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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More is better, right?

Ecologists and conservationists continually work to sustain earth's bountiful biodiversity. At present, the world supports > 200,000 species of vascular plants, perhaps as many as 30 million species of animals (mostly invertebrates, of which most are insects), and unknown numbers of micro-organisms. Several web sites provide estimates of biodiversity and information on which groups of organisms are likely becoming extinct (lost forever) before we even know they exist. Here, I consider a smaller-scale question about the role of diversity in salt marsh ecosystems.

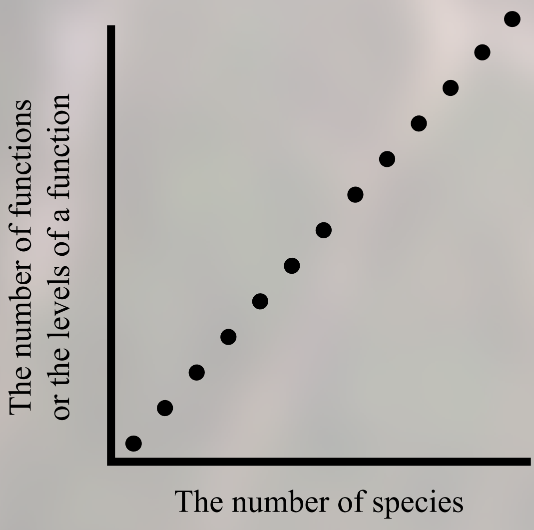
Is more always better? If the topic is *chocolate* and you're asking *me*, then the answer is yes! Note that the answer depends on *what* we're asking about and for *whom*.

For *whom*: If you ask us biological conservationists if the world is better with more species than fewer, we would say yes, absolutely! More species are better. If you then ask, *for what*? Most will say "for their own sake, because organisms have an innate (natural) right to exist." If you probe further, we will say, because they provide lots of useful functions (also called services), like producing biomass, supporting wildlife, building rich soil, and sustaining genetic diversity that might some day be tapped to create new medicines, enhance crop species' performance, or provide other ways to improve human well-being.

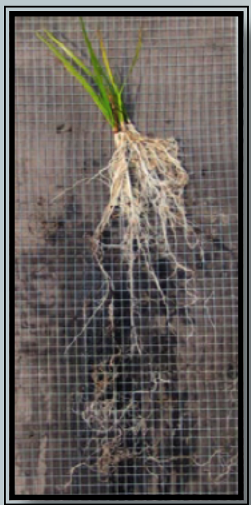
What's more difficult is to say exactly what a specific species does and why it must be sustained. In the southern CA salt marsh, we probably know more about the common plants than others know about "their" ecosystems. Why? Because there aren't many halophytes and because scientists have studied both the species and their ecosystem services.

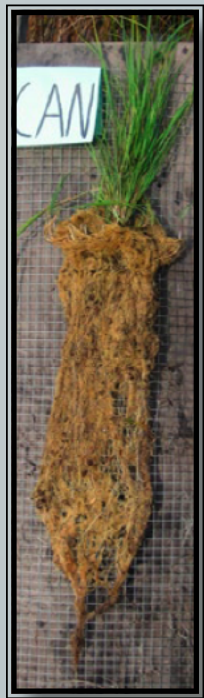
Theory about biodiversity and ecosystem function

Biodiversity theory says that species can live together and thrive in thee ways: first, if they use different resources; second, if they use the same resources, they use them in different places; or third, if they use the same resources at different times. Such species are complementary.



Plant species are complementary when their roots draw resources from different soil depths or their shoots need different amounts of light or one grows early and the other grows later. Both patterns of segregated (divided-up) resource use lead to complementarity. When first devised, biodiversity-ecosystem function (BEF) theory said that many complementary species living together would provide more functions or higher levels of a few functions, compared to a few species with less overall function. The most common argument for conserving or restoring lots of species is to provide higher net primary productivity (NPP). The graph on the left indicates the concept (general idea) that more species lead to more functions.





On the left are two freshwater wetland plants that are common in Wisconsin. We grew them separately in tall pots and then washed away the soil to compare their root systems. The species on the left has shallow roots; the species on the right has very deep roots. If grown in the same pot, we might expect them to be able to co-exist, one drawing water and nutrients from the shallow surface soil, the other able to tap water and nutrients from deeper soil.

Another factor that would probably limit growth is light. The grass on the right could grow tall in full sun and shade out shorter plants. A short plant that could tolerate shade (or grow best in shade) would be highly complementary. Two species could also use the growing season in complementary ways--one using light and nutrients early in spring, senescing (going dormant) early; another growing fastest in summer, achieving peak size in fall. Early plants could be short, because they might not be shaded by other plants until after they flower and fruit. Does this sound like a condominium time-share arrangement?

A graph showing more structure → more function was published in the 1980s by Dr. Tony Bradshaw, whom I call the "father of restoration ecology." His early thinking was that ecosystems develop, first by having few species and low levels of functioning, then moving toward many species and greater levels of functions. He described ecosystem degradation as the reverse pattern (back to few species and less functioning), and that restoration would reverse degradation. He continued to publish the concept throughout his life, despite challenges, especially for wetlands (Zedler and Lindig-Cisneros 2001).

Are our native salt marsh plants complementary?

For BEF theory to be strong, it needs support from several tests. Many ecologists have set up field experiments with plots having few, several, and many plant species--then measured the levels of one or two functions, usually including net primary productivity (NPP). Many tests show higher NPP with more plant species, at least where plots are weeded to retain the planting treatments. The typical field test also involves random groupings of species—mostly in uplands. We reasoned that a salt marsh might behave differently.

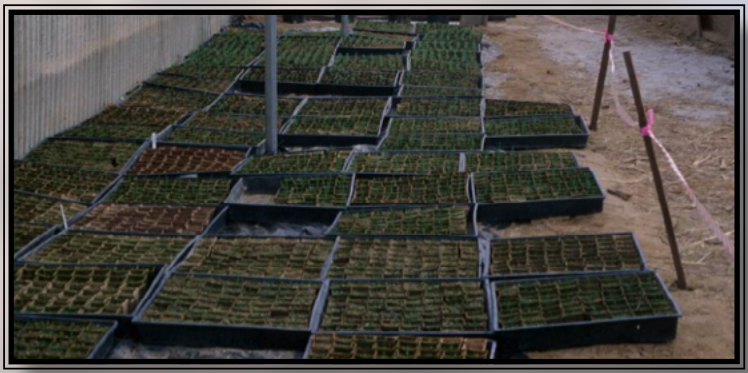
Do they use root and light space in different places or at different times? I was skeptical (doubtful), which is appropriate for a scientist--we tend to question everything. I thought we should know if the popular biodiversity-ecosystem function theory extends to salt marshes. A very important reason to know concerns salt marsh restoration: If we plant more species, will the salt marsh ecosystem provide more services? Various data suggest that productivity is higher where there is a monoculture of perennial pickleweed, not where there is a diversity of halophytes.

In 1996, we had an opportunity to plant a large field experiment--a newly excavated salt marsh plain next to the Tijuana Estuary Visitor Center. We asked the National Science Foundation (NSF) to fund a comparison plantings with 0, 1, 3 or 6 salt marsh species (from 8 common marsh plain species). NSF approved our grant proposal--Wonderful! Especially since we were already setting up the plots:

Photo: John Callaway

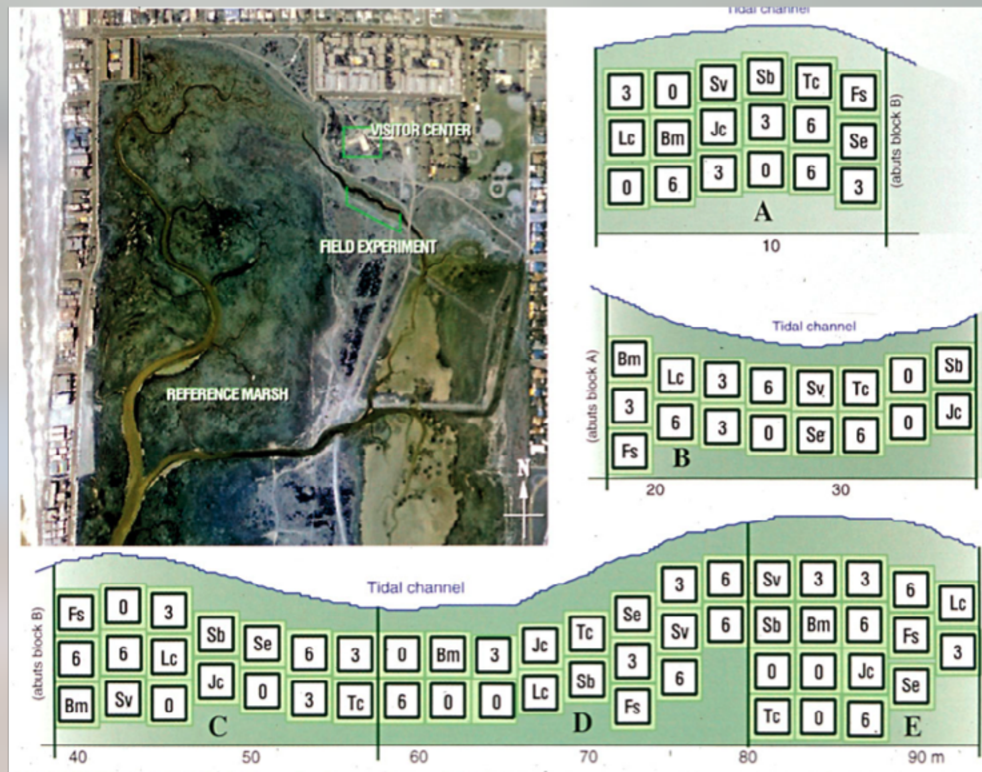
Drs. **John Callaway, Gary Sullivan** and I decided to test for complementarity among eight halophytes from the salt marsh plain. We developed five hypotheses:

> H1: Plantings with many plant species will produce more biomass than those with just a few species. Plots with 6 species will produce more aboveground biomass than plots with 3 or 1 or 0 species.
> H2: At the same time, the species-rich plots will accumulate more N in their roots and shoots.
> H3: Species-rich plots will have more complex canopies (more layers of stems and leaves).
> H4: Species-rich plots will resist invasion by unplanted seedlings.
> H5: Some species will produce seeds that establish seedlings quickly; others will not.



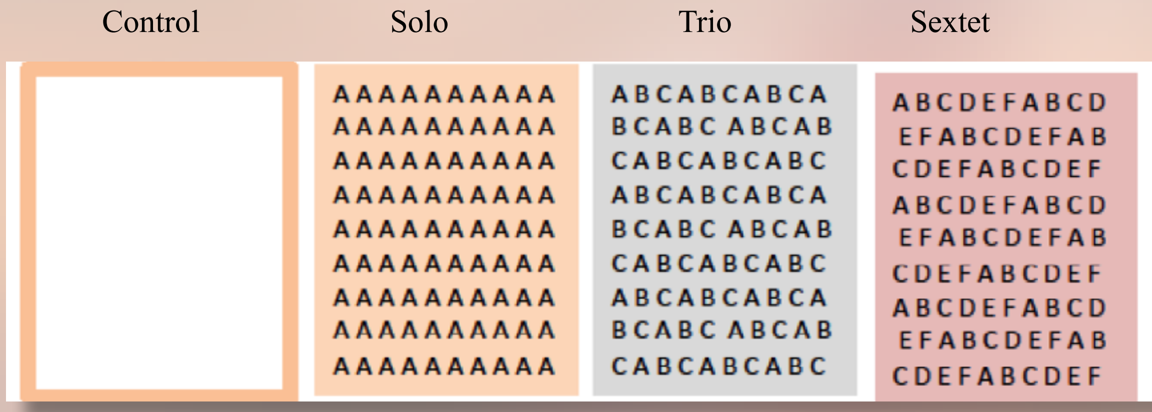
John worked out the planting plan for our species-richness treatments. This might sound easy, but there were several constraints. First, we wanted to establish all the treatments in each of five “blocks.” The blocks had to fit the long, narrow restoration site, dubbed the ”Tidal Linkage.” Can you spot blocks that had room for extra plots? We wanted to grow two combinations that were common in the salt marsh, but not included in the random draws of species.

Each plot was 2x2 m, but plots differed in composition. We randomly drew 3 or 6 species for trios and sextets. We decided to plant each of the 8 species as solos; those have initials (Genus species of each). We tried to avoid a confounded experiment (influenced by an unintended factor) by replicating treatments within 5 blocks, in case something differed from west to east (we could test for block effects). Plots differed mainly in the number of species planted.



After many iterations (repeated versions) we were satisfied with the experimental design. We had 15 plots in each block (subareas A-E, from west to east). The treatments were: controls (easy—no plants); solos (each of the species grown alone), trios (3 randomly-drawn species from the list of 8 species) and sextets (6 randomly-drawn species from the same list). Because trios and sextets were randomly drawn, each plot could have a unique composition. The total number of plots was 87. Below are a solo and a trio:

All seedlings were grown in our greenhouse, then hardened outdoors before planting. Each plot had the same spacing (20 cm), with 90 seedlings per plot (9 rows x 10 seedlings per row). John's clever spacing for trios and sextets kept species apart (not adjacent). Here's an example for five selected seedlings (A, B, C, D, E, and F).



Can you imagine how we planted 87 plots exactly as planned? We provided a map for each trio and sextet plot, and each worker had to locate and insert 90 seedlings of the right species in the right places. It took many helpers many hours, but the end result was a great reward. We found interesting patterns in the short term (Callaway et al. 2003, Keer and Zedler 2002, Lindig-Cisneros and Zedler 2002). We also found interesting changes over the long term (Doherty et al. 2010), as well as explanations (Bonin and Zedler 2008).

Here is the experimental restoration site shortly after planting in April 1997

In the first two years, we weeded the plots to retain their planting treatments (1, 3, or 6 species).

The plots filled in by 1999. Our trampling left trails between plots.

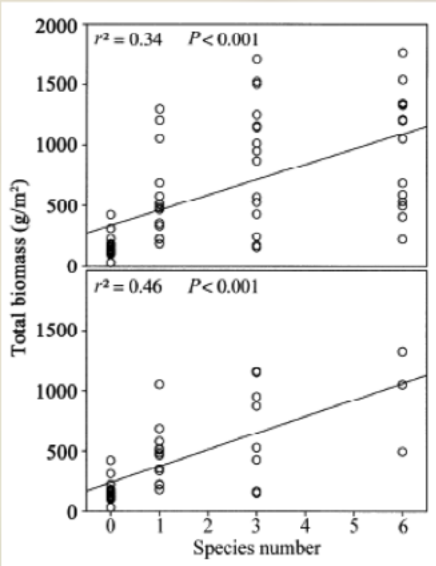
In 2000, we sampled biomass by clipping subplots above ground and excavating large soil cores below ground (photo on right).

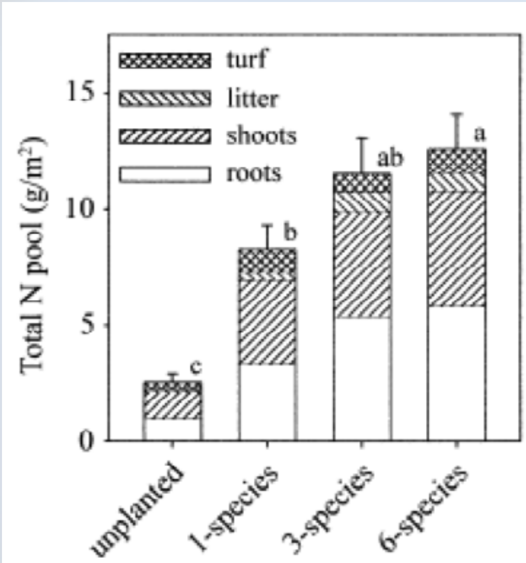
What was the result of our labor-intensive experiment?

Did any of the 5 hypotheses gain support? Let's begin with H1 and H2:

H1: A salt marsh plot with six plant species will produce more aboveground biomass…
H2: The species-rich plots will accumulate more nitrogen in their roots, stems and leaves.

In support of H1, we detected increased biomass and nitrogen accumulation where we had planted six species (Callaway et al. 2003). In 2000, the total biomass of roots plus shoots (weight after drying) averaged 996 g/m^2 for sextets, while solos averaged 572 g/m^2, and unplanted plots just 164 g/m^2). Biomass increased for trios and sextets with or without pickleweed (upper vs. lower graphs, from Callaway et al. 2003).





We concluded that ecosystem functions increased with the number of species we planted. But please read on. Later research showed and explained how things changed over the next 11 years.

Georgeann Keer tested H3 in an intensive study of canopy "architecture." It involved threading brass rods through a frame so she could count the number of times each species was hit.

H3: Species-rich plots will have more complex canopies…

Her findings supported H3: The canopy had more layers where there were more species.

The fourth hypothesis concerned the spread of new species into a planted or unplanted plot.

H4: Species-rich plots will resist invasion by volunteer seedlings...

H4 also gained support. Roberto Lindig-Cisneros found that three species produced seeds that established seedlings in many other plots, so he was able to test the function of invasion resistance. The result? Species richness reduced recruitment. As hypothesized, species-rich plots had fewer seedlings establishing (after we stopped weeding the plots).

This sea lavender plot (broad purple leaves) is being invaded by annual pickleweed (leafless stems) in the upper right corner. Not only does annual pickleweed have stems without leaves, it also has flowers without petals (close-up on right).

The fifth hypothesis was established to help restorationists decide which species to plant and which might not need to be planted.

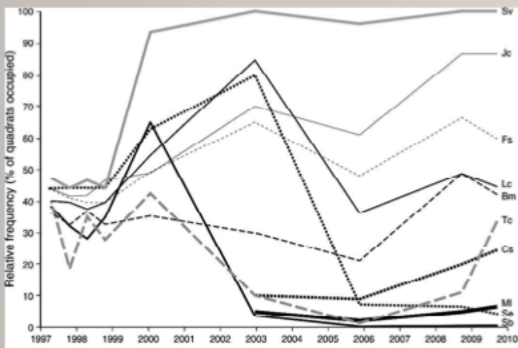
H5: Some species will produce seeds that establish seedlings quickly; others will not.

Data collected by Roberto Lindig-Cisneros supported H5. Three species with high seedling establishment were perennial pickleweed, annual pickleweed, and sea blite. The other eight showed little recruitment. Their seedlings were rare. Interpreting these results for managers, we recommended that restorationists avoid planting perennial pickleweed in restoration projects, unless there are no nearby salt marshes. If a nearby marsh has this species it will eventually export seeds that can float into marshes restored with the other species. We recommended that restorationists sow seeds of annual pickleweed and sea blite to fully-tidal restoration sites. The other five species need to be planted as seedlings (see data in chapter twenty-one).

Below is a similar view in 2004. Individual plots are no longer easy to distinguish.

What do you think happened to our test of biodiversity-function over the long term? By 2011, the experimental site did not appear to have productive patches where sextets had been planted or lower biomass where trios or solos were planted--or bare plots where nothing was planted. It was time to resample and see if the early support for the diversity-function relationship was just a short-term outcome.

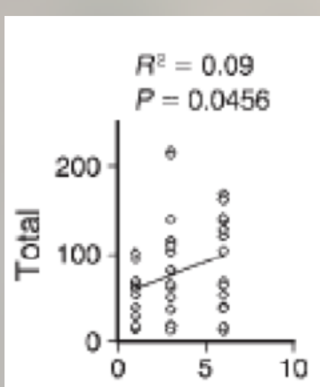
When James Doherty arrived at UW Madison, he chose to follow up the salt marsh diversity-function experiment for his MS degree. He found that the diversity–function relationships changed over 11 years' time (Doherty et al. 2011). Plots planted with a single species and plots planted with 6 species had all moved toward an average richness of 3.9 species/0.25-m²). Along the way, two short-lived species (sea blite and annual pickleweed) and love grass became rare. At the same time, three productive species became dominant (perennial pickleweed, salt marsh daisy, and alkali heath).



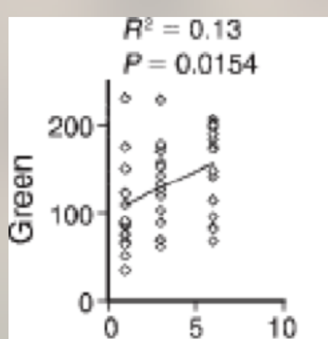
Long-term tracking of field plantings showed that all species were dynamic in their occurrences. As some became more common, others declined. This graph shows 10 species, because two volunteered themselves during the study; these were love grass (Ml) and dodder (Cs).

Although NPP was positively correlated with species richness in 2000, Jim found that, diversity–function relationships became weaker (less positive) over 11 years. The left graph below is for all biomass in 2000. The middle and right graphs are from 2008. The plots planted with 1, 3 or 6 species still had increasing green biomass, but, at the same time, decreasing brown (senesced) biomass. The pattern for total biomass disappeared between 2000 and 2008.

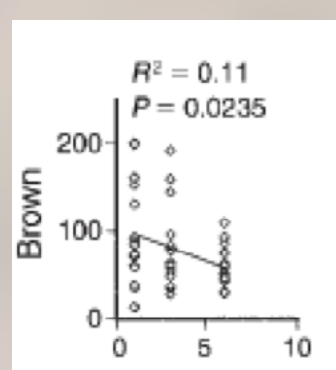
Note that R^2 estimates the percent of the variation that is explained by the regression line in the first three graphs; a P value less than 0.05 indicates that the pattern is not due to chance. The high P value (probability that a relationship is random) for total biomass in 2008 indicates no pattern.



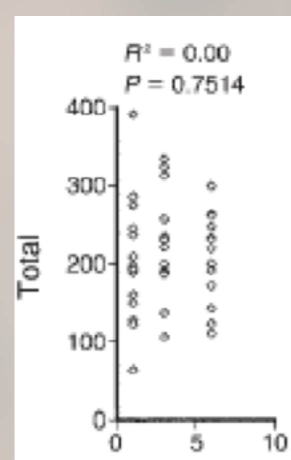
2000



2008



2008

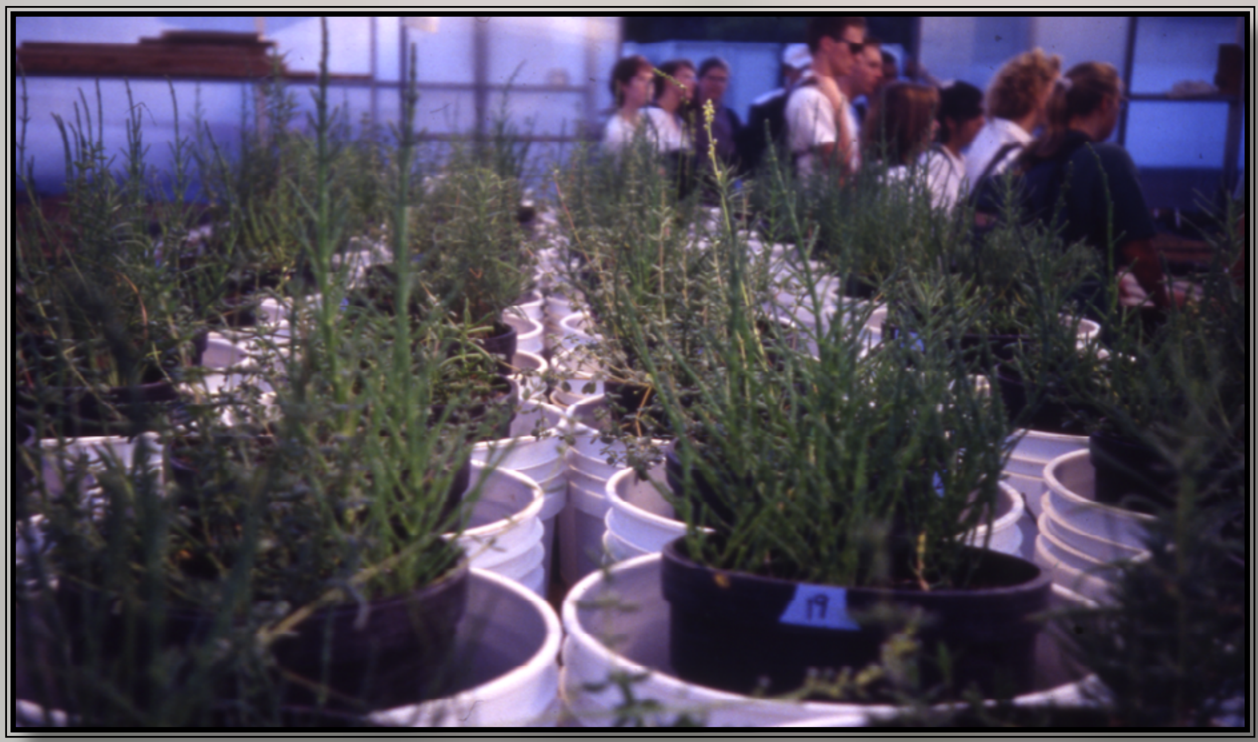


2008

It was not a coincidence that the pattern found in 2000 disappeared after we stopped weeding. Once aggressive plants are able to spread, they will. Based on our long-term study of the Tidal Linkage, we conclude that species-rich plantings don't guarantee greater functioning!

In a separate 2-year experiment, Drs. Gary Sullivan and John Callaway grew all the randomly-drawn assemblages in big pots inside our greenhouse at SDSU. The treatments included the 8 solos, 32 assemblages and an unplanted control. Each of these 41 treatments had 8 replicate pots, for at total of 328 pots (Sullivan et al. 2007).

Bravo! By replicating each randomly-drawn assemblage, we could explain variations among field plots (where we did not replicate each assemblage).



In the greenhouse, as in the field, we found more biomass and more nitrogen accumulation where we planted more species. There were some negative effects, too, on root and shoot N concentration. Plants can produce more biomass with less nitrogen if they have plenty of light, moisture and other nutrients. The study was so large and the results so complicated that the write-up grew into a monograph (very long paper). For this summary, it's enough to say that there was very little evidence for complementarity. Higher NPP was not due to the number of species present. There was, however, ample evidence that the differences among treatments were due to which species were present. Whenever perennial pickleweed was present, it took over. When the assemblage did not include perennial pickleweed, alkali heath took its place and dominated. And whenever arrow weed was present, it concentrated nitrogen, especially in its roots.

Those who work with BEF theory call these species selection effects--a variation on probability or "bet hedging." The more species you include in a random draw, the more likely a mix will include a high-performing species. So when it seemed that sextets were more productive than trios because of complementarity, it was simply that sextets tended to include the highly productive perennial pickleweed (Sv), salt marsh daisy (Jc), or alkali heath (Fs). Isn't science fascinating!

Getting to the roots of the matter. Here's Gary slicing the contents of one of our tall pots into strata (horizontal layer; singular = stratum). Each stratum was washed and sieved separately to measure roots at each depth. As in many long-term greenhouse experiments, the plants in pots tend to grow as deep as they can and accumulate at the bottom. But because the pats were sitting in water in buckets, the soil at the bottom of each pot was waterlogged.

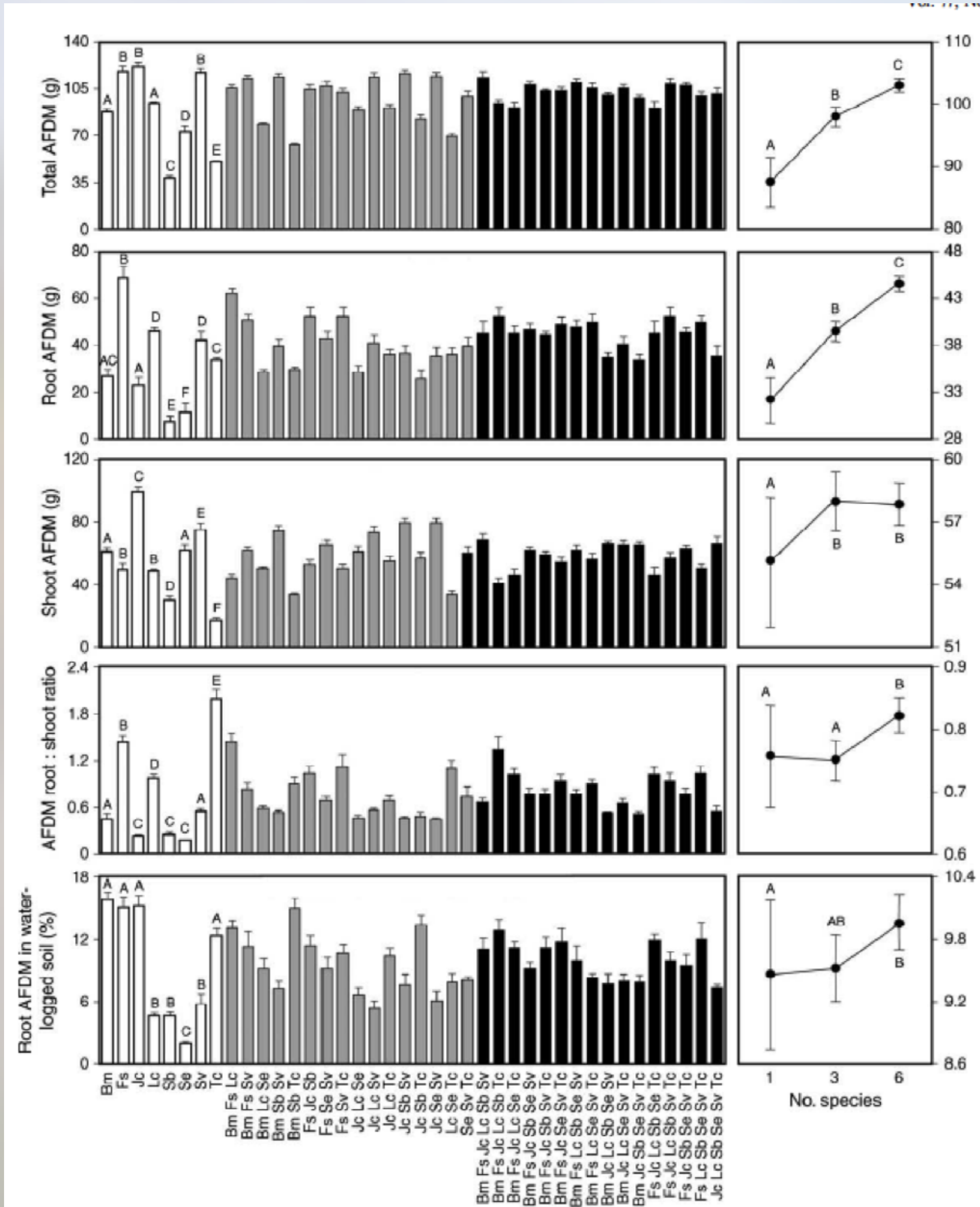
In the lowest graph on the next page, note that sea blite has the smallest proportion of roots in waterlogged soil (bottom of pot).

Do you think that's why sea blite occurs so close to tidal creeks--where water drains rapidly at ebb tide? I think so, but I also think that sea blite doesn't grow deep roots because it is a short-lived species. Usually, it lives only 2-3 years. You can often see dead "ghosts" of sea blite here and there within the marsh canopy. Belding's Savannah sparrows also see them and use them as perches, until they decompose or dislodge and float away.

Do you think a high % of roots in wet soil could indicate species that can survive rising sea level? I think so, but I'd like to know more! We noticed that sea lavender did not send many roots into the waterlogged soil. Sea lavender also tended to avoid wet soil away from tidal creeks in Volcano Marsh. That is, it seemed to need the drainage provided by a nearby creek. Avoidance of waterlogged soil in the greenhouse could be a useful indicator of avoidance of waterlogging in the field. That in turn might suggest how rising sea leel could select against such species.

Contrast the roots of salt wort (Bm, on the left and data in the graph below) with those of sea lavender (Lc). Bm should have much less difficulty tolerating waterlogging as sea level rises.

By replicating each combination in the greenhouse and testing for complementarity and selection effects, we demonstrated better than other researchers that the patterns we observed in the field were species effects. Perennial pickleweed, salt marsh daisy and alkali heath were superplants! See for yourself by comparing the bars for Sv, Jc and Fs in the graph below, as well as assemblages with and without these three species. We correctly predicted that they would dominate the restored salt marsh.



Once the data were compiled, Gary led the analysis and writing (Sullivan et al. 2007). The resulting monograph revealed dozens of secrets about species' growth patterns, differences among the randomly-drawn assemblages, and general summaries about which species were dominant among the 32 assemblages (the same ones that were planted in the field). Believe it or not, there was still more to learn about how salt marsh plants grow and why!

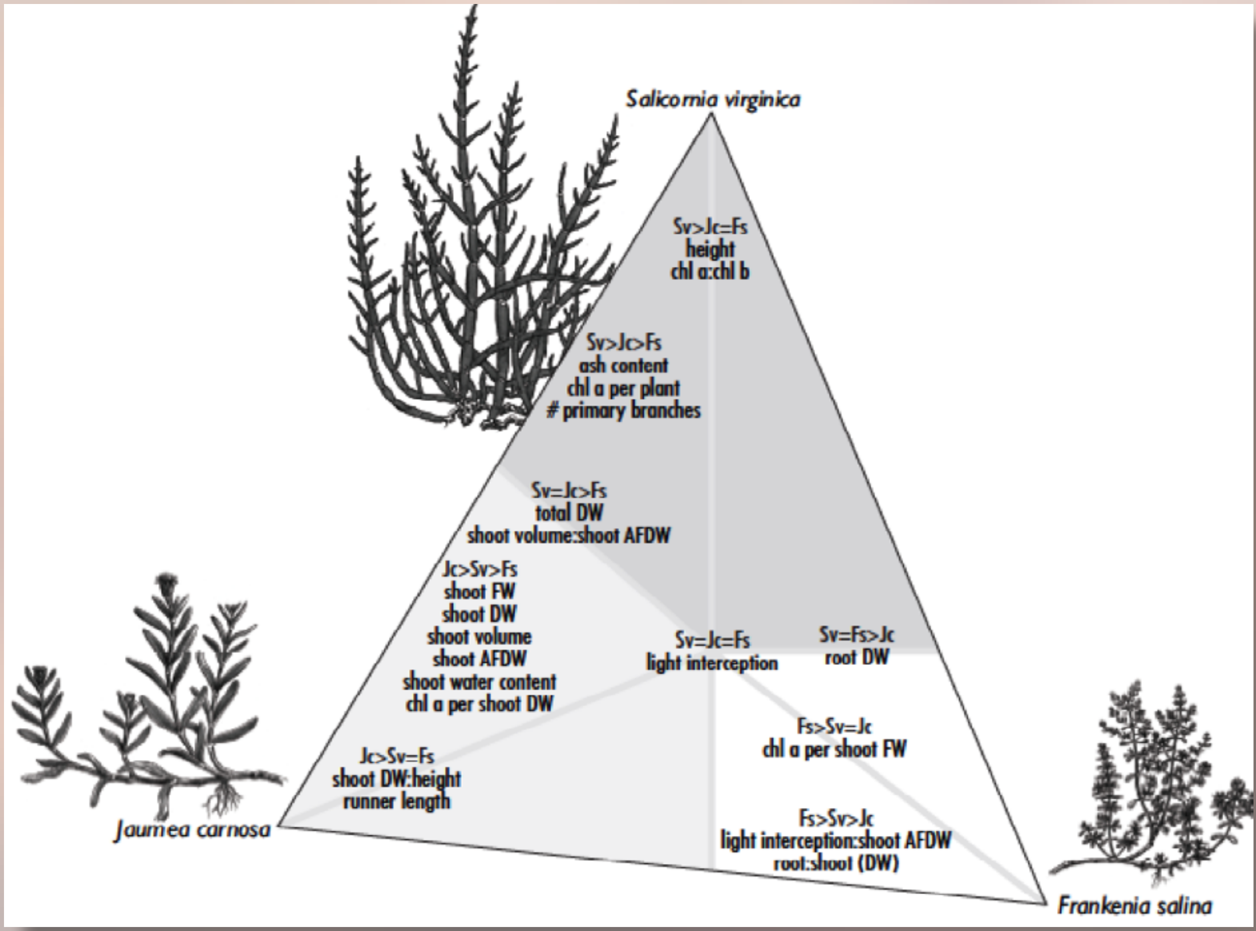
For her MS degree at UW-Madison, Cathi Bonin wanted to learn why the diverse plots were being taken over by perennial pickleweed and its top two comrades, salt marsh daisy and alkali heath. The basic question was, which of pickleweed‘s traits explains its strong tendency to dominate?

Cathi compared everything we could think of–-and that we could also measure. The 20 traits were height, number of branches, length of runners, shoot fresh weight (FW), shoot water content, shoot volume, shoot dry weight (DW), root DW, total DW, shoot ash content, shoot ash free dry weight (AFDW), light interception, chlorophyll a (chl_a) per leaf FW, chl_a per leaf DW, chl_a per shoot DW, and the ratios of root/shoot, shoot volume/shoot AFDW, light interception/ shoot AFDW, shoot DW/height, and chl_a/ chl_b. Periodically, Cathi measured canopy height and primary stem length, which are nondestructive methods that can be repeated; the destructive sampling needed to wait till the end of the growing season.

Through field and greenhouse research, perennial pickleweed revealed its secrets. This succulent grows taller by having woody (perennial) upright branches, which become stiff and strong over time as they accumulate biomass. Salt marsh daisy and alkali heath allocate more of their biomass to runners (trailing stems) and short upright branches. Their strategy is to spread horizontally into canopy gaps, subsidized by energy from the parent plant and its roots—which can be several feet away from the newest branches. We propose that salt marsh daisy persists by extending its runners throughout the understory, while alkali heath gains some advantage by allocating more of its biomass to roots. Perennial pickleweed becomes dominant by growing tall and capturing light first and being more plastic.

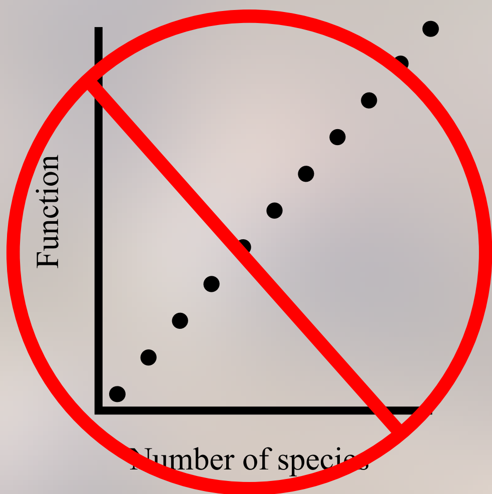
Plasticity? What’s that? It’s the ability to shift trait ratios with changing conditions, and it might be the biggest secret that Cathi revealed. Few people evaluate how a species shifts a variety of traits in response to its environment. She found that perennial pickleweed increased the ash content (probably salts) of it shoots when grown at higher salinity as well as when grown with a lower water table. Neither salt marsh daisy nor alkali heath did that. The pickleweed also decreased its root/shoot ratio when grown in high salinity and with a high water table. Salt marsh daisy decreased its root/shoot ratio only in the high salinity treatment, and alkali heath did not respond to either. In general, perennial pickleweed appeared to be more “plastic”—able to adjust its growth as conditions change. I’d call that adaptive, but the physiological advantages still need to be revealed.

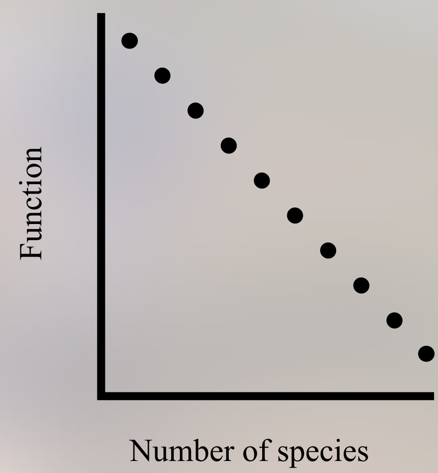
What Cathi’s detailed analyses of three competitors shows is that each is superior in various ways. Comparative studies go a long way toward explaining why some species become dominant and others remain subordinate. Also, our multi-trait approach explained abundance ranks, where focusing on a single trait could not. Salt marsh daisy and alkali heath persist and co-dominate, but perennial pickleweed’s woody branches allow maximum height, which trumps other traits (Bonin and Zedler 2008).



Comparing the early data (Callaway et al. 2003) with the long-term response (Doherty et al. 2011), we verified what was visible across the experimental salt marsh. The vegetation changed from having distinctly different patches in 2000 into a relatively homogeneous marsh in the 2000s, with pickleweed everywhere—tall, conspicuous, and dense in cover. Salt marsh daisy and alkali heath were available and able to take over where pickleweed was absent. You might think of them as "understudies."

Our salt marsh data do not support the initial claims of BEF theory. Theory predicted that increasing species richness would, due to complementarity, increase functions, such as NPP and N accumulation. That appeared to happen temporarily, while we weeded the plots (first 2 years), but not in our long-term salt marsh study. Depending on the function assessed and whether data were plotted for the number of species planted or the number that remained after a dozen years, we found either no pattern or a negative relationship:





Our greenhouse experiment revealed how individual species affected a wide variety of assemblages. The chance inclusion of a high-performing species in randomly-drawn, species-rich assemblages can explain experimental outcomes. The most informative tests of how diversity affects restoration need to follow sites that are not weeded and to be tracked over one or more decades. Here's the "bottom line":

"Superplants" explained more than complementarity

Biodiversity-ecosystem function theory now encompasses both paths of diversity effects. Jim Doherty's further explorations of this theory in freshwater wetlands suggest that nutrient-rich wetlands tend toward fewer species as productivity increases. So, when you plot function against richness, you find a negative relationship (Doherty and Zedler 2014). In this case,

cause → effect is best understood as effect → cause.

Rather than low diversity causing high productivity, the high productivity of a top-performing (super) species causes low diversity by displacing competitors.