**Impacts of inundation regime, floodplain vegetation, and burrowing animals on the incorporation of carbon into floodplain soils**

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# Introduction

Hydrological alteration from land use change, dams, irrigation, and groundwater withdrawal is affecting river health in the United States and around the world. These changes impact various ecosystem services and human social and economic systems (Naiman et al. 1995, Postel and Carpenter, 1997). Large river-floodplain ecosystems have been extensively modified in temperate regions for decades, making restoration difficult since few unimpacted systems exist to provide examples of “natural” ecosystem function.

Riverine floodplains are spatially heterogeneous and ecologically complex. Fluvial processes, such as erosion, deposition, and transport, maintain high structural diversity among floodplain elements found in the river corridor (Ward et al. 2002). Although the mechanisms are unknown (Ward et al. 2002), organisms are adapted to this spatial-temporal structural diversity (Naiman and Decamps 1997) and as a result, floodplain rivers have high biodiversity and high production rates.

The degree of aquatic and terrestrial coupling is determined by the interaction of discharge regimes and floodplain morphologies. It is the advance and retreat of water across the floodplain that controls the lateral exchange of organic matter and nutrients necessary for maintaining floodplain productivity (Junk et al. 1989). This connectivity between the main channel and lateral floodplain elements occurs, on the yearly time scale, by fluctuations in river height, although longer, decadal patterns also exist (Tockner et al. 2000, Amoros and Bornetter 2002). Higher trophic levels (invertebrates, fish) are adapted to this flood cycle and exploit the additional food resources and increased habitat availability.

In California, most floodplains are disconnected from river water because of dams, water withdrawals, and levees. The Cosumnes River however, is unique in that it has a floodplain that is hydrologically connected to its river. A stated conservation goal of the Consumes River is to restore the landscape from past agricultural use. Understanding the links between flood pulse, habitat diversity and soil invertebrate communities will be important in meeting this goal and restoring floodplain soil fertility. Invertebrate communities, directly and indirectly, affect soil fertility. Floodplain soil invertebrates must adapt to changing moisture regimes from winter floods to summer droughts. When wet, nutrients and carbon are transferred from plant derived organic matter to aquatic organisms. During dry periods, stranded aquatic algae serves as a food source, in addition to plant material, for floodplain soil organisms. My research objectives are to understand how soil invertebrate communities vary between different floodplain habitats, whether differences in the amount and type of organic matter control the density and diversity of soil invertebrates, how aquatic algae is transferred to floodplain soils, and the importance of this process in maintaining floodplain soil fertility.

The *overall objective* of this research was to understand the links between flood pulse, habitat diversity and soil invertebrate communities on floodplain soil fertility and diversity.

## Study Site

The research was conducted on the lower reaches of the Cosumnes River at the Cosumnes River Preserve (CRP), a restored floodplain ecosystem in south Sacramento County (Fig. 1). At the highest elevation (2357 m) the channel is bedrock-granite controlled while historically, at lower elevations (1.5 m), the channel was meandering. At these lower elevations, the majority of the river is leveed, except where restoration projects are ongoing. The CRP encompasses 53 km$^2$ including floodplain and uplands, and protects some of the last remaining cottonwood-willow and valley oak riparian forests in the California Central Valley. The CRP also protects many migrating waterfowl, amphibians, and wild Chinook salmon.


**Figure 1:** Map of California showing the location of the Cosumnes River Preserve.

## Methods

To measure invertebrates, organic matter, and soil properties, I established 100 m$^2$ permanent plots along 2 organic matter gradients (Fig. 2). Five plots each were established in open meadow sites that received high (HA) and low (LA) amounts of algal accumulation (algae gradient) and 5 each in the cottonwood forest (AF) and an adjacent open meadow (OM) (terrestrial to aquatic organic matter gradient). Plots were sampled for terrestrial organic matter inputs, algal inputs, soil invertebrates and soil properties, and microbial taxa over the course of the study (2003-2005).

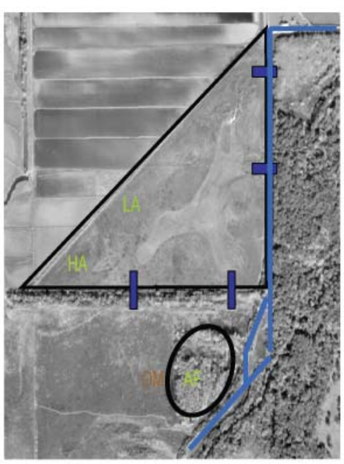


**Figure 2:** Aerial view of experimental floodplain at the Cosumnes River Preserve. The area in black is commonly referred to as the triangular floodplain and is bordered by levees on all sides. The high algae (HA) and low algae (LA) sites are contained here. Adjacent to the triangular floodplain is the lower floodplain where the accidental forest (AF, cottonwood forest) and open meadow (OM) sites are located. The Cosumnes River is outlined in light blue and levee breaches are represented as dark blue rectangles.

The forest site (AF) is dominated by cottonwood and willow trees as well as grasses. The meadow sites (HA, LA, OM) are dominated by umbrella sedge, cocklebur, grasses, and water smartweed (buckwheat family). During summer, all habitats were dry whereas during winter, each habitat flooded for varying length of time depending on flood magnitude, duration, and frequency. When flooded, mats of green algae would form in the open meadows where there was abundant light (Fig. 3A). Following flood recession, these algal mats would be deposited on the floodplain soils (Fig. 3B).

**A.**

**B.**

**Figure 3:** (A) Floating mats of green algae that develop following flooding. (B) Deposition of algae on floodplain soils.

Terrestrial litter inputs were measured by collecting fallen leaf material in a $1m^2$ plot next to each permanent plot (5 per site). Leaf material was collected approximately monthly for one year (October 2003 - October 2004). Material was returned to the lab, sorted by type and weighed after drying in a drying oven at $60^oC$ for at least 48h. Algal inputs were measured as the total amount of algae deposited on the soils following winter flooding. Soil cores were collected in June 2004 from each plot and frozen for 24h to break open the algal cells. Chlorophyll a, a measurement of algal biomass, was extracted using methanol and measured on a fluorometer. To further determine algal deposition, algal collectors were placed on the soils during the 2004-2005 flood season. Collectors were large petri dishes fixed to the floodplain soils with long stakes. Following each flood, algae were scraped from the dishes and returned for methanol extraction of chlorophyll a. Samples of both litter and algae were dried and analyzed for stable isotopes of carbon and nitrogen.

To investigate whether differences in organic matter input influenced soil microbial composition, samples from each plot were analyzed using denatured gradient gel electrophoresis (DGGE). DNA was extracted from soils using a commercial kit (Power Soil, MoBio Inc.) and subjected to PCR with universal 16S rRNA. The PCR product was run on an acrilymide gel where each band represents a microbial species. Band were excised and cloned for identification. Identifications were made based on alignments to the ribosomal database project (RDP).

Soils were sampled for oligochaetes and macroinvertebrates before (November 2003) and after (June 2004) winter flooding. Oligochaetes (worms) were sampled by removing a block of soil ($0.05m^3$) from each plot. The soils were returned to the lab and hand sorted to pick out oligochaetes and other large soil invertebrates. A soil subsample was sieved (2mm), dried, and analyzed for carbon:nitrogen and stable isotopes (carbon, nitrogen). Macroinvertebrates were preserved in ethanol and later identified to the lowest taxonomic level possible, dried, and analyzed for stable isotopes of carbon and nitrogen.

## Results and Discussion

*Organic matter inputs:*

Litter inputs were similar between meadow sites and the highest rates occurred in the AF plots (Table 1). Conversely, algal inputs were lowest in AF plots and highest in HA plots (Table 1). For all sites and litter types, litter C:N ratios were highest before and after flooding. Samples collected in between floods had the lowest C:N values (data not shown) indicating decomposition of material. Despite differences in C:N ratios of litter, differences in litter input rates and composition, and differences in the amount of algal deposition, soil C:N was not different between sites. More work is needed to understand the relationship between these organic matter inputs, decomposition rates, and soil properties.

**Table 1:** Summary of the number of days flooded, and the mean±standard error of organic matter input as a function of terrestrial material (litter) and algae (soil chl a , petri chl a). AF=accidental forest, OM=open meadow, LA=low algae, and HA=high algae

| | number days with water | Litter inputs ($(g/m^2)$/month) | soil chl a (ug/g wet soil) | | petri chl a ($ug/cm^3$) |
|---|---|---|---|---|---|
| | | | 2004 | 2005 | |
| AF | 4 | 30.73±2.76 | 0.122 | 0.189±/0.016 | 5.35±0.626 |
| OM | 14 | 27.78±5.08 | 0.672±0.054 | 1.23±0.217 | 4.37±0.552 |
| LA | 22 | 22.01±4.73 | 0.637±0.043 | 0.923±0.138 | 26.23±2.87 |
| HA | 18 | 22.51±3.74 | 1.28 | 6.14±1.34 | 43.97±5.98 |

There were differences in the stable isotopic signatures of the organic matter sources available to invertebrates (Fig. 4A, B). $\delta^{13}C$ varied more between organic matter sources than between sites (Fig. 4A). More distinctive patterns could be seen in the $\delta^{14}N$ data where increases in the $\delta^{14}N$ signature along the gradient from terrestrial to high algal deposition sites. This increase in the $\delta^{14}N$ was important for tracking algal sources through the invertebrate food web (see below).

**A.** **B.**

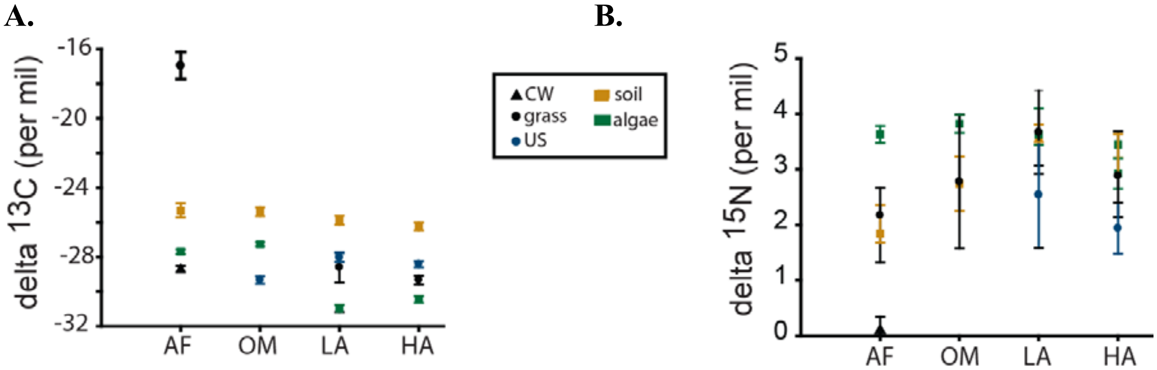


**Figure 4:** Changes in the stable isotope signatures of carbon (A) and nitrogen (B) at all 4 sites in June 2004 following winter flooding.

*Microbial communities:*

Twenty-four microbial taxa were cloned and described from the Cosumnes River floodplain soils (Table 2). Of the identified taxa, there was no one taxa that appeared at all sites; however, combinations of taxa appeared at multiple sites. More interestingly, there were taxa, for example *Buchnera spp*., that appeared only at one site (HA). Overall, clones from the forest habitat (AF) were similar to taxa already sequenced from other studies. Clones from the high algae site were the most unique where 44% of the clones did not match any sequence currently contained in the RDP. The HA site receives the highest algal inputs and remains waterlogged the longest compared to the other sites. It is unknown whether these differences have led to the selection of a different and unique microbial community compared to the other sites. The high amount of taxa variability and unknown sequences suggest that much work needs to be done in floodplain soils to begin to understand microbial diversity and any relationship to microbial function in this system.

The physiology of the taxa also varied between the forest and open meadow taxa. While the majority of cloned taxa use organics as electron donors regardless of site, taxa described for the AF soils also use sodium acetate, sodium formate, and lactate. Similarly, the AF taxa are using H2, CO2, O2, and NO3 as electron acceptors whereas taxa from the open meadows broadly use O2, NO3, and NO2. These differences could impact rates of nutrient cycling and decomposition in floodplain soils.

**Table 2:** Summary of the taxa cloned from DNA isolated from Cosumnes River Preserve floodplain soils. AF=accidental forest, OM=open meadow, LA=low algae, HA=high algae. %identified = the percentage of clones excised from the DGGE that were matched to sequences available from the ribosomal database project.

| **Taxa** | **AF** | **OM** | **LA** | **HA** |
|---|---|---|---|---|
| Acidobacterium | | X | X | |
| Actinomycetales | X | | | |
| Blastococcus spp. | | X | | |
| Bosea spp. | X | | | |
| Bradyrhizobium spp. | X | X | X | |
| Buchnera spp. | | | | X |
| Cellulomonas spp. | X | | | |
| Clostridium spp. | X | | | |
| Desulfatibacillum | | X | | |
| Firmicutes spp. | | | X | |
| Gordonia spp. | | | X | |
| Halomonas spp. | | | | X |
| Intrasporangiaceae | X | | | |
| Kitasatospora spp. | | | X | |
| Microbacterium spp. | X | | | |
| Micromonospora spp. | | X | | |

**Table 2: continued**

| Taxa | AF | OM | LA | HA |
|---|---|---|---|---|
| Prochlorococcus spp. | | | X | |
| Rhizobiales | X | | | |
| Rhizobium spp. | X | | | |
| Rhodococcus spp. | | X | | X |
| Sphingomonas spp. | X | X | | |
| Tannerella spp. | X | | | |
| Thermoanaerobacterium spp. | X | X | | |
| Uncultured bacterium | | X | | |
| % identified | 76 | 56 | 60 | 44 |

*Soil invertebrates and food web relationships:*

Twenty-one taxa of macroinvertebrates were collected from the floodplain soils. Not surprisingly, soil invertebrate abundance was highly variable between plots at the same site. There was no significant difference in the total number of invertebrates between sites (Fig. 5A). At all sites, the community was dominated by worms and beetles (adults and larvae) (Fig 5B). Some groups, such as centipedes and spiders, increased in abundance with an increase in algal deposition.

**A.** **B.**

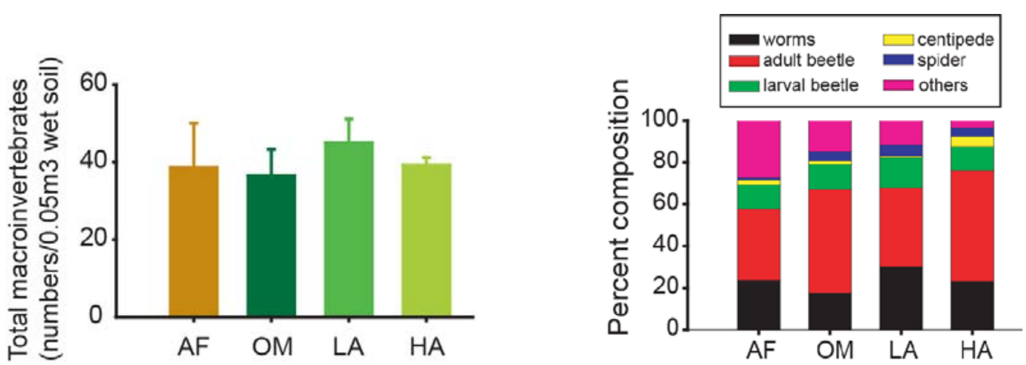


Figure 5: Total number of macroinvertebrates collected from the floodplain soils in June 2004 (A). Percent composition of the major soil invertebrate taxa collected from the floodplain soils in June 2004 (B). AF=accidental forest, OM=open meadow, LA=low algae, HA=high algae.

Macroinvertebrates were placed into functional feeding groups to investigate whether algae deposited on the floodplain was being incorporated into the food web. Figure 6 summarizes the stable isotope data for 2 feeding groups: worms (detritivores) and centipedes (predators) that were found at all sites.

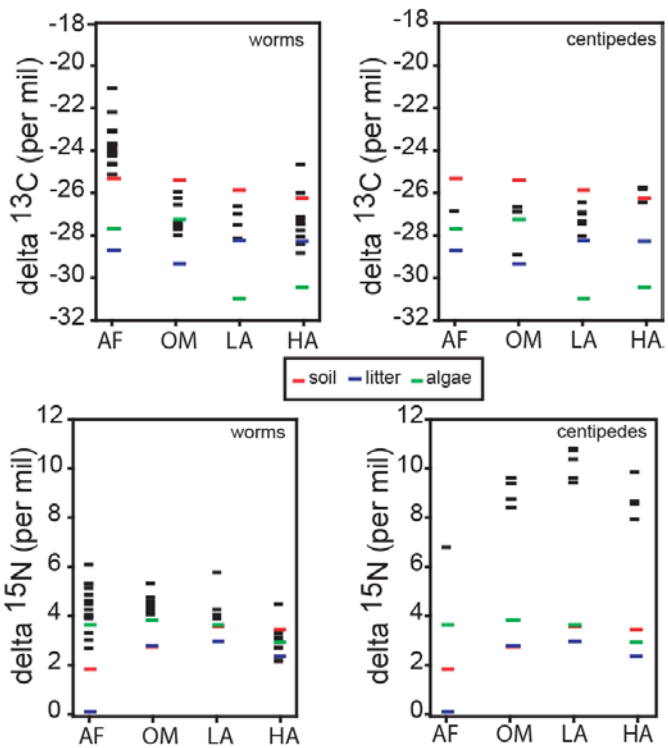


**Figure 6:** Stable isotope signatures for 2 feeding groups of invertebrates (worms and centipedes) . Each black line represents 1 individual, colored lines represent various organic matter sources.

There is a 2-4 per mil range in variation within taxa. At the AF site, worms are less negative than soil suggesting that this is their main source of carbon. At the meadow sites worms are eating some combination of the 3 organic matter sources. All centipedes were more negative than soil, suggesting that they are feeding on invertebrates that are themselves eating some combination of the 3 organic matter sources. Detritivores were generally more positive than soil or algae, often by 2 per mil, indicating that algae may be a portion of their diet. Predators showed the same increase in the 15N signal that was observed for both algae and soil along the gradient. These data indicate that algae is being incorporated into the soil food web in the open meadow habitats.

## Summary

- Timing and magnitude of flooding controls where and how much algae is deposited on floodplain soils.

- There was no difference in the total abundance of macroinvertebrates along the algal gradient

- There were some differences in the percent composition of macroinvertebrates and the presence/absence of microbial taxa along the algal gradient

- The food web has distinct trophic levels and algae seems to be incorporated into higher trophic levels in the open meadow habitats

- Management of floodplains for diverse organic matter sources, including algae, is important for the functioning of floodplain soil ecosystems

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