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Reframing plant invasion: Altered watershed biogeochemistry as a cause and consequence of giant reed Arundo donax

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Reframing plant invasion: Altered watershed biogeochemistry as a cause and consequence of giant reed *Arundo donax*

A dissertation submitted in partial satisfaction of the
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in Ecology, Evolution, and Marine Biology

by

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Vonk, J.E., Mann, P.J., **Dowdy, K.L.**, Davydova, A., Davydov, S.P., Zimov, N., Spencer, R.G.M., Bulygina, E.B., Eglinton, T.I., & Holmes, R.M. (2013). Dissolved organic carbon loss from Yedoma permafrost amplified by ice wedge thaw. *Environmental Research Letters 8*, 035023.

Hanan, E.J., D'Antonio, C.M.D., **Dowdy, K.L.**, Schimel, J.P. (2016). Effects of substrate supply, pH, and char on net nitrogen mineralization and nitrification along a wildfire-structured age gradient in chaparral. *Soil Biology & Biochemistry 19(5):* 910-926.

Homyak, P. Slessarev, E., Hagerty, S., Greene, A., Marchus, K., **Dowdy, K.,** Iverson, S., Schimel, J. Amino acids dominate diffusive nitrogen fluxes across soil depths in acidic tussock tundra. (*2021). New Phytologist* doi: 10.1111/nph.17315

ABSTRACT

Reframing plant invasion: Altered watershed biogeochemistry as a cause and consequence of giant reed *Arundo donax*

by

Kelsey Dowdy

Riparian zones are important hotspots of biogeochemical cycling, yet these systems are stressed by the compounding pressures of altered hydrology, nitrogen-rich agricultural runoff, and opportunistic introduced species. Changes in environmental conditions can favor opportunistic species and disadvantage native woody species. Once established, grasses' litter inputs and subsequent decomposition may in turn alter watershed biogeochemical cycling through differences in leaf chemistry. However, these outcomes are species- and environment-specific. A shift in the plant community from woody species toward grasses can enhance, reduce, or maintain carbon and nitrogen cycles; further, these cycles may play out differently in riparian soils and in the streams they are adjacent to. I evaluated the biogeochemical interactions of one such species that is now prolific in watersheds throughout the U.S. southwest: giant reed *Arundo donax*.

In experimental settings Arundo inhibited the growth of *Salix lasiolepis* (willow) under conditions with high N amendments characteristic of intensive upland agricultural runoff. However, Arundo did not reduce willow's growth in low N amendments or without N amendments (levels representative of upland runoff associated with sustainable farming practices or no agriculture). Arundo was able to reduce willow's growth under high N conditions by taking up more N and maintaining high photosynthetic N use efficiency as well as decreasing investment in root biomass—perhaps enabling it to allocate excess N to compete for another resource. Once established, collecting field litter and soils showed that Arundo contributed less litter C and N than woody species, but soils beneath Arundo accumulated dissolved organic C (DOC) and N (DON). These soils also hosted a relatively small microbial community and had higher silicate content, suggesting that EOC is stabilized following microbial transformations and/or in silicate complexes. In an aquatic incubation, leachates of Arundo foliage contributed less dissolved DOC and more DON than willow, but this DOC was in fact more extensively decomposed by aquatic microbes during a two-week incubation. High resolution mass spectrometry revealed that Arundo foliage's low DOC:DON, high aliphatics and peptides and low aromaticity and oxidation state contributed to its bioavailable fraction, yet over longer-term stages of decomposition Arundo foliage required more DON to break down, perhaps to create exoenzymes. Overall, Arundo material contributes a lower quantity of bioavailable DOC than willow. These results indicate that plant community shift towards Arundo could reduce soil and stream respiration, but also reduce bioavailable DOC at the base of these foodwebs.

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Introduction

Riparian zones are important ecosystems for wildlife habitat, flood control, and filtering nutrients and toxins from waterways (Bren 1993; Ranalli et al. 2010); yet these systems are increasingly stressed by compounding pressures of agricultural and urban development as well as introduced plant species (Rosenstock et al. 2013; Hood & Naiman 2000). Changes these systems are experiencing include hydrologic diversions, pollution from upstream development and nutrient-rich runoff from surrounding uplands, which modify a multitude of interacting natural cycles (Crawley 1986; Rieger & Kreager 1989; Bell 1997). They may facilitate a shift in plant community composition from predominantly native riparian forests towards opportunistic introduced species, particularly large-statured grasses (Huenneke et al. 1990; Vitousek et al. 1997; Meyerson et al. 1999; Corbin & D'Antonio 2004; Arianoutsu et al. 2013; Canavan et al. 2019).

In watersheds across the U.S. southwest, cottonwood- willow riparian forests and scrub have been converted to monotypic stands of the large-statured introduced grass *Arundo donax* (hereafter, Arundo; Rieger & Kreager 1989; Bell 1997; Quinn & Holt 2008). Originally from the Mediterranean basin and Southeast Asia, Arundo grows quickly, spreads extensively by rhizomatous growth and is dispersed during flood events that dislodge and re-distribute rhizomes. Arundo largely lacks herbivores in North America might otherwise suppress population (Perdue 1958; Hickman 1993; Bell 1997). Converting riparian forest to Arundo stands increases primary productivity and flammability, and decreases habitat for native fauna (Dudley and Collins 1995; Bell 1997; DiTomaso 1998; Dudley 2000; Herrera & Dudley 2003; Lambert et al. 2010). Less understood are the biogeochemical interactions between Arundo and the riparian landscape during its growth and decomposition, yet such a shift in biogeochemical interactions can alter ecosystem functions at several levels (Gregory et al. 1991). Arundo, like other introduced large-statured grasses, grows larger and can be competitive when subsidized with nitrogen (N; Coffman 2007). Once established, a shift in plant growth form can change carbon (C) and N litter inputs to soils and streams through decomposition (Canadell et al. 2007; Cornwell et al. 2008). Investigating how Arundo influences watershed biogeochemistry can inform land managers about upstream influences and downstream consequences: how to prioritize restoration in different N conditions and to improve predictions of watershed C flux and foodweb dynamics.

The success of opportunistic introduced species is often correlated with high N conditions (e.g. Huenneke et al. 1990; Brooks et al. 2003; Yelenik et al. 2004; August-Schmidt et al. 2015; Valliere et al. 2017) because they are able to grow rapidly and reproduce quickly when they have sufficient nutrients (Rejmanek & Richardson 1996; Van Kleunen et al. 2010). Nutrient loading to riparian and river systems from agricultural runoff can encourage introduced opportunistic species like Arundo and put native plants adapted to low N levels at a competitive disadvantage (Ambrose & Rundel 2007; diCastri 1991). When supplemented with high levels of N, Arundo can accumulate twice as much biomass as native woody species and thus outcompete them (Lambert et al. 2014; Coffman 2007); with intermediate N amendments, however, Arundo may grow less than native species (Dudley, unpublished data). In the field, Arundo spreads radially to cover large areas in nutrient-rich conditions, but in nutrient-poor conditions, it establishes dense discrete clumps (Decruyenaere and Holt 2001). Arundo’s competitive dynamics across a range of N levels are unknown yet understanding its nuanced responses to N amendment is important to management because levels of N-runoff into riparian zones vary with surrounding human activities, most commonly between agricultural practices. Large-scale, fertilizer-intensive, industrial farming methods can increase N runoff, and thereby potentially promote Arundo growth (Mondelaers & Huylenbroeck 2009). Other approaches may produce less N runoff by determining fertilizer additions based on closely-monitored crop needs and environmental conditions (precision agriculture) or by applying slower-to-leach organic N fertilizers (organic agriculture); these may limit Arundo growth (Freidenreich et al. 2019; Benoit et al. 2014; Mondelaers & Huylenbroeck 2009; Korsaeth et al. 2008; Tuomisto et al. 2012).

The extent of Arundo in riparian forests may influence nutrient cycling in riparian soils and waterways by shifting the quantity and quality of litter inputs (Hector et al. 2000; Liao et al. 2008). Leaf litter constitutes the primary organic matter (OM) input to soil and stream foodwebs (Marcarelli et al. 2011; Stanley et al. 2019), yet its chemistry can vary among plant growth forms (Stanley et al. 2012; Wymore et al. 2015; Marks 2019). The dissolved fraction (DOM) leached from leaves is particularly important for microbial metabolism and nutrient cycling because it is most immediately bioavailable (Wiegner & Tubal 2010). Differences in leaf traits between growth forms can regulate their relative biolabilities during decomposition. Molecular composition and N content control biolability: simple, straight-chain, low-molecular-weight compounds with high N content are typically readily metabolized and break down quickly, while complex, aromatic, or high-molecular-weight compounds (i.e. structural or defense compounds) are more resistant to decomposition and break down slowly (Marin-Spiotta 2014). Given the chemical compositions of different leaves, however, the relative balance of these different chemical controls on leaf litter biolability and OM contributions varies across plant assemblages. Thus, to understand how a shift in vegetation composition will influence OM dynamics, particularly in stream water adjacent to Arundo stands, an exploration of the specific chemistry and stoichiometry of leaf litter and how it regulates ecosystem processes is needed. Despite a shift from riparian forest to Arundo in watersheds in California, the U.S. Southwest, and Mexico, as well as increasing studies of Arundo's influence on community and foodweb structure, we do not know how Arundo leaf litter chemistry affects soil and stream biogeochemistry (Bedford 2005; Lan et al. 2012).

Plant resource-acquisition strategies are associated with leaf traits that translate to differences in chemistry and biolability (Cornwell et al. 2008). Introduced opportunistic plant species often have higher specific leaf areas and leaf nutrient concentrations that enable high growth rates and plant biomass compared to the riparian species they replace (Weidenhamer & Callaway 2010; Ehrenfeld 2003). Consequently, the new dominant litter is typically more nutrient-rich (most notably in N) and thus more biolabile (Liao et al. 2008). This may cause a feedback promoting the ongoing success of introduced species, which tend to thrive on N-rich soils (Huenneke et al. 1990; Ostertag & Verville 2002; Allison & Vitousek 2004; Corbin & D'Antonio 2004). However, in some cases introduced species may have an insignificant effect on decomposition rate and N availability. For example, high lignin in leaves can bond with N to make it less bioavailable and so slow overall leaf decomposition, despite high foliar N content (Castro-Díez et al. 2014).

Differences in leaf litter chemistry and consequent biolability vary between growth forms, where leaves that grow more quickly with higher nutrient content and lower structural and defense compounds decompose more quickly (Cornwell et al. 2008). Litter from herbaceous forbs tends to decompose more quickly than leaf litter of woody deciduous species, which typically decomposes more quickly than woody evergreen species, while evergreen grasses decompose more slowly than woody species (Rawlik et al. 2021). However, this varies across systems and species. For example, leaf litter from opportunistic perennial reed bamboo (*Bambusa spp* and *Sinarundinaria spp.*) has lower N content—but higher N and phosphorus (P) content per unit C—and lower mass loss in streams and in soils than native and introduced trees (O'Connor et al. 2000; Liu et al. 2000), while Japanese pampas grass (*Miscanthus sinensis*) leaf litter has similar N content to that of oak tree *Quercus crispula*, but pampas grass decomposes more slowly, likely due to greater relative abundance of acid unhydrolyzable residue (Osono et al. 2014). Such variation in the chemical controls on biolability across litter types suggests that more comprehensive chemical analyses are important in untangling how plant community shift affects watershed C and N cycling, particularly in relationship to plant growth form and resource acquisition strategies.

Arundo is an opportunistic, evergreen perennial plant in California and can grow 2-5 times faster than native riparian willow species (*Salix goodingi* and *Salix laevigata*; Coffman 2010; Reiger & Kreager 1989). This rapid growth may not necessarily result in increased litter contributions, as Arundo litter remains attached to standing stalks while native cottonwood-willow riparian forest trees drop litter seasonally; however, standing dead litter can contribute nutrients in throughfall by leaching (Hodson et al. 1984). Litter of evergreen grasses typically decomposes more slowly than leaves of deciduous, woody native riparian forest species (Cornwell et al. 2008). Arundo litter has a higher C:N (40.2) than native *Salix* and *Baccharis* litter (30.9; Lambert, unpublished data), further suggesting that Arundo might be less biolabile than native species.

Arundo's high silica content (Jackson & Nunez 1964; Schaller & Struyf 2013) may also slow down C cycling. Grasses are generally high in silica (10-20 times more than other dicots), which is stored in plant phytoliths and occludes C during photosynthesis. This phytolith-occluded C remains relatively stable during decomposition (Parr & Sullivan 2005). Slow litter decomposition can lead to C and N accumulation in surface soils (Melillo et al. 1982), although this accumulation might be counterbalanced by reduced litter inputs. The potential for changes to soil C concentration, chemistry and biolability following plant community shift means another mechanism for altering the DOM entering waterways.

Overall, any shift in plant growth form represents a shift in plant mediation of watershed biogeochemistry by way of nutrient uptake and nutrient inputs to soils and streams. Such changes in the relationship between plant community and landscape biogeochemistry are compounded by high nutrient conditions in agricultural watersheds. In response to high N conditions, opportunistic species like Arundo grow quickly and outcompete native riparian species, but their advantage is reduced in the absence of N amendments; thus lower N levels associated with less intensive agriculture may reduce Arundo's advantage. Once Arundo populations establish and replace ecologically important native woody species, differences in leaf traits and associated chemistry may slow litter decomposition in soil and waterways, because litter from large statured grasses often decomposes more slowly than native riparian tree species' litter.

In this dissertation, I explore how Arundo's establishment and inputs relate to watershed biogeochemistry. I address the following questions: (1) How does the N environment influence Arundo's competitive effects on *Salix lasiolepis*, a common woody plant in most coastal southern California streams? In Chapter 1, I evaluate how three levels of N amendment representing upland runoff from different farming methods influence Arundo growth and suppression of willow. I hypothesized that Arundo would outcompete willow in high-N conditions, but with no-N and low-N amendments willow growth would be unaffected by Arundo's presence. (2) Once established, how does Arundo's litter chemistry and subsequent decomposition affect nutrient inputs to soil and streams? In Chapter 2 I compared how long-term presence of Arundo versus native riparian forest affects soil biogeochemistry in prominent stands along the Santa Clara River. I hypothesized that Arundo would accumulate C and N in surface soils due to decreased litter biolability and higher silica content. (3) In Chapter 3, I conduct detailed DOM chemistry of Arundo and *Salix laevigata* fresh leaves and litter to evaluate how it correlates with aquatic biolability, including its influence on leachates from soil beneath the two vegetation types. I do this in wide agricultural river corridors as well as narrow, less developed creek corridors to test the generality of findings across watershed types. I hypothesized that Arundo material would be less biolabile due to the presence of more complex compounds (Chapter 3). By combining approaches of Arundo's response to watershed nutrient cycling (growth) and contributions to watershed nutrient cycling (decomposition), I aimed to understand what this shift in growth form means for watershed C and N cycling at the transitional boundary between upland and aquatic systems.

I. The interacting effects of nitrogen level and *Arundo donax* deposition on willow growth

A. Abstract

Riparian ecosystems throughout the U.S. southwest are affected by the compounding pressures of nutrient enrichment and opportunistic large statured grass *Arundo donax*. Arundo grows more with nitrogen (N) amendments and can outcompete native woody species in high-N conditions characteristic of intensive agricultural runoff, but Arundo's competitive dynamics at a range of N levels characteristic of less intensive agricultural methods have not been assessed. Here, we address how soil N levels influence Arundo competition with a dominant native woody species *Salix lasiolepis* (arroyo willow) by simulating a flooding scenario in which Arundo is deposited and establishes within an existing willow stand and is fertilized with nitrate (NO_3^-) from agricultural runoff. I added Arundo rhizomes to established willows in individual pots of riparian soil, along with a weekly addition of no, low (24 $g/m^2\ yr^{-1}$ N), or high (120 $g/m^2\ yr^{-1}$ N) nitrogen for four months in the greenhouse. Arundo significantly inhibited willow's growth by 57% in high-N conditions, but did not inhibit willow with low-N or no-N amendments. Arundo had greater leaf %N, higher potential photosynthetic N use efficiency (PNUE), and produced less root biomass than willow, suggesting that it dominated access to NO_3^- and did not need to invest in root infrastructure to acquire N. Arundo also grew 2-4 times taller than willow and may have dominated access to light. Although both species had similar net assimilation of CO_2 (A_{net}) in full light, Arundo had greater leaf biomass to increase its photosynthetic potential. These findings suggest that upstream NO_3^- management, particularly in agriculture, may

enhance the success of opportunistic introduced species such as Arundo. Native plant restoration practices could integrate upstream N dynamics into prioritizing Arundo removal areas, as well as join other conservation efforts limiting NO_3^- inputs for holistic whole watershed management.

B. Introduction

Riparian zones are important for wildlife habitat, flood control, and filtering nutrients and toxins from waterways (Gregory et al. 1991; Bren 1993; Ranalli et al. 2010). In Mediterranean regions, these areas increasingly experience high disturbance flood events and nutrient-rich agricultural and urban runoff, providing ideal conditions for opportunistic introduced species to thrive (Tickner et al. 2001). Nitrogen (N) enrichment has been linked to the competitive success of opportunistic introduced species worldwide (Huenneke et al. 1990; Vitousek et al. 1997; Corbin & D'Antonio 2004; August-Schmidt et al. 2015); such species typically grow rapidly and reproduce quickly when they have sufficient nutrients (Rejmanek & Richardson 1996; Van Kleunen et al. 2010). These species are often able to use resources more efficiently to enable higher relative growth rates; notably, they often photosynthesize more and with higher photosynthetic nitrogen use efficiency (PNUE; Vitousek 1986; Durand & Goldstein 2001; Funk et al. 2013; Lin et al. 2019). High-N conditions can also alleviate N-limitation but heighten competition for other resources, such as water and phosphorus (P); opportunistic species may invest excess N into P-acquisition and ultimately outcompete natives for P (Treseder & Vitousek 2001). In comparison, native species often have traits such as low relative growth rate and nutrient storage that may be adaptations to low-N systems, but maladaptive under current conditions in agricultural watersheds (Chapin 1980; Rejmanek & Richardson 1996; James 2008). Introduced grasses in particular compete with native woody species by quickly establishing aboveground cover and dense, shallow root systems that can dominate access to water and nutrients (Williams & Hobbs 1989; D'Antonio & Vitousek 1992).

The opportunistic introduced grass *Arundo donax* forms monotypic stands that have replaced riparian forests in watersheds throughout the southwestern U.S. (Rieger & Kreager 1989). This large-statured perennial reed reduces native flora and fauna, uses more water, and changes fire regimes via its flammability; thus millions of dollars are spent on removing Arundo and restoring native plants (Dudley and Collins 1995, Bell 1997, DiTomaso 1998, Dudley 2000; Watts & Moore 2011). However, Arundo is fast-growing, spreads easily by rhizomatous growth and by dispersing rhizome pieces during flood events, and largely lacks herbivores; hence restoration efforts are difficult and often unsuccessful (Perdue 1958; Bell 1997; Quinn & Holt 2009).

Similarly to other opportunistic introduced species, Arundo's competitive success has been linked to disturbance and high-N conditions (Bell 1997; Polade et al. 2017). Thus, the infrequent, intense storms and river flooding typical of Mediterranean climates facilitates Arundo's spread by ripping up and depositing rhizomes into new areas downstream that accumulate sediment and debris, as well as increasing pulses of N-rich agricultural runoff into riparian zones (Elton 1958, Tilman 1988, Rieger & Kreager 1989; Drake et al. 1989, Richardson et al. 2000; Ambrose & Rundel 2007; Robinson et al. 2005; Warrick et al. 2005; Moore et al. 2016). Arundo spreads radially in nutrient-rich conditions, but in nutrient-poor conditions it forms dense clumps (Decruyenaere and Holt 2001). Arundo can accumulate over twice the biomass with ammonium nitrate (NH_4NO_3) additions as without added N in riparian soils (Lambert et al. 2014). In response to varying levels of N addition, Arundo accumulates more biomass than the dominant native riparian woody plant, *Salix laevigata* (red willow) under either extreme of N availability: either no or high N amendment (12-14 g/m^2 N), but at intermediate N amendment (4 g/m^2) *Salix* outgrew Arundo (Dudley, unpublished data; Coffman 2007).

The amount of N running into riparian zones and thereby supporting Arundo growth is a function of upland land use in the watershed: enhanced Arundo growth could be associated with farming methods that produce excessive nutrients in runoff (Coffman 2007). In California, N fertilizer application has doubled since 1970, resulting in nutrient loading to riparian and river systems; excess N is readily nitrified into highly mobile NO_3^- (Rosenstock et al. 2013; Nosengo 2003). Some kinds of farming produce greater N runoff and thereby may fuel greater Arundo growth; other approaches may lead to less N runoff and may limit Arundo growth. For example, large-scale, fertilizer-intensive farming practices can increase N runoff (Mondelaers & Von Huylenbroeck 2009), while other approaches under the broad umbrella of sustainable agriculture can produce 25-50% less N runoff by determining fertilizer additions based on monitoring crop needs and environmental conditions (precision agriculture), building soil organic matter to retain nutrients, or by applying delayed-release organic N fertilizers (organic agriculture; Freidenreich et al. 2019; Magdoff & van Es 2010; Benoit et al. 2014; Mondelaers & Von Huylenbroeck 2009; Korsaeth et al. 2008; Tuomisto et al. 2012). Agricultural management is an important influence on how riparian systems work in California, yet an understanding of Arundo's competitive dynamics at the range of N inputs resulting from different land-uses and farming practices levels is lacking. Addressing this range of N levels offers the opportunity to link riparian native plant restoration with upland management decisions, as restoration efforts have historically focused on removing opportunistic introduced species without remediating environmental factors that promote their spread (Schaffner et al. 2020).

I investigated how soil N levels influence Arundo competition with *Salix lasiolepis* (Arroyo willow), a dominant native woody species. A greenhouse experiment was set up to address the following scenario: during a flood, Arundo rhizomes in riparian soils are dislodged and deposited downstream among established *Salix spp.* These areas could have different levels of N runoff depending on the land uses/agricultural methods used in the surrounding landscape. We added Arundo rhizomes to established willows (*Salix lasiolepis*) growing in pots of riparian soil, and provided weekly N-additions to span the range of N-inputs likely from different upland land uses; these spanned from none to high-N inputs reflecting the range from native upland vegetation, through sustainable farming, to intensive industrial farming (Benoit et al. 2014; Mondelaers & Huylenbroeck 2009; Korsaeth et al. 2008; Tuomisto et al. 2012). We hypothesized that Arundo inhibits willow in high N conditions through its high rates of photosynthesis and growth. We measured not only biomass responses to nutrient conditions, but also leaf C:N, net assimilation of CO_2 and potential photosynthetic nitrogen use efficiency (PNUE). If Arundo benefits from higher N, then we predict it should show lower leaf C:N and greater PNUE than willow.

C. Methods

1. Experimental Design

We set up an Arundo deposition and nitrogen amendment experiment, in which Arundo rhizomes were added to established willows (*Salix lasiolepis*) in individual pots and supplied with a weekly addition of no, low (24 g m^{-2} yr^{-1} N), or high (120 g m^{-2} yr^{-1} N) doses of potassium nitrate (KNO_3). The no nitrogen treatment reflects N levels from native upland vegetation, low-N reflects data on inputs from sustainable farming runoff, while high-N represents recent data on N levels from industrial, intensive farming runoff (Benoit et al. 2014; Mondelaers & Huylenbroeck 2009; Korsaeth et al. 2008; Tuomisto et al. 2012). This experiment took place under controlled conditions in a greenhouse, where we could control environmental variables (temperature, humidity, herbivory, soil characteristics) and monitor soil N and plant growth.

2. Soil and plant collection

Soils were collected at Sedgwick Reserve in Santa Ynez in March 2018 along Figueroa Creek, and kept air dry until potting. To understand how Arundo-N dynamics might play out across streambeds and riparian terraces with various soil properties, two soils with different textures were collected to a depth of 0.5 meters. One was a Salinas silty clay loam from a riparian terrace (a thermic Pachic haploxerol with 0-2% slope with 1-4% organic matter content to 50 cm and decreases regularly to <1% within 75 cm); the other was an adjacent sandy streambed soil which has experienced regular flooding, erosion and deposition events—it is categorized as gullied land (Web Soil Survey, USDA). Upon potting, soil %C, %N and C:N was similar between the fine and coarse soils, averaging 1.67% C, and 0.1%N (Table 1). Willow cuttings were collected from Atascadero Creek (a sub-urban waterway, comprised of a patchwork of developed and undeveloped open space) in Goleta, CA in June, August, and October 2018; cuttings were rooted hydroponically. The experimental treatments included soil texture (fine or coarse) x Arundo (+/-) x N level (no, low, high), and we had a sample size of 3-4 per treatment. However, due to similarities in plant growth metrics between textures and a loss of replicates due to willow mortality, plant growth metrics from the two soil textures were pooled for statistical analysis, resulting in treatments of Arundo x N level with a sample size of 6-8 per treatment.

3. Greenhouse conditions

To establish the mesocosms, we filled 11.2 L plastic pots 75% (approximately 8 liters) with soil, and then planted rooted willows in the soil. Pots were kept in trays containing 8 cm standing deionized water, topped off to 8cm every 3-5 days such that water was not a limiting resource. For the first three months, willows that did not survive were replaced in the same pots with the same soil. Willows were grown in a temperature and humidity controlled greenhouse for 6-9 months (variation due to willow mortality as noted). Greenhouse temperature was set to maintain a temperature near 30°C by heating if temperature dropped to 27°C and cooling if it exceeded 32°C during willow establishment; at the start of the experiment the temperature range was adjusted to maintain a range between 20°C and 27°C. The high initial temperatures may have been responsible for early willow mortality after transplanting.

In the greenhouse it was necessary to control mealy bugs. We did this initially by spot spraying affected foliage with 10% Neem and later 70% isopropyl alcohol, and then by introducing ladybeetle *Cryptolaemus montrouzieri* and green lacewing *Chrysoperla rufilabris* as biological control agents. While spraying was temporarily effective, biocontrol provided a long-term solution with no large infestations following introductions. The agents *Cryptolaemus* and *Chrysoperla* were introduced to each willow regardless of infestation.

4. Arundo and N additions

Once willows had been established for at least six months, Arundo rhizomes were dug up and collected from a recently mowed restoration plot along the Santa Clara River near Fillmore, CA. We trimmed rhizomes to a standard size of 14-17 cm with 1-4 buds and started rooting them in washed sand for one week.

We added viable (rooting and sprouting) Arundo rhizomes to half of the established willow pots and covered the rhizomes with 2 cm of soil, to simulate Arundo and sediment deposition in willow stands during flooding. Soil used to cover rhizomes had been maintained in the same conditions as that used to root willows during the establishment phase of the study (i.e., in 11.2 L pots in 8cm of standing water); this soil was homogenized before covering rhizomes.

From Arundo deposition to final harvest, the experiment ran 16 weeks (April-August 2019). KNO_3 was added weekly in concentrations of 0, 0.5, and 2.5 g/m^2 N (0, 0.025, and 0.125 g N/pot) in 250ml deionized water.

5. Soil and plant measurements

We measured soil NO_3^- and NH_4^+ in soil solution of the rooting zone at a 10cm depth at Weeks 1, 2, 3, 4, 5, 7, 10 and 16 and in the surface (0-3 cm) monthly, using Simple Luer-Lock Microsampler lysimeters (Soil Moisture Corp) followed by colorimetric analysis on a plate reader (Hood-Nowotny et al. 2010).

As a proxy for initial aboveground biomass, willows were measured for maximum height, volume, mainstem and branch diameter, and total leaf count. Established willow (6-9 months) starting biomass was determined by the allometric relationship between branch diameter, leaf area, and dry biomass in the middle of the experiment. To enable this, we subsampled branches and leaves of willows after three months (early August) and measured the diameter at the mainstem then performed scans of all leaves on each branch (along with a ruler for scale) and calculated leaf area using ImageJ. To determine the biomass component for this relationship, we dried plant material at 60°C for 72 hours, and weighed branches and leaves separately. This allometric relationship held for willows regardless of treatment (Arundo addition or N amendment). Deposited Arundo rhizomes were measured for length, number of nodes, and height and diameter of culms. We attempted to relate Arundo culm diameter to biomass with allometry, but there was no relationship, as each culm typically grows at a fixed diameter that does not vary with culm height or leaves.

Final aboveground willow biomass is reported as dry biomass accumulation (final dry mass – initial dry mass). Final aboveground Arundo biomass is simply final dry mass, as initial aboveground biomass was negligible and assumed to be zero because Arundo buds were just beginning to appear at the start of the experiment (sprouted to assure viability of rhizomes). All aboveground biomass data is reported as total (branches + leaves).

Plant height was measured at the start and end of the experiment. In order to take into account starting height we report height accumulated over the 16-week experiment as relative growth rate [(final height – initial height)/112 days].

Net assimilation (A_{net}) of CO_2 between treatments was measured during this three month subsampling by harvesting individual leaves from each plant (sample size 6-8/treatment when textures are lumped). Gas exchange rates were measured with a Licor 6400XT (Licor Industries, Lincoln, NE) while plants were in direct sunlight between 11am-1pm, and chamber conditions matched ambient conditions in the greenhouse (25°C, 400 ppm CO_2, 1600 PAR). Due to differences in willow and Arundo leaf areas, we collected leaves in the chamber and calculated leaf area post hoc, using a flatbed scanner and ImageJ (National

Institutes of Health, Bethesda, Maryland, USA, https://imagej.nih.gov/ij/). Potential photosynthetic nitrogen use efficiency (PNUE) was calculated after the final harvest by multiplying A_{net} by leaf %N.

6. Harvest

After 16 weeks, we harvested plants and soil. We measured growth in willow and Arundo, including height, number of branches/culms, and biomass. As described above, biomass was determined by drying aboveground and belowground plant material at 60°C for 72 hours. Aboveground biomass production was determined by subtracting starting biomass from final harvest biomass. Such measurements were not possible for belowground biomass, which is presented as total belowground biomass. Soil was sieved with a 4mm mesh pan to homogenize samples and remove roots, large pieces of litter and rocks prior to biogeochemical analyses.

To determine leaf C and N, we ground dried leaves to a powder using a dental amalgamator (Wig-L-Bug, Dentsply Rinn, Charlotte, NC). We weighed out 5mg of ground plant material, which was placed into foil capsules, folded, and run for high temperature combustion analysis on a CEC 440 CHN Analyzer (Control Equipment Corporation) for %C, %N and C:N. Soil C and N was analyzed similarly by drying soils at 60°C for 72 hours, grinding soil in plastic vials containing metal bars on a mill for 100 hours, weighing out 10mg soil into foil balls, and running on a CEC 440 CHN Analyzer.

We measured biogeochemical variables in the water extractable fraction as a proxy for the microbially available fraction, including water-extractable soil organic C (WEOC) and N as well as inorganic N (IN; NO_3^- and NH_4^+), and parallel extractions to determine microbial biomass C and N (MBC and MBN). To enable this, 8 g of soil was extracted in ultrapure deionized MilliQ water for four hours and filtered extracts to 1.6 µm. Microbial biomass was measured using a chloroform extraction method (Setia et al. 2012), in which we added 0.5 ml of chloroform to an 8 g sub-sample of soil and extracted it in 32 ml of MilliQ water. Parallel extracts for WEOC and total extractable N (WEON + IN), taken without chloroform, were then subtracted from chloroform extract OC and ON to obtain microbial biomass C and N values. Values were obtained using a TOC analyzer (Shimadzu TOC-V). We report biomass as flush, without applying a conversion factor. Soil inorganic N (NO_3^- and NH_4^+) was analyzed colorimetrically using a plate reader (Hood-Nowotny et al. 2010), where NO_3^- was determined by Vanadium (III) Chloride reduction and NH_4^+ was alkalized to a green indophenol. Soil IN was subtracted from soil TDN to obtain soil extractable ON.

7. Statistical analysis

Differences between treatments were analyzed using a two-way ANOVA for N level and plant species, with the exception of A_{net} where species were combined due to similarities and a one-way ANOVA for N level was performed. Tukey's honestly significant difference (HSD) was used as a post-hoc analysis for multiple comparisons. Data on the multiple time point measurements of inorganic N in soil solution as levels were always either near zero or below detection, thus they are omitted here. Due to the lack of patterns across biogeochemical variables in harvested soils and the lack of correlation with plant growth metrics, soil biogeochemical data are presented as supplemental material. $p<0.10$ was considered statistically significant, as $p<0.05$ could result in high Type-II errors with our relatively small sample sizes (Hurlbert & Lombardi 2009). All statistics were done in the JMP 12.0 Pro package (SAS Institute Inc., Core, NC, USA).

D. Results

1. Soil biogeochemistry

Over the course of the experiment, soil inorganic N (NO_3^- plus NH_4^+) was consistently low and did not vary significantly between textures, treatments, or through time, suggesting that plants took up virtually all the added N; consequently data are not shown. NO_3^- was consistently low, with immeasurably low concentrations in no N treatments and less than 2 ug/ml soil solution in low N and high N treatments, regardless of species, for all collection times and depths (rooting depth at 10cm and surface at 0-3cm). NH_4^+ was at too low of a concentration to be measured at all weeks except Week 4, which was similar across treatments, averaging 0.05 ug/ml.

Harvested soil showed no clear patterns in biogeochemical assays (WEOC, WEON, IN, MBC, MBN) with N amendment or species presence (Supplemental table 1). Biogeochemical variables tended to be higher in fine-textured than coarse-textured soils; however, soil biogeochemistry data did not follow clear patterns between treatments and there was never a significant influence on treatment in measured plant variables to this difference, so we have consolidated plant data between soil types (Supplemental table 1).

2. Growth

Total (aboveground + belowground) willow biomass was significantly reduced in the presence of Arundo by 57% in high-N treatments, but not in low-N or no-N treatments (Figure 1a; ANOVA N level: $F_{2, 50}$= 19.53, $p < 0.0001$; species: $F_{2, 50}$=11.78, $p < 0.0001$; N level*species: $F_{4, 50}$=3.96, p=0.0082; Tukey's HSD $p < 0.0001$). Total biomass of Arundo was similar between N treatments and was greater than willow biomass grown with Arundo: 2.3 times greater in no-N treatments, 2.1 times greater with low-N amendments, and 1.6

times greater with high-N amendments (Figure 1a).

Aboveground biomass behaved similarly to total biomass, where willow aboveground biomass was not inhibited in the presence of Arundo in no-N and low-N treatments, but in high-N treatments willow aboveground biomass was inhibited by 68% (Figure 1b; ANOVA N level: $F_{2,51}$= 11.00, p=0.0001; species: $F_{2,51}$=24.96, $p < 0.0001$; N level*species: $F_{4,51}$=1.28, p=0.29). In the low N treatment, willow aboveground biomass tended to be inhibited by Arundo, but this pattern was not significant. Total aboveground biomass of Arundo was similar across N levels and was always greater than willow grown in the same pots, averaging 5 times greater in no-N treatments, 6.6 times greater in low-N treatments, and 2.9 times greater in high-N treatments (Figure 1b).

Total root biomass was significantly lower in Arundo than in willow grown with Arundo in low-N, and in willow grown with and without Arundo in high-N conditions (Figure 1c; ANOVA N level: $F_{2,58}$= 5.64, p=0.0062; species: $F_{2,58}$=22.13, $p < 0.0001$; N level*species: $F_{4,58}$=2.16, p=0.088; Tukey's HSD p=0.041 for low-N and p=0.0048 for high-N between Arundo and willow grown together). Willow root biomass was not affected by Arundo presence, and was comparable across N levels; Arundo root biomass was also comparable across N levels, averaging two times less than willow in the no-N treatment, three times less in the low-N treatment; and four times less in the high-N treatment (Figure 1c).

Relative growth rate was greater in Arundo than willow (grown with or without Arundo) and in high-N conditions (Figure 2; ANOVA N level: $F_{2,46}$= 27.02, $p<0.0001$; species: $F_{2,46}$=27.25, $p<0.0001$; N level*species: $F_{4,46}$=1.92, p=0.12; Tukey's HSD $p < 0.0001$ between no/low-N and high-N level, $p < 0.0001$ between Arundo and willow). The greatest differences in relative growth rate between species were in the no-N and low-N treatments, where Arundo grew at nearly twice the rate of willow. Relative growth rate in willow was not significantly affected by the presence of Arundo (Figure 2).

3. C and N

Leaf C:N tended to be higher in willow (alone and with Arundo; C:N 50-90) than in Arundo leaves (C:N 30-40) within a given N level (Figure 3a; ANOVA N level: $F_{2, 53}$= 9.73, p=0.0003; species: $F_{2, 53}$=35.8, $p < 0.0001$; N level*species: $F_{2, 53}$=2.29, p=0.07). This interaction was significantly different between Arundo and willow (grown with or without Arundo) in no-N and low-N treatments (Tukey's HSD $p<0.0004$ and $p<0.065$, respectively), as well as in high-N conditions between Arundo and willow grown with Arundo (Tukey's HSD p=0.0004). Leaf C:N significantly decreased with any (low or high) N amendment (Tukey's HSD $p < 0.004$) and willow (grown with or without Arundo) had a higher C:N than Arundo (Tukey's HSD $p < 0.0001$).

Arundo leaves had lower %C than willow leaves (~40% vs. ~45%; Figure 3b; ANOVA N level: $F_{2, 53}$= 0.55, p=0.58; species: $F_{2, 53}$=46.5, $p < 0.0001$; N level*species: $F_{2, 53}$=1.41, p=0.25; Tukey's HSD for species $p<0.0001$ between Arundo and willow grown with or without Arundo). Any (low or high) N amendment resulted in greater leaf %N, while Arundo leaves had higher concentrations of %N than did willow leaves (1-1.4% vs. 0.5-0.8%; Figure 3c; ANOVA N level: $F_{2, 53}$= 8.63, p=0.0007; species: $F_{2, 53}$=27.2, $p < 0.0001$; N level*species: $F_{2, 53}$=1.69, p=0.17; Tukey's HSD N level $p < 0.015$, species $p < 0.0001$). High %N in Arundo leaves combined with lower leaf %C than willow resulted in the significantly lower C:N ratio in Arundo than in willow across N treatments (Figure 3a).

Our Arundo leaf C:N data with no N amendment was similar to preliminary Arundo litter C:N data collected by Lambert (unpublished data; 41.7 vs. 40.2), but our N amendments decreased Arundo leaf C:N values below this (34.8 in low N and 30 in high N). Our willow C:N was much higher than the preliminary trials with a mixture of native *Salix spp.* and *Baccharis spp.* litter (30.9) in all treatments: 81-89 in no N, 60-67 in low N, and 51.5 (lone willow) and 71 (willow grown with Arundo) in high N (Lambert, unpublished data). High C:N in willow can be attributed to low %N (Figure 4c). This may reflect differences in chemistry between live leaves and litter due to nutrient resorption and rapid loss of sugars in the early stages of litter decomposition (Hattenschwiler et al. 2008; Chauvet 1987), as well as the absence of *Baccharis* litter in our sampling (Albert et al. 2018).

4. Net assimilation of CO_2

Arundo and willow (both grown with Arundo and alone) had similar net assimilation rates (A_{net}) per unit area within a given N treatment. Adding any N increased A_{net}; this increase was significant in high N treatments regardless of species type (14 umol m^{-2} sec^{-1}), as compared to the no-N treatment (12 umol m^{-2} sec^{-1}; Figure 4; ANOVA $F_{2,55}$= 2.76, p=0.07; Tukey's HSD p=0.09). Potential photosynthetic nitrogen use efficiency (PNUE), determined by multiplying A_{net} by leaf %N, was significantly greater in Arundo than in willow (grown with or without Arundo) and with any (low or high) N amendment (Figure 5; N level: $F_{2,49}$= 7.83, p=0.0013; species: $F_{2,49}$=11.42, p=0.0001; N level*species: $F_{2,53}$=1.36, p=0.27; Tukey's HSD $p < 0.006$ for N level and $p < 0.002$ for species). In willow leaves, PNUE appeared to be lower in no-N treatment than with any N addition; however, differences in willow PNUE were not statistically significant between willow N treatments and regardless of Arundo presence (Figure 5).

E. Discussion

This experiment was designed to understand how Arundo and nitrogen (N) interact to affect the growth of established native willow growth, and thus how Arundo comes to dominate sites. It simulates a flooding scenario in which Arundo is deposited and establishes within an existing willow stand and is fertilized with N from agricultural runoff (or not). It also explored whether high N-levels enhance Arundo's growth when it establishes into a willow stand.

We hypothesized that Arundo's competitive effect on willow would increase in high-N conditions, reducing willow growth by responding to nutrient supply by producing greater biomass, and ultimately, dominating both light and belowground root space. Indeed, Arundo significantly inhibited willow growth when N enrichment was high but not when N was low (Figure 1a). Arundo's greater accumulation of leaf N (Figure 3c) and its higher PNUE (Figure 5) suggests that Arundo was able to better take advantage of nitrogen, particularly as tapping into plant-available NO_3^- reduced investment in belowground root infrastructure (Figure 3b) which allowed Arundo to shift nutrients to grow aboveground biomass and perhaps acquire P (Treseder & Vitousek 2001). Willow was slower growing, less efficient at assimilating N (Figure 3c), and produced more roots to compensate for reduced access to nutrients (Figure 1c). Lower proportions of C in Arundo leaves than willow leaves likely reflect Arundo and other grasses' relatively high incorporation of silica as a structural and defense material, which requires less energy than C-based compounds and may have further enabled Arundo to create more biomass (Jackson & Nunez 1964; Schaller & Struyf 2013; Massey et al. 2007; Minden et al. 2020). Arundo also grew taller than willow and potentially dominated access to light (Figure 2). Although both species had similar rates of A_{net} in full light (Figure 5), Arundo invests in leaf quantity over photosynthetic potential (Nackley et al. 2016), which we saw with higher leaf biomass.

These results are consistent with other studies linking the success of opportunistic introduced species with high-N conditions (Huenneke et al. 1990; Burke & Grime 1996;Vitousek et al. 1997; Corbin & D'Antonio 2004; Abraham et al. 2009; August-Schmidt et al. 2015). Similar to other such species, Arundo was able to grow rapidly when it had sufficient nutrients (Rejmanek & Richardson 1996) and to use N more efficiently in photosynthesis with higher PNUE (Vitousek 1986; Durand & Goldstein 2001; Funk et al. 2013; Lin et al. 2019). High-N conditions may also have alleviated N-limitation in Arundo and heightened competition for another resource; for example, Arundo may have allocated N to acquiring P by producing extracellular phosphatases (Treseder & Vitousek 2001). Perhaps due to excess N availability and efficient allocation strategies, Arundo did not invest in dense, shallow roots typical of other grasses in any N treatment relative to woody species, and instead quickly established aboveground cover (Williams & Hobbs 1989; D'Antonio & Vitousek 1992).

How opportunistic introduced species respond to N-enrichment at a range of levels is less understood than under saturating N conditions and may depend on interspecific interactions (James 2008; Luo et al. 2014; Zhang et al. 2017; Lee et al. 2012). Some studies have found that any N amendment results in greater competitive success of introduced species (Zhang et al. 2017), while oftentimes increasing levels of N deposition are correlated with increases in introduced species abundance (Scherer-Lorenzen et al. 2007). We found that Arundo did not inhibit willow's growth with no added N and low amounts of added N, as it did in high-N amendments; however, other metrics of Arundo's growth were variable across N levels. For example, although Arundo had higher relative growth rates than willow in all N treatments, the greatest difference was within the no-N amendment (Figure 2). Further, Arundo had greater leaf %N content and PNUE regardless of N treatment (Figure 3c). Even within high-N amendments, Arundo's competition with native woody species has been shown to vary based on other resources: Arundo can outcompete established prominent native woody species *Salix laevigata*, *Populus trichocarpa* and *Baccharis salicifolia* in high-N levels only with high soil moisture and light, but in high-N conditions without these other resources Arundo can be outcompeted by woody species (Coffman 2007). Although in this study, plants were exposed to full sun, Arundo plants were given adequate, but not excessive water (250 ml/week; willow roots had access to standing water).

Regardless of N level, Arundo proved to be an effective competitor immediately upon arrival as a rhizome segment. In the relatively short span of four months, Arundo was able to produce substantial biomass, comparable to willow that had already grown for 6-9 months and exceeding new growth by willow that was already established in the same pot (also grown 6-9 months; Figure 1); this was true under all N conditions. The capacity of Arundo rhizomes to store large quantities of C and N enable it to establish and grow rapidly at a new site, and subsequently to displace existing native vegetation (Nackley et al. 2016). While we cannot quantitatively extrapolate our findings into riparian ecosystems or into the future, our data, coupled with an understanding of Arundo's growth patterns and environmental conditions, suggest that in nutrient rich riparian systems Arundo would strongly limit willow's competitive ability, recruitment, and biomass production more than we have demonstrated here.

Arundo's substantial biomass production has been largely accredited to its lateral growth and ability to form branches off of existing culms in subsequent growing seasons following establishment (Thornby et al. 2007). While this experiment is a snapshot of one April-August growing season, over a longer time period in the field Arundo will have a further advantage: it stays green most of year and grows all year long–especially in early Spring when more water is available–while willow drops leaves seasonally. Further, several factors that alter hydrology will enhance Arundo recruitment but also reduce willow recruitment; these should include increased storm intensity, increased drought, and damming or diverting water (Polade et al. 2017; Payne et al. 2020; Cayan et al. 2010; Gage & Cooper 2005; Commander 2013). Willow often spreads with seed rain and drought conditions provide insufficient water in surface soils to promote germination and establishment (Gage & Cooper 2005).

The implications of this study for riparian vegetation dynamics are most relevant to the initial year following Arundo establishment within a native-dominated matrix. Given Arundo's success in the span of four months where rhizomes had to "start from scratch," a multi-year perspective in light of all mentioned variables is consistent with anecdotal observations of agricultural rivers throughout southern California: Arundo has done a tremendous job of outcompeting native species in these systems (Decruyenaere and Holt 2001; Dowdy, personal observations). At some point, this balance of N and spatial dominance may drive state change (Milchunas & Lauenroth 1995) via a shift in dominance to an Arundo "disclimax" community (Rieger & Kreager 1989; Young et al. 2001), where higher-N litter accumulation by Arundo may further enable favorable conditions and stability of this community (Milchunas & Lauenroth 1995; Schimel et al. 1996; Coffman 2007). Indeed, land use change has been found to alter the physical and biological composition of riparian ecosystems such that regeneration of native plant communities occurs poorly, at best, in many settings (Rieger & Kreager 1989).

F. Management implications

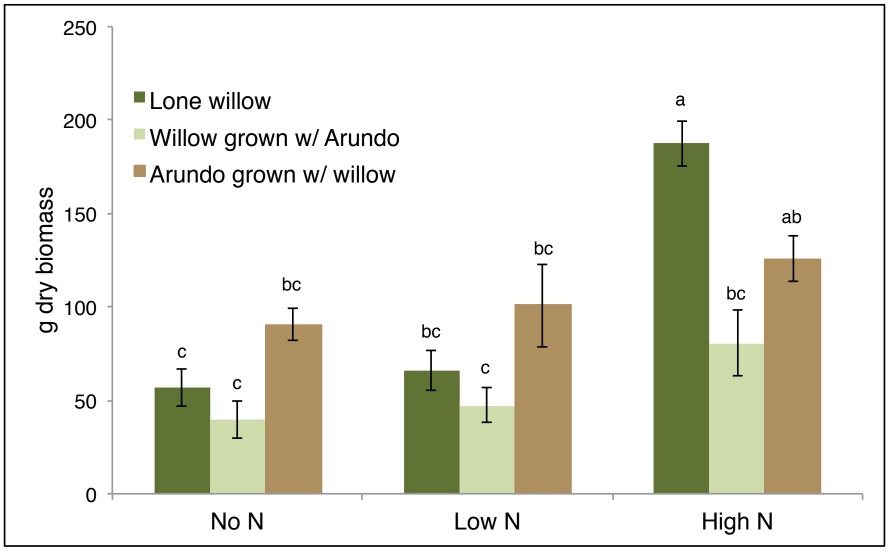
Preventing major pulses of NO_3^-, particularly at times of flooding, may be important to maintaining riparian habitat by limiting early Arundo's competitive advantage. Minimizing runoff by applying sustainable farming practices, such as carefully timing fertilizer inputs based on crop needs and environmental conditions to reduce excess and leaching, building soil OM to retain nutrients, or by adding lower concentrations of less-available organic N could limit large Arundo stands; instead, reduced N inputs could result in novel ecosystems, where Arundo establishes in dense clumps and coexists with native species (Hobbs et al. 2009; Decruyenaere and Holt 2001). The interaction of high N and Arundo is an important consideration for native plant restoration practices; for example, efforts could focus on removing nascent Arundo in areas receiving high N agricultural runoff. These findings highlight the importance of linking native plant restoration efforts and holistic whole watershed management (Wang et al. 2016; Fonseca et al. 2020). Minimizing NO_3^- in agricultural runoff has the potential to not only benefit riparian plant community resistance to invasion, but has other important implications for human health and welfare such as protecting drinking water supplies and reducing fertilizer consumption (Karydis 2009; Schaider et al. 2019).

G. Conclusions

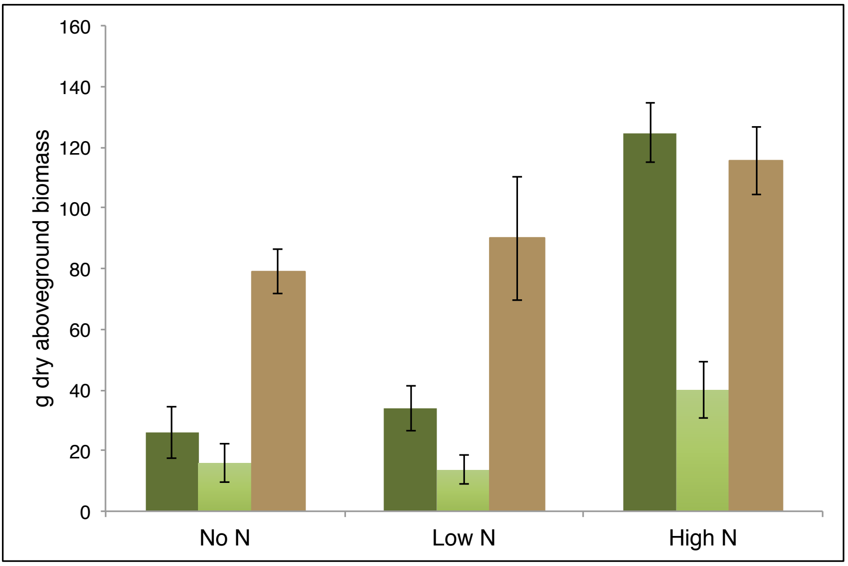
We investigated the interacting effects of non-native riparian weed *Arundo donax* and nitrate (NO_3^-) deposition on native *Salix lasiolepis* (willow) biomass production under controlled experimental conditions. Arundo is favored by high-N inputs, which may be representative of industrial agricultural runoff; under these conditions, Arundo inhibited total willow production by 57% because it used available N more rapidly and efficiently. In the treatments with no added N and low added N, representative of runoff from no upland agriculture and sustainable upland agriculture, Arundo did not significantly inhibit willow growth. These findings suggest that improved upstream N management could potentially reduce the success of introduced plant species, while native plant restoration practices focused on Arundo removal should consider upstream and upslope N dynamics to improve restoration outcomes.

Table 1: Total soil C and N. Initial soil C:N ratio, %C, and %N in fine riparian terrace soil, coarse creekbed soil, and averaged. Values are reported as means of three composite samples +/- standard errors of the mean. Note: subsequent plant data from species grown in different soil types is combined.

Soil	C:N	%C	%N
Average	16.41 ± 0.99	1.67% ± 0.04%	0.10% ± 0.01%
Fine	14.96 ± 0.18	1.73% ± 0.04%	0.12% ± 0.004%
Coarse	17.86 ± 1.66	1.61% ± 0.06%	0.09% ± 0.01%



a)



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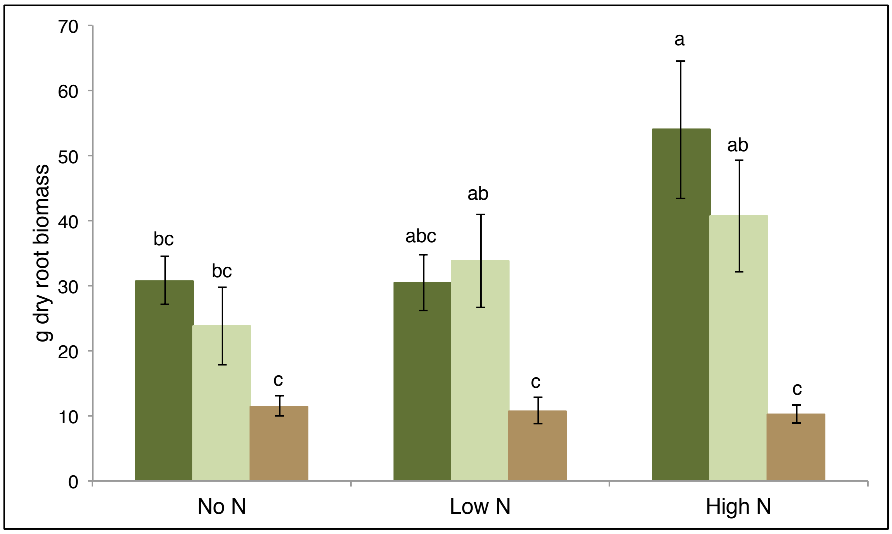


c)

Figure 1: Plant biomass. Plant biomass accumulated over 5-month experiment. a) Total (aboveground + root) biomass, b) aboveground biomass, and c) belowground root biomass, in lone willow (dark green), willow grown with Arundo (light green) and Arundo grown with willow (brown) in no, low and high N treatments. Error bars are +/- standard errors of the mean; different lowercase letters represent statistically significant differences from a posthoc Tukey's HSD ($p = 0.10$). In aboveground biomass (b), the interaction of N level*species was not significant at $p=0.10$; however, N level and species separately were significant at $p=0.0001$ and $p < 0.0001$, respectively.

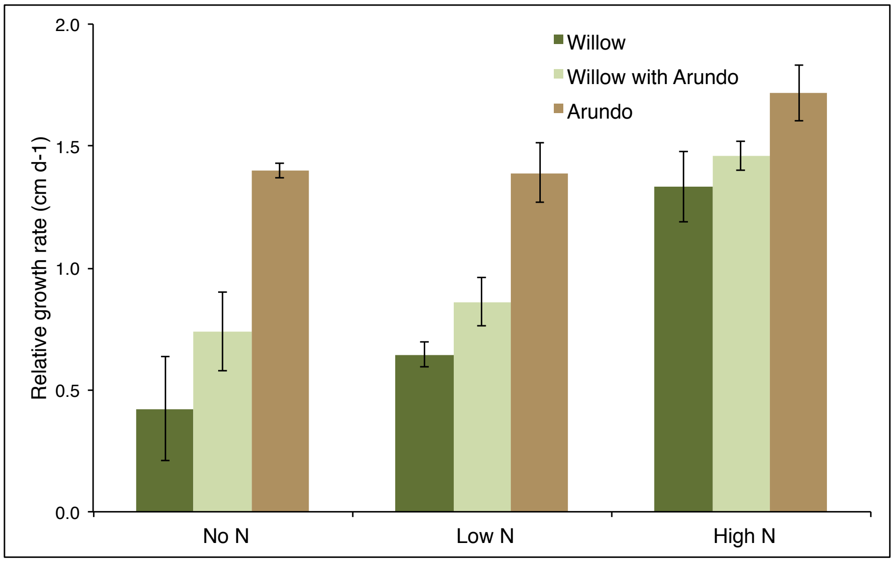


Figure 2: Relative growth rate. Relative growth rate (cm d^{-1}) in lone willow (dark green), willow grown with Arundo (light green) and Arundo (brown) in no-N, low-N and high-N treatments. Error bars are +/- standard errors of the mean; the interaction of N level*species was not significant; however, N and species separately were both significant at $p<0.0001$.

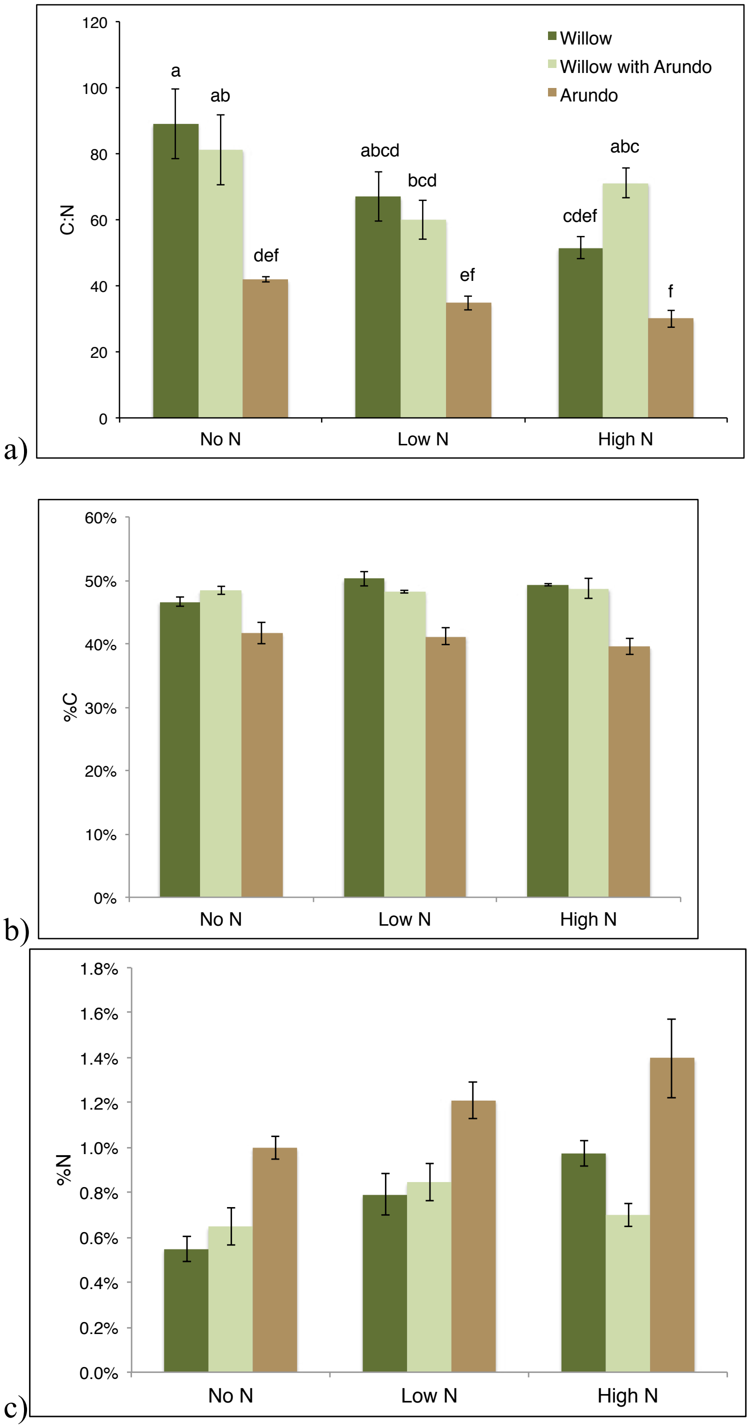


Figure 3: Total leaf C and N. Final leaf a) C:N, b) %C, and c) %N in lone willow (dark green), willow grown with Arundo (light green) and Arundo (brown) in no-N, low-N and high-N treatments. Error bars are +/- standard errors of the mean; different lowercase letters represent statistically significant differences from a posthoc Tukey's HSD ($p = 0.10$). The interaction of N level*species was not significant at $p=0.10$ in leaf %C and %N; however, species was significant in %C at $p < 0.0001$, and N level and species separately were significant in leaf %N at $p=0.0007$ and $p < 0.0001$, respectively.

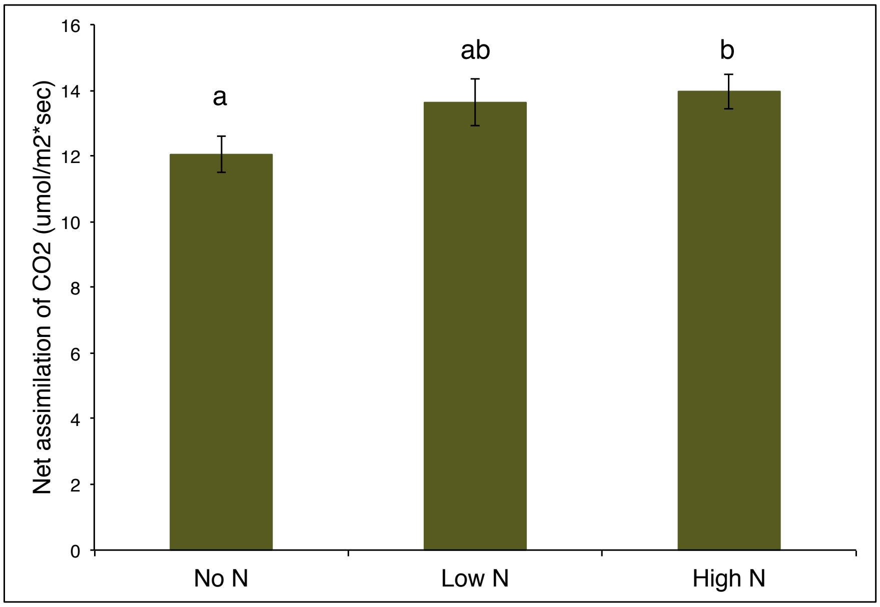


Figure 4: Net assimilation of CO_2. A_{net} between N treatments (measured at Month 2 of experiment). Lone willow, willow grown with Arundo, and Arundo data are combined due to similarities. Error bars are +/- standard errors of the mean; different lowercase letters represent statistically significant differences from a posthoc Tukey's HSD (p = 0.10).

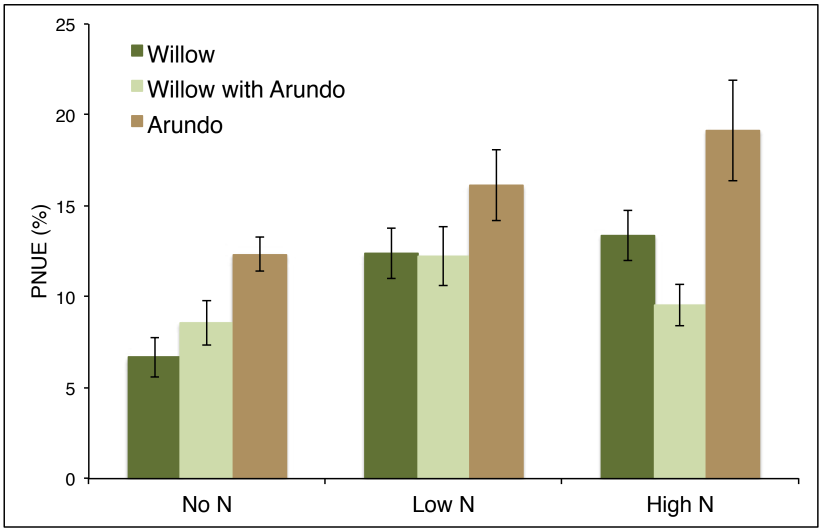


Figure 5: Potential photosynthetic nitrogen use efficiency. PNUE in lone willow (dark green), willow grown with Arundo (light green) and Arundo (brown) in no N, low N and high N treatments. Error bars are +/- standard errors of the mean. The interaction of N level*species was not significant at p=0.10, although N level and species separately were significant at p=0.0013 and p=0.0001, respectively.

Supplemental table 1: Soil biogeochemistry (harvested at the end of experiment) in no N, low N and high N treatments, in fine and coarse soils with lone willow and with Arundo + willow, including: water extractable organic C (WEOC), total N (TN), water extractable organic N (WEON), inorganic N (IN; NO_3^- and NH_4^+), microbial biomass C (MBC) and microbial biomass N (MBN). All values are reported as ug/g dry soil +/- standard errors of the mean.

N treatment	*No N*				*Low N*				*High N*			
Soil	*Fine*		*Coarse*		*Fine*		*Coarse*		*Fine*		*Coarse*	
Species	*Willow*	*Willow + Arundo*	*Willow*	*Willow + Arundo*	*Willow*	*Willow + Arundo*	*Willow*	*Willow + Arundo*	*Willow*	*Willow + Arundo*	*Willow*	*Willow + Arundo*
WEOC	110.3 ± 7.6	120.2 ± 5.9	110.6 ± 10.5	41.6 ± 1.1	357.6 ± 22.0	98.8 ± 4.4	120.6 ± 11.1	54.6 ± 4.3	175.7 ± 11.6	230.2 ± 10.1	57.9 ± 4.1	35.3 ± 3.5
TN	8.3 ± 1.9	10.2 ± 1.6	4.3 ± 0.7	3.3 ± 0.1	6.2 ± 1.0	7.2 ± 0.4	2.9 ± 0.8	2.5 ± 0.8	8.9 ± 1.4	10.7 ± 1.5	9.2 ± 2.4	2.8 ± 0.8
WEON	6.6 ± 1.4	8.5 ± 0.8	3.4 ± 0.2	2.8 ± 0.1	5.6 ± 0.3	5.5 ± 0.4	2.3 ± 0.1	2.4 ± 0.2	6.8 ± 0.2	9.0 ± 0.8	3.2 ± 0.6	2.6 ± 0.3
NO3	0.7 ± 0.3	0.6 ± 0.3	0.2 ± 0.1	0.3 ± 0.03	0.3 ± 0.1	0.4 ± 0.1	0.5 ± 0.5	0.1 ± 0.04	1.4 ± 1.1	0.4 ± 0.3	8.6 ± 2.8	0.02 ± 0.02
NH4	1.0 ± 0.7	1.1 ± 0.4	0.7 ± 0.1	0.6 ± 0.1	0.3 ± 0.2	1.3 ± 0.3	0.2 ± 0.2	0.1 ± 0.08	0.7 ± 0.1	1.3 ± 0.8	0.4 ± 0.2	0.3 ± 0.05
MBC	114.2 ± 25.4	213.4 ± 18.3	77.6 ± 40.3	76.3 ± 12.4	75.0 ± 38.4	156.0 ± 28.6	47.0 ± 22.1	71.7 ± 15.1	186.6 ± 103.9	81.1 ± 51.9	73.2 ± 35.3	79.6 ± 10.7
MBN	1.3 ± 0.8	1.0 ± 0.9	0.2 ± 0.2	0.4 ± 0.4	2.1 ± 0.4	0.5 ± 0.4	1.5 ± 0.6	2.4 ± 1.4	4.0 ± 2.5	3.5 ± 1.5	2.2 ± 2.2	1.8 ± 0.3

II. The large-statured introduced grass Arundo donax alters soil microbial cycling of carbon and nitrogen relative to native woody species

A. Abstract

Introduced opportunistic grasses have replaced woody species in riparian corridors throughout California; however, it is not well understood how this shift in plant community type may alter soil biogeochemistry. Here we address how one such grass, giant reed *Arundo donax*, alters soil microbial cycling of carbon (C) and nitrogen (N) relative to the woody species it replaces. We collected litter and soils in prominent Arundo stands and adjacent intact riparian forest, and compared Arundo materials with those of three dominant woody species: *Populus trichocarpa* (cottonwood)*, Baccharis salicifolia* (mulefat)*,* and *Salix laevigata* (willow). We found that Arundo contributed less litter than woody species with lower %C and %N, but soils beneath Arundo accumulated extractable organic C (EOC) and N (EON). Soils beneath Arundo also hosted a relatively small microbial community and had higher silicate content than those beneath woody species. These findings suggest that Arundo litter EOC is stabilized in soils by microbial transformations and/or in silicate complexes.

B. Introduction

Riparian forests throughout the U.S. southwest have been replaced by introduced opportunistic grasses as human activities modify ecosystem processes (Arianoutsu et al. 2013; Meyerson et al. 1999; Canavan et al. 2019). Aboveground effects of this shift in plant growth form are well documented, including increased primary productivity, increased flammability, and decreased habitat for native fauna (Dudley and Collins 1995; Bell 1997; DiTomaso 1998; Dudley 2000; Herrera & Dudley 2003; Lambert et al. 2010); however, fewer studies have addressed belowground effects of shifting plant growth form. Plant species replacement that differs in growth form can alter ecosystem function (Gregory et al. 1991), including dramatic changes to global carbon (C) and nutrient cycles through modified organic matter (OM) composition in litter inputs (Prentice et al. 2001; Canadell et al. 2007; Cornwell et al. 2008; Coffman 2007). Such changes in OM inputs creates the potential for positive feedbacks where such species enable their own spread (Schimel et al. 1996; Coffman 2007), as well as alter terrestrial and aquatic consumer food webs through trophic cascades (Wardell et al. 1997; Swan & Palmer 2004).

In watersheds throughout the U.S. southwest, the introduced large-statured grass *Arundo donax* has displaced willow-cottonwood forests and riparian scrub (Bell 1997). Arundo spreads rhizomatously and grows at a rate 2-5 times higher than native riparian willow species in California (*Salix goodingi* and *Salix laevigata*; Reiger & Kreager 1989). This rapid growth may not, however, result in increased litter contributions, as senescent Arundo foliage remains attached to standing culms while willow-cottonwood riparian forest trees drop litter seasonally. Further, Arundo is an evergreen grass in California (Coffman 2010), leaves of which typically decompose more slowly than leaves of deciduous, woody species (*Salix spp.*, *Populus spp.*, *Baccharis spp.*; Cornwell et al. 2008), and can result in C and N accumulation in surface soils (Melillo et al. 1982).

While little is known about Arundo and other large statured grasses' influence on biogeochemical cycles, opportunistic species typically have higher growth and photosynthetic rates, higher litter N concentrations (Ehrenfeld et al. 2001), and ultimately tend to increase decomposition rates in terrestrial ecosystems (Ehrenfeld 2003). Litter inputs between plant growth forms differ in terms of timing, physical structure, C and N stoichiometry, and chemistry and quantity of OM contributions (Hector et al. 2000; Liao et al. 2008). These factors in turn affect soil nutrient cycling (Knoepp et al. 2000; Evans et al. 2001), abundance and activity of decomposers (Melillo et al. 1982; Taylor et al. 1989), and thus decomposition rate (Pereira et al. 1998; Ehrenfeld et al. 2001; Lindsay & French 2005).

Preliminary data comparing Arundo litter and woody *Salix* and *Baccharis* litter shows that Arundo leaves have lower %C and %N, but higher C:N (40.2 vs. 30.9) than woody species (Lambert, personal communication), suggesting that Arundo might decompose more slowly and soils beneath Arundo might have lower N concentrations. However, grasses are more vulnerable to C loss via photodegradation (King et al. 2012) and can thus decompose more rapidly and completely than trees or shrubs, but this outcome is species specific and largely depends on litter chemistry and environment (Kochy & Wilson 1997). High silica content in Arundo (Jackson & Nunez 1964; Schaller & Struyf 2013) and other grasses (10-20 times that of other dicots; Russel 1961) may further affect soil C cycling. Silica stored in plant phytoliths occludes C during photosynthesis. This phytolith-occluded C remains relatively stable during decomposition (Parr & Sullivan 2005) and has been effective in experimental soil C sequestration efforts (Song et al. 2015) where silica-occluded C can build up in soils (Parr et al. 2010). Soils high in silica can also complex with soil OM, making it relatively stable (Renforth et al. 2011). In litter, silica may also decrease fungal decomposer biomass just as it is an effective fungal pathogen and herbivore deterrent in live plant tissue (Fauteaux et al. 2005; McNaughton & Tarrants 1983; Soinenen et al. 2013; Massey & Hartley 2009), but this does not inevitably result in slowed decomposition as bacterial populations in some systems may step in as the dominant decomposer group (Schaller et al. 2014), making the Si-C relationship inconclusive. Overall, the outcomes and mechanisms of how a shift from riparian forest to large statured grasses affects C and N cycling remain speculative. It is critical to understand changes in such processes resulting from a shift in growth form, especially in the riparian "hot spot" that buffers agricultural runoff and links terrestrial and aquatic biogeochemical cycles.

In this study, we address the question: how does riparian forest shift in growth form to large-statured grass Arundo alter soil microbial C and N cycling? To explore this, we assess OM contributions between Arundo and dominant woody species through surface soil biogeochemistry and qualitative OM assays. We hypothesized that higher growth rates in Arundo (Reiger & Kreager 1989) enhance litter C and N inputs to ultimately increase soil C and N and microbial biomass pools compared to woody species, while high silica in Arundo OM limits microbial availability of greater C pools. To evaluate this hypothesis, we collected litter and soil beneath *Arundo donax* and two native trees and one native shrub species: *Salix laevigata* (red willow)*, Populus trichocarpa* (black cottonwood)*,* and *Baccharis salicifolia* (mulefat). We assessed differences in soil OM quality beneath Arundo and woody species with extractable organic C and N, inorganic N (NO_3^- and NH_4^+), microbial biomass C and N, silicate (SiO_4) and respiration throughout a ten-week laboratory incubation.

C. Methods

1. Field sampling

Sampling was conducted in April 2016 in riparian terrace soils at the Hedrick Ranch

Nature Area (HRNA) along the Santa Clara River near the town of Santa Paula (34.36° N, 118.99° W) in Ventura County, Southern California. The soils are xerofluvents with a loamy sand texture in the A horizon. April sampling coincided with the growing season following the winter rains of a drought year in which Santa Paula received 54.7% of "normal" rainfall (based on 1957-1992 base period average; Ventura County Watershed Project District 2020). At this time of year, litter inputs (leaching, litter drop) to soil were expected to be at a maximum following autumn senescence and winter rains, and plant uptake of nutrients was less of a consideration, such that that soils could reflect maximal integration of litterfall differences stemming from plant species' distinct phenological traits.

We collected soil with cores (0-10cm; 5cm diameter) and litter (1 m^2 area directly below plants, centered around the mainstem) beneath Arundo and three dominant woody species, *Salix laevigata* (red willow), *Populus trichocarpa* (black cottonwood), and *Baccharis salicifolia* (mulefat) in six plots across the HRNA riparian terrace. Plots were chosen haphazardly; woody species plots were based on the criteria that all three species were present within a 10 m^2 area. Woody species were chosen for their dominance on the landscape (these riparian forests are often called cottonwood-willow forest), willow for its frequent comparison to Arundo in previous studies (e.g. Rieger & Kreager 1989; Coffman 2007), as well as because willow and mulefat are woody plants with the nearest similarity in growth form (height, branch width) to Arundo. We calculated the volume of litter in a $1m^2$ area beneath each plant species.

Arundo stands in HRNA have been persistent for >12 years (determined from Google Earth imagery); our sampling area covered six sites within 180 m^2. We sampled intact riparian forest adjacent to our Arundo sampling area, which had been restored >8 years from

Arundo stands in an area of 100 m^2, and was further surrounded by younger restored forest (>2 years; 110 m^2) and restored pasture (10 years; 180 m^2). Within this sampling area, we sampled six sites where the three woody plants in each site were within a 10m^2 area. The Arundo sampling area is upstream from and adjacent to the restored riparian forest sampling area. We prioritized sampling well-established stands with a known land use history; the natural system (older Arundo patches form large stands) and restoration process (which targets large areas rather than smaller patches to improve outcomes) did not allow for a more interspersed design.

2. Biogeochemical analyses

Soil and litter samples were returned to the laboratory for analysis. Litter and soil subsamples were air dried at 65°C for 72 hours to obtain dry weight and analyze total C (TC) and total N (TN) using an Automated Organic Elemental Analyzer (Dumas combustion method). Litter was air-dried for extractable organic C and extractable organic N.

Soil was sieved through a 4mm mesh screen to homogenize samples and remove roots organic material and rocks. Soil subsamples were taken to prepare a 10-week laboratory incubation at 20°C and 75% water holding capacity, where each sample was housed in a 32 oz. Mason jar containing soil divided into 50 ml Falcon tubes that we sampled non-destructively at Week 1, 2, 5 and 10. Mason jars were equipped with septa for sampling respiration, and jars were kept closed between sampling intervals. Soil respiration (CO_2 production) was taken at each time point by measuring the accumulation between the time points (one week, one week, three weeks, and five weeks at Week 1, 2, 5 and 10, respectively) on a Shimadzu GC 14A gas chromatograph (Nakagyoku, Japan), reported as total CO_2 respired over the incubation period.

To measure microbial C and N availability, we extracted 8 g of soil in 32 ml of 0.5 M K_2SO_4 for four hours and filtered extracts to 1.6 µm at all time points. We measured microbial biomass using a chloroform extraction method (Setia et al. 2012), in which we added 0.5 ml of chloroform to an 8 g sub-sample of soil and extracted it in 32 ml of 0.5 M K_2SO_4 for four hours. Parallel extracts taken without chloroform were then subtracted from chloroform extract OC and ON to obtain microbial biomass C and N values. We report biomass as flush, without applying a conversion factor.

We analyzed soil and litter extracts for dissolved, non-particulate OC and total dissolved N (TDN) with a TOC analyzer (Shimadzu TOC-V). Soil inorganic N (NO_3^- and NH_4^+) was analyzed colorimetrically using a plate reader (Hood-Nowotny et al. 2010), and subtracted from soil TDN to obtain soil dissolved organic N. Silicate (SiO_4) within the same extracts was measured on a Lachat autoanalyzer.

3. Statistical analyses

All statistical tests were performed using the JMP 12.0 Pro package (SAS Institute Inc., Core, NC, USA). For bulk analyses of leaf litter mass as well as %C, %N and C:N in litter and soils, woody species were combined due to similarities; comparisons between plant growth forms were then analyzed using one sided Welch's t-tests to correct for unequal variance and sample size. The relationship between plant species and biogeochemical variables in litter and in soil extracts was tested for significant differences with analysis of variance (ANOVA) with a Tukey HSD post hoc test to correct for multiple comparisons. Due to similar patterns in N cycling between soils and respiration between time points, we present initial biogeochemical data and total respiration over the incubation. $p<0.10$ was considered statistically significant, as $p<0.05$ could result in high Type-II errors in our relatively small sample size (Hurlbert & Lombardi 2009).

D. Results

1. Litter

Arundo leaf litter mass averaged less than half the volume of woody species measured in a square meter area under plants at the soil surface (Figure 1; Welch's two sample t-test, t=3.04, df=19.4, p=0.007). As seen in the standard error, all woody species had greater variance in litter mass than Arundo. Arundo litter had slightly lower % C and % N than woody species (Figure 2a; 40% C and 1%N in Arundo vs. 45% C and 1.3% N in woody species; Welch's two sample t-test %C: t=2.73, df=8.06, p=0.03; %N: t=1.88, df=7.36, p=0.10). C:N of Arundo litter was slightly higher than in woody species, but this was not statistically significant (41 vs. 35; Figure 2b; Welch's two sample t-test, t=1.16, df=5.79, p=0.29).

There were no clear trends in extractable OC (EOC) between Arundo and woody species' litter leachates per gram dry litter (Figure 3a; ANOVA $F_{3, 23}$= 0.29, p=0.83). Extractable organic N (EON) in Arundo litter leachates averaged more than twice that in the woody species' litters, but this was only statistically significant between Arundo and cottonwood (Figure 3a; ANOVA $F_{3, 22}$=2.88, p=0.06; Tukey's HSD p=0.05). Woody species' litter leachates had similar ON concentrations to one another. When adjusted for the differing litter masses, the lower amount of Arundo litter translated into lower OC and lower ON than all woodyspecies, but this was not statistically significant (Figure 3b; ANOVA EOC: $F_{3, 22}$=1.17, p=0.35; EON: $F_{3, 21}$=0.41, p=0.75).

2. Soil

Soil moisture did not significantly vary between plant species, with an average of 21% gravimetric water content (data not shown).

Soil %C and %N were higher under Arundo than woody species but this was not statistically significant (Figure 4a; 3.3%C and 0.3%N versus 2.4%C and 0.2%N; Welch's two sample t-test %C: t=1.35, df=6.82, p=0.22; %N: t=1.61, df=6.37, p=0.16). Soil C:N was not significantly different between Arundo and woody species (13 vs. 14.2; Figure 4b; Welch's two sample t-test t=1.51, df=12.00, p=0.16).

Soil EOC content beneath Arundo was over twice as high as beneath woody species (Figure 5; ANOVA $F_{3, 23}$=4.77, p=0.01; Tukey's HSD between Arundo and woody species: cottonwood p=0.01, mulefat p=0.04, willow p=0.06). EON also followed this pattern with levels twice as high beneath Arundo as beneath woody species (Figure 5; ANOVA $F_{3, 22}$=6.37, p=0.004; Tukey's HSD between Arundo and woody species: cottonwood p=0.007, both mulefat and willow p=0.01). Soil inorganic N primarily appeared as nitrate (NO_3^-), and did not differ significantly in the soils under the different plants, but tended to be highest in Arundo and mulefat, and lowest in cottonwood and willow (Fig. 6; ANOVA $F_{3, 23}$=1.16, p=0.35).

Microbial biomass C in soil under Arundo was similar to levels under cottonwood and mulefat, but willow soil had significantly higher MBC than cottonwood (Figure 7; ANOVA $F_{3, 22}$=2.53, p=0.09; Tukey's HSD p=0.09). While the patterns and proportions of MBN paralleled those for MBC, being higher in soil under willow, there were no significant differences between species (Figure 7; ANOVA $F_{3, 22}$=1.88, p=0.17). Soil %C correlates with microbial biomass C across species (Figure 8; MBC = -8.2 + 4599.9*%C, r^2 = 0.46, $F_{1, 19}$ = 17.28, p = 0.0005).

Soil respiration (CO_2 production over the ten-week incubation) appeared higher in Arundo and willow soils and lower in cottonwood and mulefat soils, but was not significantly different between soils under Arundo and any woody plant species (Figure 9; ANOVA $F_{3, 21}$=2.39, p=0.103). This pattern of higher respiration in Arundo and willow soils and lower respiration in cottonwood and mulefat soils was consistent at each time point measured (after one, two, five and ten weeks; data not shown).

Field soil EOC (a proxy for microbially accessible C) had a weak correlation with respiration in soils beneath woody species, while soils beneath Arundo had have similar respiration regardless of EOC value (Figure 10a; sum CO_2 over 10 week incubation; Woody species: CO_2 = 177.3 + 0.66*EOC, r^2 = 0.12, $F_{1, 16}$ = 1.99, p= 0.18; Arundo: CO_2 = 401.8 - 0.018*EOC, r^2 = 0.001, $F_{1, 4}$ = 0.003, p= 0.96). The correlation between microbial biomass C and total CO_2 production was similar beneath all species (Figure 10b; CO_2 = 181.3 + 1.22*MBC, r^2 = 0.19, $F_{1, 19}$ = 4.23, p = 0.05). Soil EOC correlated with microbial biomass C in woody species (Figure 10c; MBC = -29.28 + 0.98*EOC, r^2 = 0.55, $F_{1, 15}$ = 17.43, p= 0.0009). Soil EOC also correlated with MBC in soils beneath Arundo, with a lower slope and higher EOC values per MBC than in soils beneath woody species (Figure 10c; MBC = 55.12 + 0.12*EOC; r^2 = 0.70, $F_{1, 5}$ = 9.19, p= 0.04).

Soil silicate (SiO_4) was highest in Arundo soils, measuring 31 ug SiO_4/g dry soil, compared to all woody species, which ranged from 16.2-21 ug SiO_4/g dry soil (Figure 11;

ANOVA $F_{3,23}$=3.15, p=0.05; Tukey's HSD between Arundo and woody species: cottonwood p=0.29, mulefat p=0.09, willow p=0.05).

E. Discussion

We hypothesized that stands of the opportunistic introduced reed *Arundo donax* would enhance OM inputs and consequently increase soil microbial C and N cycling and microbial biomass pools, due to higher growth rates of Arundo compared to woody species. The patterns we observed by comparing Arundo stands and restored woody species' litter and soils, however, did not fully support this hypothesis. Arundo accumulated less litter than woody species (Figure 1), perhaps because litter can remain standing on the stalk for long time periods after senescence. This litter had lower %C and %N (Figure 2a), while litter leachates had comparable extractable OC and ON per unit mass (Figure 3a; Figure 3), but not per unit area (Figure 3b) due to the lower litter accumulation under Arundo. Arundo soils did have higher soil extractable organic C (EOC) and EON than woody species (Figure 5), but greater EOC was not reflected in increased soil microbial biomass, as Arundo MBC and MBN was comparable to woody species (Figure 7), and willow soils had almost twice the microbial biomass as Arundo soils (Figure 7). Soils beneath Arundo had a relatively high EOC/MBC ratio of 3.6, twice that of woody species (1.8), implying lower physical or biological availability of EOC or perhaps a low production rate.

Arundo soil respiration was the highest of any soil, although by a small margin compared to willow soil (Figure 9; Figure 10b), suggesting that some fraction of the Arundo EOC pool was in fact accessible to the microbial community, but a proportionally low fraction compared to woody species' EOC (Figure 10a; Figure 10c). Soil EOC clearly differs between woody species and Arundo, while microbial biomass is in a similar range and follows a similar pattern in woody species and Arundo soils (Figure 10). Three out of five soils beneath Arundo were similar to soils beneath woody species, up to ~400 ug EOC/g dry soil, suggesting a potential saturation (but insufficient data to ascertain), and two Arundo soils are EOC vs. CO_2 outliers. One outlier, the highest Arundo soil EOC (784 ug EOC/g dry soil; 376 mg CO_2/10 weeks), correlates with woody species' MBC (141 ug MBC/g dry soil; Figure 10b), and overall Arundo respiration is flat across and unrelated to the extractable C pool. This soil EOC accumulation, and the irrelevance of EOC pool size to respiration (Figure 10a), suggests that Arundo OM may be more difficult to decompose than that of woody species. DOC retention in soils is often attributed to sorptive stabilization (Kalbitz et al. 2000), where inherently more stable (complex, aromatic, hydrophobic) compounds are preferentially sorbed to mineral surfaces (McKnight et al. 1997; Kalbitz et al. 2003; Kalbitz et al. 2005).

Soils reflect litter differences between growth forms, which can stem from distinct patterns of chemical quality and biomass allocation that affect decomposition (Hobbie 1995; Hobbie 1996). The retention of standing dead foliage in Arundo suggests more extensive leaching than deciduous taxa, but to our knowledge leaching data for this system does not exist. We sampled after the winter rains during a drought year in which the area received 54.7% of "normal" precipitation (based on 1957-1992 base period average; Ventura County Watershed Project District 2020). The growing season in this region initiates in April, so the sampling date represents a period when litter inputs were maximally leached into soils and plant uptake of nutrients was less of a consideration. If more seasonal leaching in standing dead Arundo foliage does occur, it would follow that Arundo litter EOC and N values in our study are lower than they would be prior to leaching, and is logical that our laboratory litter leachates' EOC and EON showed statistically insignificant patterns between Arundo and woody species (Figure 3): we might expect that these patterns would be more robust before the first leaching, particularly at the peak of litter accumulation in autumn. However, in soils, where fallen and standing contributions would be integrated, extractable ON and the sum of total extractable N (DON + TIN) was higher beneath Arundo than beneath woody species.

We report litter EOC and EON dynamics both per unit mass as well as per unit ground area to untangle the complexities of Arundo litter contributions: Arundo has more EOC and EON per gram litter, but it does not drop as much litter, as much of it remains standing on the culm. Standing dead foliage in grasses makes them more subject to both throughfall leaching (e.g. Hodson et al. 1984) and photodegradation (e.g. King et al. 2012) than other plant growth forms, processes that may result in significant losses preceding OM decomposition on the forest floor where litter biogeochemistry can be more simply compared between growth forms, as in this study. Reporting litter per unit mass may be more inclusive of standing dead foliage's potential contributions, while reporting litter CN per unit area highlights biological degradation of intact leaves and is a better interpretation if the majority of C and nutrients in Arundo standing dead foliage are resorbed and stored in rhizomes (e.g. Hurst et al. 1985; Lindsay & French 2005). To our knowledge, the timing and significance of standing dead foliage's losses to abiotic processes has not been quantified in Arundo, thus it is unclear at present which representation of litter CN (per unit mass or area) is more descriptive.

Photodegradation can increase decomposition and mass loss (Henry et al. 2008) and reinforce microbial degradation (Lin & King 2014), potentially by producing labile C (King et al. 2012), or alternatively can decrease losses by hindering microbial degradation (Johnson 2003; Smith et al. 2010). Photodegradation increases with litter C:N (Brandt et al. 2009), and can change OM availability by preferentially degrading lignin (Day et al. 2007; Henry et al. 2008; Austin & Balleré 2010), as well as altering pathways of N cycling where abiotic losses of N to the atmosphere bypass N immobilization and mineralization by microbes (Brandt et al. 2009; Smith et al. 2010; King et al. 2012).

Leaching of standing dead foliage with throughfall is not well-documented in grasses, with the exception of perennial salt marsh grass, *Spartina alterniflora* (Hodson et al. 1984; Wilson et al. 1986). Lignocellulose and lignin increase in standing dead tissue relative to living tissue in *S. alterniflora* throughfall, and fungal hyphae were found in standing dead tissue, suggesting that processes are not strictly abiotic (Hodson et al. 1984). Besides *S. alterniflora*, throughfall leaching has primarily been studied *in situ* in living canopies, while litter leaching is primarily studied as a surface soil phenomenon in laboratory settings (e.g. Wickland et al. 2007; Hensgens et al. 2020). In living riparian canopies, throughfall leaching of introduced species – fern *Pteridium aquilinum* (Williams et al. 1987) and shrub *Lorinera maackii* (McNeish 2016) – leached more nutrients and C than throughfall of native tree species. Over a period of three months, *L. maackii* living canopy throughfall leached ~150 mg TOC, roughly the amount we measured in a gram of woody species' soil (Figure 5). Standing dead foliage would likely have higher concentrations of leached elements than living canopies as leaves deteriorate and compounds are more susceptible to leaching (Eaton et al. 1973). Despite the potential importance of this flux, little is known about throughfall leaching in standing dead foliage compared to fallen litter.

Dynamics observed in Arundo's fallen leaf litter can be contextualized with other grasses. For example, fallen leaf litter in bamboo, a fast-growing opportunistic reed with similar phenology to Arundo that also forms monotypic stands (Chou 1981; Gadgil & Prasad 1984) in riparian zones in the tropics, has less N and higher lignin:N and lignin:phosphorous ratios than native woody species, and decomposes more slowly in streams (Larpkern et al. 2011; O'Connor et al. 2000). This increase in lignin may reduce microbial biomass overall (except for lignin-degrading populations; Schutter & Dick 2001; DeAngelis et al. 2011). However, in Mediterranean ecosystem introduced species generally have a lower lignin:N ratio than native plants (Incerti et al. 2018), typically indicating more easily decomposable OM. Given that Arundo is both a bamboo-like reed and an introduced species originally from the Mediterranean region, it is unclear which pattern of lignin:N it resembles most, although we found leaf litter C:N to be higher in Arundo (Figure 2). We were unable to find studies investigating the effects of throughfall leaching or photodegradation losses of CN in reeds.

In the case that standing dead foliage in Arundo photodegrades or leaches nutrients, it may still be more meaningful to interpret litter CN per unit area, as the differences in growth form may affect soil pools and thus may require separate considerations: litter decomposition is the result of leaching, catabolism and fragmentation (Cotrufo et al. 2010), and standing dead foliage contributions may bias leaching over catabolism and fragmentation, thus preferentially contributing simple, soluble compounds and fewer complex structural compounds (such as lignin), in contrast with forest-floor decomposition of fallen litter. Litter leaching may be an important source of soil DOC and nutrients (Currie & Aber 1997), especially during the wet season in Mediterranean ecosystems (McComb et al. 2006). This

DOC can then form stable soil OM through microbial assimilation and products associating with mineral-associated clay and silt fractions (Kaiser & Kalbitz 2012).

This mechanism may explain the accumulation of EOC beneath Arundo plants. Recently, studies have shown that the bioavailable, non-structural compounds in litter dissolved OM are incorporated quickly into microbial biomass and then transformed into a mineral stabilized form of soil OM as microbial products (Cotrufo et al. 2013; Cotrufo et al. 2015). In fallen litter, this DOM process occurs in conjunction with the longstanding and longer-term pathway of soil OM formation, the “physical transfer pathway,” in which biophysical decomposition forms coarse particulate soil OM (Smith et al. 1997; Cotrufo et al. 2015). Following this rapid assimilation of leached Arundo litter into stable soil OM, it is possible that Arundo leaf litter decomposition on the forest floor may then be slowed by difficult to degrade structural compounds as well as a lack of diverse inputs in Arundo monotypic stands compared to diverse riparian forest – soil microbial biomass may increase per unit carbon with a high diversity of inputs (Anderson & Domsch 1986). This pattern may be further enhanced by high silica content in Arundo and other grasses (Russel 1961; Jackson & Nunez 1964), where SiO_4 complexes with OC, and these compounds remain relatively stable in soils (Renforth et al. 2011; Song et al. 2015).

Arundo soils accumulated over twice as much EOC and N as woody plant soils (Figure 5). Despite this seeming availability, higher EOC did not support a larger microbial community (Figure 5), suggesting that a large fraction of the extractable pool is not readily biodegradable. Soil incubation CO_2 data suggests that some fraction of Arundo soil OM is being used, as C is respired at similarly high levels between Arundo and willow (Figure 9); however, less CO_2 is respired in Arundo soils per unit EOC (Figure 10a) and a similar range of CO_2 is respired per unit biomass for all species (Figure 10b), and four out of five Arundo soils did not differ from woody species' soils. The high microbial biomass in willow soils may reflect its relatively labile inputs (Figure 7); conversely, proportionally low microbial biomass in Arundo soils may result from a combination of stabilized microbial products and structural compounds, as well as the high silica content in Arundo litter (Jackson & Nunez 1964; Schaller & Struyf 2013), which can decrease fungal decomposer biomass (Schaller et al. 2014).

We hypothesize that this combination of extremes – rapidly assimilated and stabilized leached litter compounds paired with fallen litter that is rich with chemically recalcitrant structural compounds – along with low diversity of plant inputs, causes the accumulation of Arundo soil EOC compared to woody species (Figure 5; Figure 10). Microbial activity in Arundo soil may then be maintained by an intermediately available C pool (here measured as respiration; Figure 9), a pool that represents a smaller proportion of Arundo C than woody species C and is not sufficient to host a large microbial community (Figure 7).

F. Conclusions

Alterations to carbon and nutrient cycles are of particular importance in the riparian zone, a nutrient cycling "hot spot" that connects terrestrial and aquatic systems and acts as a biogeochemical filter for waterways. As riparian forests shift towards dominance by large-statured grass Arundo, it is useful to understand how this shift will affect underlying and longstanding elemental cycles. A comparison of soil and litter biogeochemistry in Arundo stands versus three woody species, *Salix laevigata* (red willow), *Populus trichocarpa* (black cottonwood), and *Baccharis salicifolia* (mulefat), indicated that Arundo soil had higher extractable OC and N compared to woody species. However, this EOC did not translate into larger microbial biomass or greater soil respiration, implying lower physical or biological availability of Arundo-derived EOC. We postulate that the accumulation of EOC in Arundo soils is a combination of (i) bioavailable material leached from standing dead foliage that assimilates into stabilized microbial products; (ii) fallen litter that is relatively slow to degrade due to complex structural compounds; (iii) a lack of diversity of litter inputs that would stimulate a larger microbial community; and iv) high silica content in Arundo soils via SiO_4 litter inputs, which can complex with OC.

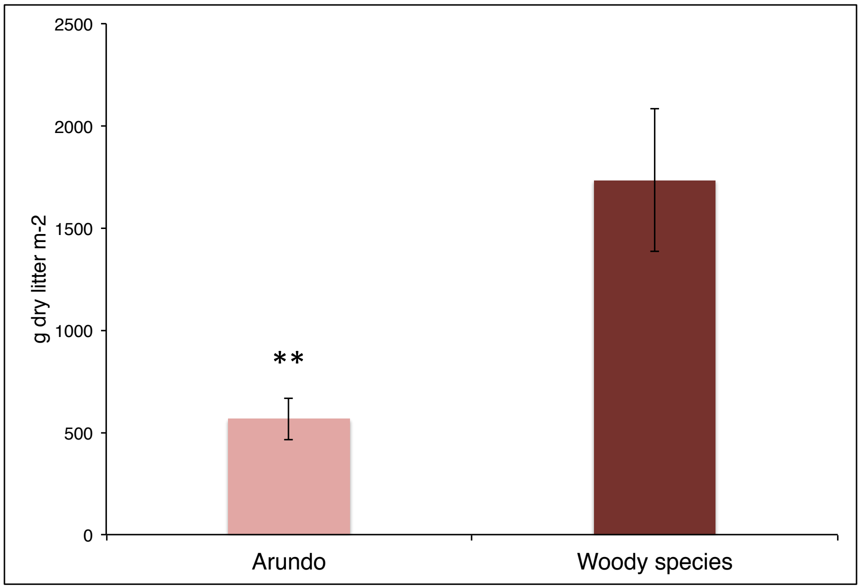


Figure 1: Litter mass. Litter (g dry weight) per m^2 directly beneath plant canopy of Arundo (n=6) versus woody species (cottonwood, mulefat, and willow combined; n=18). Woody species were combined due to similarities; Welch's unequal variances t-test was used to correct for differences in sample size. Error bars are +/- standard errors of the mean; significant differences between treatments are denoted for $p < 0.01$ (**).

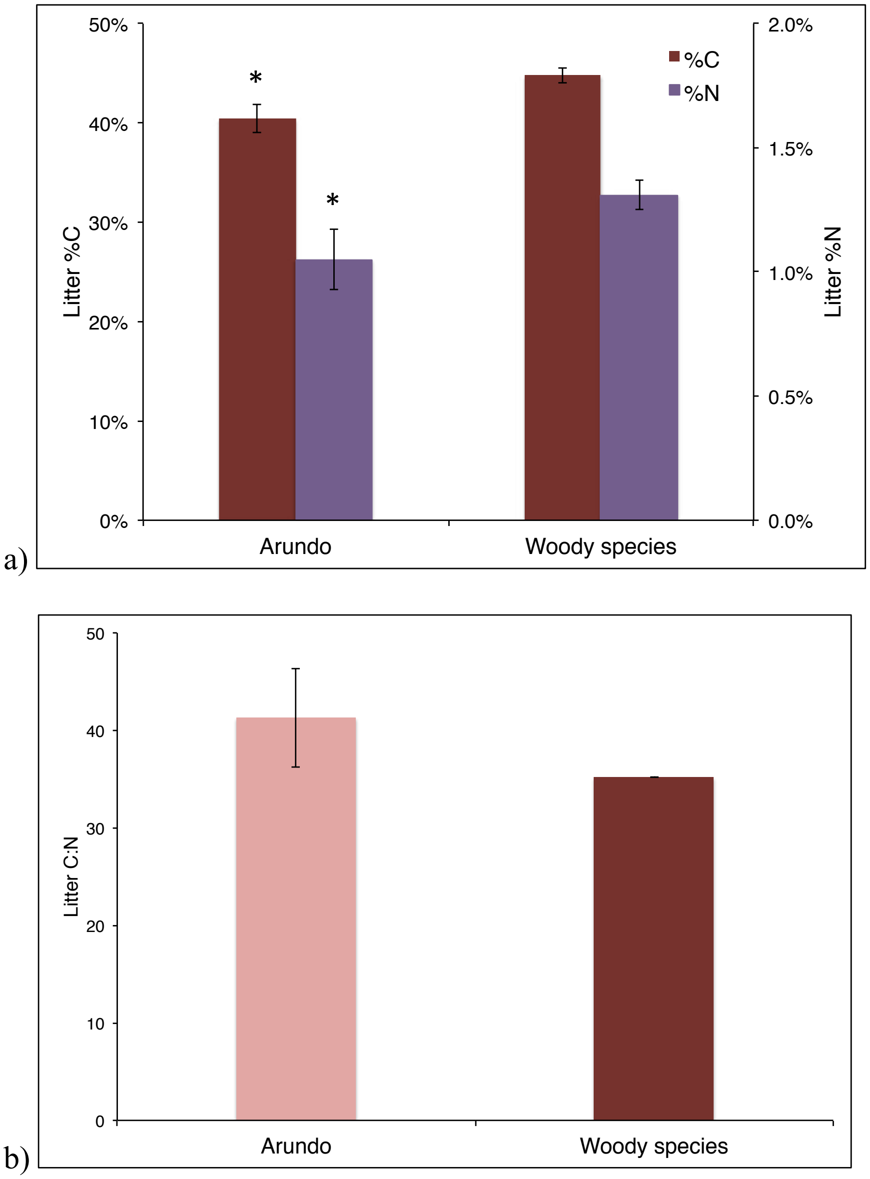


Figure 2: Litter %C, %N and C:N. (a) Litter %C (red bars) and %N (purple bars) by weight in Arundo (n=6) vs. woody species (cottonwood, mulefat and willow data combined; n=18). (b) Litter C:N in Arundo vs. woody species. Woody species were combined due to similarities; Welch's unequal variances t-test was used to correct for differences in sample size. Error bars are +/- standard errors of the mean; significant differences between treatments are denoted for $p < 0.1$ (*).

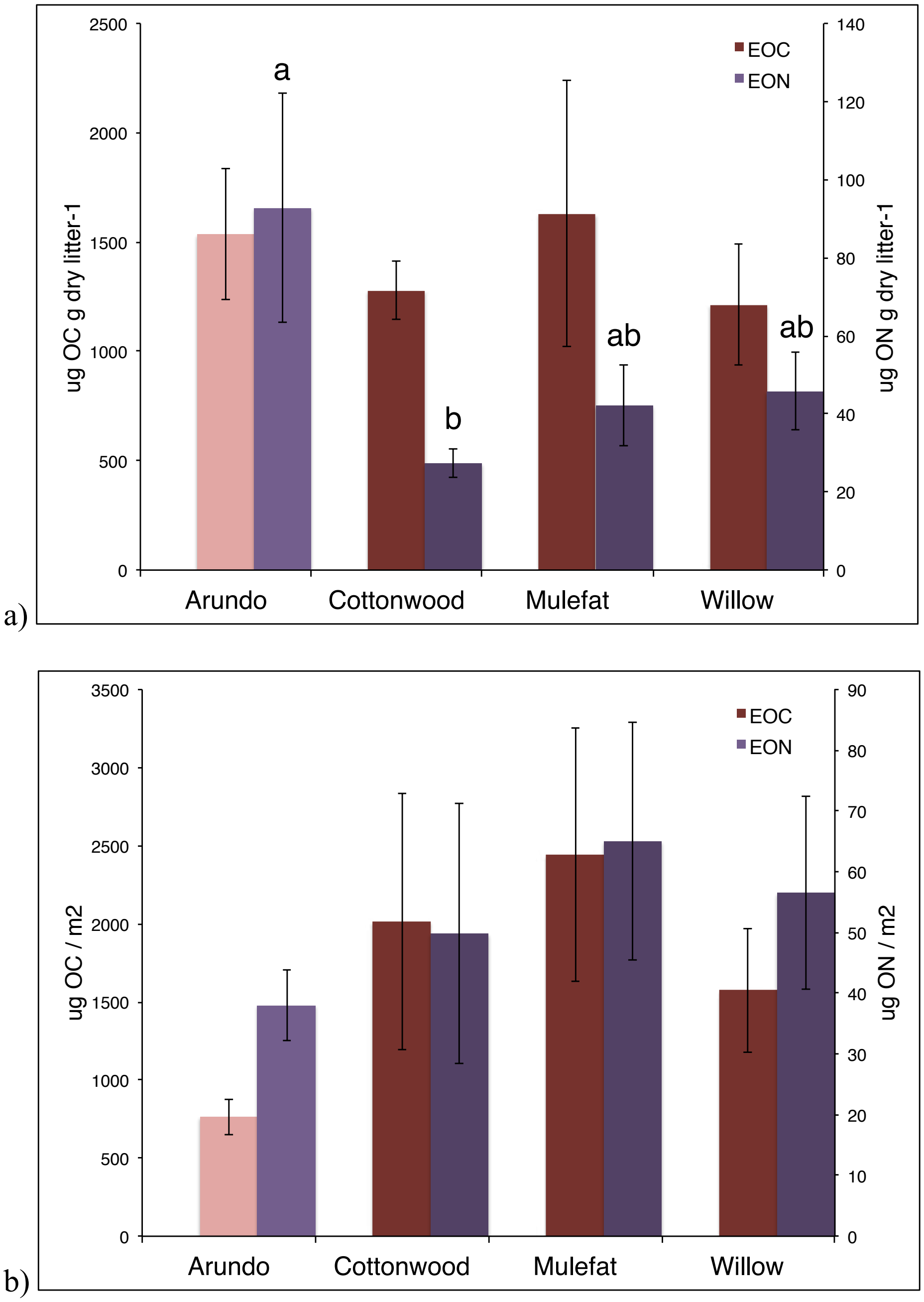


Figure 3: Litter EOC and EON. K_2SO_4-extractable OC (EOC; red bars) and ON (EON; purple bars) in dry litter of Arundo and woody species cottonwood, mulefat, and willow (a) per gram dry litter and (b) per m^2 below plant (n=6 for each species). Error bars are +/- standard errors of the mean; different lowercase letters represent statistically significant differences from a posthoc Tukey's HSD (p = 0.10).

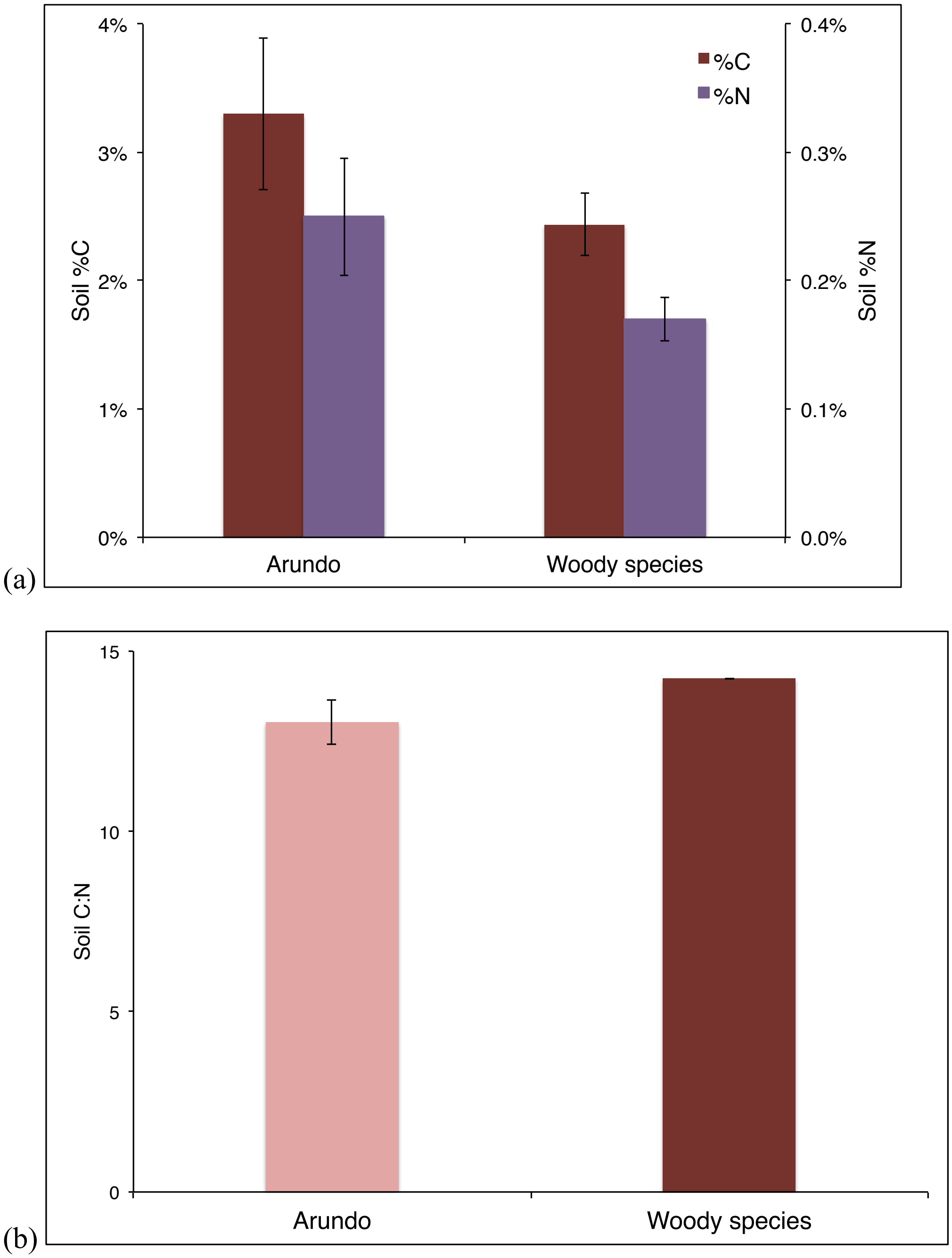


Figure 4: Soil %C, %N and C:N. (a) Soil %C (red bars) and %N (purple bars) by weight beneath Arundo (n=6) vs. woody species (cottonwood, mulefat and willow data combined; n=18). (b) Soil C:N between Arundo and native species. Woody species were combined due to similarities; Welch's unequal variances t-test was used to correct for differences in sample size. Error bars are +/- standard errors of the mean.

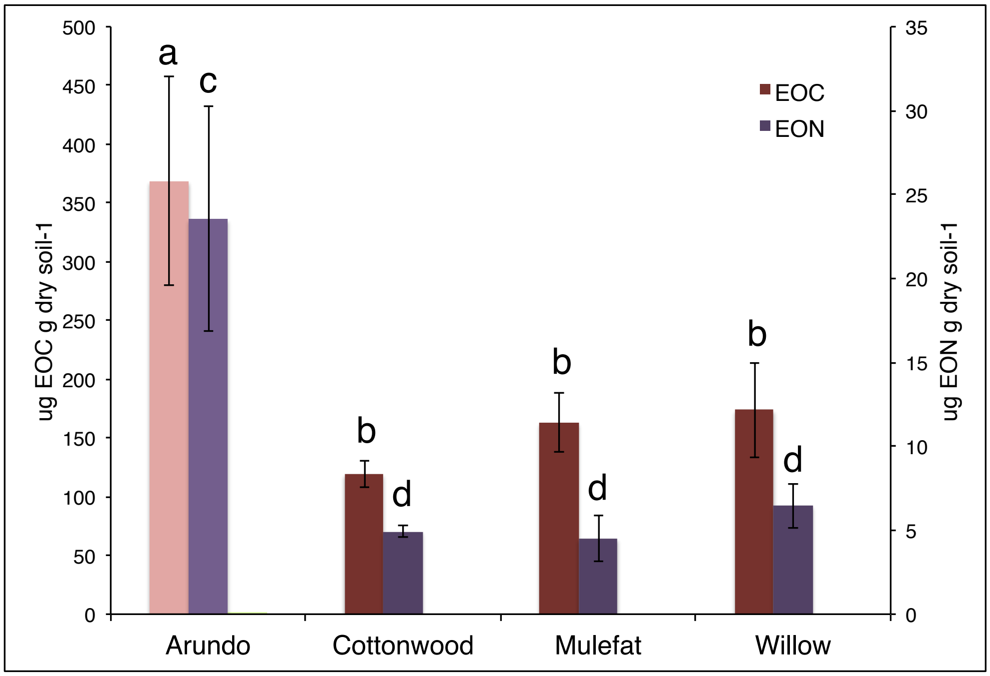


Figure 5: Soil EOC and EON. Soil K_2SO_4-extractable OC (red bars) and EON (purple bars) beneath Arundo and woody species cottonwood, mulefat and willow (n=6 for all species). Error bars are +/- standard errors of the mean; different lowercase letters represent statistically significant differences from a posthoc Tukey's HSD (p = 0.10).

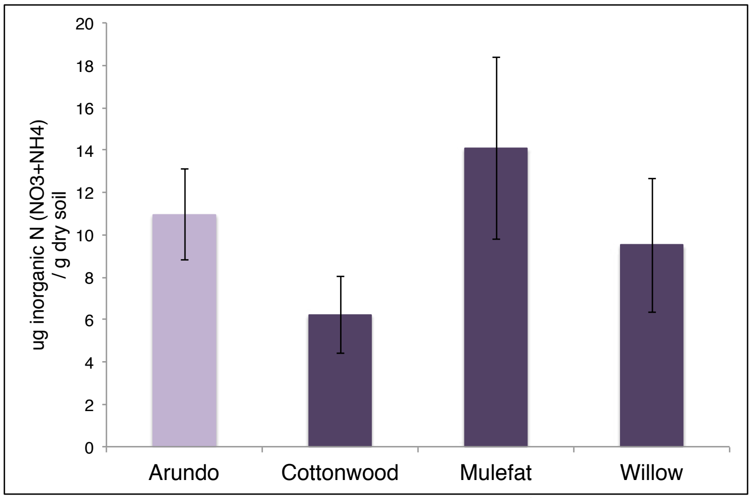


Figure 6: Soil inorganic N. $NO_3^- + NH_4^+$ beneath Arundo and woody species cottonwood, mulefat and willow (n=6 for all species). Error bars are +/- standard errors of the mean.

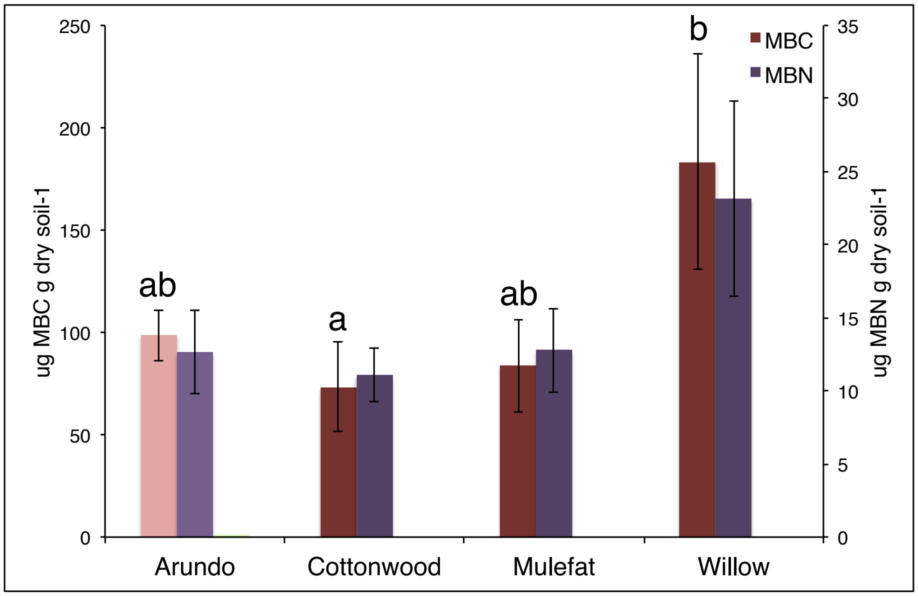


Figure 7: Soil microbial biomass. Soil microbial biomass C (MBC; red bars) and N (MBN; purple bars) beneath Arundo and woody species cottonwood, mulefat, and willow (n=6 for all species). Error bars are +/- standard errors of the mean; different lowercase letters represent statistically significant differences from a posthoc Tukey's HSD (p = 0.10).

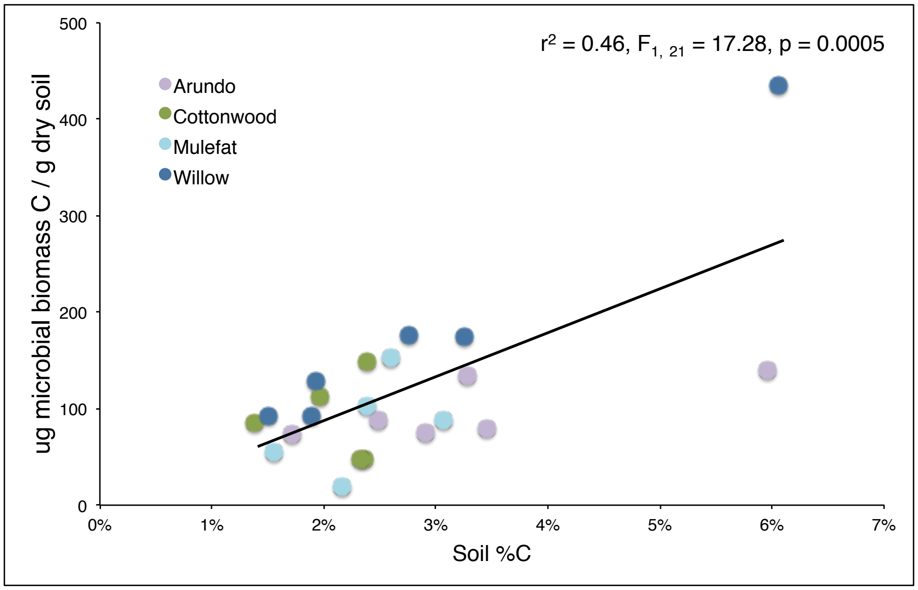


Figure 8: Soil %C vs. microbial biomass. The correlation between soil %C and soil microbial biomass C beneath Arundo (brown dots) and woody species cottonwood (green dots), mulefat (light blue dots), and willow (dark blue dots).

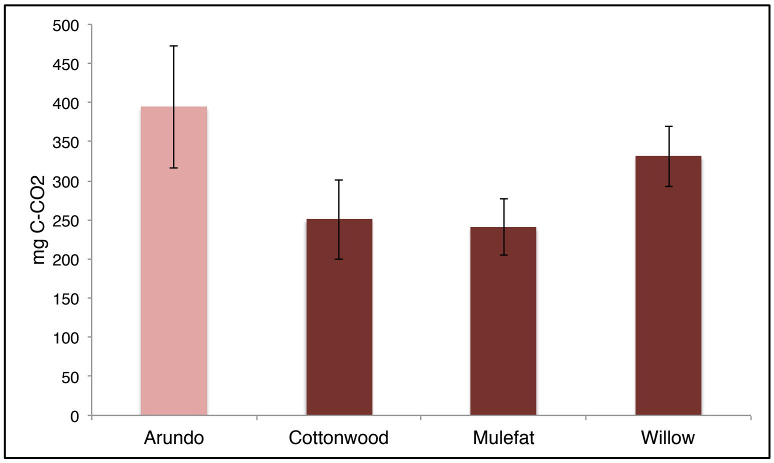
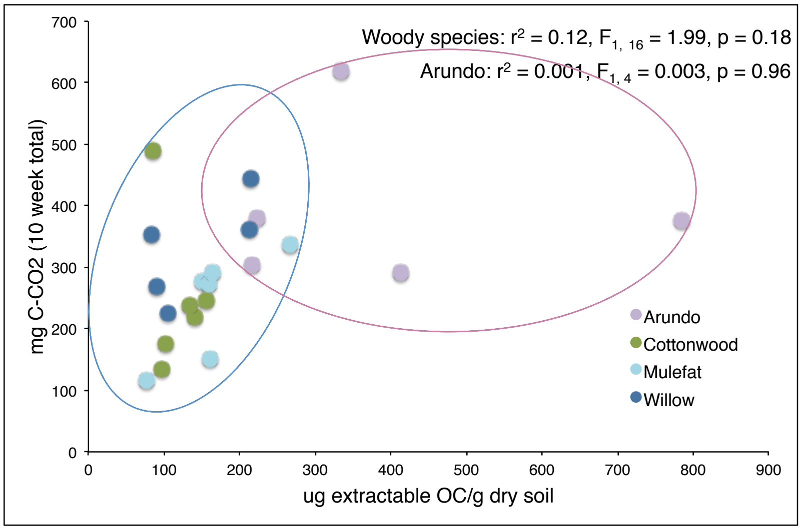
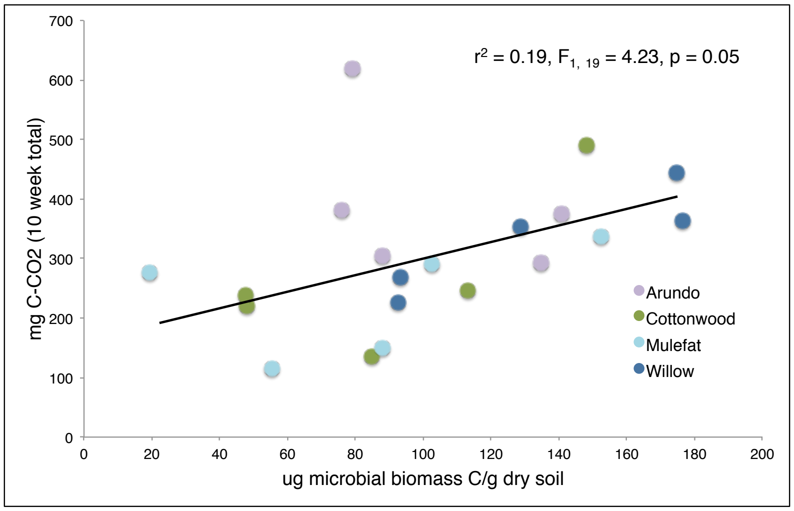


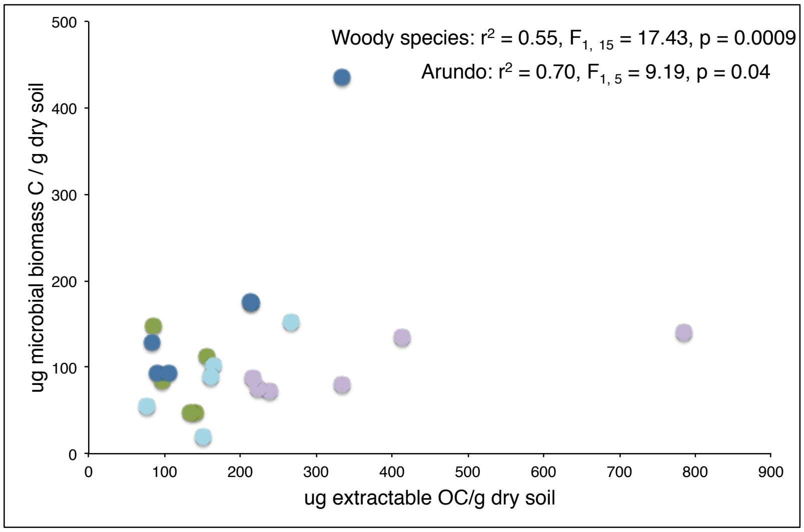
Figure 9: Total soil respiration. Soil CO_2 production over 10-week incubation between Arundo and woody species cottonwood, mulefat, and willow (n=6 for all species). Error bars are +/- standard errors of the mean.



a)



b)



c)

Figure 10: Relationships between soil EOC, MBC and respiration. The correlation between (a) soil EOC and total soil respiration (CO_2 produced over 10-week incubation), (b) microbial biomass C and total soil respiration, and (c) soil EOC and microbial biomass C in Arundo (purple dots) and woody species cottonwood (green dots), mulefat (light blue dots) and willow (dark blue dots).

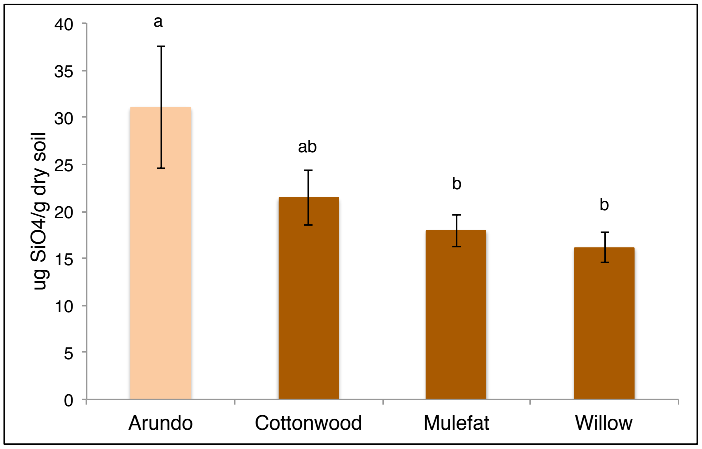


Figure 11: Soil silicate. SiO_4 beneath Arundo and woody species cottonwood, mulefat and willow (n=6 for all species). Error bars are +/- standard errors of the mean; different lowercase letters represent statistically significant differences from a posthoc Tukey's HSD (p = 0.10).

III. Large-statured grass *Arundo donax* alters plant leachate DOM relative to native riparian woody species

A. Abstract

An important regulator of riverine ecosystem function is dissolved organic matter (DOM) leached from riparian plants and soil. Differences in leaf chemistry between plant growth forms and species can alter quantity and quality of DOM, but it is unknown how introduced large statured grasses across the U.S. southwest might alter DOM cycling relative to the riparian forests these grasses displace. Here, we address how converting riparian communities in California from native woody *Salix laevigata* (willow) to stands of the large statured grass, *Arundo donax*, alters leaf, litter and soil leachate DOM chemistry and biolability. We simultaneously investigated the influence of land use adjacent to the stream to evaluate if this interacted with plant type to affect DOM chemistry. We collected willow and Arundo fresh leaves and leaf litter, as well as soils from beneath each species, in two watershed types: large agricultural rivers and smaller order, less developed creeks. We extracted DOM from these materials and explored their decomposition by a standardized microbial community in the aqueous phase. The DOM from all of these materials had high biolability (% DOC losses), with C losses ranging from 44.2% in soils to 88.0% in fresh leaves. Nearly all DOC losses in soil leachates occurred within two days, while nearly all plant DOC losses occurred within seven days. Arundo leaves and litter had 22-61% lower concentrations of DOC and 71-85% greater concentrations of DON than willow, but were 10-20% more biolabile, regardless of watershed type. Soils beneath Arundo and willow were more affected by watershed type than by species, with lower DOC and DON in large agricultural watersheds than in smaller less developed watersheds, but similar C losses. At

each phase of decomposition (fresh leaves-litter-soil), there was a lower percent relative abundance of aliphatic compounds and higher percent relative abundance of aromatic compounds. High biolability in fresh leaves and litter was correlated with DON, aliphatic and peptide-like compounds, as well as low DOC:DON, low nominal oxidation state of carbon (NOSC), and low aromaticity, while lower biolability in soils related to higher DOC:DON, high NOSC, and high aromaticity as well as low DON and low aliphatic and peptide-like compounds. A shift from willow forest to stands of the large-statured grass Arundo may contribute less – yet proportionally more biolabile – DOC and more DON to aquatic systems.

B. Introduction

Aquatic ecosystem dynamics are linked to the surrounding riparian plant community by plant inputs of organic matter (OM; Hynes 1975; Naiman & Decamps 1997; Wallace et al. 1999; Kennedy & Hobbie 2004). Fallen leaves are the primary OM source for most streams, particularly shaded ones (Marcarelli et al. 2011). Litter inputs, which vary in quantity and quality between plant types, determine the functioning of stream foodwebs, respiration, and nutrient export (Marcarelli et al. 2011; Stanley et al. 2012). Leaching of leaf litter releases dissolved OM (DOM; Gessner et al. 1999), a dominant C pool in waterways that serves as an important regulator of microbial metabolism and nutrient cycling (Wiegner & Tubal 2010). In temperate streams, dissolved organic carbon (DOC) leached from riparian leaf litter can support up to 70% of heterotrophic respiration and accounts for 30% of exported DOC (Kaplan et al. 2007; Meyer et al. 1998; Dahm 1981). The fate of leached DOM (respired or exported) is thought to largely depend upon the quality (chemical composition) of leaves, but compositional controls vary greatly between plant growth forms, and may be further complicated by the compounding stressors of diversion and nutrient enrichment present in many watersheds (Prairie 2008; Stanley et al. 2012; Wymore et al. 2015; Marks 2019).

In regions with a Mediterranean climate, differences in riparian plant growth form can be mediated by upstream watershed land use (Kominoski 2011), where changes in hydrologic flows and nutrient pollution from residential and agricultural runoff can promote plant community shifts from tree-dominated riparian forest to stands of large-statured grasses (Naiman & Décamps 1997; Jones et al. 2010; Kondolf 1995; Lambert et al. 2014). Despite the increasing prevalence of such vegetation type conversion, it is unknown how this might influence leaf-originated DOC dynamics and whether this is influenced by watershed size and land use. One of the most prolific large-statured grasses in California is giant reed, *Arundo donax*, introduced from the Mediterranean basin (Hardion et al. 2014). Arundo spreads quickly and forms high-biomass monotypic stands that can dominate riparian habitats, displacing native flora (Dudley 2000). Presently it is unknown how a shift towards dominance by large statured grasses like Arundo alters litter chemical and structural composition or how this might influence aquatic DOC cycling. Grasses are more subject to throughfall leaching than deciduous woody species due to standing dead foliage (Hodson et al. 1984); thus an understanding of how Arundo may alter soluble DOM is of particular relevance to terrestrial cycling as well.

Leaves that grow quickly with high nutrient content and low structural and defense compounds tend to decompose quickly (Cornwell et al. 2008). Thus, litter from herbaceous forbs tends to decompose more quickly than leaf litter of woody deciduous species; perhaps surprisingly, evergreen grasses often decompose more slowly than woody species (Rawlik et al. 2021). These overall patterns in decomposition are driven by litter molecular composition and N content: simple, straight-chain, low-molecular-weight compounds with high N content are typically readily metabolized and break down quickly, while complex, aromatic, or high-molecular-weight compounds (i.e. structural or defense compounds) are more resistant to decomposition and break down slowly (Marin-Spiotta 2014). Measuring chemical controls on biolability with available analytical methods typically involves targeting specific compounds; high biolability is typically associated with low lignin, a low C:N ratio, and low concentrations of tannins and phenolics (associated with defense; Neff & Asner 2001; Webster & Benfield 1986; Schindler & Gessner 2009; Frainer et al. 2015; Kuglerová et al. 2017; Migliorini & Romero 2020). However, these are not universal relationships across litter types (Bowman et al. 2003; Cleveland et al. 2004; Wiegner & Tubal 2010; Wymore et al. 2015). The relative balance of these different chemical controls on leaf litter biolability and OM contributions varies across plant communities due to the chemical compositions of different leaves (Strauss & Lamberti 2002; Wymore et al. 2015; O'Connor et al. 2000; Liu et al. 2000; Osono et al. 2014).

Temperate forest tree species leaf leachates can vary significantly in relative DOC losses (biolability; ranging from 54-86% DOC lost over 24 days), where high DOC losses correlate with indices of low aromaticity (specific ultraviolet absorbance, $SUVA_{254}$; higher values are more aromatic; Strauss & Lamberti 2002). However, within the *Populus* (cottonwood) genus, more biolabile species' leaves were *more* aromatic and had higher molecular weight (higher $SUVA_{254}$ and lower fluorescence index, FI); in these species, soluble DOC and amino acids, and low tannins and lignin correlated with biolability (>20% variation in DOC loss between *Populus* species; Wymore et al. 2015).

While opportunistic large statured grasses have not been investigated for DOC biolability, variation in decomposition controls has been documented in terms of %C mass loss. Bamboo (*Bambusa spp* and *Sinarundinaria spp.*) has lower N content—but higher N and phosphorus (P) content per unit C—and lower mass loss in streams and in soils than native and introduced trees (O'Connor et al. 2000; Liu et al. 2000), while Japanese pampas grass (*Miscanthus sinensis*) leaf litter has similar N content to that of oak tree *Quercus crispula*, but pampas grass decomposes more slowly, likely due to greater relative abundance of acid unhydrolyzable residue (Osono et al. 2014). The complexity of OM, and the interactions of different chemical components, eludes targeted analyses of a limited number of compound classes, suggesting that more comprehensive chemical analyses are important in untangling how plant community shift affects watershed C and N cycling.

To better understand these relationships between DOM chemistry and biolability, recent investigations have used detailed chemical analyses such as Fourier transform ion cyclotron resonance mass spectrometry (FT-ICR MS). This technique characterizes molecular formulae for thousands of compounds grouped into compound classes for ease of interpretation (Bhatia et al. 2010; Spencer et al. 2014; Raymond & Spencer 2015) and has yielded a wealth of information on compositional controls on DOM biolability in different systems. For example, greater losses of DOM occur with higher aliphatics and peptide-like compounds, and with lower nominal oxidation state of carbon (NOSC; an indirect measure of polarity, affecting solubility/bioavailability, that correlates with molecular weight), lower index of aromaticity (AI_{mod}), lower polyphenolics and lower average mass (Kellerman et al. 2018; Drake et al. 2018; Johnston et al. 2019; Kane et al. 2019). This approach is promising for untangling species- and situation-specific controls on leaf litter biolability and processing in waterways, particularly in the context of plant community shift.

Separately, litter leachate DOM dynamics of plant community member species (e.g. Strauss & Lamberti 2002; Cleveland et al. 2004; Wiegner & Tubal 2010; Wymore et al. 2015) and litter mass loss dynamics with vegetation type conversion (e.g. O'Connor 2000; Kennedy & Hobbie 2004; Mineau et al. 2012) have been explored in previous studies. However, we do not know how a shift in plant growth form alters leaf leachate DOC dynamics in aquatic systems. Given the importance of plant-derived DOM as the base of riverine food webs, the broad differences between plant type DOM, and the persistence of Arundo-associated DOC in soils (Dowdy et al. Manuscript in preparation), it is likely that a shift from willow-cottonwood forest towards Arundo will affect DOM processing downstream. Understanding how this shift towards Arundo leaf, litter, and soil leachate DOC biolability would tell us how terrestrial subsidies to aquatic systems might change with the prevalent vegetation.

We address the following questions: (1) how does a shift from native riparian tree *Salix laevigata* (red willow; hereafter, willow) dominance to the large-statured grass *Arundo donax* alter DOC inputs and decomposition in aquatic systems? (2) How does the watershed type and surrounding land use influence the effect of plant growth form on stream DOC cycling? We hypothesized that Arundo DOC would be less biolabile than that of willow, and that both species would break down more readily in large agricultural watersheds due to enhanced N levels. We collected fresh leaves and litter from willow and Arundo, as well as soils under each; we sampled from riparian corridors along three large agricultural rivers and three less developed small order creeks. These materials constitute terrestrial OM inputs to streams on their own and together present a decomposition continuum that offers further insights into the chemical breakdown of each growth form's leaves in terrestrial systems. We then performed bioassays to evaluate how biolability related to the chemical makeup of DOC. We leached each material and added a standardized aquatic microbial community to allow us to focus on how materials differed in chemistry. We assessed leachate chemical composition (DON, DOC:DON, FT-ICR MS formulae assignments) and biolability (C losses) of microbially-available (<0.7um) DOC over a 14-day incubation.

C. Methods

1. Sample collection

We collected fresh leaves and litter from *Arundo donax* and *Salix laevigata* (willow), as well as soil (0-10cm) from beneath them in six watersheds with established populations in Santa Barbara and Ventura counties during January and February 2018. Three watersheds contained large developed agricultural rivers: the Santa Clara River, the Santa Ynez River, and Calleguas Creek. Three watersheds contained less developed small order creeks with mixed land uses, including small-scale upland agriculture and more natural riparian vegetation: Tecolote Creek, El Capitan Creek, and Arroyo Quemada.

Samples were collected at three points along each watershed and combined to form pooled leaf, litter, and soil samples for each watershed (n=3 for each treatment [watershed type x species x material]; however, fresh Arundo leaves along one large agricultural river were lost prior to laboratory analyses, making this treatment n=2). Fresh leaves, litter and soils were collected from the same plants. Fully expanded fresh green leaves were chosen randomly; any leaves with insect damage or yellowing were avoided. Soils were broadly classified as gullied land and Agueda-Goleta complex (2-9% gradient; Tecolote Creek), Ballard stony fine sandy loam (very stony subsurface, 2-9% gradient; El Capitan Creek), Agueda silty clay loam (2-9% gradient; Arroyo Quemada), Corducci and Typic Xerofluvents (occasionally flooded, 0-5%slopes; Santa Ynez River), xerofluvents with a loamy sand texture in the A horizon (Santa Clara River), and Hueneme loamy sand with loamy substratum (Calleguas Creek; Web Soil Survey, USDA).

Sampling took place in late fall/early winter, a time chosen for maximal accumulation of leaf litter and minimal leaching. At this time, ~10% of normal winter rainfall had been received in Santa Barbara and Ventura counties. Accumulated leaf litter in deciduous native riparian forest species like *S. laevigata* was on the forest floor; in contrast *Arundo donax* is evergreen in California and does not drop leaves seasonally, and recently senesced foliage instead remains standing on the culm. These differences in litter accumulation may be important in distinguishing between plant effects on watershed C and N cycling (Dowdy et al., Manuscript in preparation).

2. Aquatic decomposition incubation

We prepared leachates of fresh leaves, litter and soils in the laboratory. Soils were sieved to 4mm to remove rocks and plant roots. We dried leaves, litter and soil for 24 hours at 50°C (Petersen & Cummins 1974; Benfield 1996; Gessner et al. 1999). For each watershed's samples, 10 g of leaves, 10 g of litter, and 20 g of soils were leached separately into 1L of 0.001 N sodium bicarbonate ($NaHCO_3$) for 24 hours in the dark at 20°C, and then filtered through pre-combusted (550°C >5 hours) 0.7um glass microfiber filters to remove the microbial biota (Spencer et al 2008). Removing microbes allowed us to focus on OM bioavailability without the confounding effects of varying microbial populations between samples. We then added a 1% standard microbial inoculate, a 50/50 mix of Calleguas Creek (large agricultural watershed) and El Capitan Creek (less developed small order watershed) water filtered to 1.6um to remove microbial grazers to each leachate. Leachates were then divided into 40ml vials for a 14-day incubation (nine vials per sample to allow for triplicate lab replication and non-destructive sampling at three time points: 2 days, 7 days, 14 days). During

3. Dissolved organic carbon and nitrogen analyses

We compared the decomposition of materials through a 14-day incubation depending on watershed type and plant species (n=3 for each treatment, with laboratory analytical triplicates; lab triplicates were used to ensure accurate DOC and DON analysis, they were not used as replicates in statistical analysis). As mentioned above, leachates were standardized by weight/biomass of soil and plants. We assessed the decomposition of DOC by measuring losses of DOC from the leachates, and by assessing N transformations throughout the incubation. Subsamples filtered to 0.7um and acidified with HCl at each time point were analyzed for DOC, total dissolved N (TDN), and inorganic N (soil leachates only). Plant material (litter and fresh leaf) TDN was assumed to primarily be in the form of DON, and exact IN/ON values were not obtained due to colorimetric interference of plant leachate organics. DOC and TDN was analyzed on a TOC analyzer (Shimadzu TOC-V) for all samples. Inorganic N (NO_3^- and NH_4^+) was analyzed colorimetrically using a plate reader (Hood-Nowotny et al. 2010), and subtracted from soil TDN to obtain dissolved organic N

(DON; soil leachates only). Separate blanks were analyzed for leachates and used to correct for background C and N concentrations.

4. 21 T Fourier Transform Ion Cyclotron Resonance Mass Spectrometry

Leachate subsamples were collected at the start (day 0; n=3 per treatment) of the incubation to analyze leachates for DOM chemical composition with 21 T Fourier Transform Ion Cyclotron Resonance Mass Spectrometry (FT-ICR MS). Subsamples were frozen at -18°C until being transported on ice to the National High Magnetic Field Laboratory in Tallahassee, FL. Subsamples were prepared for FT-ICR MS with solid phase extraction cartridges in methanol, which were evaluated with negative electrospray ionization into the magnet cell at a flow rate of 700 ng/min (Hendrickson et al. 2015; Smith et al. 2018). Mass spectra from 100 scans were accumulated and signals greater than 6σ root mean squared baseline noise were assigned formulae with a mass to charge ratio (m/z) from 120-1200 with mass error below 300 ppb. Formulae were assigned with PetroOrg (Corilo 2015) with the bounds of $C_{1\text{-}45}H_{1\text{-}92}N_{0\text{-}4}O_{1\text{-}25}S_{0\text{-}2}$. Compound classes were assigned to each molecular formula using elemental stoichiometries and modified aromaticity index (AI_{mod}; Koch & Dittmar 2006; Koch & Dittmar 2016), related to the degree of aromaticity and unsaturation of DOM (Kellerman et al. 2018). Compound classes include: highly unsaturated and phenolic with high O/C (Aromaticity Index, $AI_{mod} < 0.5$, $H/C < 1.5$, $O/C \geq 0.5$), highly unsaturated and phenolic with low O/C ($AI_{mod} < 0.5$, $H/C < 1.5$, $O/C < 0.5$), polyphenolic (AI_{mod} 0.5-0.67), condensed aromatic ($AI_{mod} > 0.67$), aliphatic ($H/C \geq 1.5$, $O/C < 0.9$, $N=0$), sugar-like ($O/C > 0.9$) and peptide-like ($H/C \geq 1.5$, $O/C < 0.9$, $N \geq 1$; O'Donnell et al. 2016). The abundance of each compound class is reported as % relative abundance, while indices of

H/C, N/C, nominal oxidation state of carbon (NOSC) and AI_{mod} are reported as weighted averages based on the relative abundance of each formula/peak in the sample and the corresponding value of that peak. NOSC is an indirect measure of polarity, which influences solubility as well as bioavailability (Riedel & Biester 2012). NOSC is primarily related to H/C and O/C ratios and secondarily to N/C and S/C ratios, and correlates with molecular weight in plant-derived DOM (Kane et al. 2019). NOSC and AI_{mod}, along with aliphatic and polyphenolic compounds (% relative abundance), can broadly describe the degree of molecular complexity and are considered bulk characteristics of DOM (Kellerman et al. 2018; Johnston et al. 2018). More biolabile samples tend to have low NOSC (e.g. aliphatics ranging from ~ -2 – 0) and AI_{mod} ($AI_{mod} < 0.5$ is considered unsaturated phenolic; available data on plant leachate AI_{mod} ranges from 0.181 – 0.316, while soil leachate AI_{mod} is ~0.4). Higher values of NOSC and AI_{mod} are thought to be more stable (e.g. NOSC ranges from 0 – 0.8 in organic acids, and lignin-like and tannin-like compounds; $AI_{mod} > 0.5$ is considered polyphenolic and $AI_{mod} > 0.6$ is considered condensed polycyclic aromatic; Riedel & Biester 2012; Kellerman et al. 2018; Johnston et al. 2019; Liu et al. 2020).

5. Statistical Analyses

Differences in initial DOC and DON were analyzed using two-way ANOVAs, comparing treatments of plant species (Arundo and willow), watershed type (large agricultural rivers vs. less developed small order creeks) and the interaction between plant species and watershed type for each material. For comparisons of DOC:DON, two-way ANOVAs were used as described above; additionally, materials (fresh leaves, litter, soil) were compared within species as was the interaction of materials*watershed type. FT-ICR MS derived bulk characteristics of DOM (NOSC, AI_{mod}, and relative abundance of aliphatics and polyphenolics) were analyzed with a two-way ANOVA with material, species, and material*species. When main effects were significant for interactions, posthoc analyses of Tukey's Honestly Significant Difference (HSD) were performed. All treatments had n=3, except fresh Arundo leaves along large agricultural rivers, where a sample was lost (n=2); analytical lab triplicates were performed for quality control but were not used in statistical analyses. To analyze effects of species and watershed type on %DOC loss over time, a repeated measures ANOVA was performed with time as a fixed effect. Correlations between DOC:DON and %DOC loss were analyzed with linear regressions. We report all values of p equal to or less than 0.10 because $p<0.05$ could result in high Type-II errors in our relatively small sample size (Hurlbert & Lombardi 2009). All statistics were done in the JMP 12.0 Pro package (SAS Institute Inc., Core, NC, USA).

To examine trends between FT-ICR MS chemical composition variables, % C loss, DON, and DOC:DON, we used principal components analysis (PCA) in the R package vegan. The PCA was done on log10(x+1) transformed FT-ICR MS derived variables that were then scaled to a range of 0 – 1 (due to negative and zero values, placing all values in the same range). %C loss, DON, and DOC:DON were then fit to the ordination over 1000 permutations. DON ($p<0.01$), DOC:DON ($p<0.0001$) and % C loss ($p<0.001$).

D. Results

1. Leachate composition

In fresh leaves, initial DOC varied significantly by plant species, where leachates from willow leaves had nearly twice the concentrations of DOC as Arundo leaves (Figure 1a; $F_{3,}$

$_{10}$= 6.69, p = 0.02; Species: p = 0.003; Watershed type: p = 0.20; Species*Watershed type: p = 0.60). TDN (assumed to be DON in plant material) concentrations were over three times higher in Arundo leaf leachates than in willow leaf leachates (Figure 1a; $F_{3, 10}$= 2.60, p = 0.13; Species: p = 0.09; Watershed type: p = 0.17; Species*Watershed type: p = 0.44). Leachates of both species' fresh leaves appeared to have higher DON concentrations along small order creeks than large agricultural rivers, but this was not statistically significant at p=0.10.

In leaf litter, initial DOC concentrations were similarly higher in willow leachates while DON was higher in Arundo leachates, and there were not significant differences in watershed type (Figure 1b; $F_{3, 11}$= 3.12, p = 0.09; Species: p = 0.03; Watershed type: p = 0.67; Species*Watershed type: p = 0.17). Along small order creeks, willow litter leachates had over two times greater DOC concentrations than Arundo litter leachates, while along large agricultural rivers the species did not appear different. TDN (considered to be DON) concentrations followed the same pattern of fresh leaves and was significantly higher in Arundo litter leachates: six times higher along small order creeks and four times higher along large agricultural rivers (Figure 1b; $F_{3, 11}$= 16.33, p = 0.0009; Species: p = 0.0001; Watershed type: p = 0.36; Species*Watershed type: p = 0.22).

Soil leachate initial DOC differed between watershed types but not between species, where soils along small order creeks had higher concentrations (Figure 1c; $F_{3, 11}$= 1.94, p = 0.20; Species: p = 0.41; Watershed type: p = 0.06; Species*Watershed type: p = 0.81). DOC concentrations in soils beneath willows appeared to be lower than DOC concentrations in soils beneath Arundo in both land uses, but not significantly so. Soil DON concentrations were also similar beneath plant species but were greater along small order creeks (Figure 1c;

$F_{3, 11} = 1.51$, $p = 0.29$; Species: $p = 0.38$; Watershed type: $p = 0.10$; Species*Watershed type: $p = 0.59$). Soil TDN concentrations followed the same pattern as soil DON concentrations, as soil inorganic N ($NO_3^- + NH_4^+$) varied little across plant species or land use type, averaging 0.68 mg/L N for all treatments (data not shown).

2. Biolability

Over a 14-day incubation, all DOC samples had high %C loss, ranging from 44.2% of soil leachate DOC to 88% of the DOC in fresh leaf leachates (Figure 2). DOC losses were similar in in fresh leaves and litter leachates (68.1-88% vs. 66.4-82.1%) and lowest in soil leachates (44.2-55.9%). Fresh leaf leachates followed similar patterns with different magnitudes of %DOC loss, where losses plateaued after day 7 (Figure 2a). After 14 days, Arundo leaf leachates had up to 20% greater %DOC losses than willow leaf leachates and each species' %DOC losses were similar despite watershed type ($F_{4, 32} = 15.77$, $p < 0.0001$; Species: $p = 0.10$; Watershed type: $p = 0.30$; Species*Watershed type: $p = 0.17$; Time: $p < 0.0001$). TDN concentrations of fresh leaf leachates did not change throughout the incubation (data not shown).

Litter leachates also followed similar patterns of %DOC loss, where losses plateaued after day 7 (Figure 2b). Arundo litter leachates had greater %DOC losses than willow, while the effect of watershed type was insignificant ($F_{4, 35} = 22.76$, $p < 0.0001$; Species: $p = 0.01$; Watershed type: $p = 0.94$; Species*Watershed type: $p = 0.27$; Time: $p < 0.0001$). By day 2, Arundo litter leachates along small order creeks had already lost 20% more %DOC than willow litter leachates in both watershed types ($F_{3, 11} = 5.81$, $p = 0.02$; Species: $p = 0.007$; Watershed type: $p = 0.41$; Species*Watershed type: $p = 0.10$; Tukey's HSD $p = 0.02$ for willow in small order creeks and $p = 0.05$ for willow in large agricultural rivers), and this pattern held through the duration of the incubation. Litter leachate TDN did not change throughout the incubation (data not shown).

Soil leachate %DOC losses were rapid over the first two days, but minimal after day two (Figure 2c). A much smaller proportion of the total DOC was lost from soil leachates than from those of plant tissues (ca. <50% compared to >70%; $F_{8, 34} = 15.08$, $p < 0.0001$; Species: $p = 0.001$; Watershed type: $p = 0.98$; Material: $p < 0 .0001$; Tukey's HSD $p < 0.0001$ for fresh leaves and litter). Soil leachates %DOC losses were similar between species and land uses, but this interaction was significant ($F_{4, 35} = 2.45$, $p = 0.07$; Species: $p = 0.35$; Watershed type: $p = 0.57$; Species*Watershed type: $p = 0.04$; Time: $p = 0.06$; Tukey's HSD n.s.). Soil leachates ranged in mineralization between 0.35-0.72 mg N/L*14-days, and rates were not significantly different between treatments (data not shown).

3. Compositional controls on biolability

Initial DOC:DON correlated strongly with fresh leaf DOC decomposition (Fresh leaf %DOC loss = 88.47 - 0.12*DOC:TDN, r^2=0.90, $F_{1, 10} = 78.03$, $p < 0.0001$) and litter leachate DOC decomposition (Litter %DOC loss = 82.24 - 0.075*DOC:TDN, $r^2 = 0.61$, $F_{1, 11} = 15.39$, $p = 0.003$), where leachates with lower DOC:DON had greater %DOC lost (Figure 3a). Conversely, high DOC:DON correlated with %DOC loss in soil leachates (Soil %DOC loss = 19.07 + 1.22*DOC:TDN, r^2=0.64, $F_{1, 11} = 17.76$, $p = 0.002$; Figure 3b). Arundo did not vary by materal, as fresh leaf, litter, and soil leachates had comparable DOC:DON with an average of 17.5, but Arundo DOC:N did vary by watershed type ($F_{5, 16}$= 2.40, $p = 0.11$; Material: $p = 0.13$; Watershed type: $p = 0.05$; Material*Watershed type $p = 0.57$). Willow fresh leaf and litter leachates had higher DOC:DON than those of Arundo (Fresh leaves $F_{3,}$

$_{10}$= 8.76, p = 0.009; Species: p = 0.003; Watershed type: p = 0.12; Species*Watershed type: p = 0.17; Litter $F_{3,\ 11}$= 18.89, p = 0.0005; Species: p = 0.0001; Watershed type: p = 0.12; Species*Watershed type: p = 0.06; Tukey's HSD p < 0.10 for all combinations of species and watershed type except Arundo between watershed types). In contrast to Arundo, willow leachate DOC:DON did vary with material but not watershed type, although this interaction was also significant ($F_{5,\ 17}$= 9.20, p = 0.0009; Material: p = 0.0003; Watershed type: p = 0.9; Material*Watershed type: p = 0.02). Along large agricultural rivers, willow plant material leachates had higher DOC:DON than soil leachates, where fresh leaf leachates averaged 167, litter averaged 127, and soils averaged 22.9. Along small order creeks, willow litter leachates had a higher DOC:DON (211) than fresh leaves and soil (86.1 and 27.0). Interestingly, Arundo leachate DOC:DON did not change with phase of decomposition (fresh leaves, litter, soil) while willow DOC:DON decreased with phase of decomposition.

Nominal oxidation state of carbon (NOSC; an indirect measure of polarity, influencing solubility, where high values are less bioavailable) was lowest in fresh leaves and litter leachates, and highest in soil leachates, with no effect of species (Figure 4a; $F_{5,\ 32}$= 5.76, p = 0.001; Material: p < 0.0001; Species: p = 0.36; Material*Species: p = 0.34). NOSC was significantly higher in soil leachates than in fresh leaves (Tukey's HSD p = 0.002) and litter (Tukey's HSD p = 0.0001), which were similar (Tukey's HSD p = 0.63). AI_{mod} was also comparably low in fresh leaves and litter leachates, and higher in soil leachates, regardless of species (Figure 4a; $F_{5,\ 32}$= 10.78, p < 0.0001; Material: p < 0.0001; Species: p = 0.36; Material*Species: p = 0.54). As with NOSC, AI_{mod} was significantly higher in soil leachates than in fresh leaves and litter (Tukey's HSD p < 0.0001 for fresh leaves and litter), but these plant materials were not significantly different (Tukey's HSD p=0.22).

Aliphatics (% relative abundance) were also similar between species, and were high in fresh leaf leachates, highest in litter leachates, and low in soil leachates (Figure 4b; $F_{5, 32}$= 3.00, p = 0.03; Material: p = 0.004; Species: p = 0.46; Material*Species: p = 0.46). Aliphatics were significantly higher in fresh leaf (Tukey's HSD p = 0.06) and litter (Tukey's HSD p = 0.004) than in soil leachates, and plant materials were not significantly different (Tukey's HSD p=0.56). Interestingly, aliphatics were more abundant in Arundo plant material leachates than in than willow across watershed types, but in soil leachates aliphatics were more abundant beneath willow; however this was not significant at p = 0.10. Polyphenolics (% relative abundance) were lowest in fresh leaf leachates, higher in litter, and highest in soil leachates but also did not differ between species (Figure 4b; $F_{5, 32}$= 16.19, p < 0.0001; Material: p < 0.0001; Species: p = 0.78; Material*Species: p = 0.99). Polyphenolic %relative abundance systematically increased between materials with phase of decomposition, from fresh leaves to litter to soil (Tukey's HSD p < 0.0001 between both plant materials and soil, p = 0.02 between fresh leaves and litter). Within each material, Arundo leachates had higher polyphenolic %relative abundance than willow leachates, but this was not significant at p = 0.10.

We related the DOM chemistry to %DOC loss by doing a PCA that incorporated FT-ICR MS derived compounds, initial DON, and initial DOC:DON (Figure 5). %DOC loss generally relates to high DON, low DOC:DON, and high aliphatic compounds with low aromaticity (Figure 5a). Principal components 1 and 2 account for 69% of the variation in data. The separation along PC1 appears to divide complex, aromatic compounds from simple aliphatics; soils' behavior appears dominated by aromatics while plant material groups with aliphatics (Figure 5). The separation along PC2 appears to divide high O/C from low O/C, where willow material (fresh leaves, litter and soil) has higher O/C while Arundo material has lower O/C compounds (Figure 4). %DOC loss corresponds with aliphatic, sugar-like and other high H/C formulae, and DON correlates with samples that have high peptide-like, CHON, and N/C (Figure 5a). Arundo leachates have more DON while willow leachates are more enriched in CHO, with the most pronounced differences in litter and fresh leaves (Figure 5b). Soils beneath Arundo in developed agricultural watersheds appears to have more N-containing formulae than the other soils (Figure 5b).

E. Discussion

We evaluated how a shift in dominant riparian vegetation from willow forest to Arundo stands may alter DOM dynamics in throughfall and/or in adjacent waterways by comparing materials from the two species in a laboratory leachate incubation. DOM from Arundo is 10-20% more biolabile than willow, with higher DON, low DOC:DON, high aliphatics and peptide-like compounds, and low oxidation state and aromaticity (Figure 2a & 2b; Figure 3a; Figure 4; Figure 5). However, Arundo leaf and litter leachates have lower DOC concentrations than willow (Figure 1), and Arundo drops less litter than willow and other native species (Dowdy et al. Manuscript in preparation). Together this suggests that a shift from woody species towards large-statured grass Arundo would decrease plant-derived DOC inputs to adjacent waterways, while potentially increasing DON inputs.

High DOM losses in the different leachates may be the result of this material alleviating C limitation to decomposers; for example, without competing sinks for DOM such as chemical sorption in soils, microbes can degrade all species at any stage of decomposition (fresh leaves, litter, soil; Cleveland et al. 2004). Low DOC:DON and high peptide-like compounds resulted in greater %C loss in plant leachates. However, the pattern in soil leachates was different—high DOC:DON correlated with greater %C loss, suggesting that readily available C was limiting. In plant leachates (live or litter), high protein content means high degradability (Webster & Benfield 1986; Kominoski et al. 2009). But in soil, where plant-derived DOM has been further processed (Wymore et al. 2015), the most degradable components are more likely acids or aliphatics (Marschner & Kalbitz 2003; Kellerman et al. 2018). Variation in this relationship likely results from the chemical form of the material available. For example, peptide-like compounds are high in N and biolabile, aliphatic compounds are C-rich but biolabile, while complex aromatic compounds require microbes to allocate N to enzyme production to make them bioavailable; thus the range of N available or required varies with the form of C compounds present.

In both Arundo and willow, high aliphatics and peptide-like compounds in plant material, presumably result from simple, sugar-like and N-rich compounds being preferentially degraded and accounting for high initial C losses (Figure 5). Aliphatic compounds are considered to be inherently biolabile due to their high ratio of hydrogen to carbon (H/C); the bioavailability of DOM in aquatic systems has been linked to high aliphatics via preferential degradation of these sugar-like compounds (Sun et al. 1997; Spencer et al. 2015; O'Donnell et al. 2016; Textor et al. 2018; Textor et al. 2019). Similarly, the relationship between leaf litter peptides and DOC loss is consistent with other findings that amino acids are easily metabolized (Balcarczyk et al. 2009; Fellman et al. 2009). Through the decomposition continuum, it is logical that simple compounds that comprise a greater percent relative abundance in fresh leaves and litter are degraded initially, leaving behind more complex molecules in soils (greater percent relative abundance polyphenols with a higher oxidation state (LaRowe & Van Cappellen 2011; Johnston et al. 2019). This is consistent with the systematic increase of polyphenols and AI_{mod} in fresh leaves, litter and soil (Figure 4b), a pattern also found by Johnson et al. (2019).

Arundo material assimilated into soils has been hypothesized to be relatively stable, due to high silica content and microbial transformation of bioavailable compounds (Dowdy et al. Manuscript in preparation). Beneath Arundo, soil DOC and DON can accumulate with relatively low soil microbial biomass and high silicate content, which can complex and stabilize OC (Dowdy et al. Manuscript in preparation; Cotrufo et al. 2013; Renforth et al. 2011; Nawaz et al. 2019). Here we show that Arundo leaves and litter DOM, as well as DOM in soils beneath Arundo, can break down to the same level as willow when suspended in solution, consistent with other findings that plant-based material often decomposes more rapidly in solution (e.g. Yue et al. 2018). This material may be available as result of OM accessibility, the absence of water stress, microbial C limitations in streams, riverine microbial community composition, and/or heightened enzyme activities in the aqueous medium (Graça et al. 2015; Tolkkinen et al. 2020).

Allocating nutrients to enzyme production to break down Arundo DOM may also explain why Arundo DOC:DON did not change with phase of decomposition (fresh leaves, litter, soil) while willow DOC:DON decreased with phase of decomposition. Preliminary analyses of total C and N mirrored this pattern of similar C:N in Arundo leaves and soils beneath them, but greater C:N in willow leaves than in soils beneath them (data not shown). It is possible that more N consumed per unit C across this continuum in Arundo material may be the result of microbes allocating N to enzyme production (Schimel & Weintraub 2003), while compounds in willow are more easily turned over. Increased N uptake during Arundo DOM processing could counterbalance enhanced Arundo N inputs. Without such a mechanism of N removal, higher N inputs from Arundo plant material could exacerbate already high N levels in agricultural watersheds (Benoit et al. 2014) and increase the turnover of other OM inputs. We found lower soil DOC and DON in soils along large agricultural rivers and an accumulation of soil DOC and DON in soils along less developed small order creeks (regardless of plant type). This suggests that DOC turns over more rapidly in some watershed types compared to others. In our case, the larger, more developed watershed contained substantially more conventional agricultural acreage so nutrient inputs to the riparian zone were likely higher.

Soils were more clearly affected by watershed type than were leaves or litter. These watersheds differ in size and consequently in the degree of intensive agriculture. Large watersheds with higher flow tend to export more DOC than small watersheds (Zarnetske et al. 2018). Agriculture is also associated with decreased storage of terrestrial OC (Ogle et al. 2005; McLauchlin 2006; Stanley et al. 2012; Drake et al. 2018) and can affect watershed DOM composition, where longstanding agricultural watersheds have more aromatic DOC (Drake et al. 2018; Vidon et al. 2008). Consistent with Vidon and others (2008), we found that soils along large agricultural rivers appear to correlate with polyphenolics, condensed aromatics, and N/C ratio of compounds (particularly beneath Arundo), as well as AI_{mod} (particularly beneath willow), while soils in less developed watersheds appear to correlate with higher NOSC and mass (Figure 5). However, these differences in soil DOC composition were not reflected in biolability. When considering watershed-scale changes in biogeochemistry from a shift toward large-statured grasses, soil DOC export may have some influence on shifts in C and N cycling, but the focal point really is on changes in leaf litter quality via decreased (yet more biolabile) DOC and increased DON.

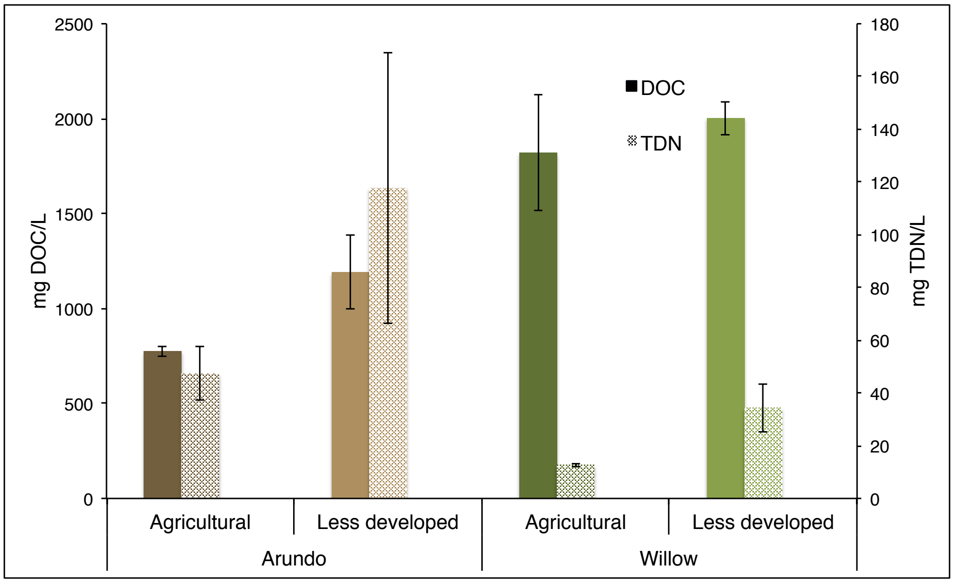
While many studies of introduced plant species focus on the effects on decomposition and soil in terrestrial environments, few consider this interface with the aqueous environment and compositional controls on DOM cycling; thus it is difficult to consider how the mechanisms we observed might play out in riparian systems. At the watershed scale, quantitative differences in leaf litter between plant species due to differences in life history strategy, rather than qualitative differences in leaf chemistry, are likely more important in altering aquatic DOC dynamics (Wiegner & Tubal 2010). Lower leaf leachate DOC and leaf litter production in Arundo than in willow could decrease available DOC in waterways, potentially lowering stream respiration and decreasing substrate supply throughout aquatic foodwebs. Similarly to Arundo, a greater portion of bamboo leaves is insoluble than those of woody species (O'Connor et al. 2000). However, greater biomass standing dead foliage in Arundo may collectively increase leached DOM contributions to soils as throughfall. While we evaluated how aquatic microorganisms break down these Arundo and willow materials, DOC loading to waterways will depend on a multitude of other variables including vertical and lateral transport to streams, leaching of in-stream plant detritus, photodegradation, and hydrology of waterways (Stanley et al. 2012). This processing will likely be complicated by waterway size where Arundo rhizomes (as well as terrestrial DOC) more readily transported, agriculture where different methods influence DOC and nutrient runoff, as well as modified flowpaths (Stanley et al. 2012).

In watersheds, DOC cycling is influenced by variables that we do not address in this mechanistic incubation, including diversity of and quantity leaf litter inputs as well as foodweb structure and dynamics. Arundo may reduce plant species biodiversity (Czech & Krausman 1997) and thereby alter DOC inputs. Different litters decompose at different rates, providing a range of C availability with more biolabile litter DOM early in the season and more chemically complex litter DOM providing resources late in the season after leaf fall (Ferreira et al. 2016; Siders et al. 2018; Marks 2019). Our study did not include particulate OC mass loss and food web dynamics, but previous work on bamboo suggests that litter is not more rapidly decomposed in the presence of macroinvertebrates (<500 um) while woody plant leaf mass losses are significantly increased by these decomposers (O'Connor et al. 2000). Consequently, Arundo's effect on shifting OC dynamics may be amplified in natural systems beyond the microbial cycling of soluble DOC we show here.

F. Conclusions

Understanding how a shift in plant growth form could influence DOM dynamics across watersheds is useful in determining the far-reaching effects of vegetation type conversion, particularly in the context of introduced species and anthropogenic change. We compared DOM dynamics of fresh leaf and litter leachates between introduced opportunistic large-statured grass *Arundo donax* and prominent native woody species *Salix lasiolepis* (willow), as well as leachates of the soils beneath them, in a laboratory decomposition experiment with a standardized aquatic microbial community. Willow plant material leached a significantly higher DOC while Arundo plant material leached significantly higher DON. Low DOC:DON in Arundo plant material, along with relatively high aliphatics and peptides, and low oxidation state and aromaticity, correlated with increased biolability. Yet Arundo DOC:DON did not change with the phase of decomposition (fresh leaves, litter, soil) while willow

DOC:DON decreased with phase of decomposition, suggesting that willow is more easily turned over overall while more N is needed to break down Arundo C. Together, these analyses demonstrate that Arundo and willow differ more in DOC and DON concentrations and chemical composition than in relative biolability; however, shifting the quantity and chemistry of DOM inputs may have a multitude of interacting downstream effects that alter DOM turnover at the watershed scale. Ultimately replacement of willow forest with Arundo stands may decrease DOC inputs and increase DON inputs from fallen leaves into waterways, potentially reducing watershed respiration of terrestrial OC yet also reducing OC available as the base of aquatic foodwebs.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Agricultural
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Arundo
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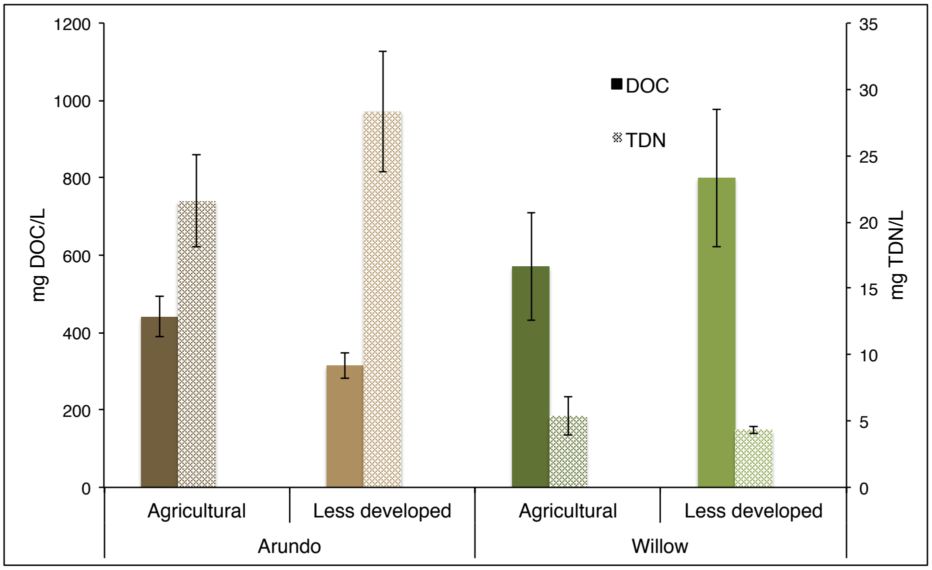
a)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Willow

b)

c)

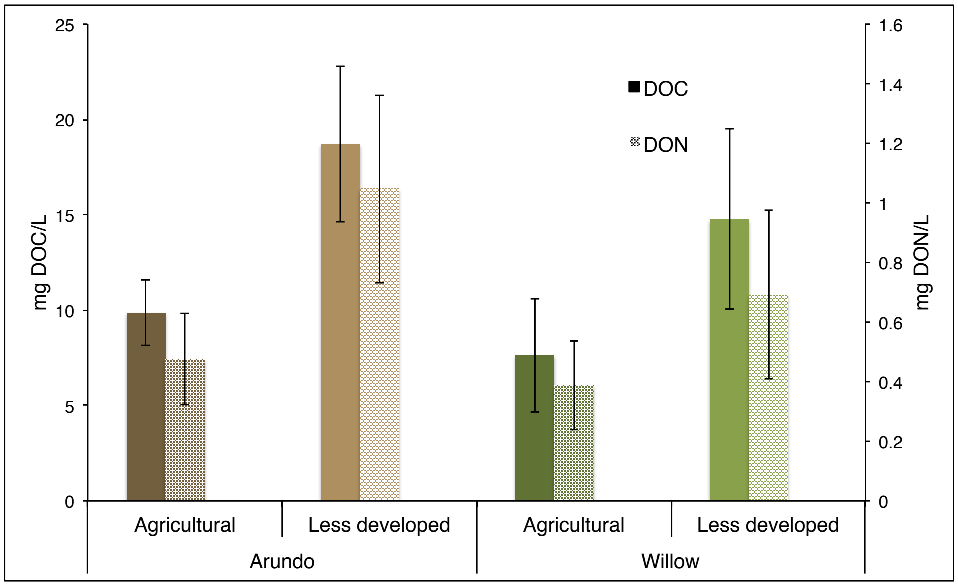
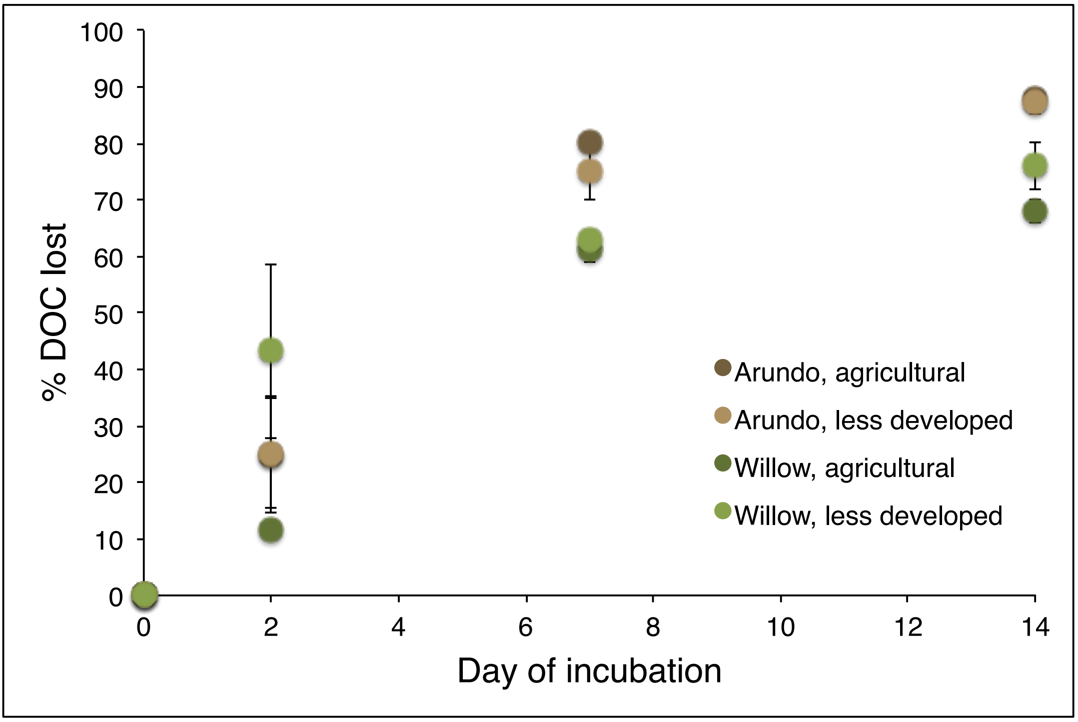


Figure 1: Initial leachate DOC and DON concentrations. DOC and DON at the start of the incubation in (a) fresh leaves (b) litter and (c) soil leachates of Arundo (brown) and willow (green) between developed agricultural watersheds and less developed watersheds. Error bars are +/- standard errors of the mean (n=3, except in Arundo fresh leaves along large agricultural rivers n=2). The interaction of species*watershed type was not significant at p=0.10; however species were significantly different in fresh leaves (a) and litter (b) at p = 0.09 and p = 0.03, respectively, while watershed types were significantly different in soils at p = 0.06.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10
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% DOC lost
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10
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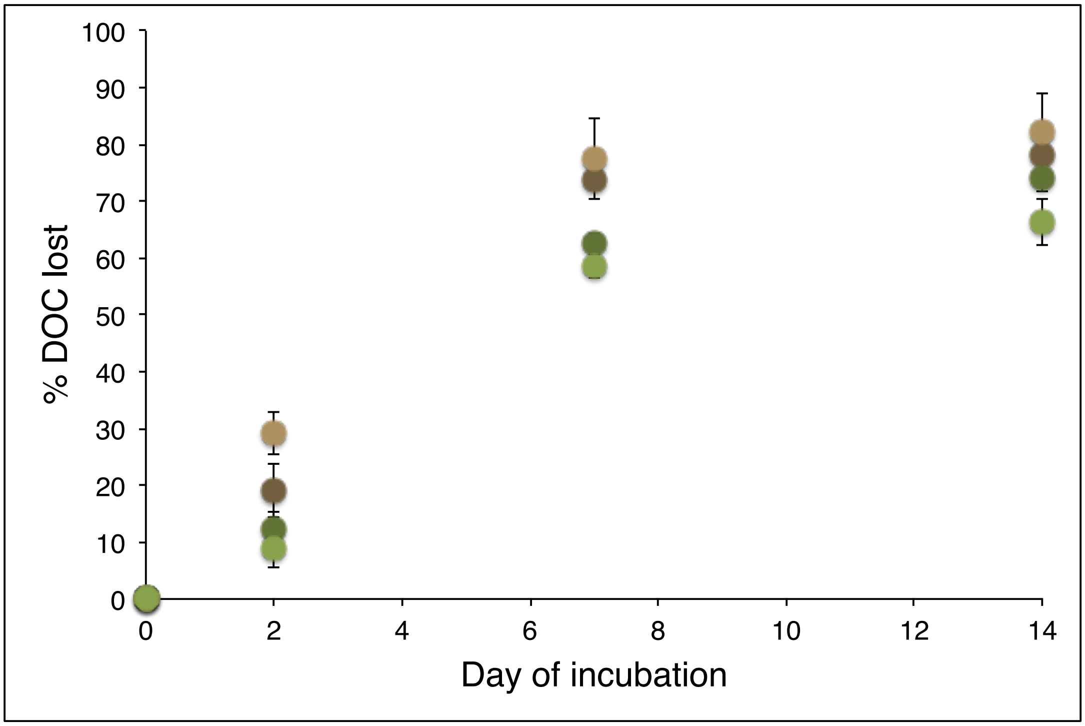
Day of incubation
● Arundo, agricultural
● Arundo, less developed
● Willow, agricultural
● Willow, less developed

a)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% DOC lost
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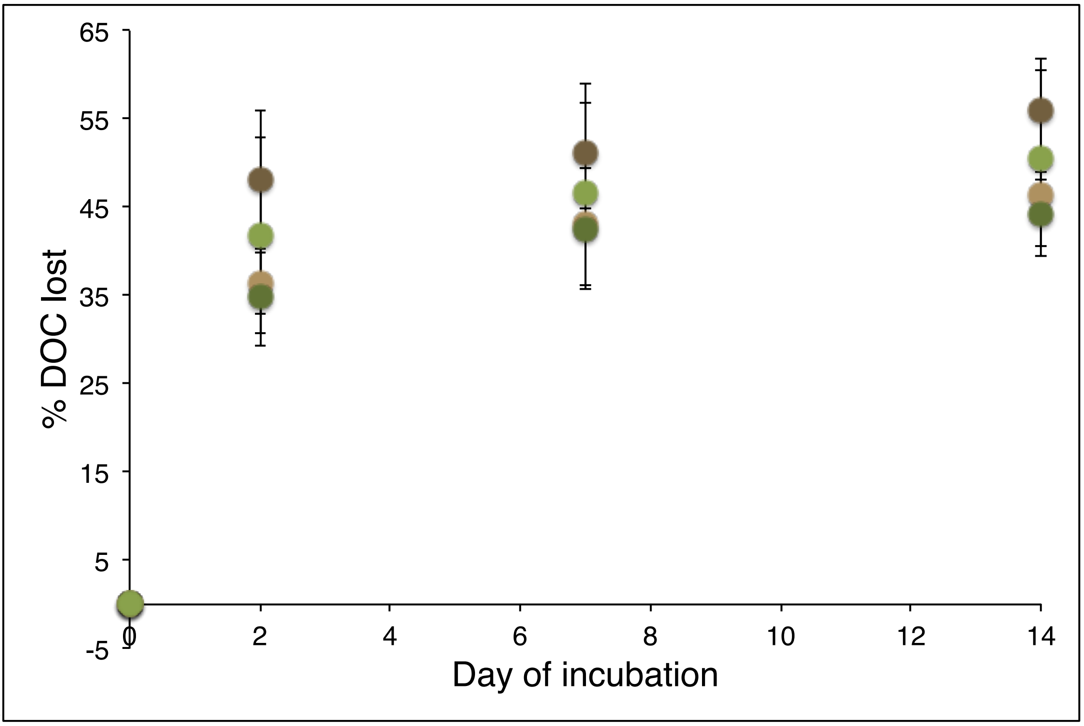
Day of incubation

b)



c)

Figure 2: DOC biolability. % DOC lost over 14-day incubation in (a) fresh leaves, (b) litter and (c) soil leachates in Arundo (brown) and willow (green) between developed agricultural watersheds (darker shades) and less developed watersheds (lighter shades). Error bars are +/- standard errors of the mean (n=3, except in Arundo fresh leaves along large agricultural rivers n=2). The interaction of species*watershed type on %DOC losses was not significant at p=0.10; however species were significantly different in fresh leaves (a) and litter (b) at p = 0.10 and p = 0.01, respectively, while watershed types were significantly different in soils at p = 0.06. Soils had significant interactions between species*watershed type in ANOVA but not in Tukey's HSD. Soils lost significantly less %DOC than fresh leaves or litter (p < 0.0001).

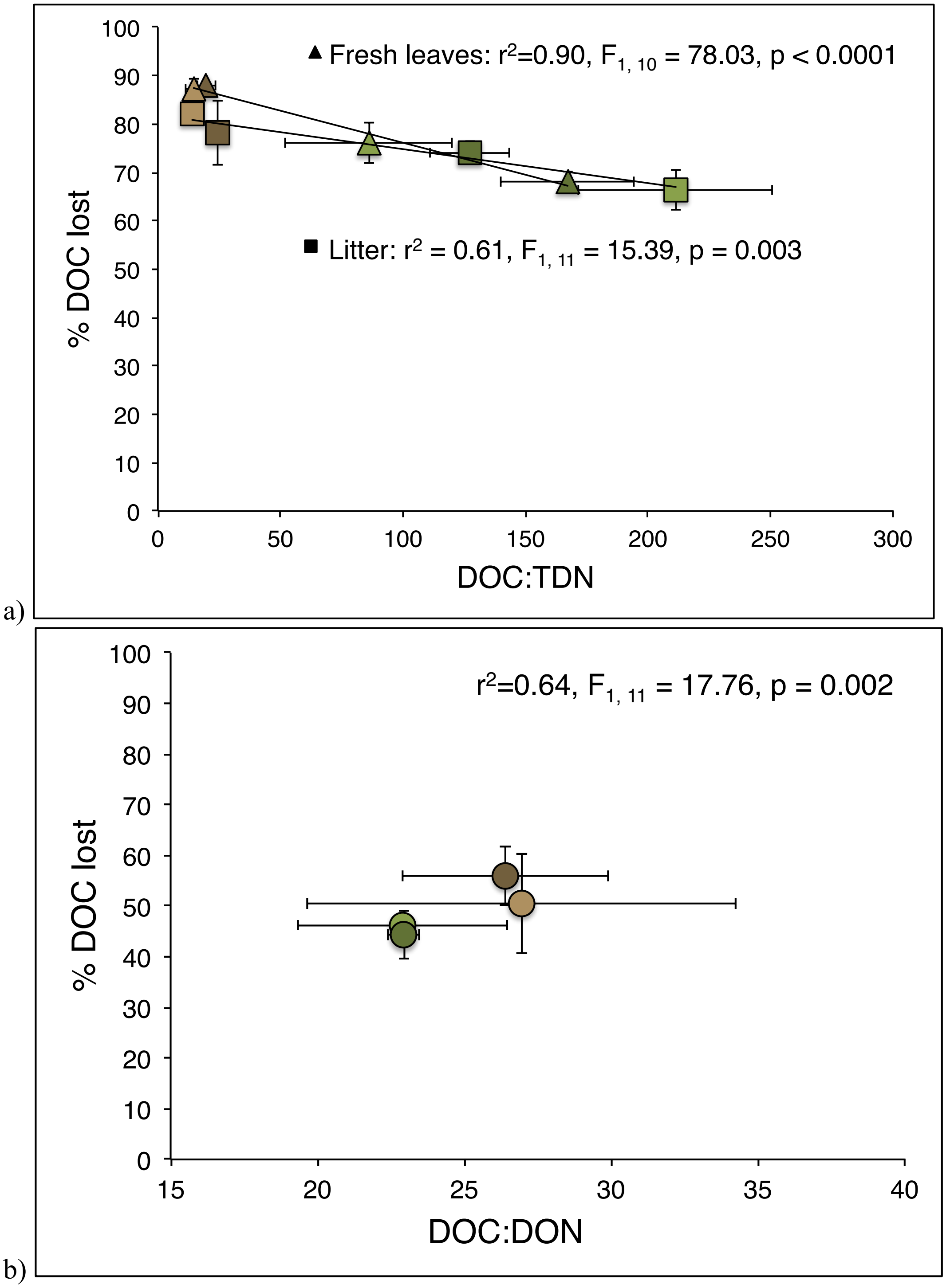


Figure 3: Leachate DOC:DON as a predictor of % DOC loss. DOC:DON vs. %DOC loss in (a) fresh leaves (triangles) and litter (squares) and (c) soil of Arundo (brown) and willow (green) in agricultural (dark dots) and minimally developed creek (light dots) watersheds. In leaves and litter, N is reported as TDN (due to minimal IN contributions in plant material) while in soil N is reported as DON. Error bars are +/- standard errors of the mean (n=3, except in Arundo fresh leaves along large agricultural rivers n=2).

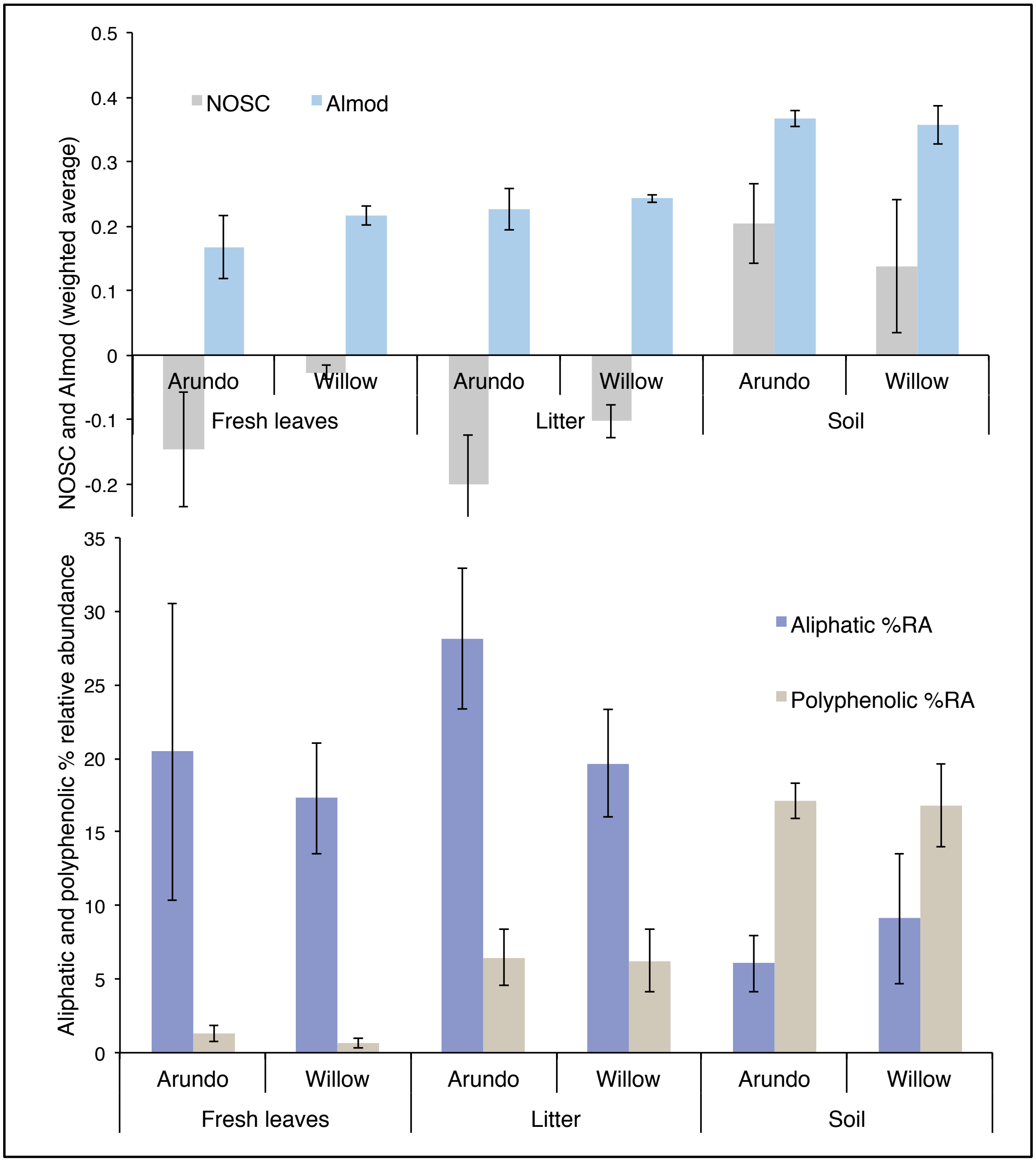


Figure 4: Bulk characteristics of DOM. a) nominal oxidation state of carbon (NOSC) and aromaticity index (AI_{mod}), and b) aliphatic and polyphenolic % relative abundance, between Arundo and willow fresh leaves, litter, and soil. Watershed land use is combined within species due to similarities. Error bars are +/- standard errors of the mean (n=6, except in Arundo fresh leaves n=5). The interaction of material*species was not significant at p=0.10; however materials were significantly different in plant materials (fresh leaves and litter) and soils in all variables: NOSC (Tukey's HSD $p = 0.002$ and $p = 0.0001$), AI_{mod} (Tukey's HSD $p < 0.0001$), aliphatics (Tukey's HSD $p < 0.06$ and $p = 0.004$), and in polyphenolics all materials were significantly different (Tukey's HSD $p < 0.0001$ between plant materials and soil, $p = 0.02$ between fresh leaves and litter).

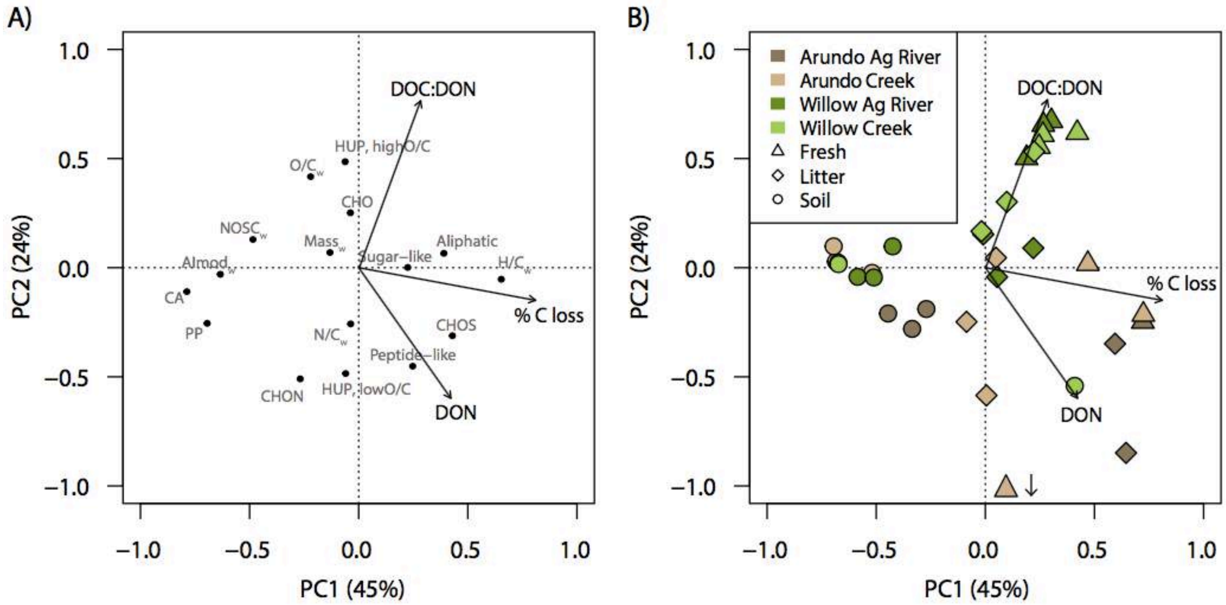


Figure 5: DOM composition related to biolability in principle component analysis. PCA plot with a) loadings and b) scores relating %C loss over 14-day incubation, DON, DOC:DON and FT-ICR-MS derived carbon composition variables in fresh leaves (triangles), litter (diamonds), and soil (circles) of Arundo in ag rivers (dark brown), Arundo in creeks (light brown), willow in ag rivers (dark green), and willow in creeks (light green). FT-ICR-MS variables include O/C of compounds (weighted average), highly unsaturated & phenolic with high O/C (HUP, high O/C; % relative abundance), CHO compounds (% relative abundance), nominal oxidation state of carbon (NOSC; weighted average), mass (weighted average), sugar-like compounds, aliphatic, H/C of compounds (weighted average), modified aromaticity index (AI_{mod}; weighted average), condensed aromatics (CA; % relative abundance), polyphenols (PP; % relative abundance), N/C of compounds (weighted average), peptide-like compounds, CHOS compounds (% relative abundance), CHON compounds (% relative abundance), and highly unsaturated & phenolic with low O/C (HUP with low O/C; % relative abundance).

Conclusion

The findings presented in this dissertation showed that replacing native riparian forests with the introduced large statured grass, *Arundo donax*, changes the way C and N move into, and are processed within, soil and stream ecosystems. High-NO_3^- conditions characteristic of runoff from intensive agriculture enabled Arundo to outcompete *Salix lasiolepis* (willow), while low-NO_3^- conditions typical of riparian zones surrounded by less intensive upland agriculture did not enable Arundo to readily inhibit willow growth (Chapter 1). When established, a native woody species such as willow drops leaf foliage seasonally, contributing litter with mid-range C:N ratios (~35). When these leaves are leached by rain or streamwater, they release relatively bioavailable DOC and DON; the DOC decomposes from fresh leaves to litter to soil without requiring much DON to break down complex molecules. The soils beneath these woody species support a microbial community with an average DOC to microbial biomass C (MBC) ratio of 1.8, implying relatively high bioavailability of DOC and perhaps a slow production rate.

In contrast, when Arundo displaces woody species, it can take up more NO_3^- from runoff and transform it into organic N in leaves, resulting in lower leaf C:N than woody species. Arundo drops less leaf litter than woody species, which has a higher C:N ratio than woody species perhaps due to resorption or standing dead litter on the culm leaching N. When they are leached, Arundo leaves and litter release more DON and less—but more labile—DOC. Despite reduced DOC inputs, soils beneath Arundo accumulate DOC, which supports a proportionally small microbial community with a relatively high DOC/MBC ratio of 3.6, implying lower physical or biological availability of DOC. This soil DOC accumulation and relatively low microbial biomass, along with an accumulation of soil DON and silicate (SiO_3), lead us to postulate that Arundo-derived DOC has been stabilized by microbial transformations as well as in silicate complexes. Overall, Arundo may transform more inorganic N into foliar N, and reduce watershed DOC cycling by reducing and stabilizing DOC inputs, which would potentially reduce respiration but also DOC available as the base of aquatic foodwebs.

Chapter 1 revealed that Arundo is competitive with established willows within one growing season, but it does not readily outcompete willow in low-N conditions in this time frame. In high-N conditions, Arundo reduced willow biomass by assimilating more N and photosynthesizing more efficiently with that N. Readily available NO_3^- shifted Arundo's C investment from belowground to aboveground tissue, while willow was less efficient at assimilating N and invested more C in belowground biomass. Both species photosynthesized at similar rates per unit area, which increased with N availability, but Arundo invested more in leaf quantity, enabling it to photosynthesize more overall (Nackley et al. 2016; Chapter 1). Across N conditions, Arundo was an effective competitor; even starting at time zero as a rhizome fragment it was able to outgrow recently established willows. Arundo generally grows more in subsequent growing seasons than in its first growing season (Thornby et al. 2007); thus its early success demonstrated here confirms observations in agricultural watersheds that Arundo outcompetes native species (Decruyenaere and Holt 2001; Ambrose & Rundel 2007; Coffman 2007).

These results are consistent with findings across ecosystems worldwide that opportunistic introduced species are favored by high-N conditions, as they have traits that enable rapid growth in nutrient-rich conditions (Rejmanek & Richardson 1996; Fenn et al. 2003; Corbin & D'Antonio 2004; Van Kleunen et al. 2010). The effects of a range of N levels are less well studied and more nuanced across systems and species, particularly regarding plant species competition (James 2008; Luo et al. 2014; Zhang et al. 2017). While Arundo grown alone responds positively to any N amendment (Lambert et al. 2014), I show that it takes a relatively high N amendment for Arundo to outcompete willow (Chapter 1). The N levels in riparian zones thus regulate the success of riparian opportunists, such as Arundo; these N levels are typically directly correlated with upland land-use practices (particularly agriculture). While high-N conditions associated with intensive agriculture favor Arundo's spread, Arundo may in turn ameliorate N loading to waterways by assimilating and transforming more mobile NO_3^- into ON as leaf litter (Chapter 1-3).

The shift from native woody species leaf litter to Arundo leaf litter will likely reduce overall litter inputs to riparian zones, as well as decrease bioavailable dissolved OC and increase ON within that litter (Chapters 2-3). Chapter 2 revealed that soils beneath Arundo accumulated DOC and DON compared to native woody riparian species. The soil DOC and DON pool beneath Arundo appears to be more stable, as indicated by lower microbial biomass and respiration as well as higher silicate content that can complex OC (Parr et al. 2010; Song et al. 2015; Chapter 2-3). Furthermore, along the decomposition continuum of fresh leaves-litter-soil, more N is needed to break down Arundo DOC, perhaps to produce enzymes (Schimel & Weintraub 2003), as evidenced by a consistent DOC:DON ratio in Arundo along this continuum and a decreasing DOC:DON ratio in willow (Chapter 3). Greater N and peptide-like compounds in Arundo leaf and litter leachates, along with high aliphatic compounds, appear to enable more rapid decomposition of Arundo DOC—although with overall lower DOC concentrations than that of willow foliage (Chapter 3). This biolabile DOC may be readily transformed and stabilized as microbial products, which combined with the remaining less bioavailable fraction stabilized in silicate compexes results in more persistent DOC.

Decomposition dynamics can vary according to leaf traits tied to life history strategy, where fast-growing plants (such as introduced, opportunistic species) produce leaf tissue that prioritizes photosynthesis over defense and thus decomposes more quickly (Rawlik et al. 2021; Ehrenfeld 2003); however, this may be an oversimplification for introduced large-statured grasses such as Arundo (Windham et al. 2004). Here I show that Arundo foliage contains a bioavailable fraction that indeed turns over more readily than slower-growing willow, but also contains a less available fraction that accumulates in soils; this may be because of silicate-based structural and defense compounds that require minimal C investment (Chapter 2-3). Additionally, greater N assimilation that enabled photosynthesis also enabled decomposition (Chapter 1), but N accumulated when biolabile C had turned over (Chapter 2). This accumulation of N in soils beneath Arundo may have a feedback effect promoting its spread while hindering native species, ultimately driving state change towards an Arundo climax community (Rieger & Kreager 1989; Milchunas & Lauenroth 1995; Schimel et al. 1996; Coffman 2007; Chapter 1).

Alterations to C and N cycles are particularly important in riparian ecosystems, nutrient cycling “hot spots” that connects terrestrial and aquatic systems and act as a biogeochemical filter between upland landscapes and waterways. High-N conditions that enable Arundo to outcompete native riparian species may drive state change towards Arundo dominance, shifting underlying and longstanding elemental cycles by providing leaf litter that is less DOC- but more DON-rich. The biolabile fraction of Arundo DOC may be readily transformed by microbes which, along with a DOC fraction complexed with silicate, may contribute to a more stable soil DOC pool. Consequently, a plant community shift towards Arundo could reduce soil and stream respiration yet also reduce OC available as the base of riparian foodwebs.

Management implications

Arundo can outcompete native willow in nitrate-rich conditions, yet it may mitigate nitrate-rich runoff in agricultural watersheds by transforming inorganic N into less available organic N in foliage. Nitrate-rich runoff is usually high in intensive industrial agriculture and can be minimized with practices such as precision agriculture, which closely monitors timing of fertilizer additions depending upon crop needs and environmental conditions, or organic agriculture, which uses fertilizer containing less available organic N instead of more readily available inorganic N that is subject to leaching (Freidenreich et al. 2019; Mondelaers & Huylenbroeck 2009). Minimizing nitrate-rich runoff may help to reduce Arundo's spread and improve native plant restoration outcomes. Incorporating what is known about surrounding land use may be useful in considering restoration priorities as well as in indicating larger Arundo stands with more pronounced downstream effects on DOC cycling and foodweb dynamics.

References

Abraham, JK, Corbin, JK, & D'Antonio, CM. (2009). California native and exotic perennial grasses differ in their response to soil nitrogen, exotic annual grass density, and order of emergence. *Plant Ecolog*y, 201:445-456.

Albert, LP, Wu, J, Prohaskaet, N, et al. (2018). Age-dependent leaf physiology and consequences for crown-scale carbon uptake during the dry season in an Amazon evergreen forest. *New Phytologist*, 219:870-884.

Allison, SD, Vitousek, PM. (2004). Rapid nutrient cycling in leaf litter from invasive plants in Hawaii. *Oecologia*, 141:612-619.

Ambrose, RF, & Rundel, PW. (2007). Influence of Nutrient Loading on the Invasion of an Alien Plant Species, Giant Reed (Arundo donax), in Southern California Riparian Ecosystems. UC Water Resources Center Technical Completion Report Project No. W-960.

Anderson, T-H, & Domsch, KH. (1986). Carbon assimilation and microbial activity in soil. *J. Plant Nut. and Soil Sci*., 149:457-468.

Arianoutsou, M, Delipetrou, P, Vila, M, et al. (2013). Comparative Patterns of Plant Invasions in the Mediterranean Biome. *PLoS ONE*, 11:e79174.

August-Schmidt, EM, Haro, G, Bontrager, A, & D'Antonio, CM. (2015). Preferential Associations of Invasive Lantana camara (Verbenaceae) in a Seasonally Dry Hawaiian Woodland. *Pacific Science,* 69:385-397.

Austin, AT, & Ballaré, CL. (2010). Dual role of lignin in plant litter decomposition in terrestrial ecosystems. *Proc. Natl. Acad. Sci. USA.,* 107:4618–4622.

Bedford, AP. (2005). Decomposition of phragmites australis litter in seasonally flooded and exposed areas of a managed reedbed. *WETLANDS*, 25:713–720.

Bell, GP. (1998). Ecology and management of Arundo donax, and approaches to riparian habitat restoration in southern California. In Brock, J. H., Wade, M., Pysek, P., and Green, D. (Eds.): *Plant Invasions: Studies from North America and Europe*. Blackhuys Publishers, Leiden, The Netherlands, 103-113.

Benfield, EF (1997). Comparison of litterfall input to streams. *Journal of the North American Benthological Society*, 16:104–108.

Benoit, M, Garnier, J, Anglade, J, & Billen, G. (2014). Nitrate leaching from organic and conventional arable crop farms in the Seine Basin (France). *Nutr. Cycl. Agroecosyst.*, 100:285–299.

Bhatia, MP, Das, SB, Longnecker, K, Charette, MA, & Kujawinski, EB. Molecular characterization of dissolved organic matter associated with the Greenland ice sheet. *Geochimica et Cosmochimica Acta*, 74(13):3768-3784.

Bowman, WD, Steltzer, H, Rosentiel, TR, Cleveland, CC, & Meier, CL. (2003). Litter effects of two co-occurring alpine species on plant growth, microbial activity and immobiilization of nitro- gen. *Oikos*, 104:336–344.

Brandt, LA. (2009). The role of photodegradation in plant litter decomposition in grassland ecosystems. A dissertation submitted to the faculty of the graduate school of the university of Minnesota.

Bren, LJ. (1993). Riparian zone, stream, and floodplain issues: a review. *Journal of Hydrology*, 150(2–4):277–299.

Brooks, ML, D'Antonio, CM, Richardson, DM, Grace, JB, Keeley, JE, DiTomaso, JM, Hobbs, RJ, Pellant, M, & Pyke, D. (2004). Effects of invasive plants on fire regimes. *Bioscience*, 54:677–688.

Burke, MJW, & Grime, JP. (1996). An experimental study of plant community 530 invasibility. *Ecology*, 77:776-790.

Canadell, JG, Le Quere, C, Raupach, MR, Field, CB, Buitenhuis, ET, Ciais, P, et al. (2007). Contributions to accelerating atmospheric CO2 growth from economic activity, carbon intensity, and efficiency of natural sinks. *Proc. Natl Acad. Sci. USA*, 104:18866–18870.

Canavan, S, Meyerson, LA, Packer, JG, et al. (2019). Tall-statured grasses: a useful functional group for invasion science. *Biol Invasions*, 21:37–58.

Castro-Díez, P, Godoy, O, Alonso, A, Gallardo, A, & Saldana, A. (2014). What explains variation in the impacts of exotic plant invasions on the nitrogen cycle? A meta-analysis. *Ecology Letters*, 17:1–12.

Cayan, DR, Das, T, Pierce, DW, Barnett, TP, Tyree, M, & Gershunov, A. (2010). Future dryness in the southwest US and the hydrology of the early 21st century drought. *Proceedings of the National Academy of Sciences*, 107(50):21271-21276.

Chapin III, S. (1980). The Mineral Nutrition of Wild Plants: Annual Review of Ecology and Systematics. *Annual Review of Ecology and Systematics*, 11:233-260.

Chauvet, E. (1987). Changes in the chemical composition of alder, poplar and willow leaves during decomposition in a river. *Hydrobiologia*, 148:35-44.

Chou, CH. Allelopathic potential of bamboo vegetation in Taiwan. XIII International Botanical Congress, Sydney, Australia, 21-28 August, 1981. Abstracts.

Cleveland, CC, Neff, JC, Townsend, AR, & Hood, E. (2004). Composition, Dynamics, and

Fate of Leached Dissolved Organic Matter in Terrestrial Ecosystems: Results from a Decomposition Experiment. *Ecosystems*, 7:275–285.

Coffman, GC. (2007). Factors influencing invasion of giant reed (*Arundo donax*) in riparian ecosystems of Mediterranean-type climate regions. Dissertation, University of California, Los Angeles.

Coffman, GC, Ambrose, RF, & Rundel, PW. (2010). Wildfire promotes dominance of invasive giant reed (Arundo donax) in riparian ecosystems. *Biological Invasions,* 12:2723–2734.

Commander, CJC. (2013). The influence of dams on the abundance of *arundo donax* (giant reed) in riparian corridors. *Masters Thesis*, California State University, Sacramento.

Corbin, JD, & D'Antonio, CM. (2004). Effects of Exotic Species on Soil Nitrogen Cycling: Implications for Restoration. *Weed Technology*, 18, 464-1467.

Cornwell, WK, Cornelissen, CHC, Amatangelo, K, et al. (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, 11: 1065–1071.

Cotrufo, MF, Del Galdo, I, & Piermatteo, D. (2009). Litter decomposition: concepts, methods and future perspectives. In: *Soil Carbon Dynamics. An integrated methodology* (eds Krutz W, Bahn M, Heinemeyr A), pp. 76–90. Cambridge University Press, Cambridge.

Cotrufo, MF,Wallenstein, M, Boot, MC, Denef, K, & Paul, EA. (2013). The Microbial E_ciency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: Do labile plant inputs form stable soil organic matter? *Glob. Change Biol.*, 19:988-995.

Cotrufo, MF, Soong, JL, Horton, AJ, et al. (2015). Formation of soil organic matter via biochemical and physical pathways of litter mass loss. *Nature Geoscience*, 8:776–779.

Crawley, MJ. (1986). The population biology of invaders. Philosophical Transactions of the Royal Society of London, *B. Biol. Sci.*, 314:711-731.

Currie, WS, & Aber, JD. (1997). Modeling leaching as a decomposition process in humid montane forests. *Ecology*, 78:1844–60.

Czech, B, & Krausman, PR. (1997). Factors influencing invasion of giant reed (arundo donax) in riparian ecosystems of mediterranean climates regions. *Science,* 277:1116-1117.

D'Antonio & Vitousek (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, 23:63-87.

Dahm, CN. (1981). Pathways and mechanisms for removal of dissolved organic carbon from leaf leachate in streams. *Can. J. Fish. Aquat. Sci.,* 38:68-76.

Day, TA, Zhang, ET, & Ruhland, CT. (2007). Exposure to solar UV-B radiation accelerates mass and lignin loss of Larrea tridentata litter in the Sonoran Desert. *Plant Ecol.*, 193:185–194.

DeAngelis KM, Allgaier M, Chavarria Y, Fortney JL, Hugenholtz P, Simmons B, et al. (2011) Characterization of Trapped Lignin-Degrading Microbes in Tropical Forest Soil. *PLoS ONE*, 6(4):e19306.

Decruyenaere, JG, & Holt, JS. (2005). Ramet demography of a clonal invader, *Arundo donax* (Poaceae), in Southern California. *Plant Soil*, 277:41–52.

diCastri, F. (1991). An ecological overview of the five regions with a mediterranean climate. Pages 3-16 *in* R. H. Groves and F. diCastri, editors. *Biogeography of Mediterranean Invasions*. Cambridge University Press, Cambridge.

DiTomaso, JM. (1998). Biology and ecology of giant reed. Pages 1-5 *in* Proceedings of the Arundo and Saltceder: The Deadly Duo Workshop. June 17, 1998, Ontario, California.

Drake, JA, Mooney, HA, diCastri, F, Groves, R, Kruger, FJ, Rejmanek, M, & Williamson, M. (1989). Biological Invasions: a Global Perspective. John Wiley & Sons Ltd., Chichester.

Dudley, TL. (2000). *Arundo donax*. Pages 53-58 *in* C. C. Bossard, J. M. Randall, and M. C. Hoshovsky, editors. Invasive Plants of California's Wildlands. University of California Press, Berkeley.

Dudley, TL, & Collins, B. (1995). Biological Invasions in California Wetlands: The Impacts and Control of Non-indigenous Species (NIS) in Natural Areas. Pacific Institute for Studies in Development, Environment and Security, Oakland, CA, 62p.

Durand, LZ, & Goldstein, G. (2001). Photosynthesis, photoinhibition, and nitrogen use efficiency in native and invasive tree ferns in Hawaii. *Oecologia*, 126:345–354.

Eaton, J, Likens, G, & Bormann, F. (1973). Throughfall and Stemflow Chemistry in a Northern Hardwood Forest. *Journal of Ecology*, 61(2):495-508.

Ehrenfeld, JG, Kourtev, P, & Huang, WZ. (2001). Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological Applications*, 11:1287–1300.

Ehrenfeld, JG. (2003). Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6:503-523.

Elton, C. S. 1958. The Ecology of Invasions by Animals and Plants. Methuen, London.

Evans, RD, Rimer, R, Sperry, L, & Belnap, J. (2001). Exotic Plant Invasion Alters Nitrogen Dynamics in an Arid Grassland. *Ecological Applications*, 11:1301-1310.

Fauteux, F, Remus-Borel, W, Menzies, JG, & Belanger, RR. (2005). Silicon and plant disease resistance against pathogenic fungi. *Fems Microbiology Letters*, 249:1–6.

Fenn, ME, Baron, JS, Allen, EB, Rueth, HM, Nydick, KR, Geiser, L, Bowman, WD, Sickman, JO, Meixner, T, Johnson, DW, Neitlich, P. (2003). Ecological Effects of Nitrogen Deposition in the Western United States. *BioScience*, 53(4): 404–420.

Fonseca, AR, Santos, JA, Varandas, SGP, Monteiro, SM, Martinho,JL, Cortes, RMV, & Cabecinha, E. (2020). Current and Future Ecological Status Assessment: A New Holistic Approach for Watershed Management. *Water,* 12, 2839; doi:10.3390/w12102839

Frainer, A, Moretti, MS, Xu, W, & Gessner, MO. (2015). no evidence for leaf-trait dissimilarity effects on litter decomposition, fungal decomposers, and nutrient dynamics. *Ecology*, 96:550–561.

Freidenreich, A, Barraza, G, Jayachandran, K, & Khoddamzadeh, AA. (2019). Precision Agriculture Application for Sustainable Nitrogen Management of Justicia brandegeana Using Optical Sensor Technology. Agriculture 2019, 9, 98; doi:10.3390/agriculture9050098

Funk, JL, Glenwinkel, LA, & Sack, L. (2013). Differential Allocation to Photosynthetic and Non-Photosynthetic Nitrogen Fractions among Native and Invasive Species. *PLoS ONE*, 8, e64502.

Gadgil, M, & Prasad, SN. (1984). Ecological determinants of life history evolution of two Indian bamboo species. *Biotropica*, 16:161-172.

Gage, EA, & Cooper, DJ. (2005). Patterns of willow seed dispersal, seed entrapment, and seedling establishment in a heavily browsed montane riparian ecosystem. *Can. J. Bot.*, 83:678–687.

Gessner, MO, Chauvet, E, & Dobson, M. (1999). A Perspective on Leaf Litter Breakdown in Streams. *Oikos*, 85:377-384.

Giweta, M. (2020). Role of litter production and its decomposition, and factors affecting the processes in a tropical forest ecosystem: a review. *Journal of Ecology and Environment*, 44:11.

Graça, MAS, Ferreira, V, Canhoto, C, Encalada, AC, Guerrero-Bolaño, F, Wantzen, KM, & Boyero, L. (2015). A conceptual model of litter breakdown in low order streams. *Internat. Rev. Hydrobiol.*, 100:1-12.

Gregory, SV, Sawanson, FJ, McKee, WA, & Cummins, KW. (1991). An ecosystem perspective of riparian zones. *BioScience*, 41:540–551.

Hattenschwiler, S, Aeschlimann, B, Coûteaux, MM, Roy, J, & Bonal, D. (2008). High variation in foliage and leaf litter chemistry among 45 tree species of a neotropical rainforest community. *New Phytologist*, 179:165-175.

Hector, A, Beale, AJ, Minns, A, Otway, SJ, & Lawton, JH. (2000). Consequences of the Reduction of Plant Diversity for Litter Decomposition: Effects through Litter Quality and Microenvironment. *Oikos*, 90:357-371.

Henry, HAL, Brizgys, K, & Field, CB. (2008). Litter Decomposition in a California Annual Grassland: Interactions between Photodegradation and Litter Layer Thickness. *Ecosystems,* 11:545-554.

Hensgens, G, Laudon, H, Peichl, M, Gil, IA, Zhou, Q, & Berggren, M. (2020). The role of the understory in litter DOC and nutrient leaching in boreal forests. *Biogeochemistry,* 149:87–103.

Herrera, AM, & Dudley, TL. (2003). Reduction of riparian arthropod abundance and diversity as a consequence of giant reed (Arundo donax) invasion. *Biological Invasions*, 5:167–177.

Hickman, JC. (1993). The Jepson manual: higher plants of California. University of California Press, Berkeley, California.

Hobbs, RJ, Higgs, E, & Harris, JA. (2009). Novel ecosystems: implications for conservation and restoration. *Trends in Ecology and Evolution*, 24, doi:10.1016/j.tree.2009.05.012

Hobbie, SE. (1996). Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs*, 66:503-522.

Hodson, RE, Christian, RR, & Maccubbin, AE. (1984). Lignocellulose and lignin in the salt marsh grass Spartina alterniflora: initial concentrations and short-term, post-depositional changes in detrital matter. *Marine Biology*, 81:1-7.

Hood, WG, & Naiman, RJ. (2000). Vulnerability of riparian zones to invasion by exotic vascular plants. *Plant Ecology*, 148:105–114.

Hood-Nowotny, R, Umana, NH, Inselbacher, E, Oswald-Lachouani, P, & Wanek, W. (2010). Alternative Methods for Measuring Inorganic, Organic, and Total Dissolved Nitrogen in Soil. *Soil Science Society of America Journal*, 74:1018-1027.

Huenneke, LF, Hamburg, SP, Koide, R, Mooney, HA, & Vitousek, PM. (1990). Effects of Soil Resources on Plant Invasion and Community Structure in Californian Serpentine Grassland. *Ecology*, 71:478-491.

Hurlbert, SH, & Lombardi, CM. (2009). Final collapse of the Neyman-Pearson decision theoretic framework and rise of the neoFisherian. *Annales Zoologici Fennici*, 46:311-349.

Hurst, JL, Pugh, GJF, & Walton, DWH. (1985). The Effects of Freeze-Thaw Cycles and Leaching on the Loss of Soluble Carbohydrates from Leaf Material of Two Subantarctic Plants. *Polar. Biol.*, 4:27-31.

Hynes, HBN. (1975). The stream and its valley. *SIL Proceedings,1922-2010*, 19:1–15.

Incerti, G, Cartenì, F, Cesarano, G, Sarker, TC, Abd El-Gawad, AM, D'Ascoli, R, Bonanomi, G, & Giannino, F. (2018). Faster N Release, but Not C Loss, From Leaf Litter of Invasives Compared to Native Species in Mediterranean Ecosystems. *Frontiers in Plant Science*, 9:534.

Jackson, GC, & Rivera Núñez, J. (1964). Identification of Silica Present in the Giant-Reed (Arundo donax L.). *The Journal of Agriculture of the University of Puerto Rico*, 48(1):60–62.

James, JJ. (2008). Leaf nitrogen productivity as a mechanism driving the success of invasive annual grasses under low and high nitrogen supply. *Journal of Arid Environments,* 72:1775–1784.

Johnson, D. (2003). Response of terrestrial microorganisms to ultraviolet-B radiation in ecosystems. *Research in Microbiology*, 154:315–320.

Johnston, SE, Bogard, MJ, Rogers, JA, et al. (2019). Constraining dissolved organic matter sources and temporal variability in a model sub-Arctic lake. *Biogeochemistry*, 146:271–292.

Jones, TA, Monaco, TA, & James, JJ. (2010). Launching the Counterattack: Interdisciplinary Deployment of Native-Plant Functional Traits for Repair of Rangelands Dominated by Invasive Annual Grasses. *Rangelands*, 32(1):38–42.

Kaiser, K, & Guggenberger, G. (2000). The role of DOM sorption to mineral surfaces in the preservation of organic matter in soils. *Org. Geochem.*, 31:711–725.

Kaiser, K. & Kalbitz, K. (2012). Cycling downwards—dissolved organic matter in soils. *Soil Biol. Biochem.*, 52:29–32.

Kalbitz, K, Schmerwitz, J, Schwesig, D, & Matzner, E. (2003). Biodegradation of soil-derived dissolved organic matter as related to its properties. *Geoderma*, 113:273-291.

Kalbitz, K, Schwesiga, D, Rethemeyerb, J, & Matzner, E. (2005). Stabilization of dissolved organic matter by sorption to the mineral soil. *Soil Biology and Biochemistry*, 113:1319-1331.

Kaplan, LA, Wiegner, TN, Newbold, JD, Ostrom, PH, & Gandhi, H. (2007). Untangling the complex issue of dissolved organic carbon uptake: A stable isotope approach. *Freshwater Biol.*: doi:10.1111/j.1365-2427.2007.01941.x.

Karydis, M (2009). Eutrophication assessment of coastal waters based on indicators: a literature review. *Global NEST Journal*, 11:373-390.

Kellerman, AM, Guillemette, F, Podgorski, DC, Aiken, GR, Butler, KD, & Spencer, RGM. (2018). Unifying concepts linking dissolved organic matter composition to persistence in aquatic ecosystems. *Environ. Sci. Technol.*, 52:2538–2548.

Kennedy, TA, & Hobbie, SE. (2004). Saltcedar (Tamarix ramosissima) invasion alters organic
matter dynamics in a desert stream. *Freshwater Biology*, 49:65–76.

King, JY, Brandt, A, & Adair, EC. (2012). Shedding light on plant litter decomposition: advances, implications and new directions in understanding the role of photodegradation. *Biogeochemistry*, 111:57–81.

Knoepp, JD, & Clinton, BD. (2009). Riparian zones in southern Appalachian headwater catchments: carbon and nitrogen response to forest cutting. *Forest Ecology and Management*, 258:2282–2293.

Köchy, M, & Wilson, SD. (1997). Litter decomposition and nitrogen dynamics in aspen forest and mixed-grass prairie. *Ecology*, 78:732–739.

Kominoski, JS, Marczak, LB, & Richardson, JS. (2011). Riparian forest composition affects stream litter decomposition despite similar microbial and invertebrate communities. *Ecology*, 92:151-159.

Kondolf, GM, & Larson, GM. (1995). Case Studies And Reviews: Historical channel analysis and its application to riparian and aquatic habitat restoration. *Aquatic conservation: marine and freshwater ecosystems*, VOL. 5, 109-126.

Korsaeth, A. (2008). Relations between nitrogen leaching and food productivity in organic and conventional cropping systems in a long-term field study. *Agric. Ecosyst. Environ.*, 127:177–188.

Kuglerová, L, Garc, L, Pardo, E, Mottiar, Y, & Richardson, JS. (2017). Does leaf litter from invasive plants contribute the same support of a stream ecosystem function as native vegetation? *Ecosphere,* 8:e01779.

Lambert, AM, Dudley, TL, & Saltonstall, K. (2010). Ecology and impacts of the large-statured invasive grasses Arundo donax and Phragmites australis in North America. *Invasive Plant Sci. Manag.*, 3:489–494.

Lambert, AM, Dudley, TL, & Robbins, J. (2014). Nutrient enrichment and soil conditions drive productivity in the large-statured invasive grass Arundo donax. *Aquatic Botany*, 112:16–22.

Lan, Y, Cui, B, You, Z, et al. (2012). Litter Decomposition of Six Macrophytes in a Eutrophic Shallow Lake (Baiyangdian Lake, China). *Clean – Soil, Air, Water*, 40:1159–1166.

Larpkern, P, Moe, SR, & Totland, O. (2011). Bamboo dominance reduces tree regeneration in a disturbed tropical forest. *Oecologia*, 165:161–168.

Liao, CZ. (2007). The effects of invasive alien plants on ecosystem carbon and nitrogen cycles. A case study of *Spartina alterniflora* invasion in the Yangtze estuary and a meta-analysis. *PhD Thesis*. Shanghai, China: Fudan University.
Lin, T, Klinkhamer, PGL, Pons, TL, Mulder, PPJ, & Vrieling, K. (2019). Evolution of Increased Photosynthetic Capacity and Its Underlying Traits in Invasive Jacobaea vulgaris. *Frontiers in Plant Science*, 10:1016.

Lin, Y, & King, JY. (2014). Effects of UV Exposure and Litter Position on Decomposition in a California Grassland. *Ecosystems*, 17: 158–168.

Lindsay, EA, & French, K. (2005). Litterfall and Nitrogen Cycling Following Invasion by Chrysanthemoides monilifera ssp. rotundata in Coastal Australia. *Journal of Applied Ecology*, 42:556-566.

Liu, W, Fox, JED, & Xu, Z. (2000). Nutrient Fluxes in Bulk Precipitation, Throughfall and Stemflow in Montane Subtropical Moist Forest on Ailao Mountains in Yunnan, South-West China. *Journal of Tropical Ecology*, 18:527-548.

Luo, Y, Guo, W, Yuan, Y, Liu, J, Du, N, & Wang, R. (2014). Increased nitrogen deposition alleviated the competitive effects of the introduced invasive plant Robinia pseudoacacia on the native tree Quercus acutissima. *Plant and Soil,* 385:63–75.

Magdoff, F, & Van Es, H. (2010). Building Soil For Better Crops (3 ed.): Sustainable Agriculture Research and Education.

Marcarelli, AM, Baxter, CV, Mineau, MM, & Hall, RO. (2011). Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. *Ecology*, 92:1215–1225.

Marschnera, B, & Kalbitz, K. (2003). Controls of bioavailability and biodegradability of dissolved organic matter in soils. *Geoderma*, 113:211 –235.

Marks, JC. (2019). Revisiting the Fates of Dead Leaves That Fall into Streams. *Annu. Rev. Ecol. Evol. Syst.*, 50:547–68.

Marín-Spiotta, E, Gruley, KE, Crawford, J, et al. (2014). Paradigm shifts in soil organic matter research affect interpretations of aquatic carbon cycling: transcending disciplinary and ecosystem boundaries. *Biogeochemistry*, 117:279–297.

Massey, FP, Ennos, AR, & Hartley, SE. (2007). Grasses and the resource availability hypothesis: the importance of silica-based defences. *Journal of Ecology*, 95:414–424.

Massey, FP, & Hartley, SE. (2009). Physical defences wear you down: progressive and irreversible impacts of silica on insect herbivores. *Journal of Animal Ecology*, 78:281–291.

McComb, AJ, Qiu, S, Bell, RW, & Davis, JA. (2007). Catchment litter: a phosphorus source mobilized during seasonal rainfall. *Nutr. Cycl. Agroecosyst.*, 77:179–186.

McKnight, DM, Harnish, R, Wershaw, RL, Baron, JS, & Schiff, S. (1997). Chemical characteristics of particulate, colloidal, and dissolved organic material in Loch Vale Watershed, Rocky Mountain National Park. *Biogeochemistry*, 36:99–124.

McNaughton, SJ, & Tarrants, JL. (1983). Grass leaf silicification: Natural selection for an inducible defense against herbivores. *Proc. Natl. Acad. Sci., USA*, 80:790-791.

Melillo, J.M, Aber, JD, & Muratore, JF. (1982). Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology*, 63:621– 626.

Meyer, JL, Wallace, JB, & Eggert, SL. (1998). Leaf litter as a source of dissolved organic carbon in streams. *Ecosystems*, 1:240–249.

Meyerson, LA, Chambers, RM, & Vogt, KA. (1999). The effects of Phragmites removal on nutrient pools in a freshwater tidal marsh ecosystem. *Biol. Invasions*, 1:129–136.

Migliorini, GH, & Romero, GQ. (2020). Warming and leaf litter functional diversity, not litter quality, drive decomposition in a freshwater ecosystem. *Sci. Rep.* 10, 20333.

Milchunas, DG, & Lauenroth, WK. (1995). Inertia in Plant Community Structure: State Changes After Cessation of Nutrient-Enrichment Stress. *Ecological Applications*, 5:452-458.

Minden, V, Schaller, J, & Venterink, HO. (2020). Plants increase silicon content as a response to nitrogen or phosphorus limitation: a case study with Holcus lanatus. *Plant Soil*, https://doi.org/10.1007/s11104-020-04667-1

Mineau, MM, Baxter, CV, Marcarelli, AM, & Minshall, GW. (2012). An invasive riparian tree reduces stream ecosystem efficiency via a recalcitrant organic matter subsidy. *Ecology*, 93:1501–1508.

Mondelaers, K, Aertsens, J, & Van Huylenbroeck, G. (2009). A meta-analysis of the differences in environmental impacts between organic and conventional farming. *Br. Food. J.*, 111:1098–1119.

Moore, G, Li, F, Kui, L, & West, J. (2016). Flood water legacy as a persistent source for riparian vegetation during prolonged drought: an isotopic study of Arundo donax on the Rio Grande. *Ecohydrology*, 9:909–917.

Nackley, L, Hough-Snee, N, & Kim, S-H. (2016). Competitive traits of the invasive grass Arundo donax are enhanced by carbon dioxide and nitrogen enrichment. *Weed Research*, 57:67–71.

Naiman, RJ, & Decamps, H. (1997). The Ecology Of Interfaces—Riparian Zones. *Annual Review of Ecology and Systematics*, 28:621-658.

Neff, J, & Asner, G. (2001). Dissolved Organic Carbon in Terrestrial Ecosystems: Synthesis and a Model. *Ecosystems*, 4:29–48.

Nosengo, N. (2002). Fertilized to death. *Nature*, 425:894–895.

O'Connor, PJ, Covich, AP, Scatena, FN, & Loope, LL. (2000). Non-Indigenous Bamboo along Headwater Streams of the Luquillo Mountains, Puerto Rico: Leaf Fall, Aquatic Leaf Decay and Patterns of Invasion. *Journal of Tropical Ecology*, 16:499-516.

Osono, T, Azuma, J-I, & Hirose, D. (2014). Plant species effect on the decomposition and chemical changes of leaf litter in grassland and pine and oak forest soils. *Plant Soil*, 376:411–421.

Ostertag, R, & Verville, JH. (2002). Fertilization with nitrogen and phosphorus increases abundance of non-native species in Hawaiian montane forests. *Plant Ecology*, 162:77–90.

Parr, JF, & Sullivan, LA. (2005). Soil carbon sequestration in phytoliths. *Soil Biol. Biochem.*, 37:117–124.

Parr, JF, Sullivan, LA, Chen, B, Ye, G, & Zheng, W. (2010). Carbon bio-sequestration within the phytoliths of economic bamboo species. *Global Change Biol.*, 16:2661–2667.

Payne, AE, Demory, ME, Leung, LR, et al. (2020) Responses and impacts of atmospheric rivers to climate change. *Nat. Rev. Earth Environ.* 1:143–157.

Perdue, RE. (1958). *Arundo donax*—source of musical reeds and industrial cellulose. *Econ. Bot.*, 12:157–172.

Pereira, AP, Graca, MAS, & Molles, M. (1998). Leaf litter decomposition in relation to litter physio-chemical properties, fungal biomass, arthropod colonization, and geographical origin of plant species. *Pedobiologia*, 42:316–327.

Petersen, RC, & Cummins, KW. (1974). Leaf processing in a woodland stream. *Freshw. Biol.*, 4:343–68.

Polade, SD, Gershunov, A, Cayan, DR, Dettinger, MD, & Pierce, DW. (2017). Precipitation in a warming world: Assessing projected hydro-climate changes in California and other Mediterranean climate regions. *Sci. Rep*., 7:10783.

Prairie, YT. (2008). Carbocentric limnology: looking back, looking forward. *Canadian Journal of Fisheries and Aquatic Sciences*, 65:543–548.

Prentice, IC, Farquhar, GD, Fasham, MJR, Goulden, ML, Heimann, M, Jaramillo, VJ, et al. (2001). The carbon cycle and atmospheric carbon dioxide. In: *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change* (eds Houghton, JT, Ding, Y, Griggs, DJ. Noguer, M, van der Linden, PJ, Dai, X, Maskell, K, & Johnson, CA). Cambridge University Press, Cambridge, pp. 185–225.

Quinn, LD, & Holt, JS. (2009). Restoration for Resistance to Invasion by Giant Reed (Arundo donax). *Invasive Plant Science and Management,* 2:279–291.

Ranalli, AJ, & Macalady, DL. (2010). The importance of the riparian zone and in-stream processes in nitrate attenuation in undisturbed and agricultural watersheds – A review of the scientific literature. *Journal of Hydrology*, 389(3–4):406-415.

Rawlik, K, Nowiński, M, & Jagodziński, AM. (2021). Short life–fast death: decomposition rates of woody plants leaf and herb-litter. *Annals of Forest Science*. 78:6.

Raymond, PA, & Spencer, RGM. (2015). Riverine DOM. In *Biogeochemistry of Marine Dissolved Organic Matter* (Second Edition), Academic Press, 509-533.

Rejmanek, M, Richardson, DM. (1996). What attributes make some plant species more invasive? *Ecology*, 77:1655–1661.

Renforth, P, Washbourne, C-L, Taylder, J, & Manning, DAC. (2011). Silicate Production and Availability for Mineral Carbonation. *Environmental Science & Technology*, 45:2035-2041.

Richardson, J, & Moore, D. Stream and Riparian Ecology Chapter 3.

Riedel, T, & Biester, H. (2012). Molecular Fractionation of Dissolved Organic Matter with Metal Salts. Environ. *Sci. Technol*., 46:4419‒4426.

Rieger, JP, Kreager, DA. (1989). Giant reed (Arundo donax): a climax community of the riparian zone. In: Abell DL (ed) USDA Forest Service Gen Tech Rep PSW–110. Proceedings of the California riparian systems conference: protection, management, and restoration for the 1990 s. Berkeley, California, pp 222–225.

Robinson, TH, Leydecker, A, Keller, AA, & Melack, JM. (2005) Steps towards modeling nutrient export in coastal Californian streams with a Mediterranean climate. *Agricultural Water Management*, 77(1–3):144–158.

Rosenstock T, Liptzin D, Six J, & Tomich T. (2013). Nitrogen fertilizer use in California: Assessing the data, trends and a way forward. *Calif. Agr.*, 67(1):68–79.

Russel, EW. (1961). Soil Conditions and Plant Growth. Longmans Green, New York.

Schaffner, U, Hill, M, Dudley, T, & D'Antonio, C. (2020). Post-release monitoring in classical biological control of weeds: assessing impact and testing pre-release hypotheses, *Current Opinion in Insect Science*, 38:99–106.

Schaider, LA, Swetschinski, L, Campbell, C, & Rudel, RA. (2019). Environmental justice and drinking water quality: Are there socioeconomic disparities in nitrate levels in U.S. drinking water? *Environ. Health*, 18:3.

Schaller, J, Hines, J, Brackhage, C, Ba¨ucker, E, & Gessner, MO. (2014). Silica decouples fungal growth and litter decomposition without changing responses to climate warming and N enrichment. *Ecology*, 95:3181–3189.

Schaller, J, & Struyf, E. (2013). Silicon controls microbial decay and nutrient release of grass litter during aquatic decomposition. *Hydrobiologia*, 709:201–212.

Scherer-Lorenzen, M, Veneterink, HO, & Buschmann, H. (2007). Nitrogen Enrichment and Plant Invasions: the Importance of Nitrogen-Fixing Plants and Anthropogenic Eutrophication. In *Ecological Studies*, W.Nentwig (Ed.), Biological Invasions, Springer-Verlag Berlin Heidelberg, 193:163-180.

Schimel, JP, Keith Van Cleve, Rex G. Cates, Thomas P. Clausen, and Paul B. Reichardt, PB. (1996). Effects of balsam poplar (Populus balsamifera) tannins and low molecular weight phenolics on microbial activity in taiga floodplain soil: implications for changes in N cycling during succession. *Can. J. Bot.*, 74:84-90.

Schindler, MH, & Gessner, MO. (2009). Functional leaf traits and biodiversity effects on litter decomposition in a stream. *Ecology*, 90:1641–1649.

Schutter, M, & Dick, R. (2001). Shifts in substrate utilization potential and structure of soil microbial communities in response to carbon substrates. *Soil Biology and Biochemistry*, 33:1481–1491.

Setia, R, Verma, SL, & Marschner, P. (2012). Measuring microbial biomass carbon by direct extraction–comparison with chloroform fumigation-extraction. *European Journal of Soil Biology*, 53:103-106.

Smith, P, Smith, JU, Powlson, DS, McGill, WB, & Arah, JRM. (1997). A comparison of the performance of nine soil organic matter models using datasets from seven long-term experiments. *Geoderma*, 81:153–225.

Smith, WK, Gao, W, Steltzer, H, Wallenstein, MD, & Tree, R. (2010). Moisture availability influences the effect of ultraviolet-B radiation on leaf litter decomposition. *Glob. Chang Biol.*, 16:484–95.

Soininen, EM, Bråthen, KA, Jusdado, JGH, Reidinger, S, & Hartley, SE. (2013). More than herbivory: levels of silica-based defences in grasses vary with plant species, genotype and location. *Oikos*, 122:30–41.

Song, A, Ning, D, Fan, F, Li, Z, Provance-Bowley, M, & Liang, Y. (2015). The potential for carbon biosequestration in China's paddy rice (Oryza sativa L.) as impacted by slag-based silicate fertilizer. Scientific Reports, DOI: 10.1038/srep17354.

Spencer, RGM, Guo, W, Raymond, PA, Dittmar, T, Hood, E, Fellman, J, & Stubbins, A. (2014). Source and biolability of ancient dissolved organic matter in glacier and lake ecosystems on the Tibetan Plateau. *Geochimica et Cosmochimica Acta*, 142:64-74.

Stanley, EH, Powers, SM, Lottig, NR, Buffam, I, & Crawford, JT. (2012). Contemporary changes in dissolved organic carbon (DOC) in human-dominated rivers: is there a role for DOC management? *Freshwater Biology*, 57(Suppl. 1):26–42.

Strauss, EA, & Lamberti, GA. (2002). Effect of dissolved organic carbon quality on microbial decomposition and nitrification rates in stream sediments. *Freshwater Biology*, 47, 65-74.

Swan, CM, & Palmer, MA. (2004). Leaf diversity alters litter breakdown in a Piedmont stream. *J. N. Am. Benthol. Soc.*, 23:15–28.

Taylor, BR, Parkinson, D, & Parsons, WFJ. (1989). Nitrogen and lignin content as predictors of litter decay-rates – a microcosm test. *Ecology*, 70, 97–104.

Thornby, D, Spencer, D, Hanan, J, & Sher, A. (2007). L-DONAX, a growth model of the invasive weed species, Arundo donax L. *Aquatic Botany,* 87:275–284.

Tickner, DP, Angold, PG, Gurnell, AM, & Mountford, J. (2001). Riparian plant invasions: hydrogeomorphological control and ecological impacts. *Progress in Physical Geography,* 25:22–52.

Tilman, D. (1988). Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press, Princeton, New Jersey.

Treseder, KK, & Vitousek, PM. (2001). Effects of soil nutrient availability on investment in acquisition of n and p in Hawaiian rain forests. *Ecology*, 82:946–954.

Tuomisto, HL, Hodge, ID, Riordan, P, & Macdonald, DW. (2012). Does organic farming reduce environmental impacts? A meta-analysis of European research. *J. Environ. Manage,* 112:309–320.

Valliere, JM, Irvine, IC, Santiago, L, & Allen, EB. (2017). High N, dry: experimental nitrogen deposition exacerbates native shrub loss and nonnative plant invasion during extreme drought. *Global Change Biology*, 23:4333–4345.

Van Kleunen, M, Weber, E, & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, 13:235-245.

Vitousek, P, & Sanford, RL. (1986). Nutrient cycling in tropical forest. *Annu. Rev. Ecol. Syst.*, 17:137–67.

Vitousek, PM, Dantonio, CM, Loope, LL, Rejmanek, M, & Westbrooks, R. (1997). Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology*, 21:1–16.

Wagener, SM, et al. (1998). Rivers and soils: parallels in carbon and nutrient processing. *BioScience*, 48:104–108.

Wallace, JB, Eggert, SL, Meyer, JL, & Webster, JR. (1999). Effects of resource limitation on a detrital-based ecosystem. *Ecological Monographs*, 69:409–442.

Wang, G, Mang, S, Cai, H, Liu, S, Zhang, Z, Wang, L, & Innes, JL. (2016). Integrated watershed management: evolution, development and emerging trends. *J. For. Res.*, 27:967–994.

Wardle, DA, Bonner, KI, & Nicholson, KS. (1997). Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos*, 79:247–258.

Warrick, JA, Washburn, L, Brzezinski, MA, & Siegel, DA. (2005). Nutrient contributions to the Santa Barbara Channel, California, from ephemeral Santa Clara River. *Estuarine, Coastal and Shelf Science,* 62:559-574.

Watts, DA, & Moore, GW (2011). Water-Use Dynamics of an Invasive Reed, Arundo donax, from Leaf to Stand. *Wetlands,* 31:725–734.

Webster, JR, & Benfield, EF. (1986). Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics*, 17:567–594.

Weidenhamer, JD, Callaway, RM. (2010). Direct and indirect effects of invasive plants on soil chemistry and ecosystem function. *J. Chem. Ecol.*, 36:59–69.

Wickland, KP, Neff, JC, & Aiken, GR. (2007). Dissolved Organic Carbon in Alaskan Boreal Forest: Sources, Chemical Characteristics, and Biodegradability. *Ecosystems*, 10:1323–1340.

Wiegner & Tubal 2010). Comparison of Dissolved Organic Carbon Bioavailability from Native and Invasive Vegetation along a Hawaiian River. *Pacific Science,* 64:545–555.

Williams, AG, Kent, M, & Ternan, JL. (1987). Quantity and Quality of Bracken Throughfall, Stemflow and Litterflow in a Dartmoor Catchment. *Journal of Applied Ecology*, 24:217-229.

Williams, K, & Hobbs, RJ. (1989). Control of shrub establishment by springtime soil water availability in an annual grassland. *Oecologia*, 81:62–66.

Wilson, JO, Valiela, I, & Swain, T. (1986). Carbohydrate dynamics during decay of litter of Spartina alterniflora. *Marine Biology*, 92:277-284.

Windham, L, Weis, JS, & Weis, P. (2004). Metal dynamics of plant litter of *Spartina alterniflora* and *Phragmites australis* in metal-contaminated salt marshes. Part 1: patterns of decomposition and metal uptake. *Environmental Toxicology and Chemistry*, 23:1520–1528.

Wymore, AS, Compson, ZG,McDowell, WH, Potter, JD, Hungate BA, et al. (2015). Leaf-litter leachate is distinct in optical properties and bioavailability to stream heterotrophs. *Freshw. Sci.*, 34:857–66.

Xiong, S, & Nilsson, C. (1997). Dynamics of Leaf Litter Accumulation and Its Effects on Riparian Vegetation: A Review. *The Botanical Review*, 63:240-264.

Yelenik, SG, Stock, WD, & Richardson, DM. (2004). Ecosystem level impacts of invasive *Acacia saligna* in the South African fynbos. *Restor. Ecol.,* 12:44–51

Young, TP, Chase, JM, & Huddleston, RT. (2001) Community succession and assembly: comparing, contrasting and combining paradigms in the context of ecological restoration. *Ecol. Restor.,* 19:5–18

Yue, K, García-Palacios, P, Parsons, SA, Yang, W, Peng, Y, Tan, B, Huang, C, & Wu, F. (2018). Assessing the temporal dynamics of aquatic and terrestrial litter decomposition in an alpine forest. *Functional Ecology*. 00:2464–2475.

Zhanga, H, Changa, R, Guoc, X, Lianga, X, Wanga, R, & Liua, J. (2017). Shifts in growth and competitive dominance of the invasive plant Alternanthera philoxeroides under different nitrogen and phosphorus supply. *Environmental and Experimental Botany,* 135:118–125.