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DETERMINANTS OF PLANT SPECIES ASSEMBLAGES IN THE CALIFORNIAN MARSH PLAIN: IMPLICATIONS FOR RESTORATION OF ECOSYSTEM FUNCTION

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The composition and richness of plant assemblages (defined as the mix of species found in a particular location) are both important to ecosystem functions such as productivity, N dynamics and canopy architecture.

Plant community theory suggests that assemblage composition is first determined by environmental factors, then biotic interactions limit co-occurrence.

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In salt marshes vegetation patterns have been correlated with tidal inundation, elevation and salinity. Other factors include seed availability, physical disturbance and biotic interactions.

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The marsh plain in Californian salt marshes, which extend from Point Concepción near Santa Barbara, down to Baja California, are well suited to the study of species composition and species assemblages and their relationship to ecosystem function because: The herbaceous vegetation is easily sampled. The marsh plain coexists without interference from invasive species. Halophyte traits are well known, major environmental changes occur within a relatively short distance due to the effects of tidal inundation on soil salinity and moisture. Species composition is constant in time (shifts in composition occur only in response to major disturbance events like flooding), and disturbance is rare.

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These marshes are characterized by a small plant species pool, 6 perennial (in the yellow background), 1 short lived (in blue) and 1 annual species (in purple). *Salicornia virginica* is the dominant species. These species are not readily sorted into functional groups, they differ in biomass and N allocation, shoot:root ratio, and show phenotypic and functional plasticity in response to environmental factors. Thus, research has found that functions such as canopy complexity and N accumulation increase with species richness.

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In southern California marshes, over 90% of coastal wetlands have been destroyed. Many of the remaining sites, like Tijuana Estuary in San Diego and Ballona Wetland in Los Angeles, are surrounded by urban development. In these sites, biodiversity is being lost due to the effects of coastal development, including eutrophication, freshwater inflow and sedimentation. Plans for ecosystem restoration are no underway, for example in Tijuana Estuary there is a plan to restore ~200 hectares of former salt marsh.

Restoration ecologists could benefit from predictions on how species composition affects community structure and function.

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My general objective was to investigate three categories of the factors that determine composition and richness of plant assemblages and provide recommendations for salt marsh restoration.

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“Topographic heterogeneity”

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Topographic heterogeneity can create a complex mosaic of substrates with varying physical characteristics. In salt marshes the most obvious features of topographic heterogeneity are tidal creeks. Creeks control tidal flow into the marsh and influence flooding and drainage. Zedler et al (1999) found that specie richness was higher near the tidal creek edge (< 1m) and that the distribution of four of the marsh plain species varied in relation to elevation and distance from a tidal creek (*S. bigelovii*, *S. esteroa*, *F. salina*, and *L.californicum*).

This led us to question the spatial extent of tidal creeks on species richness, species abundance, and species assemblages. I will be focusing on the effect of tidal creeks on species assemblages.

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A team of researchers from the Pacific Estuarine Research Lab at San Diego state University surveyed vegetation in Bahia San Quintin Mexico, a relatively pristine salt marsh in May 1999.

As a comparison Tijuana Estuary the least fragmented coastal wetland in Southern California has ~ 700 ha of wetland area.

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We sampled cover in plot of 5 spatial scales and in a nested design in areas with or without creeks.

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We asked if species assemblages differed in areas with and without creeks. Where assemblage composition is the identity of species in a plot. Here illustrated by the circles of different colors.

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We found 188 unique assemblages (of a possible 8191). The assemblages were distinctly different between cells with and without creeks. Only 14% of assemblages were found in common between these areas.

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This table shows the frequency and composition of the most common assemblages. The most common assemblage had 6 species. This (map thumbnail) represents what appears to be a previously un-described *Salicornia* species that we considered separately in our analysis. Differences in assemblage composition can be a result of differential responses to physical gradients resulting from variations in flooding (such as salinity, redox, sulfides), as well as tidal dispersal as seeds can deposit in areas along creek banks.

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“Seed availability”

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Seed dispersal influences recruitment and the formation of seed banks in the soil. Particularly, in restored marshes, like this site in Tijuana Estuary, seed dispersal may play a key role because areas that were historically salt marsh do not retain a seed bank because seeds are short lived.

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Plants either have to be planted

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or seeds have to come in on their own and establish.

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Studies in the Netherlands and New England have found three main patterns for the transport of salt marsh seeds, the most common pathway are the tides because seeds can float in the water, that salt marsh seeds can travel considerable distances and float for long periods of time, and that tidal dispersal was possible for many species.

We asked if dispersal of Californian marsh plain seeds was possible into a restored site by tidal transport and what was the temporal variation of seed transport.

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We sampled the incoming tide into a restored marsh and the outgoing tide from a reference marsh, monthly for two years. We then assessed the identity, and quantity of emergent seedlings from the tidal material collected.

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Seedling emergence from tidal material was characterized by low richness and density. Over 90% of seeds were *Salicornia virginica*, the marsh plain dominant. Six other marsh species were present. This pattern is likely the function of high abundance of *Salicornia* in nearby sites and seed characteristics. *Salicornia* seeds can float and have hooks on their surface that can latch on to passing debris.

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I am only presenting *Salicornia virginica* seedling density because density for other marsh plain species was very low <0.1 seedling m^3 . *Salicornia virginica* seedling density was highest in winter, when rain events occur and tidal amplitude is highest. This species also produces seeds between June and December, so this pattern is likely a combination of seed production and environmental factors.

We conclude that for most species tidal dispersal limits seed availability, for species other than *Salicornia virginica* dispersal events are likely episodic and rare. Establishment in restored marshes results from the coincidence of seed production, dispersal vectors (flooding or high tide) and rain that lowers soil salinity.

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“Biotic interactions”

Once seeds have entered a site and germinated biotic interactions can limit co-occurrence. Particular species might contribute more to one ecosystem process than other species and in turn affect assemblage composition.

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For example in the marsh plain *Triglochin* has low biomass, low height and few canopy layers, high N% (17-52 mg g⁻¹), and sparse cover but has high frequency of occurrence in natural marshes. In a reference marsh there was a significant negative relationship between canopy cover of *Triglochin* and *Salicornia*, this and other studies suggest that *Triglochin* can open up canopy gaps for germination.

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Based on this evidence Zedler et al. (2001) proposed a model where *Triglochin* influences community dynamics by decreasing biomass of neighboring species and facilitating seedling recruitment, particularly of the annual *Salicornia bigelovii*.

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The authors suggested that *Triglochin* accumulates large N stores as it grows during the winter and reaches peak biomass in June. Thereby, increasing N competition and reducing biomass of competitive species. N stored in *Triglochin* tissue becomes available following decomposition of *Triglochin* shoots which dieback by mid summer. This N can then be used by other plant species, particularly *S. bigelovii* the marsh annual which begins germination around November.

We tested this hypothesis by growing assemblages of the 7 common-marsh species, with and without *Triglochin* and comparing biomass. At the same time we used ¹⁵N stable isotope to demonstrate N translocation between *Triglochin* and other common marsh plain species. We carried out one greenhouse and one field experiment and I will be focusing on the greenhouse results.

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We planted *Triglochin plants* that had been previously enriched with ¹⁵N in pots with the other 7-species and harvested them after 13 months, after *Triglochin* shoots had died back.

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Plants grown with *Triglochin* in the greenhouse had reduced shoot biomass. We suggest that the increase of plants grown in pots without *Triglochin* was due to enhanced N availability.

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Uptake of N recycled from *Triglochin* tissue was measured as an increase of delta 15N in the plant tissue relative to background levels. Stable isotope technique takes advantage of the low abundance of 15N isotope relative to the 14N isotope in the atmosphere. Enriching a sample provides a way to track the movement of N. Data for the 15N tissue content are presented as delta 15N which is simply an expression of the 15N/14N ratio in the sample vs the standard. So a higher N15 delta means higher abundance of 15N.

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Natural abundance of 15N in the tissue of marsh plants of the same age (≤ 3 years) as the ones used in the experiment ranges between -2 and 7. These are values from plants collected in the field and include all species except *Salicornia bigelovii*. Other authors have found delta 15N as high as 17.

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The results from the translocation experiment show that delta values of plants grown with enriched 15N *Triglochin* were significantly higher than those grown without *Triglochin*. As a means of comparison the red dotted line in the +*Triglochin* graph indicates the largest delta value found in -*Triglochin* pots.

This suggests that N mineralized after senescence of shoots or through decomposition of roots was a source of N for the 7-species assemblage. This provides evidence for the model where *Triglochin* regulates N availability on the marsh plain. A clonal species like *T. concinna* could concentrate N over a large area, creating long-lived nutrient enriched patches and contributing significantly to spatial variability in N availability to plants. The differential ability of plant species to compete for nutrients within nutrient rich patches created by *T. concinna* could be expected to produce shifts in species abundance and identity, and could increase diversity.

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Finally, I investigated the interaction between *Triglochin* and *Salicornia*. As we saw in the previous section the interaction between these two species can have implications for ecosystem function. There has been no test of the interaction between these two species. I have already mentioned the characteristics of *Triglochin*. *Salicornia* grow year round and reproduces vegetatively, it withstands extreme shifts in salinity and is a strong competitor for N. It also has a wide distribution from marsh plain to high marsh.

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In salt marshes N is limiting so we would expect competition for N. Theory also suggests that competition will shift across stress gradients, but in salt marshes areas of low and high stress are not easily defined as flooding and redox potential are more severe in the low marsh, and in pools and depressions along the marsh plain. While soil salinity increases with marsh height.

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We investigated how the interaction between *Salicornia* and *Triglochin* varied across a gradient of water levels and N-supply. I will focus on one greenhouse experiment, where we tested the specific hypothesis that when N was limiting and as the interaction time increased *Triglochin* would dominate and *Salicornia* biomass would be reduced. We also suggested that *Triglochin* would have higher biomass in high water levels and *Salicornia* in low based on their observed distributions in the field. This one-year experiment used an additive design with plants grown in monotypes or in mix with equal numbers of plants of each species in the mix.

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N was added as 15 g/m² at the beginning of the experiment and we applied three water level treatments. Water levels were supposed to recreate the stress imposed by the action of repetitive tidal inundation, in three greenhouse and one field experiment. This hydrograph shows the daily variation in water levels and the variation in hydroperiods of two weeks. For example, the high water treatment oscillated daily between 25 and 20 cm for two weeks and then the water level dropped for another two weeks.

After 1-year we assessed above and belowground biomass, seed production, and tissue N content. I will not present the results for seed production.

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There was no effect of water levels on aboveground biomass, and overall *Salicornia* biomass was higher than *Triglochin*. Biomass of *Salicornia* decreased in the mix relative to the monotype.

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Belowground, biomass was higher for *Triglochin*. I should point out than in other experiments when N was added in higher concentrations belowground *Salicornia* biomass was higher than *Triglochin*. Overall, belowground biomass was highest in the medium water level.

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We suggest that competitive dominance of *Triglochin* over *Salicornia* occurs primarily when nitrogen is limiting, resulting from *Triglochin*'s superior ability to allocate belowground biomass and to sequester available N. As we can see *Triglochin* allocates a larger proportion of its biomass belowground relative to aboveground and it sequesters more N in its tissue.

So the two other greenhouse experiments we tested the hypothesis that an increase in N supply would shift the competitive interaction, increasing *Salicornia* dominance below and aboveground. Also, as in the 1-year experiment we predicted that biomass of *Triglochin* would increase with water levels and that of *Salicornia* would decrease. I will only give a general overview of the results.

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These are the results for a 4-month replacement experiment. Where total pot density was kept constant but density of each species varied in the mix. Here we have mix pots across the gradient of increasing N-supply and water levels. Overall the results matched the expectations, *Salicornia* aboveground and belowground biomass increased with fertilization, but belowground biomass of *Salicornia* was only higher than *Triglochin* when N was added. Contrary with what might appear, there was no increase of *Triglochin* biomass with water level. We conclude that competitive dominance of *Triglochin* occurs primarily belowground when N is limiting resulting from *Triglochin*'s ability to sequester N, and that in the Californian marsh plain changes in N can shift competitive interactions.

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We can draw recommendations for marsh restoration of Californian salt marshes from these results. Concur with Zedler et al. (1999) and Sanderson et al. (2001) that tidal creeks should be incorporated into restoration designs. Target (and plant) multispecies assemblages, not monocultures. Emphasize species that are non-tidally-transported, avoid *Salicornia virginica* because this species was common in the emergent seedling from tidal marsh, and plant *Triglochin concinna* to increase N retention. Landscape position matters; consider surrounding vegetation and means of dispersal of each species.