4, and 5 years of N addition (as urea).

As in our short-term experiment, the cordgrass grew tall while we were adding N, but as soon as we stopped, the cordgrass was short the next year. Each year, we wondered if just one more year of N addition would produce tall cordgrass. It did not. Because the project was required to provide self-sustainable nesting habitat, we could not recommend longer-term N additions. Annual fertilization is not "self-sustainability."

The result is explained by coarse, sandy soil that is unable to build up N supplies. Others have since shown that soil organic matter takes decades to accumulate in restoration sites that have coarse mineral substrates as starting points. It will take a long time for soils to mature in gravel pits, on mine spoils, over hurricane-washed dunes, and anywhere that topsoil is removed. Increased effort did not reverse the degradation caused by coarse soil, so our study lent support to the warning that ‘‘states with thresholds of degradation can be crossed only with difficulty" (Hobbs and Norton 1996).

Kathy Boyer and Julie Desmond maintained the plots, added N, and sampled the plants. After completing his Ph.D. degree, Dr. Roberto Lindig-Cisneros contributed robust statistical analyses that passed peer review by a top journal (see Lindig-Cisneros et al. 2003).

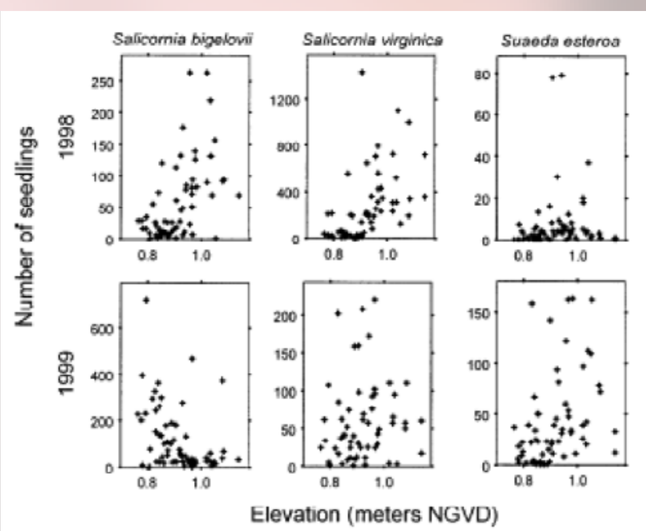
Simultaneously testing dispersal-limitation and biodiversity-ecosystem function (BEF) theory

DISPERSAL LIMITATION. At Tijuana Estuary, we tested dispersal limitation at the Tidal Linkage site (described and pictured in chapter ten). We asked: Which species would readily recruit on their own and which might be dispersal-limited? Of course, it was also possible that some species would be intermediate, with limited seed dispersal but broad vegetative spread or vice versa (the reverse).

Here are the recruitment data for eight species planted at the Tidal Linkage:

Species	Sb	Sv	Se	Bm	Jc	Lc	Tc	Fs
Number planted	720	840	810	720	840	825	780	765
1998 Total seedlings observed	15,978	17,703	1,668	26	33	24	73	2
1999 Total seedlings observed	7,586	3,445	2,685	8	33	178	8	8

Planting each of 8 species in approximately the same numbers and leaving some plots bare allowed us to compare establishment ability via seeds (Lindig-Cisneros and Zedler 2002). The two top seedling recruiters were perennial pickleweed (Sv) and annual pickleweed (Sb), both with over 15,000 seedlings counted by Roberto Lindig-Cisneros. Sea blite (Se) was a distant third contender with 1,668 seedlings counted. What was surprising were the low numbers of all other species. Clearly, five marsh-plain species have limited seed-dispersal capability.



Perhaps you're wondering whether the seedings were restricted to narrow elevation ranges (Roberto was). Here is the answer. All three top recruiters produced seedlings across the site's elevation range.

From the data above, why do you think there were fewer seedlings in 1999 than in 1998? Recall that the site was planted with young seedlings of each species in 1997. They were planted 20 cm apart, with 90 seedlings per 2x2-m plot. The canopy was still quite open in 1998, but much denser in 1998. Seedings had less light in 1999!

We also explored vegetative (clonal) dispersal, which is more limiting than seed dispersal, but still allows some expansion. Salt marsh daisy (Jc) and salt wort (Bm) produce the longest runners over the soil surface, sometimes >2 m. Other species spread more slowly by adding stems near the parent ramet; these include perennial pickleweed, alkali heath, arrow grass, and sea lavender. Note that neither short-lived species (annual pickleweed, sea blite) can reproduce vegetatively. That's typical; short-lived species put much of their energy into seed production! Vegetative spread is limited for four of the perennials and both short-lived species.

BIODIVESITY-ECOSYSTEM FUNCTION (BEF): In 1997, BEF theory said that planting groups of species would provide more ecosystem services than planting fewer species. We wanted to test BEF theory. The practical implication would be that restorationists could plant a diverse species mix and expect a site to provide more ecosystem services than a monoculture. Wouldn't that be great—achieving more biodiversity and more functions simultaneously? Unfortunately, it didn't turn out that way.

In chapter ten, I described our extensive field and greenhouse test of BEF theory that more species provide more functions (or higher levels of selected functions). Our work advanced theory in the following ways:

• We found a positive BEF relationship in the first 2 years while plots were being weeded to sustain our initial plantings of 1, 3, or 6 species (Callaway et al. 2003). However, after 2 years, the pattern was lost or negative (Doherty et al.2011). We found little evidence for complementarity among salt marsh plant species that would lead to greater functioning. It is true that no two halophyte species are identical and that they have very different behaviors and forms (e.g., annual and perennial, evergreen and deciduous, upright and trailing, basal rosette and branching). Such differences among species might lead to complementarity in "resilience" (the ability to resist or respond to disturbance). That function was not tested in our field experiment. Elsewhere (Zedler et al. 2001), we argue that the many differences among species lead to resilience. Different disturbances (a flood or a fire) might be accommodated by different species. With lots of species, at least one should be able to sustain a dense canopy when there's a specific disturbance.

• We found strong effects of two dominant species, perennial pickleweed and alkali heath. Later versions of BEF theory adopted this outcome, saying that increasing the diversity of plantings increases the chance that an influential species will be included. BEF theory became more confusing by shifting from a basis in complementarity to a basis in bet hedging (the more species you plant, the more likely you'll find one that grows well).

• Our research was unique in accumulating knowledge of a small group of halophytes that make up our region's tidal marsh plain; we came to know each one well. Perhaps that is the most important lesson from our test of BEF theory: Learn how each species contributes to an ecosystem so you can explain outcomes. We still need to understand the high marsh halophytes.

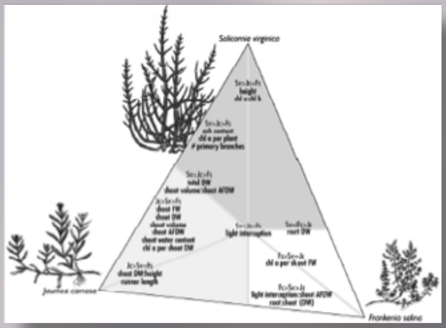
FUTURE RESEARCH: Because restorationists would not want to weed out native species, I do not recommend further tests of BEF theory (based on complementarity) to inform the practice of salt marsh restoration. Instead, I recommend experiments to identify the most influential species based on long-term monitoring of plantings that begin with each species grown alone, as well as in groups.

Testing theory about plant dominance

In textbooks, dominants are the most abundant species; they control the habitat and other species. Our BEF experiment showed that when we planted eight species with near-equal numbers in 1997 (Callaway et al. 2003), three gradually became dominant. In 2005, the dominants ranked as follows: perennial pickleweed > salt marsh daisy > alkali heath, based on their frequency of occurrence and estimated cover (Zedler and West 2008).

Theory suggests that such outcomes are based on productivity, with the most productive species becoming the most dominant. However, productivity could not explain the pattern in the field, because our 2-year greenhouse study indicated no differences in productivity for these three halophytes (Sullivan et al. 2007). There were no differences in ash free dry weight after 2 years, or nitrogen (N) accumulation, or root-N concentration, or shoot-N concentration.

The secrets of dominance were revealed by Cathi Bonin, who compared traits other than productivity. Might the key factors leading to dominance be morphological (structure), physiological (functional), or phenological (timing)? In an earlier chapter, I showed our triangle of results about how perennial pickleweed dominates without being the most productive. No single trait explained why these three species differ in abundance. Instead, the strongest traits of each species helped explain their ranks: perennial pickleweed (tallest, most "plastic") > salt marsh daisy (longest runners) > alkali heath (high root:shoot biomass).



I wonder how much more we would learn by comparing photosynthesis rates, salt tolerance mechanisms, root-fungi associations, avoidance of herbivores, and plasticity. Which other traits that might complete the puzzle?

Testing theory on topographic heterogeneity

We wanted to know how tidal creek networks influenced all aspects of salt marsh development (a basic question with practical implications). At the same time that we designed a 20-acre excavation to have areas with and without tidal creeks, we added experiments to test proximity of plantings to creeks, the addition of soil amendment to the marsh plain, and planting seedlings in tight clusters vs. loose clusters (a spacing experiment). Later, we added experimental pools of 5 cm (which favored an annual plant), 10 cm, and 20-cm depth (where inverts and fishes could thrive), which taught us that different levels of topographic heterogeneity favored different species—a finding of value to the basic researchers as well as restorationists.

Elkhorn Slough (franslanting.photoshelter.com) S

Dan Larkin et al. (2006) stated topographic heterogeneity theory as “areas with more heterogeneous topography will have greater surface space, environmental variability and fractal dimensions.” Fractals are similar patterns that occur at multiple spatial scales. In salt marshes, the meanders of tidal channels are mimicked at smaller scales in tidal creeks and even smaller scale in tidal rivulets. Areas with high topographic heterogeneity should support more species and more ecosystem functions--directly by providing more kinds of environments and indirectly by supporting more species.

Flat, smooth topography is rare in nature. In the salt marsh, the salt pans are flat, smooth places, but even they become heterogeneous at the micro-scale when plants and animals occupy the substrate. Tiger beetles and rove beetles are small critters, but you can see microtopographic variations that they create by digging a burrow and kicking the excavated sediment into a heap aboveground.

In restoration, it is sometimes difficult to design and implement “rough” topography. Bulldozer operators push big, wide blades to create perfectly-smooth surfaces for roads and foundations of buildings. Trying to explain heterogeneity can be difficult. I recall the attempts to restore dunes at Tijuana Estuary. Bulldozer operators agreed to make bumps, and they created a row of regularly spaced mounds.

I also recall how my request for heterogeneous topography in four experimental wetland swales at the UW-Madison Arboretum was misinterpreted. I asked that all four swales have the same rough substrates. The engineering drawings called for perfectly undulating surfaces (like sin waves). The drawings went out for construction bids, and two of the bidders called me to ask "how are we supposed to build perfectly smooth mounds?" That's when I learned about the sin waves. The bids came back with astronomical price tags! Lesson: Allow ecologists to talk directly with planners.

The drawings were revised, and the new bids fit the budget. Even with appropriate drawings, however, the contractors needed more information—Could they simply disc or plow the site? Could they use the forked teeth of a backhoe? Should mini-ditches be parallel to water flow? We agreed that backhoe teeth scraped perpendicular to flow would provide topographic heterogeneity to facilitate growth of 27 native plant species. By the end of construction, however, rainfall, ponding water, and wind quickly flattened the soil surface. Then, unexpectedly, woody roots that were buried in the topsoil floated to the surface, where the wind blew them to the east side of each swale. Another lesson: Nature will create its own heterogeneity, despite plans for uniform roughness!

A FIELD TEST OF TOPOGRAPHIC HETEROGENEITY. When the California Coastal Conservancy helped the Tijuana Estuary managers plan an 8-hectare (20-acre) excavation called the Model Marsh, there was an opportunity to test for the effects of topographic heterogeneity at real-world scales—we agreed on six subunits, each about a hectare in size with ample flat buffer space in between. Three would have tidal creek networks and three would be flat. The design was relative simple and construction efforts were superb!

On the left, Dr. John Callaway and Michelle Cordrey are inspecting what would become a tidal creek. Below, a backhoe is being used to excavate creeks.

Some of our research on topographic heterogeneity appears in other chapters. For example, Julie Desmond's work showed the importance of tidal creeks for fish habitat. Our studies of Sweetwater Marsh and CalTrans' attempts to construct habitat for the light-footed clapper rail showed the need to provide creekbanks for foods and large patches of low-elevation topography for cordgrass. And islands should not be smooth domes.

Our direct experimental test of creek versus no-creek topography showed that:

• Creeks facilitated sediment transport out of the site during the 2004 floods.

• Creeks provided habitat for longjaw mudsuckers.

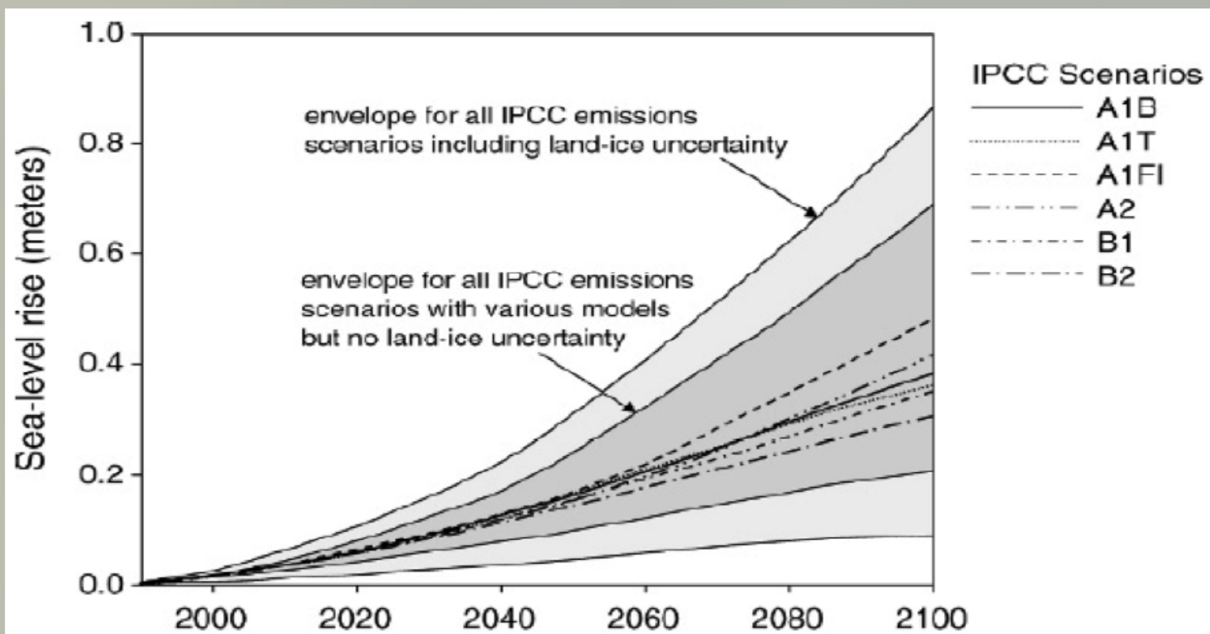
• Creeks gave mudsuckers and California killifush access to feeding "oases" on the marsh plain.

• Creeks increased survival of halophytes planted near creeks, compared to planting several meters away from creeks.

Topographic heterogeneity theory goes beyond the statement that "areas with more heterogeneous topography will have greater surface space and environmental variability." The theory also predicts that more heterogeneous areas will have greater diversity and enhanced food webs. Given even larger salt marsh restoration projects, tests of topographic heterogeneity theory could include observations on fractal dimensions, as well. Because the Model Marsh's excavated creeks changed rapidly in width and depth, I recommend experiments to jumpstart tidal creek formation by excavating just the mouth of a creek as it enters the main tidal channel. Much could be learned about channel, creek, and rivulet structure by watching an excavated site evolve complex creek networks with fractal features.

Theory needed to predict the future: Sea level rise

Salt marshes are perched on the edges of continents where they are extremely vulnerable to global change, especially rapidly rising sea level. While physical scientists are continually improving models to predict rates of sea level rise, our current biological theories lag behind. This graph of SLR shows results of six models conducted by the Intergovernmental Panel on Climate Change (IPCC 2001 in Callaway et al. 2007).



From these predictions of global average sea level rise, what's the earliest we might expect a 30-cm rise in sea level? Hint: Draw a horizontal line from 30 on the y axis and mark where it hits the top curve. Then see where that point falls on the x axis. It looks like about 2050. Yikes! The worst-case scenario could occur in 35 years. I say "worst," because no one expects rising sea level to be a good thing. Too much real estate sits at the water's edge. More than the world's salt marshes are vulnerable to increased inundation.

In general, biologists know that salt marshes won't persist where they exist now, unless sedimentation matches SLR. But we cannot predict which plants and animals will persist with greater inundation or which ones will be able to migrate upslope/inland. Mobile animals (chapter fifteen) should have more options than stationary ones, and algae should adapt more quickly than vascular plants.

We need a more comprehensive theory to predict how salt marsh diversity and functions (processes) will change with sea level rise (SLR), and which species will persist in situ (where they are now) and which will migrate upslope where there is space to do so. Below, I try to use existing research to make such predictions. One of my objectives is to show where research is needed. By pointing out "holes" in salt marsh science, perhaps future researchers will be inspired to fill those gaps.

First, some cautions:

• Sea level rises gradually along with global warming because: (1) cold ocean water heats up and expands in volume (called thermal expansion); (2) ice caps, icebergs, and glaciers melt (collectively called ice melt) and increase the ocean's volume. These are slow processes, and the oceans are very large, so the surface water rises very slowly. Munk (2002) estimated that SLR at 20 cm per century (that averages <2 mm per year, but yearly changes are highly variable and not reliable).

• Average sea level will rise gradually, but other, more catastrophic changes will also occur along the coast (storm surges and waves) and from upstream weather events that result in flooding downstream. These other sea level anomalies (beyond predicted tides) will occur more frequently.

• Sea-level extremes have greater impacts than gradual SLR, especially when a storm surge coincides with a predicted high water level that is unusually high due to other climatic fluctuations such as El Niño/Southern Oscillation. We saw many examples of flooding at Tijuana Estuary during stormy decades, so we have evidence that extreme events have major impacts on salt marshes.

Here are three quotes from experts (see Cayan et al. 2008):

• "Gradual sea level rise progressively worsens the impacts of high tides, surge and waves resulting from storms, and also freshwater floods from Sierra and coastal mountain catchments. The occurrence of extreme sea levels is pronounced when these factors coincide. The frequency and magnitude of extreme events, relative to current levels, follows a sharply escalating pattern as the magnitude of future sea level rise increases"

• "Climate change is likely to raise mean sea levels, which would lead to inundation of some low-lying areas and adversely affect coastal aquifers. However, some of the most serious impacts would result from the extreme sea levels associated with tides, winter storms, and other episodic events that would be super-imposed upon the higher baseline sea level."

• "Extreme high water levels (measured by any fixed threshold) will occur with increasing frequency (i.e., with shorter return period) as a result of higher mean sea level. Many California coastal areas are at risk from sea level extremes, especially in combination with winter storms."

Here's what a sea storm looked like along a shallow coastline in Cornwall, United Kingdom (UK), in January 2014.

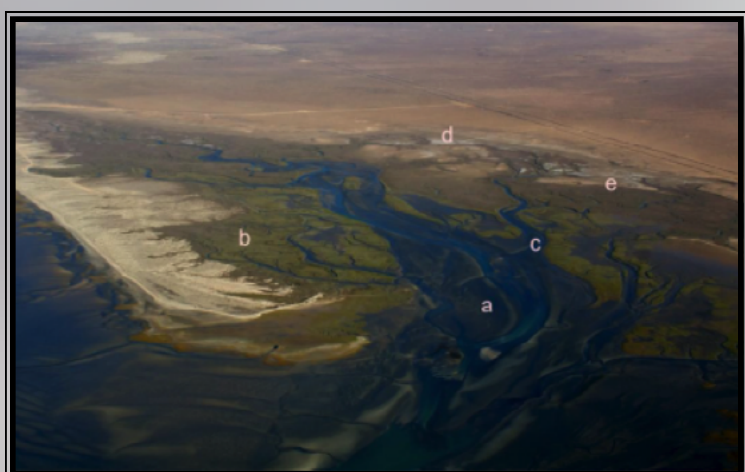
The UK has a program called managed realignment, meaning that some low-lying coastal villages that are highly vulnerable to SLR will be moved inland over several decades.

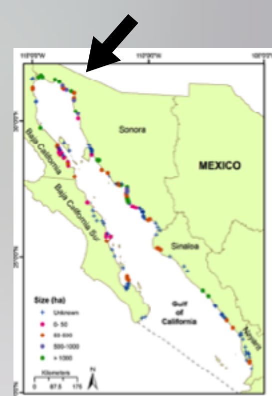
Cautions, continued:

• Predicting impacts of combined SLR and extreme events is extremely difficult. Considering just the extreme events, I identified direct effects (like sediment filling tidal pools), additive effects (like several sedimentation events leading to substantial ccumuation and increased elevation), indirect effects (like the marsh plain being elevated to that perennial pickleweed formed a monotype), interactive effects (like drought and salinity multiplying the stress on marsh plants), unseasonal effects (like prolonged flooding in April 1983, causing cattails to displace salt marsh in the San Diego River), sequence effects (where the order of 2 extremes makes a difference). For example, river mouth closure followed by a growing season without rainfall caused an extreme drought in Tijuana Estuary, but the reverse would have little effect. Comparing these six extreme-event effects to gradual SLR, we should be more concerned about extremes. Is there much concern about extreme events? Or do people just think that all is well once the storm is over? Just clean up that mess and all will return to normal?

• There are few places left for salt marshes to migrate inland, because the adjacent uplands are too steep (like the bluffs around Upper Newport Bay salt marsh) or covered by urban structures, including roads and buildings. The salt marshes of the Gulf of California might offer the best chances for inland migration. In this photo of Estero Almejos, you can see gently sloping upland topography near the salt marsh labeled “e.” However, the area marked “b” seems to be threated by dune sands during strong winds or high-water washovers. This photo illustrates how both extreme events and SLR threaten salt marshes.

Photo: A. Castillo-Lopez, July 2009





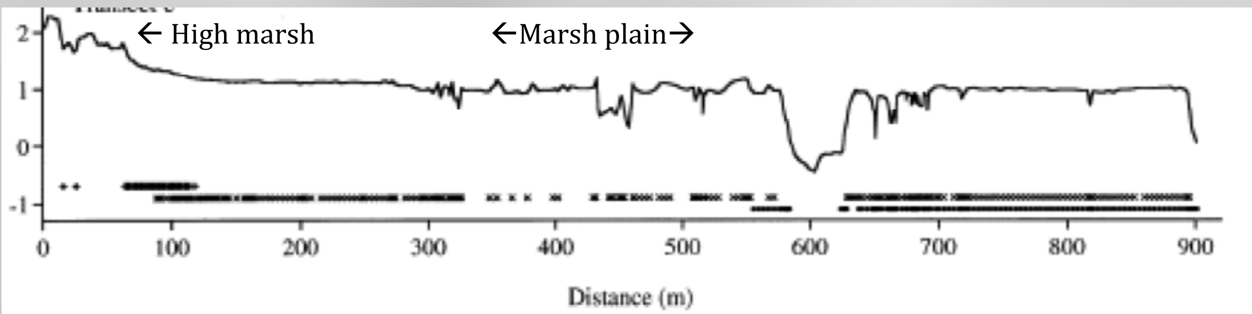
Which plants will persist in situ or migrate inland?

We don’t have a comprehensive theory to predict such outcomes. Still, I can guess that some species will persist longer than others as the marsh plain gets wetter, and some species will use their dispersal skills to move upslope, either via seeds or vegetative “runners.” Some species might even do both. Other species will succumb, especially when extreme events accompany gradually rising sea level.

Let's try to predict impacts of 30 cm of SLR. This scenario could occur by 2050. What would that look like? Recall that, at Volcano Marsh, the marsh plain has a 30-cm elevation range (below is one 900-m transect).

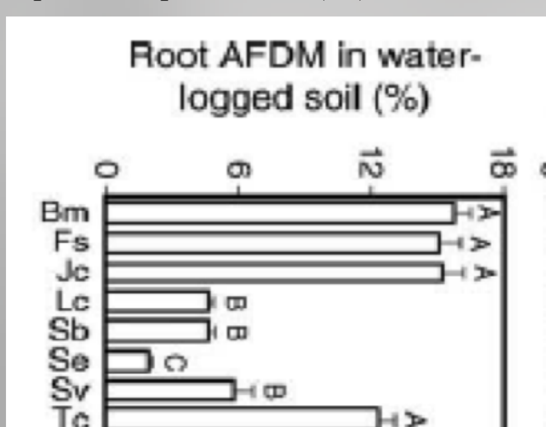
• Notice is how extensive the marsh plain is compared to high marsh (not much room to migrate).

• Also note that the marsh plain is not flat; it is riddled with pools and creeks.



WHICH SPECIES MIGHT PERSIST? Using theory of limiting factors, including effects of nitrogen and competitors, we can predict salt marsh plant species that might be the most stressed. Some of the most useful data were from the 2-year greenhouse study, where Gary Sullivan measured the proportion of roots that grew in waterlogged soil at the botto of 35-cm-deep pots.

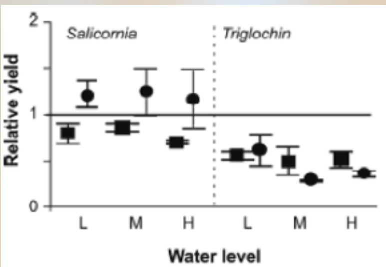
Four species appeared to tolerate waterlogging; these were salt wort (Bm), alkali heath (Fs), salt marsh daisy (Jc) and arrow grass (Tc). One species is an annual that would not grow deep roots in a single growing season. The other three species did not send much root biomass into wet, anoxic soil. These were sea lavender (Lc), sea blite (Se), and perennial pickleweed (Sv).

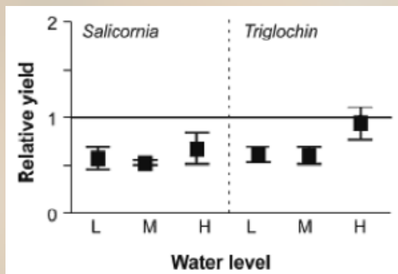


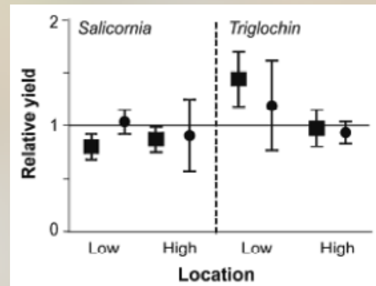
I predict that, when 30 cm of SLR will waterlog the marsh plain, three species will not tolerate the resulting anoxic soil. I hypothesize that four species that tolerated waterlogging will persist for at least the early stages of a 30-cm rise in sea level.

Hem Morzaria's test of competition across a stress gradient suggested that high water reduced perennial pickleweed both above and below ground. However, there was less effect given extra N. Suitable growing conditions could help relieve stress of SLR.

Some of the shortcomings of current theory are visible in the following graphs of relative yield for perennial pickleweed (*Salicornia*) and arrow grass (*Triglochin*) grown in the lab (L, M, H, water levels) and field (Low, High elevation). Relative yield summarizes competition outcomes. Each symbol shows each species' total biomass (above + below ground) grown with its potential competitor divided by total biomass without its potential competitor. Here are the three graphs that Hem prepared for the two greenhouse experiments and in the field. Squares indicate N addition; circles indicate no N addition.







Obviously, arrow grass is not a strong competitor; it rarely produced less biomass when grown with perennial pickleweed than by itself. The one exception (discussed earlier) was in the field at low elevation with N added. In the 4-month experiment (far left), perennial pickleweed outcompeted arrow grass with no N added, but that result reversed when N was added. In the year-long experiment, continuing the 4-month experimental treatment that had a one-time addition of N, both species grew better alone (RY <1). Recall that this was an additive experiment, with the competitor added to a constant number of plantings. So, 10 plants in a pot or plot with two species could certainly have fewer resources than 5 plants grown alone.

We can explain away many of the findings one by one, but the fact remains that three experiments produced different outcomes. This tells me that we have limited ability to devise and test comprehensive theory about how a salt marsh will respond to increased tidal inundation. We don't know how each pair of species might interact with waterlogged soil, and we certainly don't know how nitrogen or other nutrients might alter the outcomes. We don't know how long experiments have to run to make reliable predictions, and we don't know which factors that differ between greenhouses and field sites affect experimental outcomes.

WHICH SPECIES MIGHT MIGRATE UPSLOPE? Can we expect the marsh plain vegetation to migrate onto what is now the high marsh within 35 years? From theory, we would predict that the soils and topography would need to be similar in order for all species to migrate into what is now high marsh. But it isn't. Why not?

• High marsh elevations lack pools and creeks, although the topography can be bumpy for other reasons, including animal mound-building (Zedler and Cox 1984, Cox and Zedler 1986). Topographic heterogeneity theory is relevant here. Recall that Alison Varty showed that 10-cm pools were too wet for perennial pickleweed but that annual pickleweed could thrive in shallow pools where the perennial competitor was suppressed. I think annual pickleweed will persist in situ (where it is now) longer than the perennial.

• High marsh soils are not as clayey as those on the marsh plain, because clay settles out of water where it stands the longest (at lower elevations). The clay deposits make the marsh plain relatively flat. Existinges high marsh have steeper slopes with sandier soil that drains more readily. It won't have shallow pools or creeks, at least not right way. In short, a high tide won't produce as wet a substrate when it covers high marsh topography as it does on a marsh plain. I conclude that migrating upslope won't be as simple as spreading horizontally. There'll be new ground to cover--a new frontier. Plant-soil and plant-plant interactions will likely differ from those on the marsh plain. Anyone care to predict how? Hmmmm. We need theory to rise to the occasion. Wouldn't it be great if we could just plug slope and soil texture into a comprehensive model that would spit out relative abundances of each species? A team of researchers might tackle that some day.

Here's a more solid basis for predicting "migrators." Migration requires dispersal, either from seed or vegetative propagules. We can infer dispersal from (1) regional distributions and (2) local expansion of plantings.

• Regional distributions. In 2001, John Callaway, Gary Sullivan and I reported the number of southern California coastal wetlands where each species was present. If dispersal is a primary cause of regional distribution, then there were three broad dispersers that occurred in 22-23 sites (perennial pickleweed, salt marsh daisy and alkali heath) and five restricted dispersers that occurred in just 7-11 sites (sea lavender, sea blite, annual pickleweed, and salt wort). I think it is very interesting that the first three broad dispersers are the same three species that came to dominate the Tidal Linkage.

Let's consider local expansion of plantings next for further insights. We learned in the Tidal Linkage that only 3 of the 8 marsh plain species were good colonizers from seeds (Lindig-Cisneros and Zedler 2002). These were perennial pickleweed > annual pickleweed >> sea blite. So if the habitat were suitable, and if seeds were available, these species should establish and spread. Those are big "ifs."

(usnews.tumblr.com)

We also compared dispersal via runners (horizontal shoots along the soil surface) for the top three dominants of that marsh a decade after planting. The runners produced by salt marsh daisy were much longer than those of either perennial pickleweed or alkali heath. So the daisy might be the first to invade habitats uphill looking for a gap in the canopy. It practices the "guerilla" form of clonal expansion. Another species with guerilla tactics is salt wort, but it tends to like wetter soil, so it might be first to expand upslope, but only along the fringe. The daisy might move farther upslope into "enemy territory." Meanwhile, perennial pickleweed and alkali heath might expand more slowly and surely, using the "phalanx" tactic.

A SUMMARY OF SPECULATIONS: In the absence of comprehensive theory, we can use accumulated data to predict responses of marsh plain species to 30 cm of SLR withing 35 years.

• Species that might persist on the marsh plain by tolerating waterlogged soil appear to be:

annual pickleweed (waterlogging will create canopy gaps)
salt marsh daisy
alkali heath
salt wort
arrow grass (especially where competitors are lacking).

• Species that could spread upslope rapidly into sloped and better-drained high marsh areas appear to be:

perennial pickleweed (by seed, more slowly vegetatively)
snnusl pickleweed (by seed; but it won't persist without pools)
sea blite (by seed, but it might not persist—its seedlings will need canopy gaps)
salt marsh daisy (by long runners)
salt wort (by very long runners, given a rhizome subsidy from plants at lower elevation)

• Potential "losers" in the long term: sea lavender, sea blite, annual pickleweed

Next steps

What are the priorities for new, more comprehensive theory? I recommend working to predict responses to sea level rise (SLR) and extreme events. That includes monitoring changes in the region's salt marshes to test and refine such theory, plus understanding effects of SLR in combination with extreme events over long time frames. Another high priority is to understand how animals and micro-organisms interact and how they will change with SLR. I know I have short-changed the animals and micro-organisms of the ecosystem in trying to predict the future, so those are also priorities for others who have studied invertebrates, vertebrates, and microbial functions.

I am a strong proponent of biodiversity conservation, but most of the species in salt marshes are not vascular plants. My collaborators and I got to know a few species well through experimentation and monitoring, and we learned a lot in our 2-yr greenhouse study about16 trios and 16 sextets in random combinations. Those who are curious can consult our monograph (Sullivan et al. 2007), which uncovers more secrets! That paper and many more studies of southern California salt marshes are listed in chapter twenty (References). Other researchers have explored southern California salt marshes and have more stories to tell. I've written down my favorite stories; I hope others will do the same.

The future is bright for making new discoveries. Each of the researchers I've introduced in this e-book played a critical role in revealing previously-unknown information. Collectively, we came a long way from Edith Purer's (1942) descriptions and hypothesized cause → effect relationships. But there's still much more to know. So please: Explore, ask questions, suggest hypotheses, test your ideas, interpret your results in light of the larger scientific knowledge, and write about the secrets you've uncovered. Make your news available to others using multiple formats, including e-books for broad audiences!