



Title:

Influence of Nutrient Loading on the Invasion of an Alien Plant Species, Giant Reed (*Arundo donax*), in Southern California Riparian Ecosystems

Author:

[Ambrose, Richard F.](#), University of California, Los Angeles
[Rundel, Philip W.](#), University of California, Los Angeles

Publication Date:

11-01-2007

Series:

[Technical Completion Reports](#)

Publication Info:

Technical Completion Reports, University of California Water Resources Center, UC Berkeley

Permalink:

<http://escholarship.org/uc/item/3qt3s5c4>

Additional Info:

Technical Completion Report W-960

Abstract:

Giant reed, *Arundo donax* L., is one of the greatest threats to riparian ecosystems of Mediterranean-type climate regions, including California. Forming extensive monotypic stands, *A. donax* increases the risks of flooding and fire, uses prodigious amounts of water, and reduces habitat value for wildlife. Urban and agricultural development adjacent to riparian ecosystems may contribute to its invasion success. The main hypothesis of this project is that the current abundance of nutrients, water, light, and fire in riparian ecosystems of Mediterranean-type climate promotes *A. donax* invasion. Analysis of the influence of nutrient enrichment from residential and agricultural land use types on *A. donax* infestation throughout several coastal watersheds in Southern California revealed that floodplains with enriched soil NO₃-N supported *A. donax* infestations whereas sites with lower N levels did not. Unlike the native red willow (*Salix laevigata* Bebb.), *A. donax* may take advantage of anthropogenically enriched N (and K) levels in riparian ecosystems. Regarding response to fire, *A. donax* began regrowth from rhizomes immediately after being burned in October 2003 along the Santa Clara River whereas native riparian plants remained dormant for several months, and *A. donax* grew 3–4 times faster than native riparian plants. A year after the fire, *A. donax* dominated these burned areas (99% relative cover and a 24% increase in relative cover compared to pre-fire conditions). *Arundo donax* infestations appear to create an invasive plant-fire regime. These results help elucidate the optimal conditions for *A. donax* invasion of riparian ecosystems, which in turn can help prioritize control strategies and revegetation of riparian ecosystems.

Supporting material:

"Factors Influencing Invasion of Giant Reed (*Arundo donax*) in Riparian Ecosystems of Mediterranean-type Climate Regions" (Dissertation by Gretchen Christina Coffman, UCLA, 2007.)



Project Title: **Influence of Nutrient Loading on the Invasion of an Alien
Plant Species, Giant Reed (*Arundo donax*), in Southern
California Riparian Ecosystems**

Principal Investigators: Richard F. Ambrose
Environmental Science and Engineering Program
Department of Environmental Health Sciences

and

Philip W. Rundel
Department of Ecology and Evolutionary Biology

University of California, Los Angeles
Los Angeles, CA 90095

UC Water Resources Center Technical Completion Report Project No. W-960

November 2007

Abstract

Giant reed, *Arundo donax* L., is one of the greatest threats to riparian ecosystems of Mediterranean-type climate regions, including California. Forming extensive monotypic stands, *A. donax* increases the risks of flooding and fire, uses prodigious amounts of water, and reduces habitat value for wildlife. Urban and agricultural development adjacent to riparian ecosystems may contribute to its invasion success. The main hypothesis of this project is that the current abundance of nutrients, water, light, and fire in riparian ecosystems of Mediterranean-type climate promotes *A. donax* invasion. Analysis of the influence of nutrient enrichment from residential and agricultural land use types on *A. donax* infestation throughout several coastal watersheds in Southern California revealed that floodplains with enriched soil NO₃-N supported *A. donax* infestations whereas sites with lower N levels did not. Unlike the native red willow (*Salix laevigata* Bebb.), *A. donax* may take advantage of anthropogenically enriched N (and K) levels in riparian ecosystems. Regarding response to fire, *A. donax* began regrowth from rhizomes immediately after being burned in October 2003 along the Santa Clara River whereas native riparian plants remained dormant for several months, and *A. donax* grew 3–4 times faster than native riparian plants. A year after the fire, *A. donax* dominated these burned areas (99% relative cover and a 24% increase in relative cover compared to pre-fire conditions). *Arundo donax* infestations appear to create an invasive plant-fire regime. These results help elucidate the optimal conditions for *A. donax* invasion of riparian ecosystems, which in turn can help prioritize control strategies and revegetation of riparian ecosystems.

Table of Contents

CHAPTER 1 INTRODUCTION	1
1. Problem Statement.....	1
2. Objectives	2
3. Organization of this Report	3
CHAPTER 2 - INFLUENCE OF ANTHROPOGENIC NUTRIENT ENRICHMENT ON INVASION OF RIPARIAN ECOSYSTEMS BY <i>ARUNDO DONAX</i> IN SOUTHERN CALIFORNIA	4
1. Introduction	5
2. Methods	7
2.1. Study Area.....	7
2.2. Study Design and Sampling Locations.....	8
2.3. Sampling Methods.....	8
2.4. Statistical Analyses.....	10
3. Results	11
3.1. Naturally Occurring Nutrient Levels.....	11
3.2. Shallow Groundwater Nutrients	12
3.3. Soils Nutrients and Grain Size	13
3.4. Relationship between Shallow Groundwater, Soil, and Leaf Tissue Nutrients	15
3.5. Leaf tissue Nutrients.....	15
3.6. N:P and N:K Ratios	17
4. Discussion	17
4.1. Natural Nutrient Levels	18
4.2. Nutrient Limitation.....	18
4.3. Anthropogenic Nutrient Levels	19
4.4. Factors Controlling Nutrient Availability.....	21
4.5. Nutrient Supply and Availability.....	23
5. Management and Restoration Implications	24
CHAPTER 3 - WILDFIRE PROMOTES GIANT REED (<i>ARUNDO DONAX</i>) INVASION IN RIPARIAN ECOSYSTEMS	26
1. Introduction	27
2. Methods	28
2.1. Study area.....	28
2.2. Study design	28
2.3. Study species	29
2.4. Sampling methods	29
2.5. Statistical analyses.....	31

3.	Results	31
3.1.	Pre- versus post-fire plant abundance.....	31
3.2.	Post-fire density.....	32
3.3.	Post-fire shoot length.....	32
3.4.	Post-fire shoot elongation rate and RGR.....	32
3.5.	Post-fire productivity.....	33
3.6.	Soil nutrients	33
4.	Discussion	33
4.1.	Change in Plant Composition and Structure.....	33
4.2.	Soil Nutrients Stimulate Growth	34
4.3.	Mechanisms of Invasion.....	35
5.	Conclusions and Management Implications	36
	Literature Cited	38
	Tables.....	51
	Figures.....	62
	List of Publications	80

CHAPTER 1

INTRODUCTION

1. Problem Statement

Indigenous to southern Eurasia, giant reed (*Arundo donax*) has been introduced and is now successfully invading riparian ecosystems in many climates worldwide, from tropical to temperate (Polunin and Huxley 1987). In the United States, *A. donax* has become especially devastating to riparian habitats in California's mediterranean-type climate. *A. donax* has successfully invaded streams of Southern California in the last 30 years, following an era of human alterations along river courses, including channelization of streams and rivers, levee construction, floodplain alteration, and encroachment of agricultural and urban development into river systems.

River and stream systems of coastal Southern California are fragile yet dynamic, typically characterized by a network of braided streams. Due to the intense but infrequent storm event patterns of the mediterranean-type climate, these braided stream corridors become scoured, exposing sandy floodplains, channels and terraces, making them vulnerable to disturbance colonizers, primarily invasive, weedy plants. Weedy plants are able to establish and grow quickly in these disturbed areas, often physically outcompeting the native riparian plant species for light and other necessary resources before natives have a chance to establish.

Arundo donax is one of the most successful of these riparian invaders. Although its seeds are sterile in California, *A. donax* spreads rapidly downstream when small pieces of the plant break off and land on a bare, moist substrate (Bell 1997). Growing at an extremely high rate (up to 7cm per day), *A. donax* quickly establishes on unvegetated or sparsely vegetated soil and grows to >8m in height after only a few months (Reiger and Kreager 1989). It then expands outward in area, quickly displacing native shrubs, herbs and grasses, and eventually even trees. In this manner, *A. donax* forms extensive stands or monocultures in riparian ecosystems, along floodplains and terraces of Southern California's river and stream systems.

Stands of *A. donax* have created serious problems along rivers in Southern California, both physically and biologically. Where it grows extensively along floodplains, *A. donax* causes physical obstructions to natural water flow and increases the risk of flooding to adjacent lands. As the above ground biomass dies back in the hot, dry summer months, characteristic of mediterranean-type climates, *A. donax* creates an unnatural fire hazard where riparian corridors used to form natural fire breaks. Natural riparian ecosystem functioning may be impaired by *A. donax* due to its higher water requirements and transpiration rates than native riparian species (Perdue 1958; Iverson 1994). *Arundo donax* has very little known wildlife habitat value (Bell 1997) compared to the native trees, such as willow (*Salix* spp.) and cottonwood (*Populus* spp), and shrubs, like mule fat (*Bacharris salicifolia*)(Bell 1994) and its stems and leaves contain a large array of inorganic noxious chemicals (Jackson and Nunez 1964) which reduce herbivory by most native insects and grazers. Due to its dense population growth form, it

physically displaces indigenous wildlife that depend on the riparian corridor and river floodplain for foraging, nesting, and cover.

In the last century, nutrient inputs to river systems have increased dramatically due mainly to agriculture and municipal sewage. These same nutrient inputs are present in high quantities in the rivers of Southern California's watersheds (Pederson 2001, Suffet and Sheehan 2000). Nationwide, the use of fertilizer in agricultural areas has increased from 20 to 40 million tons annually. The average percent of nitrogen, the main constituent in commercial fertilizers, has risen from 6.1 to 20.4 % (Texas Water Resources Institute 1986). This increase in use and composition of fertilizer alone has led to a loading of river systems with nutrients, mainly nitrogen and phosphorus. Nitrogen, found in the form of nitrate in fertilizer, poses unique risks to river systems; it is soluble and moves quickly through soils in the shallow groundwater between agricultural practices and rivers. Phosphorus, on the other hand, is not very soluble and typically adheres to soil particles. Other anthropogenic and natural sources are thought to have also contributed to nutrient loading in river systems, including: nitrogen enriched rainfall and air; manure from animal feedlots and corrals; fertilizer applied to lawns; leaky septic tanks; oxidation of organic materials; and the symbiotic nitrogen fixation by plants.

2. Objectives

A combination of factors is thought to cause the invasion of *A. donax* in river systems of Southern California. The main hypothesis of this study is that increased nutrient inputs have made a significant contribution to the invasion of *A. donax* throughout river systems in mediterranean-type climates. To test this hypothesis, the research had the following objectives:

- 1) To relate nutrient concentration of soil and shallow groundwater to *A. donax* abundance from different sampling locations throughout three watersheds, based on land use type and location in the floodplain versus terrace.
- 2) To compare the effect of a range of anthropogenic nutrient inputs on *A. donax* versus dominant native plants abundance in riparian communities within subwatersheds of the Santa Clara River Watershed, Calleguas Creek Watershed, and Topanga Canyon Watershed (with predominantly different land uses)
- 3) To compare nutrient concentrations in riparian communities in which *A. donax* is present and absent in order to correlate nutrient concentrations with *A. donax* establishment
- 4) To relate *A. donax* abundance (patch size/density, plant size/vigor, and biomass) to nutrient concentrations in the surrounding environment (soils and shallow groundwater)
- 5) To correlate *A. donax* presence and abundance with high nitrogen versus high phosphorus in the soil and shallow groundwater

In addition to the above objectives, in 2004 we received supplemental funding to evaluate the impacts of fire on *Arundo* recovery in riparian habitats. This supplement enabled us to follow study sites that were burned in the large October 2003 fire. We addressed the following objectives:

- 1) To observe the change in vegetation (native versus nonnative) after fire in a riparian ecosystem
- 2) To study the effect of sediment load after fire on Southern Steelhead habitat
- 3) To research methods for cost-effective management solutions to effects of fire on riparian systems (especially in relation to giant reed eradication from terraces post-fire)

3. Organization of this Report

Because this project had two distinct phases, one focused on nutrients and the other on recovery after the October 2003 fire, we have presented the results in two separate chapters. Chapter 2 addresses the influence of anthropogenic nutrient enrichment on the invasion of riparian ecosystems by *Arundo donax* in southern California. Chapter 3 addresses the degree to which wildfire promotes *Arundo donax* invasion in riparian ecosystems.

The research presented here forms a portion of Gretchen Coffman's doctoral dissertation (Coffman 2007), with R. Ambrose serving as her advisor and P. Rundel serving as committee member. Chapter 2 of this report was modified from Chapter 3 of her dissertation, and Chapter 3 of this report was modified from Chapter 4 of her dissertation.

**CHAPTER 2 -
INFLUENCE OF ANTHROPOGENIC NUTRIENT ENRICHMENT ON
INVASION OF RIPARIAN ECOSYSTEMS BY *ARUNDO DONAX* IN
SOUTHERN CALIFORNIA**

Abstract: One of the greatest threats to riparian ecosystems of Mediterranean-type climate regions, including California, is a member of the grass family (Poaceae), giant reed (*Arundo donax* L.). We tested the hypothesis that anthropogenic nutrient enrichment is one of the most significant factors contributing to the recent invasion of riparian ecosystems by *A. donax* in southern California. We examined the influence of nutrient enrichment of shallow groundwater and soil from various land use practices on the degree of infestation of *A. donax* throughout several coastal watersheds. Elevated levels of N (nitrogen) found in shallow groundwater and soils of floodplains were associated with adjacent land use and watersheds with higher anthropogenic nutrient inputs. Both large and small *A. donax* infestations on floodplains contained higher soil NO₃-N concentrations than did non-infested areas. Higher N and K (potassium) leaf tissue content of *A. donax* in large and small infestations compared to native red willow (*Salix laevigata* Bebb.) in non-infested and reference sites suggests that these nutrients may be more available to *A. donax*. Unlike *S. laevigata*, *A. donax* may take advantage of anthropogenically enriched N levels in riparian ecosystems, as illustrated by its positive response to all forms of shallow groundwater N in floodplains and soil N on riparian terraces. Results of this study suggest that N limiting conditions may naturally occur in riparian ecosystems in this geologically young landscape, but anthropogenic nutrient inputs have elevated groundwater N:P ratios in study watersheds. Results of this study can help predict optimal nutrient conditions for *A. donax* invasion. Reducing excess N supply to riparian ecosystems associated with agricultural and residential land use activities may aid in the long-term control of *A. donax*.

1. Introduction

Both natural and anthropogenic disturbances along rivers in Mediterranean-type climate regions are thought to promote the spread of invasive plant species (Drake et al. 1989, Gregory et al. 1991, Pysek and Prach 1994, Else 1996, Else and Zedler 1996, Dudley 1998). Several experimental studies in wetland ecosystems have demonstrated higher response to nitrogen by clonal, invasive plants than natives (Green and Galatowitsch 2002, Maurer and Zedler 2002, Minchinton and Bertness 2003). Elevated nutrient levels have been linked to plant invasion in many ecosystems (Kolb et al. 2002, Booth et al. 2003, Brooks 2003, Kolb and Alpert 2003, Suding et al. 2004), however little is known about the role of nutrients in promoting invasion in riparian ecosystems (Wang 1998). In this paper, we explore the influence of anthropogenic nutrient enrichment on the invasion of riparian ecosystems by the clonal grass species *Arundo donax* in southern California.

Due to the intense but infrequent winter storm patterns characteristic of Mediterranean-type climates, rivers are heavily scoured every few years. Strong floods remove and disperse riparian vegetation downstream, creating open floodplains for colonization. Weedy plant species are able to establish and grow quickly in disturbed areas such as these (Elton 1958, Tilman 1988, Drake et al. 1989, Richardson et al. 2000), the most invasive of which often physically compete with native species for light, nutrients, and water. Historically, riparian ecosystems in Mediterranean-type climates have been severely altered by human perturbation. Since early human settlement of these areas, rivers have been dammed, channelized, mined, diverted, and subjected to residential and commercial development in Mediterranean-type climates (Palmer 1993, Mount 1995). These alterations have magnified their susceptibility to plant invasions by weedy plant species (Randall et al. 1998, Rundel 1998). Currently, one of the greatest invasive threats to riparian ecosystems in Mediterranean-type climates is a tall, perennial bamboo-like member of the grass family (Poaceae) called giant reed (*Arundo donax* L.).

Indigenous to southern Eurasia, *A. donax* was introduced extensively to other locales and now thrives in many warm climates worldwide (Perdue 1958, Crampton 1974, Polunin and Huxley 1987, Hickman 1993, Sharma et al. 1998). In the United States, *A. donax* has become especially devastating to riparian habitats in California's Mediterranean-type climate region, creating significant impacts to natural-river functioning and sustainability (Rundel 2000). *Arundo donax* was introduced to agricultural landscapes in the Los Angeles area for building materials and erosion control along irrigation canals. Carried by floodwaters, *A. donax* eventually made its way to adjacent streams and rivers and by the 1820s patches were commonly found along floodplains of many streams (Robbins et al. 1951). However, it appears that *A. donax* has only recently succeeded in invading (i.e., expanding its distribution and displacing native vegetation) riparian ecosystems along floodplains and terraces in southern California after large floods in 1969 (Sanger Hedrick pers. comm.) (Bell 1997).

Arundo donax is one of the most successful weedy invaders in the disturbance-defined riparian ecosystems of Mediterranean-type climates (Bell 1997, Boose and Holt 1999). Although inflorescences (0.5 m long terminal panicles) are not known to produce

seed in California (Johnson et al. 2006), *A. donax* reproduces readily by vegetative propagation; it is dispersed downstream when small pieces of rhizomes or culms break off during flooding and land on bare, moist substrates (Else 1996, Else and Zedler 1996, Bell 1997, Boose and Holt 1999, Wijte et al. 2005). Growing at an extremely fast rate (up to 10 cm per day under optimal conditions), *A. donax* quickly establishes on exposed or sparsely vegetated soil and grows to more than 4 m in height after only a few months (Rieger and Kreager 1989) and may attain heights of up to 8 m a few years after establishment (Perdue 1958). Once established, *A. donax* then expands outward in area by clonal propagation (Decruyenaere and Holt 2001), crowding and displacing indigenous shrubs, herbs and grasses, and trees under elevated soil moisture, nutrient, and light conditions (Rieger and Kreager 1989). In this manner, *A. donax* forms extensive stands, or monocultures, along floodplains and terraces of California's river and stream systems.

Infestations of *A. donax* have created serious physical and biological problems along rivers in Mediterranean-type climate regions (Dudley and Collins 1995, DiTomaso 1998, Dudley 2000, Rundel 2003). Where it grows extensively along floodplains, *A. donax* physically obstructs natural water flow, thereby increasing the risk of flooding. As the aboveground biomass dries in the hot, dry summer months, *A. donax* creates a fire hazard where moisture-rich riparian corridors would normally form natural barriers to fire (Scott 1994, Rundel and Gustafson 2005). Furthermore, *A. donax* may outcompete native riparian species for scarce water resources (Iverson 1994, Coffman in press), thereby decreasing biodiversity and reducing the value of riparian habitats for wildlife (Kisner 2004).

Millions of dollars have been spent in efforts to remove *A. donax* from riparian ecosystems in southern California. Although these attempts have been successful in removing small infestations of *A. donax* on riparian terraces, it continues to thrive in floodplains. An understanding of the ecological conditions that promote continued growth and invasion of *A. donax* is needed for its effective control. Ever expanding residential and agricultural development in coastal southern California and other Mediterranean-type climates has led to increased water import and discharge into rivers, declining water quality, and removal of the once vast low-lying areas of riparian forest. The result – increased nutrient, water, and light availability – may promote invasion of riparian ecosystems by *A. donax* (Bell 1997, Wang 1998, Rundel 2003, Coffman et al. 2004). This study investigated one of the most important factors influencing *A. donax* invasion: elevated nutrient levels in riparian ecosystems caused by anthropogenic inputs.

Soils in Mediterranean-type climates commonly contain low levels of nitrogen (N) and phosphorus (P) (Day 1983, diCatri 1991, Dallman 1998). In southern California, the young sedimentary geology is naturally high in P, but has N-limiting conditions (Pettijohn 1975). Nutrient enrichment of riparian ecosystems (especially by N) from adjacent land use practices may promote *A. donax* growth and invasion in river systems of southern California. Excess N, P, and potassium (K) are transported in surface and shallow groundwater from various land use activities to adjacent riparian ecosystems (Schlosser and Karr 1981, Correll 1984, Correll et al. 1992, Triska et al. 1994, Rodda 1995, Basnyat et al. 1999). Weedy and invasive plant species often differ in

their nutrient requirements and uptake efficiency compared to native plants, resulting in a competitive advantage for the former in nutrient rich environments (Claridge and Franklin 2002). Thus, elevated nutrient levels in riparian ecosystems are thought to promote invasion of plants such as *A. donax*.

This study investigated the influence of anthropogenic nutrient enrichment on invasion of *A. donax* in three river systems of southern California. We hypothesized that nutrient enrichment of riparian ecosystems from anthropogenic sources has contributed significantly to invasion of river systems by *A. donax* in southern California. To test this hypothesis, we examined relationships between the degree of *A. donax* infestation and nutrient levels in the associated shallow groundwater, soil, and leaf tissue using a correlational approach.

2. Methods

2.1. Study Area

The study area lies northwest of Los Angeles in Ventura and Los Angeles Counties, California. Three river systems (Calleguas Creek, the Santa Clara River, and Topanga Canyon) located in watersheds with varying compositions of land use were studied (Figure 1). Ten reference subwatersheds from within this region where *A. donax* is absent were used as indicators of natural conditions.

The Calleguas Creek watershed drains an area of approximately 888 km², predominantly in southern Ventura County. It contains a roughly equal mix of three main land use categories: ~30% residential development, ~32% agricultural areas (both row crops and orchards mostly in the western and lower watershed), and ~38% open space (mainly in the mountains of the upper watershed) (Figure 2). This watershed was chosen for its relatively high level of anthropogenic nutrient input.

The Santa Clara River is one of southern California's last remaining large, unregulated river systems. The river and its tributaries drain a watershed of approximately 4,185 km², the second largest coastal watershed in southern California. The 187-km long river flows in a westerly direction from its headwaters on the northern slopes of the San Gabriel Mountains in Los Angeles County to the Oxnard Plain in Ventura County, emptying into the Pacific Ocean near the City of Ventura. The Santa Clara River contains a mix of land use types representing moderate anthropogenic nutrient input, although over 80% of the watershed (mainly upper and higher elevation portions) remains as open space (Figure 2). The floodplain of the lower watershed is dominated by agricultural land use (orchards and row crops), and urban and residential development is rapidly expanding in the mid to upper watershed.

The Topanga Canyon Watershed, approximately 91 km², is located in the heart of the Santa Monica Mountains in western Los Angeles County. Topanga Canyon is a low anthropogenic nutrient input system. The watershed is composed primarily of low-density rural residential development (6%) and open space (93%) in the upper parts of the watershed, with almost no agricultural land use (Figure 2).

To fully test our hypothesis that riparian ecosystems in developed watersheds were invaded due to increased nutrient supply from anthropogenic inputs, we documented reference conditions in undeveloped watersheds throughout the study area to compare to developed watersheds. In this coastal geographic region, none of the undeveloped watersheds contained *A. donax*, so they were not true controls for testing our hypothesis. However to establish reference conditions, we sampled shallow groundwater, soil, and leaf tissue nutrients within ten undeveloped watersheds (reference sites) in the region: three subwatersheds (tributaries) of the Santa Clara River Watershed and seven smaller undeveloped watersheds in the Santa Monica Mountains. Reference sites were located in open space areas containing no upstream anthropogenic nutrient inputs and were dominated by red willow, *Salix laevigata* (no *A. donax* was present). We could not control for N inputs from atmospheric deposition, but based on model results for dry atmospheric N deposition for watersheds in the Los Angeles Region, we assumed similar levels of atmospheric N dry deposition among watersheds (Lu et al. unpublished data).

2.2. Study Design and Sampling Locations

We established stratified sampling locations along the main stem of each of the three river systems based on three factors and different levels within each factor: adjacent land use type (agricultural, residential development, and open space); fluvial geomorphic landform (floodplains and terraces); and degree of *A. donax* infestation (none, small, and large) (Table 1; Figure 2). Effects of nutrient inputs from land use activities on *A. donax* invasion were thought to be more directly related to adjacent land use type in higher riparian terraces (called terraces), whereas the watershed factor was used to address cumulative effects of upstream land use activities on floodplain sampling locations (lower terraces immediately adjacent to main channels with baseflow).

Each sampling location was approximately 600 m². Floodplain sampling sites were roughly 30 m in length (parallel and immediately adjacent to the main stream channel, containing baseflow) by 20 m in width (perpendicular to the channel). Terrace sampling sites had similar dimensions but were located immediately adjacent to upland land use areas. We also selected locations where *A. donax* was: (1) completely absent and native riparian vegetation (*Salix laevigata*) dominated, (2) only present as small infestations (between 1–9 m²), and (3) the dominant component of the vegetation (> 100 m²), representing heavily invaded river reaches. *Salix laevigata* Bebb. (Salicaceae family) was selected because it is the most common woody plant consistently found throughout riparian ecosystems in the study area. Roots of the phreatophyte *S. laevigata* can reach up to 30 m when the groundwater table is deep, whereas *A. donax* roots have been observed to grow to only 8 feet in depth (Figure 3) (See Appendix 3-1 in Coffman 2007 for site locations).

2.3. Sampling Methods

Samples of *A. donax* or *S. laevigata* leaf tissue and associated shallow groundwater and soils were taken once at each sampling location from July to September 2003. Ten *A. donax* or *S. laevigata* leaves from at least three plants were collected at

each sampling location for leaf tissue nutrient analyses. *Arundo donax* leaves were collected at large and small infestation sampling sites. *Salix laevigata* leaves were collected from riparian ecosystem sampling sites with no *A. donax* and at reference sites where *A. donax* was absent. Only newly mature, healthy, full sun leaves were collected from the top of *A. donax* culms and the middle of *S. laevigata* canopies. Leaf tissue was analyzed for relative nutrient content to evaluate nutrient use and availability to plants (Taiz and Zeiger 1991).

Shallow groundwater samples were collected in the center of each sampling location next to the target plant (either *A. donax* or *S. laevigata*). An 8-cm diameter bucket auger was used to create sampling holes, and a temporary stainless steel piezometer connected to a bailer was used to collect the groundwater samples. After purging the bailer several times, a groundwater sample was collected. Each day, these samples were kept on ice until delivered to a local laboratory for immediate analysis. Because groundwater was too deep to sample at terrace study sites, only soil and leaf tissue nutrient contents were collected in these areas. Five subsamples of soil were collected adjacent to target plants and combined into a composite sample by mixing together thoroughly in a stainless steel bowl. Each soil subsample was collected with an 8-cm diameter bucket auger from the upper 30 cm of the soil surface, where nutrient concentrations are expected to be greatest (Day 1983).

Leaf tissue and soil samples were air-dried and ground to a powder in preparation for nutrient content analyses at the DANR Analytical Laboratory in Davis, California. Leaf tissue was analyzed for total percent N, P, and K. Total N content of leaf tissue was determined using a Nitrogen Gas Analyzer combustion method (LECO FP-528) (AOAC International 1997a), total P content by microwave acid digestion/dissolution of leaf tissue samples and quantitative determination by AAS and ICP-AES (Meyer and Keliher 1992, Sah and Miller 1992), and total K content by the 2% acetic acid extraction method and a quantitative determination using atomic emission spectrometry (Johnson and Ulrich 1959).

Soil samples were analyzed for total N (%), nitrate-N ($\text{NO}_3\text{-N/ppm}$), ammonia-N ($\text{NH}_4\text{-N/ppm}$), orthophosphate ($\text{PO}_4\text{-P/ppm}$), and pH. Total N in the soil was determined by the combustion gas analyzer method (Method 972.43) (AOAC International 1997b). Concentrations of $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ in the soil were determined by equilibrium extraction of soil with potassium chloride and a flow-injection analyzer (Hofer 2003, Knepel 2003). Because the soils studied were neutral to alkaline, the Olsen-P method was used to estimate the relative availability of inorganic $\text{PO}_4\text{-P}$ in soils (Olsen and Sommers 1982, Prokopy 1995). Soil pH was determined using a saturated paste prepared from the soil and a pH meter (USDA 1954). Soil grain size was analyzed using a hydrometer to determine the particle size distribution of sand, silt, and clay in soil suspension (Sheldrick and Wang 1993).

Shallow groundwater samples were analyzed for $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$, $\text{PO}_4\text{-P}$, total Kjeldahl nitrogen (TKN), total N (total N = TKN + $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$), and pH by Fruit Growers Environmental Laboratories in Santa Paula, California. $\text{NH}_4\text{-N}$ (4500NH3H), $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$ (SM4500-NO3 F/EPA 300.0), and pH (Method 4500-H

B) were analyzed according to the *Standard Methods for the Examination of Water and Wastewater* (Franson et al. 1998). TKN (EPA Method 351.1) and PO₄-P (Olsen P Methods 300.0 and 4500) were analyzed per *Methods for Chemical Analysis of Water and Wastes* (USEPA 1983).

2.4. Statistical Analyses

In this study, we used a multifactorial design in which combinations of four fixed factors (Model 1) were crossed with each other. The factors and associated levels were: watersheds (Santa Clara River, Calleguas Creek, Topanga Canyon, and reference watersheds), land use types (agricultural, residential, and open space), fluvial geomorphic location (floodplain and terrace), and degree of *A. donax* infestation (none, small, and large). Sampling sites with small *A. donax* infestations represented areas where *A. donax* presence may indicate different invasion trajectories (i.e., depending on site conditions *A. donax* will either invade the area or persist as a small patch). ANOVA tests were used to analyze effects of various combinations of the four factors (independent variables) on nutrient concentrations in shallow groundwater, soil, and leaf tissue, soil grain size, pH, and leaf tissue and shallow groundwater N:P (dependent or response variables) (Systat Statistical Program [Version 10]).

Since data for terrace locations were only collected within the Santa Clara River Watershed, four-way ANOVAs could not be conducted. Instead, two three-way ANOVAs (watershed x land use x degree of infestation and land use x fluvial geomorphic location x degree of infestation) were performed on a combination of the fixed factors and response variables. To further investigate differences between invaded and non-invaded sites, small *A. donax* infestation data were removed and three-way ANOVAs repeated. Because soil nutrients can be strongly influenced by soil grain size, three-way ANOVAs for soil nutrients were conducted using soil grain size (percent silt + clay) as a covariate. This parameter covaried significantly with all soil nutrient analytes. Since *A. donax* and *S. laevigata* leaves were not collected from the same sample locations to test species specific variation in leaf tissue nutrients, one-way ANOVAs were performed by the species factor (*A. donax* and *S. laevigata*, data from all infestation types combined) using groundwater nutrient analytes as covariates. *Arundo donax* leaf tissue nutrient content was significantly greater than *S. laevigata* in all cases. Therefore, *A. donax* and *S. laevigata* leaf tissue nutrient results were compared separately in ANOVAs because variation in species nutrient uptake and use efficiency could potentially confound results (Chapin et al. 1986). F tests were performed to evaluate contrasts between means of grouping variables and levels in three-way ANOVA results.

We conducted one-way ANOVAs for watershed identity using all response variables to analyze the main effects of three study watersheds compared to reference watersheds. Nutrient content of leaf tissue was analyzed and reported separately by species in this one-way ANOVA. In addition, one-way ANOVAs by degree of infestation across all watersheds were conducted for *A. donax* leaf tissue nutrients in small and large infestations to compare foliar nutrient concentrations between infestation levels. Tukey's post hoc tests were conducted to determine significant differences between factor means in these one-way ANOVAs.

Linear regression analyses were performed to investigate relationships between *A. donax* and *S. laevigata* leaf total N and P content and various shallow groundwater and soil nutrient analyte concentrations on floodplains and terraces. Significance levels for regressions were determined from P values (ANOVA). We selected shallow groundwater and soil nutrient analytes with the strongest relationships to leaf tissue nutrients to analyze further in one- and three-way ANOVAs. All forms of N and P in the shallow groundwater in floodplains were analyzed. However, only soil NO₃-N and PO₄-P were analyzed along floodplains and terraces on the Santa Clara River.

Probability plots were used to test for normality of data and to identify data that required transformation. Most of the data were log₁₀ base transformed. Raw data were used for leaf tissue N and K and shallow groundwater PO₄-P and pH. Square root transformations were used on percent silt + clay. When means and standard errors were used to describe or present statistical differences, data were back-transformed and reported in original units as an asymmetrical range.

3. Results

3.1. Naturally Occurring Nutrient Levels

We used reference watershed data collected in this study to represent natural conditions for comparison to study watersheds, since historic data on natural conditions in neither study watersheds nor other watersheds in the southern California region were not available. Mean total soil N was much higher in reference watersheds than in floodplain or terraces of study watersheds (Table 2). However, NO₃-N and PO₄-P levels in reference watersheds were similar to study floodplains but much lower than levels found on terraces. N and P levels of the shallow groundwater in reference watersheds were low (mean 0.13-1.11 mg/L) compared to study watersheds (mean 0.37-5.74 mg/L). The mean shallow groundwater molar N:P ratio (NO₃-N:PO₄-P) from reference sites was 2.4:1 (SE 2.0:1–3.0:1), which is considered to be N limiting according to the Redfield ratio (< 15:1 = N limiting and > 15:1 = P limiting for sea water or 15 atoms of N for every 1 atom of P). The N:P ratio of shallow groundwater in study watersheds was higher than found in reference watersheds but also in the range of N limiting [4.4:1 (SE 3.9:1–5.0:1)].

The mean N:P ratio of *S. laevigata* leaf tissue from the reference sites was 12.1:1 (SE 11.5:1–12.8:1), which is also considered to be N limiting (< 14:1 = N limiting and > 16:1 = P limiting on a per mass basis) (Koerselman and Meuleman 1996) (Table 3). Mean leaf tissue of both *S. laevigata* and *A. donax* collected from study watersheds had much higher N:P ratios, but considered neither N nor P limiting. The *S. laevigata* leaf tissue N:K ratio of 1.5:1 (SE 1.4:1–1.6:1) from the reference sites was optimal for plant growth (< 1.5:1 = N limiting and > 1.5:1 = K limiting) (Knecht and Goransson 2004). However, the N:K ratio is below the N limiting threshold for *A. donax* in study watersheds [0.99:1 (SE 0.96:1.02)].

3.2. Shallow Groundwater Nutrients

The three-way ANOVA (watershed x land use x degree of infestation) showed that the two-way interaction of watershed and land use factors best explained total N distribution in the shallow groundwater along the floodplains studied (Table 4). Concentrations of total N in the shallow groundwater were significantly higher in Calleguas Creek than in the Santa Clara River adjacent to agricultural and open space land uses (Figure 4a). No variation between the two watersheds existed for total N concentrations adjacent to residential land uses. However, shallow groundwater total N levels were significantly lower adjacent to residential land uses compared to agriculture and open space within Calleguas Creek. Results of the one-way ANOVA by watershed indicated that reference sites contained significantly lower total N in the shallow groundwater compared to any of the three study watersheds (Table 5). TKN results in shallow groundwater were similar to those of total N.

The watershed main effect for the three-way ANOVA was very highly significant for $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$ concentration in the shallow groundwater (Table 4). These concentrations were significantly higher throughout Calleguas Creek (1.08 mg/L, SE 0.80–1.46 mg/L) compared to the Santa Clara River watershed (0.27 mg/L, SE 0.23–0.31 mg/L). When data from small *A. donax* infestations were removed, the interaction of watershed and land use type was significant for the three-way ANOVA ($F_{(2,50)} = 3.866$; $P = 0.027$). $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$ concentrations in the shallow groundwater adjacent to agricultural land uses were significantly higher along Calleguas Creek than any other combination of land use and watershed (Figure 4b). The one-way ANOVA for $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$ concentrations by watershed was very highly significant (Table 5). Shallow groundwater $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$ levels were significantly higher along floodplains in Calleguas Creek compared to levels measured along the Santa Clara River, Topanga Canyon, or reference watersheds.

The three-way ANOVA resulted in a significant three-way interaction for shallow groundwater $\text{NH}_4\text{-N}$ levels found in floodplains (Table 4). Significantly higher mean $\text{NH}_4\text{-N}$ concentrations in the shallow groundwater were associated with small infestations next to open space along Calleguas Creek compared to sites with any other combination of land use and degree of infestation (Figure 4d and e). Large infestations adjacent to open space on Calleguas Creek contained higher shallow groundwater $\text{NH}_4\text{-N}$ levels than many other combinations of factors. However, the one-way ANOVA by watershed indicated that levels of $\text{NH}_4\text{-N}$ in shallow groundwater did not differ significantly between reference watersheds and any of the main study watersheds (Table 5). Reference watersheds contained an average of 0.26 mg/L (SE 0.21–0.33) $\text{NH}_4\text{-N}$ in shallow groundwater, which is lower only than levels found within small *A. donax* infestations on floodplains adjacent to open space within the Calleguas Creek watershed.

The main effect of watershed was very highly significant for $\text{PO}_4\text{-P}$ in the three-way ANOVA (Table 4). The watershed with the highest proportion of total anthropogenic land cover, Calleguas Creek, contained the highest shallow groundwater $\text{PO}_4\text{-P}$ concentrations (Figure 2). Orthophosphate concentrations in the shallow groundwater were significantly higher along Calleguas Creek ($2.67 \pm \text{SE } 0.38$ mg/L) than

Santa Clara River ($0.64 \pm \text{SE } 0.10 \text{ mg/L}$). The one-way ANOVA for shallow groundwater $\text{PO}_4\text{-P}$ levels by watershed was also very highly significant (Table 5). Shallow groundwater $\text{PO}_4\text{-P}$ concentrations on floodplains were significantly lower at reference sites and along the Santa Clara River compared to Calleguas Creek.

The one-way ANOVA for shallow groundwater pH levels by watershed was very highly significant (Table 5). Calleguas Creek and the Santa Clara River had significantly more acidic shallow groundwater than did Topanga Canyon and the reference watersheds.

3.3. Soils Nutrients and Grain Size

3.3.1. Nutrients

The relative availability of nutrients in soil made the soil nutrient results quite complex, due to variability in soil grain size and pH levels among sites, as well as different rooting depths of the two plant species (Figure 3). Availability of nitrogen varies considerably depending on soil grain size, which determines cation exchange capacity and moisture holding capacity. NH_4^+ and NO_3^- are highly charged ions that readily dissolve in water. Percent silt + clay grain size was used as a covariate in ANOVAs for soil nutrients to account for variation due to soil grain size. Significant relationships between *A. donax* leaf tissue N and soil total N, $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ found on riparian terraces suggested that this species may rely more heavily on soil nutrients in the upper 30 cm of soil on terraces than *S. laevigata*, which may have much deeper roots in these areas (Figure 5).

HPO_4^{2-} adsorbs readily to soil particles (especially finer textured soils) and is most available to plants when dissolved in water at pH ~ 6.5 (Havlin et al. 1999). The mean soil pH of floodplains of reference watersheds was 7.38 (SE 7.26–7.50), which was similar to floodplains (7.41, SE 7.38–7.45) and terraces (7.38, SE 7.33–7.43) along the Santa Clara River. Higher than optimal pH levels in these areas may cause lower $\text{PO}_4\text{-P}$ availability for both plant species. The three-way ANOVA (land use x location x degree of infestation) of soil pH resulted in a very highly significant land use main effect (Table 6). Mean soil pH levels varied significantly from one another by land use type as follows: open space (7.57, SE 7.51–7.62), agricultural (7.40, SE 7.35–7.45), and residential (7.23, SE 7.18–7.28). Thus, $\text{PO}_4\text{-P}$ may be more available to plants adjacent to land use with higher anthropogenic inputs due to lower soil pH.

In the three-way ANOVA (watershed x land use x degree of infestation), the main effect of watershed was significant for percent total N content in the soil (Table 4); floodplain soils in Calleguas Creek (0.05%, SE 0.047–0.052%) contained significantly lower levels of mean total N than did soils along the Santa Clara River ($0.06 \pm \text{SE } 0.003\%$). $\text{NO}_3\text{-N}$ levels in the soil varied significantly by all factors (all main effects significant). The mean content of $\text{NO}_3\text{-N}$ was significantly higher in Calleguas Creek (2.1 ppm, SE 1.8–2.6ppm) than the Santa Clara River (0.7 ppm, SE 0.6–0.9 ppm). Floodplains adjacent to agricultural ($1.6 \pm 0.4 \text{ ppm}$) and open space (1.4 ppm, SE 1.1–1.8 ppm) contained significantly higher levels of $\text{NO}_3\text{-N}$ than those adjacent to residential

land uses (0.9 ± 0.2 ppm). Both large and small degrees of infestation were found to contain significantly higher mean $\text{NO}_3\text{-N}$ soil levels ($1.6 \pm \text{SE } 0.4$ ppm and 1.5 ppm, 1.1–1.8 ppm, respectively) than non-infested areas (0.8 ppm, SE 0.7–1.1 ppm). Levels of $\text{NH}_4\text{-N}$ were found to be significantly higher in floodplain soils of Calleguas Creek (1.5 ± 0.1 ppm) compared to the Santa Clara River (1.4 ± 0.1 ppm). The three-way interaction for mean $\text{PO}_4\text{-P}$ levels found in floodplain soils was significant (Table 4). In most cases, levels of soil $\text{PO}_4\text{-P}$ were higher in Calleguas Creek than along the Santa Clara River (Figure 6). Levels of $\text{PO}_4\text{-P}$ in floodplain soils adjacent to agricultural land uses in Calleguas Creek were higher than levels found in soil anywhere along the Santa Clara River. Large infestations of *A. donax* were associated with higher soil $\text{PO}_4\text{-P}$ levels than small or non-infested floodplains next to open space along the Santa Clara River.

Soil $\text{NO}_3\text{-N}$ and $\text{PO}_4\text{-P}$ concentrations were significantly higher on terraces versus floodplains of the Santa Clara River for all degrees of *A. donax* infestation according to the land use x fluvial geomorphic location x degree of infestation three-way ANOVA (Figure 7a and c). Soil nutrient levels did not differ significantly along floodplains, with the exception of lower $\text{PO}_4\text{-P}$ levels adjacent to residential compared to agricultural land uses (Figure 7d). However, soil associated with the deeper-rooted *S. laevigata* from non-infested riparian terraces contained significantly higher $\text{NO}_3\text{-N}$ and $\text{PO}_4\text{-P}$ concentrations than soil associated with either *A. donax* infestation stage (Figure 7a and c). Soil $\text{PO}_4\text{-P}$ levels associated with all land uses were significantly higher on terraces compared to floodplains (except between terrace open space and floodplain agricultural areas) (Figure 7d). Terrace sites adjacent to anthropogenic land uses had significantly higher soil $\text{PO}_4\text{-P}$ concentrations (as well as lower pH values allowing for greater availability) versus open space. Small and large *A. donax* infestations contained significantly more soil $\text{PO}_4\text{-P}$ adjacent to agricultural versus open space land use (Figure 7e).

One-way ANOVAs for mean soil $\text{NO}_3\text{-N}$ and $\text{PO}_4\text{-P}$ content by watershed were very highly significant (Table 5). Mean $\text{NO}_3\text{-N}$ content of soil along the floodplains of Calleguas Creek was significantly higher than content of soil along Santa Clara River. Soils sampled along Calleguas Creek contained significantly higher mean $\text{PO}_4\text{-P}$ content than soils along the Santa Clara River or Topanga Canyon.

3.3.2. Grain Size

In general, soil grain size was highly correlated with the watershed from which it was sampled and adjacency to certain land use types. However, the combination of fluvial geomorphic location and degree of infestation affected soil grain size distribution in the 3-way ANOVA (land use x geomorphic location x degree of infestation, Santa Clara River only) (Table 6). Percent silt + clay content was significantly higher on terraces versus floodplains in non-infested sites and small infestations of *A. donax* (Figure 7b). However, this parameter did not differ significantly by geomorphic landform within large infestations of *A. donax*. In addition, percent silt + clay did not differ by degree of infestation within floodplains but was significantly higher in non-infested sites versus large *A. donax* infestations on terraces. Reference sites contained 20.1% (SE 17.4–22.9%) silt + clay in floodplains, which was similar to small infestations of *A. donax* along floodplains but much lower than non-infested sites and small infestations along

terraces. One-way ANOVAs for mean percent silt + clay in floodplains by watershed were very highly significant (Table 6). Mean silt + clay content found in floodplain soils along the Santa Clara River was significantly higher than silt + clay content found along Calleguas Creek or Topanga Canyon floodplains.

3.4. Relationship between Shallow Groundwater, Soil, and Leaf Tissue Nutrients

Various forms of N and P found in the shallow groundwater and soils had positive linear relationships with N and P content of *A. donax* and *S. laevigata* leaves (Figure 5 and Figure 8). However, pools of N and P available to plants varied considerably by species, medium, and fluvial geomorphic location. In floodplains, linear regressions showed significant positive relationships between *A. donax* leaf tissue N and each form of N individually (total N, $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$, and $\text{NH}_4\text{-N}$) in the shallow groundwater (Figure 8). In fact, as groundwater nutrients increased, *A. donax* N content increased more than *S. laevigata* N content in each case. However, only relationships between total N and $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$ in the shallow groundwater and *S. laevigata* leaf tissue N content were significant. Relationships between P content of *S. laevigata* leaves and shallow groundwater $\text{PO}_4\text{-P}$ levels were highly significant in floodplains, but were not found between *A. donax* leaves and shallow groundwater $\text{PO}_4\text{-P}$ levels. A strong positive relationship was found between *A. donax* leaf N content and soil $\text{NO}_3\text{-N}$ on riparian terraces (Figure 5). Also, *A. donax* leaf N content indicated a positive relationship with both soil total N and $\text{NH}_4\text{-N}$ on terraces and $\text{NO}_3\text{-N}$ on floodplains; similar trends were not found for *S. laevigata*. No significant relationships were found between mean P content found in leaves of either species and soil $\text{PO}_4\text{-P}$ concentrations in terrace or floodplain locations.

3.5. Leaf tissue Nutrients

3.5.1. Total Nitrogen

Mean leaf tissue N content of *A. donax* varied by watershed and land use in the three-way ANOVA (watershed x land use x degree of infestation – non-infested sites excluded) (Table 4). N content of *A. donax* leaves was significantly higher adjacent to open space land use within Calleguas Creek than any other land use types along either stream (Figure 9a). The three-way ANOVA (land use x fluvial geomorphic location x degree of infestation – non-infested sites excluded) for *A. donax* leaf tissue N content revealed significant main effects for land use and degree of infestation on the Santa Clara River (Table 6). Mean leaf tissue N content was higher in sites adjacent to agricultural ($2.54 \pm \text{SE } 0.08\%$) and residential ($2.64 \pm \text{SE } 0.08\%$) land uses compared to open space ($2.21 \pm \text{SE } 0.09\%$). Large *A. donax* infestations ($2.59 \pm \text{SE } 0.07\%$) contained significantly higher mean leaf tissue N than small infestations ($2.36 \pm \text{SE } 0.08\%$).

The one-way ANOVA for mean N content of *A. donax* leaf tissue by infestation stage for all study watersheds was highly significant ($F_{(1,79)} = 8.858$; $P = 0.004$). Mean N of *A. donax* leaves was higher in large infestations ($2.67 \pm \text{SE } 0.06\%$, $n = 62$) than in small infestations ($2.38 \pm \text{SE } 0.07\%$, $n = 60$). The one-way ANOVAs for mean N leaf

content by watershed were very highly significant for *A. donax* only and *S. laevigata* only (Table 5). N content of *S. laevigata* leaves in reference sites and from Topanga Canyon was significantly lower than N content sampled along the floodplains of Calleguas Creek or the Santa Clara River. *Arundo donax* leaves sampled in Calleguas Creek contained significantly higher N content than leaves from either the Santa Clara River or Topanga Canyon. Although leaf tissue nutrient content could not be compared statistically between species because species-specific differences might confound comparisons, N content of *A. donax* leaves from all watersheds was higher than that of *S. laevigata* leaves in reference sites.

3.5.2. Total Phosphorus

Mean P content of *A. donax* leaves varied by watershed only in the three-way ANOVA (watershed x land use x degree of infestation – non-infested sites excluded)(Table 4). Leaf tissue mean P content was higher in Calleguas Creek (0.19%, SE 0.184–0.193%) than in the Santa Clara River (0.17 ± SE 0.006%). The three-way ANOVA (land use x fluvial geomorphic location x degree of infestation – non-infested sites excluded) for *A. donax* leaf tissue P content was not significant for any main effects or interactions (Table 6).

The one-way ANOVA for mean P content of *A. donax* leaf tissue by degree of infestation for all study watersheds was significant ($F_{(1,79)} = 4.817$; $P = 0.031$). Mean P of *A. donax* leaves was higher in large infestations (0.18% SE 0.173–0.180%, $n = 62$) than in small infestations (0.16% SE 0.155–0.164%, $n = 60$).

One-way ANOVAs for mean P content of leaves by watershed were significant for *S. laevigata* only and *A. donax* only (Table 5). *Salix laevigata* leaves contained higher P content along floodplains of Calleguas Creek than along floodplains of the Santa Clara River, Topanga Canyon, or reference sites. Mean leaf P content of *A. donax* leaves was significantly higher in Calleguas Creek than in the Santa Clara River. Although leaf tissue nutrient content could not be compared statistically between species, P content of *A. donax* leaves from all watersheds was higher than that of *S. laevigata* leaves in reference sites.

3.5.3. Total Potassium

Mean K content of leaf tissue varied by land use and degree of infestation in the three-way ANOVA (watershed x land use x degree of infestation – non-infested sites excluded) (Table 4). Leaf tissue K content was significantly higher in large infestations adjacent to residential land uses than in any other combination of land use and infestation stage (Figure 9b). The degree of infestation main effect was highly significant in the three-way ANOVA (land use x fluvial geomorphic location x degree of infestation – non-infested sites excluded) for *A. donax* leaf tissue K (Table 6). Mean leaf tissue K content was significantly higher in large *A. donax* infestations (2.94 ± SE 0.08%) than in small infestations (2.66 ± SE 0.06%).

Although the one-way ANOVA for mean K content of *A. donax* leaf tissue by degree of infestation for all study watersheds was not significant ($F_{(1,79)} = 3.578$; $P = 0.062$), mean K of *A. donax* leaves was higher in large infestations ($2.79 \pm \text{SE } 0.07\%$, $n = 62$) than in small infestations ($2.55 \pm \text{SE } 0.05\%$, $n = 60$). The one-way ANOVA for K content by watershed was not significant for *S. laevigata* leaves, but K content of *A. donax* leaves was significantly higher in the Santa Clara River compared to Calleguas Creek or Topanga Canyon (Table 5). Leaf tissue nutrient content could not be compared statistically between species, but K content of *A. donax* leaves from all watersheds was higher than that of *S. laevigata* leaves from reference sites or any of the study watersheds.

3.6. N:P and N:K Ratios

Shallow groundwater molar N:P ratios did not vary significantly in either three-way ANOVA or the one-way ANOVA by watershed. However, reference watersheds [2.1:1 (SE 2.0–3.0:1)] had lower mean N:P ratios than all study watersheds and Calleguas Creek [5.7:1 (SE 4.4:1–7.5:1)] had the highest ratio (Table 3). All mean N:P ratios were in the N limiting range (<15:1) according to the Redfield Ratio.

Arundo donax leaf tissue N:P ratios did not vary significantly in either of the three-way ANOVAs performed for the study watersheds (Table 3). When only *S. laevigata* leaves from floodplain locations were examined in the one-way ANOVA by watershed, leaf N:P ratios within reference watersheds were significantly lower than those within the Santa Clara River, and N:P ratios in Calleguas Creek were significantly lower than those in the Topanga Canyon or the Santa Clara River. In addition, the mean N:P ratio of *A. donax* leaf tissue was significantly higher in Calleguas Creek and the Santa Clara River compared to Topanga Canyon. Although statistical comparisons could not be made between the plant species, the mean N:P ratios of *S. laevigata* leaf tissue in reference sites were lower than the N:P ratio of *A. donax* leaf tissue in all study watersheds.

The land use x location x degree of infestation ANOVA for N:K revealed a significant land use main effect ($F_{(2,60)} = 4.589$; $P = 0.014$). Higher N:K ratios of *A. donax* leaf tissue were observed adjacent to residential (0.93:1, SE 0.89:1–0.96:1) and agricultural land uses (0.91:1, SE 0.88:1–0.94:1) compared to open space (0.78:1, SE 0.75:1–0.82:1). Mean N:K ratios of *S. laevigata* leaf tissue from floodplains did not vary among watersheds in the one-way ANOVA by watershed (Table 3). However, *A. donax* leaf tissue mean N:K was significantly higher in Calleguas Creek compared to either Santa Clara River or Topanga Canyon. Although statistical comparisons were not possible, the mean leaf N:K of *S. laevigata* was much higher in reference watersheds compared to *A. donax* leaf mean N:K ratios found in other watersheds.

4. Discussion

Anthropogenic nutrient enrichment of natural ecosystems has been linked to plant invasions worldwide (Mooney et al. 1986, Drake et al. 1989, D'Antonio and Vitousek 1992, Hobbs and Huenneke 1992, Vitousek et al. 1996, Brooks 2003). However, little is known about the influence of elevated nutrients on invasions in river systems of

Mediterranean-type climates such as California (Rundel 2000, Kim 2003, Robinson et al. 2005). This analysis of nutrient levels in several river systems in southern California supports the hypothesis that excess nutrients associated with anthropogenic land use activities have helped promote the recent invasion of riparian ecosystems by *A. donax* in southern California. We tested this hypothesis by evaluating N and P pools in shallow groundwater and soil within riparian ecosystems invaded to various degrees by *A. donax* adjacent to several land uses. All factors investigated – land use, watershed, and fluvial geomorphic location – were important in explaining nutrient distribution and *A. donax* invasion. Furthermore, our results indicate that the greater supply and availability of N and K to *A. donax* compared to native plants may contribute to invasion of riparian ecosystems by *A. donax* in southern California (Charbonneau and Kondolf 1993, CRWQCB-LA 1995).

4.1. Natural Nutrient Levels

Naturally occurring nutrient levels essential for terrestrial plant growth (primarily N and P) vary widely in soils and shallow groundwater due to climate, topography, organisms, parent material, and soil texture. Precipitation and nitrogen fixation are the main natural sources of N, but all other essential soil nutrients (including P and K) are inherited from the parent material or added anthropogenically (Day 1983, Rundel et al. 1983, Stark 1994). Soils in Mediterranean-type climate regions of the world are naturally deficient in N and/or P compared to other regions (Day 1983, diCatri 1991, Dallman 1998), but vary considerably within these regions especially in the extent to which they are available to plants.

Historical soil and shallow groundwater nutrient data for natural or undisturbed riparian ecosystems in southern California were not available for comparison with our study results. The highly erosive soils found throughout this region likely transport associated nutrients to the alluvium of low-lying river systems, especially after fire. Average total N levels found in floodplain soils of our reference watersheds were within the range of levels (slightly nutrient-rich) found in adjacent shrubland ecosystems of California (Day 1983, diCatri 1991) (Table 2). The young sedimentary geology of our study region is composed primarily of marine deposits containing organisms very high in P (Pettijohn 1975), creating soils higher in P than found in older more weathered geologies (Walker and Syers 1976, Groves et al. 1983). N and P levels found in the shallow groundwater of reference watersheds were low, although slightly higher than flow-weighted nutrient concentrations found in streams of many other small undeveloped basins in the U.S. (Williams et al. 1998, Clark et al. 2000) (Table 2).

4.2. Nutrient Limitation

N, P, and K alone and in combination were found to limit terrestrial and wetland plant production in the eastern U.S. and Europe (Koerselman and Meuleman 1996, Verhoeven et al. 1996, Svengsouk and Mitsch 2001, Knecht and Goransson 2004). Researchers have shown that N limits plant production on young substrates, such as southern California, whereas P is limiting on older substrates (Walker and Syers 1976, Vitousek 1996). Although nutrient limitations in riparian ecosystems of southern

California are undocumented, they may provide important insight into the invasion process; anthropogenic N inputs may be relatively more important to plant production than P in younger geologies of southern California.

Results of this study indicate that N limiting conditions (relatively higher P levels) may naturally occur in riparian ecosystems in this geologically young landscape as suggested by several researchers (Walker and Syers 1976, Vitousek 1996). The N:P (molar ratio) in shallow groundwater of reference sites in this study (2.4:1) was much lower than levels in sea water (<15:1 = N limiting conditions) or freshwater (19-48:1) reported in the literature, indicating naturally N limiting conditions in floodplains of southern California (Redfield 1958, Hecky et al. 1993). Also, leaf tissue N:P for *S. laevigata* in reference sites [12:1 (SE 11.5–12.8:1)] suggests that N may be naturally limiting to plants in this region (<14:1 = N limiting) (Koerselman and Meuleman 1996, Verhoeven et al. 1996).

Groundwater and leaf tissue N:P ratios found in this study suggest that N is naturally limiting in riparian ecosystems of southern California, but anthropogenic nutrient inputs have contributed to elevated ratios in more developed watersheds. Shallow groundwater N:P ratios were higher in study watersheds with higher anthropogenic nutrient inputs compared to no nutrient input reference sites. Mean surface water N:P ratios for rivers worldwide were much higher (24:1 or P limited according to the Redfield Ratio) than in our reference or study watersheds (Hecky et al. 1993). Warrick et al. (2005) found N:P molar ratios in the surface water of the Santa Clara River to be 5:1 during a winter storm event and <1:1 during the low-flow summer months, in a similar range (N limiting) to results found for reference and study watersheds.

The N:P and N:K ratios in leaf tissue have been used to indicate nutrient limitations in freshwater wetland plant communities (Koerselman and Meuleman 1996, Verhoeven et al. 1996, Svengsouk and Mitsch 2001, Knecht and Goransson 2004). According to Koerselman and Meuleman (1996), N:P ratios by mass $\leq 14:1$ (molar ratio 31:1) indicate N limiting conditions and ratios $\geq 16:1$ indicate P limitations. Similar to the trend in shallow groundwater N:P ratios, *S. laevigata* and *A. donax* leaf tissue N:P ratios found in reference watersheds were in the N limiting range (12:1) and adequate levels for both nutrients (14:1). Knecht and Göransson (2004) suggested optimal N:K nutrient ratios should be around 1.5:1 for deciduous and herbaceous plants based on a free supply of these nutrients under laboratory conditions. N:K ratios associated with *S. laevigata* leaf tissue in this study were similar to this optimal index (1.4:1–1.7:1) and did not differ by watershed. The *A. donax* leaf tissue N:K ratio was much lower (1:1) than that of optimal N:K, indicating that *A. donax* can assimilate K in excess of requirements (luxury consumption) or N may be limiting in relation to K.

4.3. Anthropogenic Nutrient Levels

Nutrient enrichment of rivers due to land use inputs is a global phenomenon. Increased use and composition of N and P in fertilizer have contributed to nutrient enrichment in rivers in agricultural landscapes (Charbonneau and Kondolf 1993, USEPA

1999, Nicola 2003). Surface and shallow groundwater run off from both agricultural and residential land use types contains excess N and P from fertilizers and drains into streams. Sewage treatment plants discharge treated wastewater that contains N, P, and K constituents into streams and rivers in southern California. Rural residential development throughout all of the studied watersheds may contribute $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, and $\text{NO}_2\text{-N}$ from septic tank leakage. In addition, levels of atmospheric N deposition are known to be high (from 1-45 kg/ha/year) around the Metropolitan Los Angeles Area (Padgett et al. 1999, Bytnerowicz et al. 2001, Meixner 2003, Lu et al. unpublished data). Although not widely known, K is required for biological phosphorus removal processes in sewage treatment plants (Brdjanovic et al. 1996). Thus, excess amounts of K may be associated with wastewater discharged into rivers in this study, especially Calleguas Creek or the Santa Clara River that receive sewage discharge throughout their course. Alternatively, if not enough K is used in wastewater treatment, treated water may contain higher levels of P. Levels of K were not measured in shallow groundwater or soil in this study but may be important in understanding higher K content of *A. donax* versus *S. laevigata* leaf tissue found and thus invasion success of *A. donax*.

Higher levels of N and P in the shallow groundwater and soil of riparian ecosystems were associated with sites invaded by *A. donax*. However, nutrient levels in riparian ecosystems were found to vary considerably by watershed, land use, and fluvial geomorphic location. These factors helped explain the influence of nutrients from anthropogenic inputs on invasion of riparian ecosystems by *A. donax* on both floodplains and terraces throughout the study area.

4.3.1. Watershed

Many studies have shown that nutrient inputs from agricultural and urban land uses result in elevated N and P concentrations in adjacent water bodies (Peterjohn and Correll 1984, Fail et al. 1986, Frink 1991, Correll et al. 1992, Rodda 1995, Warrick et al. 2005), but few have focused on variation among multiple watersheds or cumulative effects of upstream land use inputs (Correll 1984, Correll et al. 1992, Basnyat et al. 1999, Ahearn et al. 2005, Robinson et al. 2005). Although many similarities exist between watersheds located within a given region (i.e., geology, climate, riparian vegetation), variation in factors such as land use composition and soil type can greatly influence nutrient levels found in riparian ecosystems (Ahearn et al. 2005, Robinson et al. 2005). By comparing multiple watersheds with varying levels of anthropogenic nutrient inputs, our findings help disentangle the cumulative effects of both agricultural and residential land use on nutrient supply in floodplains at a watershed-scale. The general trend observed in total N, $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$, $\text{NH}_4\text{-N}$, and $\text{PO}_4\text{-P}$ concentrations in the shallow groundwater and soil on floodplains was Calleguas Creek > Santa Clara River > Topanga Canyon > reference sites. In addition, pH of the shallow groundwater was more acidic in the watersheds with the highest anthropogenic land use.

Shallow groundwater and soil in floodplains of Calleguas Creek contained much higher levels of $\text{PO}_4\text{-P}$ than the other study and reference watersheds. The higher percentage of agricultural and residential land uses and associated nutrients in this watershed compared to the other study watersheds might account for the observed P

enrichment and lower pH levels. Agricultural nutrient sources may be the primary contributor to the elevated $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$ levels found in groundwater in the floodplains of Calleguas Creek. Similar relationships between agricultural inputs and elevated nitrate were reported in other watershed-scale studies (Correll 1984, Peterjohn and Correll 1984, Correll et al. 1992, Rodda 1995, Basnyat et al. 1999, Ahearn et al. 2005, Robinson et al. 2005, Warrick et al. 2005).

4.3.2. Land Use

At a more local scale, adjacency to land uses was found to be important in characterizing nutrient supply on riparian terraces and floodplains. Adjacency to land use helped explain variation in nutrient supply in shallow groundwater total N and $\text{NH}_4\text{-N}$ in floodplain locations. Although $\text{NO}_3\text{-N}$ and $\text{PO}_4\text{-P}$ levels were higher in groundwater and soil on floodplains adjacent to agriculture than next to residential and open space land use in several cases, clearer trends were found on terraces in which $\text{PO}_4\text{-P}$ levels were higher adjacent to both agriculture and residential land use than next to open space.

4.3.3. Fluvial Geomorphic Location

N and P levels in the soil were much higher on riparian terraces than on floodplains regardless of land use type or degree of infestation. $\text{NO}_3\text{-N}$ and $\text{PO}_4\text{-P}$ soil content was lower in floodplains of reference sites than on riparian terraces of the rivers with anthropogenic inputs. Lower soil pH as well as percent silt + clay grain size (no and small infestations) on terraces contributed to higher availability of $\text{PO}_4\text{-P}$ on terraces compared to floodplains.

4.3.4. Degree of Infestation

Riparian ecosystems infested by *A. donax* contained higher $\text{NO}_3\text{-N}$ levels in floodplain soils than did non-infested or reference sites, which may be the result of high nutrient input and adjacency to agricultural land use of invaded sites. Non-infested riparian terrace sites contained higher $\text{NO}_3\text{-N}$ and $\text{PO}_4\text{-P}$ levels than did sites invaded by *A. donax* on the Santa Clara River. This trend likely reflects the better utilization of surface soil nutrients on terraces by the shallow, extensive root system of *A. donax* compared to the much deeper tap root of *S. laevigata* trees (Phillips 1963, Russell 1963) (Figure 3). Conversely, *A. donax* and *S. laevigata* are likely to derive nutrients from similar depths in floodplains where available nutrients (and water) are much closer to the surface. Relationships among nutrient sources, nutrient pools, and *A. donax* infestation level also were controlled by differences in nutrient availability to plant species, which in turn were controlled by physical constraints in the environment and species-specific rates of nutrient uptake, assimilation, metabolism, and limitation.

4.4. Factors Controlling Nutrient Availability

Nutrient availability in relation to supply of nutrients is key to understanding the *A. donax* invasion process, but quantification of nutrient availability is complex (Day 1983). Wetting and drying cycles, high soil temperatures, and wildfires characteristic of Mediterranean-type climates promote the release of nutrients by increasing the turnover

of microbial biomass and organic matter that is otherwise sequestered (Stark 1994). Decomposition of litter releases nutrients, but quantities may vary by leaf species. Nutrients are thought to be most available in spring and autumn when water availability and temperature do not limit plant productivity (Day 1983). However, nutrient supply to floodplains of river systems in California was found to be greatest during winter storms (Robinson et al. 2005, Warrick et al. 2005). Supply to riparian terraces may occur throughout the year due to nutrient inputs from agricultural runoff, and supply to floodplains may occur year round due to sewage treatment plant releases. Ash from wildfires may contribute high proportions of N to riparian ecosystems and is considered to be a main factor promoting growth after fire (Day 1983).

Supply of N and P in the soil and their availability to plants vary greatly based on grain size, pH, and rooting depth (Metz et al. 1966). Variability in soil grain size and associated cation exchange and moisture holding capacity affects rates of diffusion transport of nutrients in the soil. Soil grain size has a strong influence on water and nutrient retention in soils: Coarser soils retain less water than finer particle soils, such as clay and silt, and have a lower cation exchange capacity due to lower surface area (Kozlowski et al. 1991, Taiz and Zeiger 1991). Soils with higher cation exchange capacity supply more minerals to roots. In this study, nutrient content in the soil was strongly correlated with grain size. On riparian terraces, different degrees of infestation had similar trends in soil grain size and NO₃-N and PO₄-P concentrations. The relatively higher amount of finer soil particles in non-infested terrace sites relative to infested sites may have contributed to the higher soil nutrient levels found in the former.

Rate of P uptake by plants is strongly related to soil pH. Typically, basic soil pH values result in lower solubility of phosphate salts and thus a lowered ability of plant roots to assimilate P (Taiz and Zeiger 1991). At soil pH levels near 7.5 found in this study, P was slightly less available to plants than at optimal pH conditions (optimal pH = 6.5). However, native plants that have evolved under these conditions may have adapted mechanisms to extract P under lower than optimal pH conditions (Koerselman and Meuleman 1996). The ability to assimilate nutrients available in the surrounding soil and groundwater depends on development of an extensive root system and rooting structure, as well as mycorrhizal symbionts that maximize uptake (Kozlowski et al. 1991). For example, higher root surface area increases uptake rates and high P influx and root/shoot ratio results in higher P efficiency. Root morphology and architecture differ between monocots, such as *A. donax*, and dicots, like *S. laevigata* (Taiz and Zeiger 1991). Roots of *A. donax* are composed primarily of fibrous roots and tend to be much shallower than those of *S. laevigata*, which has a taproot that can extend 20 m or more to groundwater (Figure 3). Physiological strategies of these plants differ greatly due to their inherent structure. Although *A. donax* has a shallower and less extensive rooting system, it is aided by a large rhizome that stores carbohydrates, water, and minerals under stressful conditions (Else 1996, Wijte et al. 2005). In contrast, *S. laevigata*, a large woody phreatophyte, has a long taproot and well-developed root system that can reach deeper groundwater and associated nutrients (Robinson 1958). Nutrient availability of N, P, and K to terrestrial plants is usually higher in surface layers of the soil, due to the more neutral pH, ease of root penetration, and accumulation of organic matter. Thus, *A. donax* may utilize nutrients in the upper soil profile and shallower groundwater, whereas *S.*

laevigata may rely on a greater percentage of nutrients from deeper sources where a higher percentage of its roots are distributed.

On riparian terraces in which shallow groundwater occurs at a much greater depth than in floodplains, the differences in rooting structure of *A. donax* versus *S. laevigata* must be considered. *Salix laevigata* can use much deeper water (and associated nutrient sources) than *A. donax*. Results of this study reflect this difference, indicating significantly higher concentrations of NO₃-N and PO₄-P in terrace soils associated with *S. laevigata* in non-infested sites. However, higher soil nutrient levels observed next to non-infested sites may be due partly to variation in nutrient fluctuation rates as well. It follows that growth and invasion of *A. donax* depends more on shallower soil moisture and associated nutrients than *S. laevigata* (Figure 3). Soil nutrient results suggest that these two species may avoid competition for nutrients on riparian terraces after establishment, due to their varying rooting depths at maturity (Verhoeven et al. 1996). However, *A. donax* may have other adaptations as well, such as higher growth response to N or nitrogen-use efficiency that result in its invasion success on terraces.

Variation in availability of N, P, and K to *A. donax* versus native *S. laevigata* is important in understanding the invasion process. Rates of nutrient assimilation and efficiency vary genetically by plant species (Duncan 1994). Plants adapted to more-fertile soils exhibit higher maximum potential growth rates compared with plants that have evolved under low soil nutrient conditions (Chapin et al. 1986). Thus, levels of available N, P, and K may vary greatly in their importance to the growth response of *A. donax* compared to *S. laevigata*. Data are not currently available on species-specific growth response of *A. donax* or *S. laevigata*, but fertilization studies should be conducted to measure their growth response to N, P, and K levels. Due to unknown species-specific assimilation rates and efficiency, leaf nutrient content of *A. donax* and *S. laevigata* could not be compared statistically to evaluate nutrient content of leaf tissue with respect to degree of infestation and other factors. However, several analyses are presented below in which availability to both species could be assessed.

4.5. Nutrient Supply and Availability

The nutrient content of leaf tissue is closely correlated with changes in nutrient availability due to supply during the growing season (Bouma 1983, Chapin and Cleve 1989). Relationships between N and P content of *A. donax* and *S. laevigata* leaf tissue and concentrations of nutrient in the surrounding shallow groundwater and soil indicate relative sources of N and P that may be used by each species on riparian floodplains versus terraces in this study. In floodplains, *A. donax* exhibited a significant positive response to all forms of N in the shallow groundwater and NO₃-N in the soil, whereas *S. laevigata* showed a significant positive response to only NO₃-N + NO₂-N and PO₄-P pools in shallow groundwater. No significant relationships were found between soil N or P and *S. laevigata* leaf tissue nutrients in either floodplains or terraces, which suggests that this species may use primarily deeper nutrient pools. On riparian terraces, *A. donax* appears to use all forms of soil N, unlike *S. laevigata*. Relationships between nutrient supply and nutrient status of leaves support the assertion that these two plants may use different sources of nutrients on riparian terraces. These findings suggest that *A. donax*

may have two main advantages over *S. laevigata*: (1) it is better able to uptake nutrients in the surface soils of riparian terraces due to different root distribution of the two species; and (2) it does not appear to require as much P.

Analysis of leaf tissue nutrient content revealed a clear link between *A. donax* invasion and anthropogenic supply of nutrients. In general, for both species percent total N, P, and K content of leaf tissue was higher in watersheds with greater anthropogenic inputs. In addition, *A. donax* leaf tissue N was higher in riparian ecosystems adjacent to both agricultural and residential land use types compared to open space. Total N, P, and K content of leaf tissue were much higher in areas heavily infested by *A. donax* than in areas with small infestations. These results suggest that a greater supply of N, P, and K from anthropogenic nutrient sources may be more available to *A. donax* in highly invaded riparian ecosystems than elsewhere. Preliminary analyses show that *A. donax* leaf litter contains significantly lower N content and higher C:N than litter from a mix of native species including *Salix* spp. (Lambert unpublished data). However, species-specific nutrient assimilation and efficiency may vary and must be considered when comparing results for both species.

High levels of K found in *A. donax* leaf tissue were of particular interest and may be critical to the invasion process. Spencer et al. (2005) found that soluble K levels in the soil were higher where *A. donax* relative growth rate was greatest in northern California. K fertilization studies indicate a positive growth response and an increase in tissue K with increasing K availability in forest soils (Tripler et al. 2006). Although soil K was not measured in this study, *A. donax* leaves exhibited higher K levels in heavily infested sites adjacent to residential land use compared to areas with small infestations and were found to contain almost twice as much K as the native *S. laevigata*. Terrestrial plants use large amounts of K for various physiological activities, including stomatal regulation, but uptake mechanisms and efficiencies vary among plant species (Stark 1994). Adequate K is also known to prevent drought stress in crop plants (Spencer et al. 2005). High levels of K supply may give *A. donax* a competitive advantage during the hot, dry summer months in southern California. *Arundo donax* may either assimilate K more effectively than *S. laevigata* and/or levels of K in the soil or shallow groundwater may have been higher around *A. donax*. Fertilization studies measuring K uptake by *A. donax* compared to other native riparian species are needed to further understand its role in *A. donax* invasion.

5. Management and Restoration Implications

This study elucidated the influence of anthropogenic nutrient inputs on invasion of riparian ecosystems of southern California by an alien plant species. Enrichment of shallow groundwater with excess total N, NO₃-N, and NH₄-N from adjacent land appeared to have facilitated the rapid expansion of *A. donax* in the riparian ecosystems studied. Riparian terraces heavily invaded by the large, perennial grass *A. donax* were associated with nutrient inputs from adjacent agricultural and residential land uses. Contribution of nutrients from a combination of land use practices had an even stronger cumulative effect on invasion in floodplains at a watershed scale. Although not

addressed in this study, the role of atmospheric N deposition as an important source of NO_3^- around large urban areas in *A. donax* invasion requires further attention.

Arundo donax will likely continue to spread rapidly in watersheds and locations within watersheds with higher anthropogenic nutrient loading regardless of the source. Reducing nutrient inputs to riparian ecosystems in California and other Mediterranean-type climate regions may help reduce the rate of spread of *A. donax* in watersheds where its distribution is low or it is not yet present. Within these watersheds, evaluation of nutrient levels in riparian ecosystems may help predict the threat of invasion; however, other factors (i.e., water availability) likely contribute to the invasion process. Results of this study indicate that riparian ecosystems adjacent to intensive agricultural operations or wastewater treatment plant discharge on terraces are at the greatest risk of invasion by *A. donax* if this species is introduced. Also, watersheds with high percentage of agricultural and residential land use composition are at risk. Recent expansion of urbanization and agricultural practices in watersheds of other Mediterranean-type climate regions, such as the Western Cape of South Africa, has resulted in similar trends in rapid expansion of *A. donax* in more urbanized streams and rivers (Samuels and Knight 2003). Land management practices related to both agricultural and residential development should be evaluated to determine their nutrient inputs to riparian ecosystems, and best management practices should be employed to lower nutrient inputs to help control *A. donax* invasion along river systems.

Fluvial processes of flooding or scouring of streams in years with heavy rainfall are certainly primary factors in promoting spread of *A. donax*. The results showed that higher supply and availability of N, P, and K may also contribute to *A. donax* invasion after it is dispersed. However, manipulative experiments are needed to determine clear causal relationships between nutrient supply and availability to *A. donax* compared to dominant native riparian species under various water availability conditions. Further experimental investigation of the effects of light, water, and fire relative to nutrients on invasion of riparian ecosystems by *A. donax* will help elucidate the invasion process. Investigation of *A. donax* distribution and age of infestation related to land use change over time throughout watersheds in Mediterranean-type climates may provide further insight into contribution of anthropogenic land use to the invasion process.

Removal of invader species is often the initial step and prime component of stream restoration and mitigation in southern California (Coffman et al. 2004). Restoration plans for river systems and associated riparian revegetation must address anthropogenic nutrient levels if eradication or control of *A. donax* is a desired objective. In watersheds where nutrient levels are high, dam or levee removal projects need to consider the possibility that restoration actions might further distribute *A. donax* and promote its invasion. Revegetation or restoration on high terrace locations should proceed with caution; high levels of nutrients added by land use practices or released by wildfires may promote *A. donax* invasion. With nutrient enrichment that exists throughout urbanized watersheds in southern California, aggressive maintenance programs and native riparian plant revegetation are essential elements of comprehensive *A. donax* removal and control programs.

CHAPTER 3 - WILDFIRE PROMOTES GIANT REED (*ARUNDO DONAX*) INVASION IN RIPARIAN ECOSYSTEMS

Abstract: Invasion of riparian ecosystems by the large bamboo-like grass species *Arundo donax* L. has caused major alterations to structure and ecosystem functions in streams of arid and Mediterranean-type climate regions. Although healthy riparian ecosystems function as natural barriers to wildfire, the extensive wildfires in southern California in October 2003 burned large expanses of riparian ecosystems along the Santa Clara River and appeared to promote *A. donax* invasion. We investigated post-fire plant colonization of riparian areas along the Santa Clara River to determine the influence of wildfire on *A. donax* invasion. Growth of *A. donax* was compared to native plants for 1 year after the fire. Pre- and post-fire plant abundance and soil nutrient concentrations were analyzed to ascertain the role of fire-derived nutrients in the invasion process. Due to its immediate re-growth after the fire and its high growth rate compared to native riparian plants, *A. donax* dominated these burned riparian ecosystems within a few months after the fire and reached 99% cover a year later. *Arundo donax* grew an average of 3–4 times faster than native woody riparian plants – up to 2.62 cm/day (average 0.72 cm/day) – and reached up to 2.3 m in height less than 3 months after the fire. One year post-fire, *A. donax* density was nearly 20 times higher and productivity was 14–24 times higher than native plants. Elevated soil NH₄-N and P levels post-fire may have stimulated the high growth rate of *A. donax*. Large quantities of *A. donax* biomass that have replaced native woody species after wildfire have increased susceptibility of riparian ecosystems along the Santa Clara River to fire, creating an invasive plant-fire regime cycle. Wildfire not only promotes dominance of riparian ecosystems by *A. donax*, but also alters vital ecosystem processes and increases the risk of fire spreading to surrounding shrublands, towns, and agriculture.

1. Introduction

Historically, dense cover of chaparral biomass accumulating over a 30–50 years or more provided fuel for high-intensity wildfires in shrublands of southern California and in similar shrublands of other Mediterranean-type climate regions (Minnich 1983, Keeley et al. 1999, Keeley and Fotheringham 2001, 2005). However, riparian corridors may have acted as natural firebreaks (Dudley 1998, Rundel 2000, 2003) and refuge for wildlife in the landscape because of their low-lying topographic position and relative absence of flammable fuels. Lightning was the primary cause of wildfires, especially during dry, low humidity conditions that occur in the late summer and fall (Naveh 1975, Keeley 1982, Keeley et al. 1999). Currently, most wildfires in these areas are anthropogenic in origin (Rugen 1987, D'Antonio and Vitousek 1992, Keeley et al. 1999).

Invasion of annual grass species has been linked to altered fire regimes in rangelands, deserts, and wildlands of California and the western U.S. (Brooks and Pyke 2001, Brooks et al. 2004, Dukes and Mooney 2004). Grass/fire cycles, more recently termed invasive plant-fire regime cycles, may ensue when alien grass species colonize an area and provide fuel for fire propagation, increasing frequency, area, and intensity of fires (D'Antonio and Vitousek 1992, D'Antonio 2000, Brooks 2002, Brooks et al. 2004, Keeley 2004, Keeley and Fotheringham 2005). Rapid recovery of alien grass species compared to native species after fire leads to increased susceptibility of that ecosystem to fire.

In coastal shrubland watersheds in California, a large invasive grass species *Arundo donax* may be an even bigger problem in riparian ecosystems due to its perennial growth form with a large volume of biomass produced, flammability compared to natives, and immediate rapid growth after fire (Rieger and Kreager 1989). *Arundo donax* was introduced from southern Eurasia into the Los Angeles region several hundred years ago for erosion control and building materials (Robbins et al. 1951, Perdue 1958, Dudley and Collins 1995), and now infests many stream and river system in coastal California (Gaffney 2002). The natural flood disturbance regime in this climate regime successfully distributes it along rivers, where it establishes readily on bare substrates (Else 1996, Else and Zedler 1996). Studies suggest that increased water and nutrient delivery to these systems have increased its invasion success (see Chapter 2 and 3), yet the influence of fire on its invasion in river systems remains relatively unexplored and undocumented. Several accounts suggest that infestations of *A. donax* have increased fuel load as well as fire frequency and intensity along riparian corridors (Robbins et al. 1951, Bell 1994, Scott 1994, D'Antonio 2000). Growing to between 4–8 m in height and as fast as 10 cm per day (Perdue 1958, Crampton 1974, Hickman 1993), it produces abundant flammable biomass that accumulates during the summer and fall months (Rundel 2000). The ability of its rhizomes to recover more rapidly than native plants after fire likely contributes to its invasion success, but no evidence exists to document this response to fire. Furthermore, increased post-fire nutrient effects may promote a positive feedback cycle (invasive plant-fire regime) in these ecosystems.

Although little research exists on the effects of fire in riparian ecosystems, several authors have suggested that fire may increase the ability of *A. donax* to invade natural

riparian systems (Rieger and Kreager 1989, Scott 1994, Bell 1997). The large amount of highly flammable biomass that *A. donax* produces and that accumulates during most of the year, as well as the ability of its rhizomes to respond quickly after fire, likely contribute to its invasion success by creating an invasive plant-fire regime cycle. DiTomaso (1998) suggests that *A. donax* invasion is changing riparian ecosystems from primarily flood-defined (Mount 1995) to fire-defined systems. The Simi/Verdale wildfire of October 2003 (Ventura County, CA) (Keeley and Fotheringham 2005) provided a unique opportunity to study the contribution of fire to invasion of riparian terrace ecosystems of the Santa Clara River by *A. donax*. In this study, we compared growth and recolonization of *A. donax* to that of native plant species in riparian ecosystems burned in a southern California wildfire. We hypothesized that high adjacent soil nutrient content, immediate post-fire resprouting phenology, and higher growth rate than native plants promote invasion of *A. donax* in riparian corridors of southern California.

2. Methods

2.1. Study area

Study sites were located in the approximately 700-acres of riparian ecosystem of the Santa Clara River that was burned in the late October 2003 Simi/Verdale fire (Keeley and Fotheringham 2005) (Figure 10). The 187 km-long Santa Clara River and its tributaries drain a 4,185 km² watershed, the second largest coastal watershed in southern California. Hundreds of acres of *A. donax* infest floodplains and terraces along the Santa Clara River. Natural riparian vegetation on terraces consisted of large riparian trees, both black cottonwood (*Populus balsamifera* (L.) ssp. *trichocarpa* Torrey & A. Gray) and red willow (*Salix laevigata* Bebb) in the canopy layer. A mixture of smaller trees and shrubs comprised the understory layer, including arroyo willow (*Salix lasiolepis* Benth.), sandbar willow (*Salix exigua* Nutt.), shining willow [*Salix lucida* Muhl. ssp. *lasiandra* (Benth.) E. Murray], mulefat [*Baccharis salicifolia* (Ruiz Lopez & Pavon) Pers.], and blue elderberry (*Sambucus mexicana* C. Presl.).

2.2. Study design

Six sites established in a previous study along the Santa Clara River (see Chapter 3) were burned during the 2003 wildfire. These study sites were all located on riparian terraces, and five out of six sites were adjacent to shrubland ecosystems. The wildfire crossed the river through one site located near the Los Angeles-Ventura County line and the other five sites were located near the town of Santa Paula. We compared pre-fire plant composition and soil nutrient data collected in summer 2003 at these six permanent monitoring sites to data collected in these sites during the year after the wildfire (2004). We established eight additional study sites along riparian terrace areas burned to the west of these sites in a river reach that did not contain previous study sites to make sure sites were well-distributed throughout the riparian areas burned and represented the range of environmental conditions found in the study area. We monitored recolonization of all sites from November 2003-October 2004 (Figure 10) (see Appendix 4-1 in Coffman 2007 for study site locations and descriptions). The 14 study sites were approximately 600 m² (most sites were 30 m long x 20 m wide) and all but one was

located next to open space land use types; the one exception was adjacent to a citrus orchard.

2.3. Study species

Arundo donax is a robust, perennial, bamboo-like member of the Poaceae family (grass family) that occurs throughout the floodplains and terraces of rivers in California and other warm, temperate climates worldwide (Crampton 1974, Hickman 1993). It has erect, stout yet hollow culms that are 1–4 cm in diameter and 2–8 m or more tall. Culms branch, forming ramets, typically at the end of the first year of growth or after a culm is damaged. Leaf blades are broad (2–6 cm wide), less than 1 m long, flat, clasping at the base, strongly scabrous along their margins, and evenly spaced along the culm (Faber and Holland 1992, Hickman 1993). *Arundo donax* reproduces vegetatively through a network of large thick rhizomes that grow horizontally just below the surface of the soil. Under some conditions it produces a large (3–6 dm), terminal, plume-like inflorescence (panicle) at the end of the growing season (Faber and Holland 1992, Hickman 1993); however, seeds of the inflorescence are primarily sterile in California (Johnson et al. 2006).

In addition to *A. donax*, we studied several native riparian plant species commonly found on terraces of rivers in southern California and in terraces that were burned in the fire: *Salix laevigata*, *S. lasiolepis*, *S. exigua*, *Populus balsamifera* ssp. *trichocarpa*, and *Baccharis salicifolia*. *Salix laevigata* is a riparian tree that reaches heights up to 15 m and is dominant in both floodplains and terraces along southern California rivers, and *Populus balsamifera* ssp. *trichocarpa* grows to a height of 30 m in alluvial plains and terraces along rivers in southern California (Faber et al. 1989, Faber and Holland 1992, Hickman 1993). *Salix lasiolepis* is a widely distributed plant that occurs as a small tree in wetter areas and a spreading shrub in drier locations (Faber et al. 1989). *Salix exigua* is a shrub-sized willow that commonly grows on sandy substrates along active floodplains (Faber et al. 1989). *Baccharis salicifolia* is one of the most dominant shrubs found throughout floodplains and terraces of streams and rivers of southern California. A member of the Asteraceae, it usually grows to a height of less than 4 m.

2.4. Sampling methods

We took plant measurements monthly from November 2003 to October 2004 in all 14 study sites to examine the effects of fire on recolonization of riparian terraces. We determined change in plant abundance in burned areas by comparing pre- and post-fire (summer 2003 and July 2004) percent cover of *A. donax* and native woody plant species in the six long-term study locations. Ocular estimates of percent cover by species were taken within 1 m² quadrants placed randomly throughout six permanent study sites during summer 2003 and all 14 study sites during each post-fire sampling period. Post-fire mean shoot density (stems m⁻²) of *A. donax* and all native species were sampled monthly within six 1m² quadrants (placed randomly each time) within all 14 study sites. We measured mean shoot length (cm) and basal diameter (mm) of 20 randomly selected *A. donax* and 20 native individuals of each dominant native woody species at each study site

and post-fire sampling period. In addition, we measured shoot height and basal diameter for three permanently marked *A. donax* and native plant shoots (three of each species) at each sampling period. Basal diameter measurements were taken 10 cm above the surface of the soil. We calculated mean shoot elongation rate (cm d⁻¹) for each species using data from the permanently marked individuals.

We calculated the aboveground biomass, relative growth rates (RGRs), and productivity of plants within the study sites using the plant dimension data collected during the study. Non-destructive dimensional analyses were used to estimate aboveground biomass dry weight of plants in study sites with minimal interference to plant growth (Whittaker 1961, 1965, Whittaker and Marks 1975, Sharifi et al. 1982, Spencer et al. 2006). We created regression models for each species using basal diameter, shoot length, and aboveground biomass of culm/branch samples measured in the field experiment to predict biomass of each individual plant sampled in the study sites. Regression models for aboveground biomass were very highly significant for all species ($r^2 = 0.971$ to 0.990 , $P < 0.001$) (see Chapter 2 for study design and Appendix 2-1 in Coffman 2007 for equations). *Arundo donax* biomass was estimated based on both basal diameter and shoot length measurements taken at all study sites, and native species biomass estimates were based on basal stem diameter. All data were log transformed in regression models.

We calculated RGRs for all permanently marked individuals using the following differential equation, where W is the total aboveground biomass dry weight (g) of each shoot and t is time (day⁻¹ post-fire).

$$\text{RGR} = \frac{dW}{dt} \frac{1}{W} = \frac{d(\ln W)}{dt}$$

Mean productivity (kg m⁻² year⁻¹) for each species was calculated at approximately 1 year post-fire. We estimated biomass (kg) for the 20 randomly sampled culms/stems for each species measured during September 2004. For each species, mean biomass per shoot (kg shoot⁻¹) was multiplied by mean density (shoots m⁻²) at each study site and then divided by time (year). We averaged productivity calculations for each species across study sites.

Five soil subsamples were collected at each study site adjacent to *A. donax* and each native woody plant species immediately after fire (November through January). Subsamples were collected in the upper 20 cm of the soil where nutrient concentrations are greatest (Day 1983). For each species, soil samples were combined into a composite sample by thorough mixing in a stainless steel bowl. Each soil subsample was collected with an 8-cm diameter bucket auger. Soil samples taken before the fire (summer 2003) were taken adjacent to *A. donax* and *S. laevigata* according to the same sampling protocol.

Soil samples were air-dried and ground to a powder in preparation for nutrient content analyses at the DANR Analytical Laboratory in Davis, California. Soil samples were analyzed for total N (%), nitrate-N (NO₃-N - ppm), ammonia-N (NH₄-N - ppm), and

orthophosphate (PO₄-P - ppm). Total N in the soil was determined by the combustion gas analyzer method (Method 972.43) (Hofer 2003, Knepel 2003). Concentrations of NO₃-N and NH₄-N in the soil were determined by equilibrium extraction of soil with potassium chloride and a flow-injection analyzer (Olsen and Sommers 1982, Prokopy 1995). Because the soils studied were neutral to alkaline, the Olsen-P method was used to estimate the relative availability of inorganic PO₄-P in the samples. Soil grain size was analyzed using a hydrometer to determine the particle size distribution of sand, silt, and clay in soil suspension (Sheldrick and Wang 1993).

2.5. Statistical analyses

One-way and two-way analysis of variance (ANOVA) tests were used to analyze effects of various combinations of factors (plant type and time) on plant performance and growth data (dependent or response variables) (Systat Statistical Program [Version 10]). Factors tested include plant type (*A. donax* and native plant species) and time (pre-fire vs. post-fire or months post-fire). Dependent variables included plant abundance (percent cover), density (stem m⁻²), shoot length (cm), shoot elongation rate (cm d⁻¹), RGR (g g⁻¹ day⁻¹), productivity (kg m⁻² yr⁻¹), and soil nutrient concentrations (NH₄-N, NO₃-N, and phosphate in ppm).

We conducted a one-way ANOVA of productivity by species (*A. donax*, *B. salicifolia*, and *S. laevigata*) and two way-ANOVAs for all plant performance metrics by factors of plant type and time to determine differences in plant growth by species over time post-fire. Tukey's post-hoc test was used for pairwise comparisons of means in the one-way ANOVA. We performed ANOVA hypothesis tests to evaluate contrasts between means of grouping variables and levels in two-way ANOVA results. Probability plots were examined to test for normality of data and to identify any data that required transformation. All biomass, soil NH₄-N, and NO₃-N data were ln transformed. When means and standard errors were used to describe or present statistical differences, data were back-transformed and reported in original units.

3. Results

3.1. Pre- versus post-fire plant abundance

In the two-way ANOVA (plant type x time period) of plant abundance, both main effects were significant (Table 7). Percent cover of *A. donax* was much higher than native plant cover both before and after the study sites were burned (Figure 11). Although both *A. donax* (65.0 ± SE 6.7% cover) and the native plants (21.7 ± SE 6.0% cover) were in greater abundance before the fire, less than a year after the fire *A. donax* (42.8 ± SE 4.3% cover) was the dominant plant species in these riparian ecosystems (Figure 11). Native species comprised 25.0% of the total vegetation before the fire and less than 1% (0.4 ± SE 0.2% cover) of the vegetation in burned riparian terraces only 9 months after the fire.

3.2. Post-fire density

The two-way ANOVA (plant type x time period) of plant density revealed a significant two-way interaction (Table 7). The mean density of *A. donax* (stems m⁻²) was much greater than that of native plant species for all months sampled (March–September 2004) (Figure 12). Mean density of native plant species declined somewhat over time during the first year after the fire, although differences between sampling periods were not significant. However, mean density of *A. donax* shoots increased significantly over time. A year after the wildfire, *A. donax* density ($26.3 \pm \text{SE } 3.2$ stems m⁻²) was an order of magnitude greater than that of native species ($1.4 \pm \text{SE } 0.4$ stems m⁻²) within the burned riparian ecosystems sampled.

3.3. Post-fire shoot length

Post-fire resprout timing and shoot length over time differed significantly between *A. donax* and the native plants studied (Figure 13). *Arundo donax* began growing within days after being burned to the ground, whereas native plants did not start to appear (a few seedlings/resprouts at eight sites) until January (over two months after they burned). The two-way ANOVA of shoot length by plant type and time period resulted in a very highly significant two-way interaction (Table 7). Shoot length was 1.7–5.2 times greater (over 2.5 times greater on average) for *A. donax* than for natives during all months sampled (Figure 13).

3.4. Post-fire shoot elongation rate and RGR

Arundo donax shoots grew at a much faster rate than the native riparian plant species within the first year after fire (Figure 14 and Figure 15). The two-way ANOVA (plant type x month post-fire) for the shoot elongation rate revealed a significant two-way interaction due to variation in rate between species for each time period (Table 8). The highest *A. donax* shoot elongation rates were observed immediately post-fire (first two months) and in April 2004 at the beginning of the growing season. During the first 3 months post-fire, *A. donax* exhibited very high shoot elongation rates. Native plant species did not emerge until January 2004 and grew much more slowly than *A. donax*. Mean shoot elongation rates of *A. donax* were significantly higher than those of native plant species except during the winter (between January and March) when rates did not differ significantly. A series of heavy frosts occurred in late February 2004 (4 months post-fire), and they appeared to have lowered *A. donax* shoot elongation rates substantially. In April, shoot elongation rates for both *A. donax* and native plant species increased from winter levels, corresponding with warmer spring growing conditions. From April 2004 until the end of the year, elongation rates decreased for all plants, with *A. donax* maintaining higher rates (up to two times higher) than native species until December 2004.

In the two-way ANOVA (plant type x month post-fire) of RGR, the two-way interaction was very highly significant (Table 8). The mean RGR of *A. donax* was much greater initially (first three months) than that of the native plant species (Figure 15). *Arundo donax* mean RGR was extremely high ($0.094 \pm \text{SE } 0.005$ g g⁻¹ day⁻¹) immediately

after being burned, whereas the native plants did not emerge until the third month after the fire and then grew at a much more moderate rate. Mean RGR of native plants was highest five months after the fire and significantly higher than *A. donax* during the spring. As mentioned above, a series of very heavy frosts in February 2004 appeared to curtail *A. donax* growth but had little effect on the RGR of native plants. The mean RGR of both *A. donax* and native plants was very low at the end of the growing season, from mid-summer (July) to late fall (November).

3.5. Post-fire productivity

Approximately one year after the fire, *A. donax* productivity was much higher than that of any of the native species ($F_{(2,295)} = 43.291$; $P < 0.001$) (Figure 16). Productivity of *A. donax* was 14 times higher than that of *B. salicifolia* and 24 times higher than that of *S. laevigata* in burned areas. Due to initial low abundance and significant mortality during the year, *S. exigua*, *S. lasiolepis*, and *P. balsamifera* ssp. *trichocarpa* were at such a low density in burned sites that their productivity was undetectable one year after the fire.

3.6. Soil nutrients

Mean pre- and post-fire soil nutrient levels surrounding *A. donax* compared to native plants differed significantly (Figure 17; Table 9). Mean soil nutrient levels ($\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, and $\text{PO}_4\text{-P}$) adjacent to *A. donax* plants increased substantially after the study sites burned. However, no significant differences in nutrient concentrations were observed between pre- and post-fire soil adjacent to native plant species. After the study sites burned, both $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ concentrations were more than twice as high in the soil adjacent to *A. donax* plants compared to native plant species.

4. Discussion

In this study, we explored the role of fire in the *A. donax* invasion process in riparian ecosystems of southern California where wildfire is naturally prevalent in adjacent shrubland ecosystems. Burning through nearly 300 ha of *A. donax* infested riparian terraces, the October 2003 Verdale-Simi fire provided an opportunity to examine ecosystem-level effects of wildfire, namely the change in native versus invasive plant composition, and mechanisms responsible for invasion by *A. donax*. Comparisons of post-fire *A. donax* and native plant performance demonstrate several physiological and morphological characteristics that give *A. donax* an advantage over native species after fire. Elevated nutrient levels found surrounding *A. donax* compared to native plants, likely resulting from greater pre-fire biomass, may have maintained its immediate post-fire growth. These findings indicate how fire promotes invasion of *A. donax* in riparian terraces adjacent to shrubland ecosystems and may help in establishing an invasive plant-fire regime cycle (Brooks et al. 2004).

4.1. Change in Plant Composition and Structure

Results of this study indicate a strong and potentially lasting effect of fire on plant composition in riparian areas burned along the Santa Clara River study area. Less than a

year after the fire, *A. donax* was clearly increasing its dominance in these ecosystems. *Arundo donax* increased in abundance by almost 25% and comprised more than 99% of the vegetative cover in study sites a year after fire. The much higher biomass or productivity of *A. donax* a year after the fire compared to the two most abundant native species, *S. laevigata* and *B. salicifolia*, suggests that native riparian trees and shrubs might eventually be excluded by *A. donax* in fire-prone riparian ecosystems. Similar examples of post-fire competitive exclusion of native plant species by invasive grasses have been documented in many ecosystems in which fire is an unnatural or altered process (i.e., enhanced frequency) (D'Antonio and Vitousek 1992, D'Antonio 2000). Although smaller in stature, the invasive annual grass *Bromus tectorum* L. (cheatgrass) has caused an increase in wildfire occurrence followed by a decrease in native species abundance in sagebrush shrublands of the western United States (Whisenant 1990, Brooks and Pyke 2001). The dominant species in sagebrush shrublands, *Artemisia tridentata* (sagebrush), does not resprout after fire (Booth et al. 2003), whereas *B. tectorum* successfully germinates from seed and grows in harsh conditions in interspaces between shrubs after fire (Brooks et al. 2004). Successive fire cycles and increased fire return intervals have led to dominance by the invader.

4.2. Soil Nutrients Stimulate Growth

Elevated nutrient levels in surface soil provide high nutrient levels that increase or maintain plant growth immediately after fire in shrubland ecosystems (Rundel and Parsons 1980, Boerner 1982). Wildfires are known to alter nutrient budgets and cycling by volatilizing some nutrients and mobilizing the levels of others (Boerner 1982, D'Antonio and Vitousek 1992, D'Antonio 2000). Volatilization of nutrients depends on fire temperature but is thought to be high for nitrogen, carbon, and sulfur because of the low temperatures at which they become volatile (Rundel et al. 1983). Ammonium and phosphate levels in surface soils may increase rapidly after fire in shrubland ecosystems due to mineralization (Christensen 1973, Debano and Dunn 1982, Rundel et al. 1983), but post-fire nitrate levels are highly dependent on vegetation type and quantity (Romanya et al. 2001). Nitrogen losses in shrubland ecosystems may occur after fire due to leaching by rainfall and soil erosion (Debano and Conrad 1978, Romanya et al. 2001). Because of the low-lying nature of riparian ecosystems in the landscape, nutrient-rich ash may collect in these areas or nutrients in the ash may run off into these systems from surface erosion and soil leaching (Boerner 1982).

Mechanisms contributing to increased abundance of *A. donax* compared to native plant species in burned areas a year after fire were examined, including response to elevated nutrient levels, differing phenology, and high growth rates. A positive feedback cycle was observed, whereby *A. donax* contributes higher nutrient levels to soil post-fire and these high levels promote rapid growth compared to native riparian species. Evidence suggests that large differences in pre- and post-fire soil nutrient levels may have stimulated and/or helped maintain high growth rates of *A. donax* following fire. Levels of ammonia, nitrate and phosphate in the soil surrounding *A. donax* were much higher in riparian study sites after the fire, whereas soil nutrient levels adjacent to the native plants species did not change. Higher soil nutrient levels found next to *A. donax* versus native plants were likely due to quality and quantity of fuel (vegetation) burned,

fire intensity, and resulting ash deposited (Debano and Conrad 1978). Although not measured, these high post-fire levels were likely indicative of nutrient content contained in the pre-fire aboveground biomass of varying species, influencing nutrient content of ash (Christensen and Muller 1975, Debano and Conrad 1978). Variation in fire intensity between patches of *A. donax* (Bell 1997, D'Antonio 2000) and native plants mixed with *A. donax* observed may have also influenced nutrient content. In mature California chaparral, elevated post-fire soil nitrogen levels from addition of ammonium and phosphorus-rich ash (Christensen 1973) provide favorable nutrient conditions for plant growth (Christensen and Muller 1975, Rundel and Parsons 1980). The high proportion of nutrients, such as ammonium, in the ash remaining after fire is thought to mineralize rapidly, especially after the first rainfall, and become available to plants (Rundel and Parsons 1984), and be readily available to plants, if not lost from the system (Rundel et al. 1983). Higher soil ammonium and phosphate concentrations associated with *A. donax* compared to native plants post-fire may help explain higher initial growth rate of *A. donax* compared to native species immediately after fire, but causation cannot be definitively determined from these results.

4.3. Mechanisms of Invasion

We found clear evidence of three mechanisms, response to nutrients, fire-adapted phenology, and high growth rate of *A. donax*, that promote its preemption of natives after fire. Fire appears to stimulate *A. donax* growth immediately, whereas native plant species recover much slower after burned. Native species did not begin resprouting or germinating until several months after the October 2003 wildfire. In areas containing high nitrogen levels, Decruyenaere & Holt (2005) found that *A. donax* exhibited no dormancy during the year, although recruitment of new shoots (from rhizomes) was higher in the summer than in winter months. Accordingly, high nutrient levels in soils surrounding *A. donax* post-fire may have led to high growth rates and maintenance of shoot growth after rhizomes burned. Conversely, native woody riparian species, such as *S. laevigata*, *P. balsamifera* spp. *trichocarpa* and *B. salicifolia*, are dormant in the winter months and are leafless (G. Coffman personal observation). Resprouting and germination of these species in southern California occurs between late winter and early spring, corresponding with declining river flows (Braatne et al. 1996, Stella et al. 2006). Resprouting and germination of native species after fire appeared similar to the natural phenology (no burn effect) of these species and nutrient levels did not appear to effect regrowth. In chaparral ecosystems, several sprouter non-seeder species (clonal growth form similar to *A. donax*) appear within weeks after fire (Hanes 1971, Naveh 1975, Zedler et al. 1983, Thomas and Davis 1989).

Growth rates and other measures of plant performance of *A. donax* were much higher than native species during the first year after fire, resulting in a higher aboveground biomass a year later. Mean monthly growth rates of *A. donax* were up to three times higher than native riparian plant species in the winter and twice as high in spring through summer. Most native species growth occurred in the spring and early summer and corresponds to phenology under non-burned conditions (Braatne et al. 1996). The pattern and mean RGRs of *A. donax* were similar to those measured for

recruits that emerged in April in a Northern California study (Spencer et al. 2005) (see Chapter 3).

Riparian ecosystems infested by *A. donax* adjacent to fire-prone shrublands in southern California appear to be on a trajectory to an invasive plant-fire regime cycle (Brooks et al. 2004). Introduction of the unique habit of *A. donax*, a clonal tall grass species, into an ecosystem naturally dominated by woody trees and shrubs has altered fuel types, layers, and loads (Scott 1994, DiTomaso 1998, Brooks et al. 2004). Decreased moisture content and increased surface to volume ratio of *A. donax* versus native vegetation may lead to an altered or increased length of fire susceptibility or increased probability of ignition in these systems, although no data currently exists to document this assertion. Addition of this novel fuel characteristic to the riparian ecosystem has increased vertical continuity (structure of fuel allows fire to spread from surface to crowns of shrubs and trees), which can in turn increase the frequency and extent of fires (Brooks et al. 2004). Due to its tall growth form, infestations of *A. donax* mixed with native species may spread fire vertically into the canopy of riparian trees instead of mainly burning trunks of riparian species near the ground surface. As *A. donax* abundance increases in fire-prone areas due to increased nutrient levels, fire-adapted phenology and high growth rate of *A. donax*, increased fire return intervals may eventually lead to exclusion of native species in riparian ecosystems. Evidence of this positive-feedback cycle suggests that *A. donax* may create an invasive plant-fire regime cycle in streams and rivers of Mediterranean-type climates similar to this southern California example.

5. Conclusions and Management Implications

That fire promotes invasion of riparian ecosystems by the large alien grass species, *Arundo donax* L., has long been speculated, but no data existed to support this premise. Although fire was once a natural part of shrubland ecosystems that characterize the coastal southern California landscape, large riparian ecosystems provided natural firebreaks because native vegetation retains foliar water that resists ignition (Hanes 1971, Naveh 1975, Bell 1997, Rundel 1998, Keeley and Fotheringham 2001). In October 2003, however, a wildfire burned more than 700 acres of vegetation on riparian terraces along the Santa Clara River. One year after the fire, *A. donax* dominated the vegetation in burned areas. This study illustrates how wildfire promotes invasion of this large alien grass species in riparian ecosystems of southern California.

Removal of *A. donax* from riparian ecosystems adjacent to fire-prone shrublands in Mediterranean-type climates should be a key management priority. Negative effects on other ecosystem functions, such as wildlife habitat reduction (Knick et al. 2005), follow fire regime changes (Brooks et al. 2004) and associated plant invasions (Herrera and Dudley 2003, Kisner 2004). Infestations of *A. donax* located on riparian terraces adjacent to towns or agricultural practices pose an increased risk of fire to people and property. Immediate post-fire removal of *A. donax* reduces future fire risk and greatly reduced the amount of biomass removal necessary. However, time of year is critical to selection and success of appropriate removal techniques. Active planting of removal areas with a diverse composition of native species may be required to prevent reinvasion

by *A. donax* or other exotic species due to enhanced nutrient levels in these burned riparian ecosystems (Chapter 2 in Coffman 2007).

LITERATURE CITED

- Ahearn, D. S., R. W. Sheibley, R. A. Dahlgren, M. Anderson, J. Johnson, and K. W. Tate. 2005. Land use and land cover influence on water quality in the last free-flowing river draining the western Sierra Nevada, California. *Journal of Hydrology* 313:234-247.
- AOAC International. 1997a. Official Methods of Analysis of the Association of Official Analytical Chemists. Combustion Method 990.03, 16th edition. AOAC International, Arlington, Virginia.
- AOAC International. 1997b. Official Methods of Analysis of the Association of Official Analytical Chemists. Method 972.43, 16th edition. AOAC International, Arlington, Virginia.
- Basnyat, P., L. D. Teeter, K. M. Flynn, and B. G. Lockaby. 1999. Relationships between landscape characteristics and nonpoint source pollution inputs to coastal estuaries. *Environmental Management* 23:539-549.
- Bell, G. P. 1994. Biology and growth habits of giant reed (*Arundo donax*). Pages 1-6 in N. E. Jackson, P. Frandsen, and S. Douthit, editors. *Arundo donax* Workshop Proceedings. November 19, 1993, Ontario, California.
- Bell, G. P. 1997. Ecology and management of *Arundo donax*, and approaches to riparian habitat restoration in Southern California. Pages 103-113 in J. H. Brock, M. Wade, P. Pysek, and D. Green, editors. *Plant Invasions: Studies from North America and Europe*. Blackhuys Publishers, Leiden, The Netherlands.
- Boerner, R. E. J. 1982. Fire and nutrient cycling in temperate ecosystems. *Bioscience* 32:187-192.
- Boose, A. B., and J. S. Holt. 1999. Environmental effects on asexual reproduction in *Arundo donax*. *Weed Research* 39:117-127.
- Booth, M. S., M. M. Caldwell, and J. M. Stark. 2003. Overlapping resource use in three Great Basin species: Implications for community invasibility and vegetation dynamics. *Journal of Ecology* 91:36-48.
- Bouma, D. 1983. Diagnosis of mineral deficiencies using plant tests. Pages 120-146 in A. Lauchli and R. L. Bielecki, editors. *Inorganic Plant Nutrition, Encyclopedia of Plant Physiology*. Springer-Verlag, Berlin, Germany.
- Braatne, J. H., S. B. Rood, and P. E. Heilman. 1996. Life history, ecology, and conservation of riparian cottonwoods in North America. Pages 57-85 in R. F. Stettler, H. D. Bradshaw, P. E. Heilman, and T. M. Hinckley, editors. *Biology of Populus and its Implications for Management and Conservation, Part I, Chapter 3*.

NRC Research Press, National Research Council of Canada, Ottawa, Ontario, Canada.

- Brdjanovic, D., C. M. Hooijmans, M. C. M. v. Loosdrecht, G. J. Alaerts, and J. J. Heijnen. 1996. The dynamic effects of potassium limitation on biological phosphorus removal. *Water Resources* 30:2323-2328.
- Brooks, M. L. 2002. Peak fire temperatures and effects on annual plants in the Mojave Desert. *Ecological Applications* 12:1088-1102.
- Brooks, M. L. 2003. Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. *Journal of Applied Ecology* 40:344-353.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive plants on fire regimes. *Bioscience* 54:677-688.
- Brooks, M. L., and D. A. Pyke. 2001. Invasive plants and fire in the deserts of North America. Pages 1-14 in G. K.E.M. and T. P. Wilson, editors. *Proceedings of the Invasive Plant Workshop. The Role of Fire in the Control and Spread of Invasive Species.*, Tallahassee, Florida: Tall Timbers Research Station.
- Bytnerowicz, A., P. E. Padgett, S. D. Parry, M. E. Fenn, and M. J. Arbaugh. 2001. Concentrations, deposition, and effects of nitrogenous pollutants in selected California ecosystems. *The Scientific World Journal* 1:304-311.
- Chapin, F. S., and K. V. Cleve. 1989. Approaches to studying nutrient uptake, use and loss in plants. Pages 186-287 in R. W. Pearcy, J. R. Ehleringer, H. A. Mooney, and P. W. Rundel, editors. *Plant Physiological Ecology: Field Methods and Instrumentation.* Chapman and Hall Ltd., New York.
- Chapin, F. S., P. M. Vitousek, and K. V. Cleve. 1986. The nature of nutrient limitations in plant communities. *The American Naturalist* 127:48-58.
- Charbonneau, R., and G. M. Kondolf. 1993. Land use change in California, USA: Non-point source water quality impacts. *Environmental Management* 17:453-460.
- Christensen, N. L. 1973. Fire and the nitrogen cycle in California chaparral. *Science* 181:66-68.
- Christensen, N. L., and C. H. Muller. 1975. Effects of fire on factors controlling plant growth in *Adenostoma* chaparral. *Ecological Monographs* 45:29-55.
- Claridge, K., and S. B. Franklin. 2002. Compensation and plasticity in an invasive plant species. *Biological Invasions* 4:339-347.

- Clark, G. M., D. K. Mueller, and M. A. Mast. 2000. Nutrient concentrations and yields in undeveloped stream basins of the United States. *Journal of the American Water Resources Association* 36:849-860.
- Coffman, G.C. 2007. Factors Influencing Invasion of Giant Reed (*Arundo donax*) in Riparian Ecosystems of Mediterranean-type Climate Regions. Ph.D. Dissertation, University of California, Los Angeles.
- Coffman, G. C. in press. Giant reed (*Arundo donax*) invasion: Effects on streams and water resources. *Encyclopedia of Water Science*.
- Coffman, G. C., R. F. Ambrose, and P. W. Rundel. 2004. Invasion of *Arundo donax* in river systems of Mediterranean climates: causes, impacts and management strategies. Pages 138 (full text on cd) in M. Arianoutsou and V. P. Papanastasis, editors. 10th International Conference on Mediterranean Climate Ecosystems. Millpress, Rhodes, Greece.
- Correll, D. L. 1984. N and P in soils and runoff of three coastal plain land uses. Pages 207-224 in R. L. Todd, R. Leonard, and L. Asmussen, editors. *Nutrient Cycling in Agroecosystems*. University of Georgia Press, Athens, Georgia.
- Correll, D. L., T. E. Jordan, and D. E. Weller. 1992. Nutrient flux in a landscape: Effects of coastal land use and terrestrial community mosaic on nutrient transport to coastal waters. *Estuaries* 15:431-442.
- Crampton, B. 1974. Grasses in California. *California Natural History Guides*: 33. University of California Press, Berkeley, California.
- CRWQCB-LA. 1995. Water Quality Control Plan, Los Angeles Region. Basin Plan for the Coastal Watersheds of Los Angeles and Ventura Counties.
- D'Antonio, C. M. 2000. Fire, plant invasions, and global changes. Pages 65-93 in H. A. Mooney and R. J. Hobbs, editors. *Invasive Species in a Changing World*. Island Press, Washington, D.C.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63-87.
- Dallman, P. R. 1998. *Plant Life in the World's Mediterranean Climates: California, Chile, South Africa, Australia, and the Mediterranean Basin*. University of California Press, Berkeley, California.
- Day, J. A. 1983. Mineral nutrients in mediterranean ecosystems. South African National Scientific Programmes Report No. 71. Cooperative Scientific Programmes, Council for Scientific and Industrial Research, Pretoria, South Africa.

- Debano, L. F., and C. E. Conrad. 1978. The effect of fire on nutrients in a chaparral ecosystems. *Ecology* 59:489-497.
- Debano, L. F., and P. H. Dunn. 1982. Soil and nutrient cycling in Mediterranean-type ecosystems: A summary and synthesis. *in* Gen. Tech. Rep. PSW-58. Berkeley, California: Pacific Southwest Forest and Range Experiment Station, Forest Service. U.S. Department of Agriculture.
- Decruyenaere, J. G., and J. S. Holt. 2001. Seasonality of clonal propagation in giant reed. *Weed Science* 49:760-767.
- Decruyenaere, J. G., and J. S. Holt. 2005. Ramet demography of a clonal invader, *Arundo donax* (Poaceae), in Southern California. *Plant and Soil* 277:41-52.
- diCatri, F. 1991. An ecological overview of the five regions with a mediterranean climate. Pages 3-16 *in* R. H. Groves and F. diCatri, editors. *Biogeography of Mediterranean Invasions*. Cambridge University Press, Cambridge.
- DiTomaso, J. M. 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, J. A., H. A. Mooney, F. diCatri, R. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson. 1989. *Biological Invasions: a Global Perspective*. John Wiley & Sons Ltd., Chichester.
- Dudley, T. 1998. Exotic plant invasions in California riparian areas and wetlands. *Fremontia* 26:24-29.
- Dudley, T., and B. Collins. 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, 62 p.
- Dudley, T. L. 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.
- Dukes, J. S., and H. A. Mooney. 2004. Disruption of ecosystem processes in western North America by invasive species. *Revista chilena de historia natural* 77:411-437.
- Duncan, R. R. 1994. Genetic manipulation. Pages 1-38 *in* R. E. Wilkinson, editor. *Plant-Environment Interactions*. Marcel Dekker, Inc., New York.
- Else, J. A. 1996. Post-flood establishment of native woody species and an exotic, *Arundo donax*, in a Southern California riparian system. M.S. Thesis. San Diego State University, San Diego.

- Else, J. A., and P. Zedler. 1996. Dynamics of the flood disturbed zone of a riparian system: Vegetative establishment and resprouting of woody native species and the exotic, *Arundo donax*. Bulletin of the Ecological Society of America (1996 Annual Combined Meeting, Providence, RI. 10-14 August 1996) 77:129.
- Elton, C. S. 1958. The Ecology of Invasions by Animals and Plants. Methuen, London.
- Faber, P. M., and R. F. Holland. 1992. Common Riparian Plants of California: A Field Guide for the Layman. Pickleweed Press, Mill Valley, California.
- Faber, P. M., E. Keller, A. Sands, and B. M. Massey. 1989. The ecology of riparian habitats of the Southern California coastal region: A community profile. U.S. Fish and Wildlife Service Biological Report 85(7.27). 152 pp.
- Fail, J. L., B. L. Haines, and R. L. Todd. 1986. Riparian forest communities and their role in nutrient conservation in an agricultural watershed. American Journal of Alternative Agriculture 2:114-121.
- Franson, M. A. H., L. S. Clesceri, A. E. Greenberg, and A. D. Eaton. 1998. Standard Methods for the Examination of Water and Wastewater, 20th Edition. American Public Health Association, Washington, DC.
- Frink, C. R. 1991. Estimating nutrient exports to estuaries. Journal of Environmental Quality 20:717-724.
- Gaffney, K. A. 2002. Invasive Plants in Riparian Corridors: Distribution, Control Methods and Plant Community Effects. M.A. Thesis. Sonoma State University, Rohnert Park, California.
- Green, E. K., and S. M. Galatowitsch. 2002. Effects of *Phalaris arundinacea* and nitrate-N addition on the establishment of wetland plant communities. The Journal of Applied Ecology 39:134-144.
- Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystems perspective of riparian zones. Bioscience 41:540-551.
- Groves, R., J. S. Beard, H. J. Deacon, J. J. N. Lambrechts, A. Rabinovitch-Vin, R. L. Specht, and W. D. Stock. 1983. Introduction: The origins and characteristics of Mediterranean ecosystems. Pages 1-18 in Mineral Nutrients in Mediterranean Ecosystems. South African National Scientific Programmes Report No. 71, Hermanus, South Africa.
- Hanes, T. L. 1971. Succession after fire in chaparral of Southern California. Ecological Monographs 41:27-52.
- Havlin, J. L., J. D. Beaton, S. L. Tisdale, and W. L. Nelson. 1999. Soil Fertility and Fertilizers, 6th edition. Prentice Hall, Upper Saddle River, New Jersey, 499 pp.

- Hecky, R. E., P. Campbell, and L. L. Hendzel. 1993. The stoichiometry of carbon, nitrogen, phosphorus in particulate matter of lakes and oceans. *Limnology and Oceanography* 38:709-724.
- Herrera, A. M., and T. L. Dudley. 2003. Reduction of riparian arthropod abundance and diversity as a consequence of giant reed (*Arundo donax*) invasion. *Biological Invasions* 5:167-177.
- Hickman, J. C. 1993. *The Jepson Manual: Higher Plants of California*. University of California Press, Berkeley.
- Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* 6:324-337.
- Hofer, S. 2003. Determination of Ammonia (Salicylate) in 2M KCl soil extracts by Flow Injection Analysis. QuikChem Method 12-107-06-2-A. Lachat Instruments, Loveland, Colorado.
- Iverson, M. E. 1994. Effects of *Arundo donax* on water resources. Pages 19-25 in N. E. Jackson, P. Frandsen, S. Douthit, editor. *Arundo donax* Workshop Proceedings, Ontario, California. November 1993.
- Johnson, C. M., and A. Ulrich. 1959. Analytical methods for use in plant analysis. Bulletin 766. University of California, Agricultural Experiment Station, Berkeley, California.
- Johnson, M., T. Dudley, and C. Burns. 2006. Seed production in *Arundo donax*? *Cal-IPC News* Fall:12-13.
- Keeley, J. E. 1982. Distribution of lightning and man-caused wildfire in California. Pages 431-437 in C. E. Conrad and W. Oechel, editors. *Proceedings of the Symposium on Dynamics and Management of Mediterranean-type Ecosystems*. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, General Technical Report PSW-58.
- Keeley, J. E. 2004. Invasive plants and fire management in California Mediterranean-climate ecosystems. Pages 128 (full text on cd) in M. Arianoutsou and V. P. Papanastasis, editors. *10th International Conference on Mediterranean Climate Ecosystems (MEDECOS)*. Millpress, Rhodes, Greece.
- Keeley, J. E., and C. J. Fotheringham. 2001. Historic fire regime in Southern California shrublands. *Conservation Biology* 15:1536-1548.
- Keeley, J. E., and C. J. Fotheringham. 2005. Lessons learned from the wildfires of October 2003. Pages 112-122 in R. W. Halsey, editor. *Fire, Chaparral, and Survival in Southern California*. San Diego, California, Sunbelt Publications.

- Keeley, J. E., C. J. Fotheringham, and M. Morais. 1999. Reexamining fire suppression impacts on brushland fire regimes. *Science* 284:1829-1931.
- Kim, J. G. 2003. Response of sediment chemistry and accumulation rates to recent environmental changes in the Clear Lake watershed, California, USA. *Wetlands* 23:95-103.
- Kisner, D. A. 2004. The Effect of Giant Reed (*Arundo donax*) on the Southern California Riparian Bird Community. M.S. Thesis. San Diego State University, San Diego.
- Knecht, M. F., and A. Goransson. 2004. Terrestrial plants require nutrients in similar proportions. *Tree Physiology* 24:447-460.
- Knepel, K. 2003. Determination of Nitrate in 2M KCl soil extracts by Flow Injection Analysis. QuikChem Method 12-107-04-1-B. Lachat Instruments, Loveland, Colorado.
- Knick, S. T., A. L. Holmes, and R. F. Miller. 2005. The role of fire in structuring sagebrush habitats and bird communities. *Studies in Avian Biology* 30:63-75.
- Koerselman, W., and A. F. M. Meuleman. 1996. The vegetation N:P ratio: A new tool to detect the nature of nutrient limitations. *Journal of Applied Ecology* 33:1441-1450.
- Kolb, A., and P. Alpert. 2003. Effects of nitrogen and salinity on growth and competition between a native grass and an invasive congener. *Biological Invasions* 5:229-238.
- Kolb, A., P. Alpert, D. Enters, and C. Holzapfel. 2002. Patterns of invasion within a grassland community. *Journal of Ecology* 90:871-881.
- Kozłowski, T. T., P. J. Kramer, and S. G. Pallardy. 1991. *The Physiological Ecology of Woody Plants*. Academic Press, Inc., San Diego, California.
- Lu, R., K. Schiff, and K. Stolzenbach. unpublished data. Nitrogen deposition on coastal watersheds in the Los Angeles Region.
- Maurer, D. A., and J. B. Zedler. 2002. Differential invasion of a wetland grass explained by tests of nutrients and light availability on establishment and clonal growth. *Oecologia* 131:279-288.
- Meixner, T. 2003. Landscape level controls on nitrate-nitrogen in forested and chaparral catchments of southern California. University of California Water Resources Center. Technical Completion Report - W-931.
- Metz, L. J., C. G. Wells, and B. F. Swindell. 1966. Sampling soil and foliage in a pine plantation. *Soil Science Society of America Proceedings* 30:397-399.
- Meyer, G. A., and P. N. Keliher. 1992. An overview of analysis by inductively coupled plasma-atomic emission spectrometry. Pages 473-505 in A. Montaser and D. W.

- Golightly, editors. Inductively Coupled Plasmas in Analytical Atomic Spectrometry. VCH Publishers Inc., New York, New York.
- Minchinton, T. E., and M. D. Bertness. 2003. Disturbance-mediated competition and the spread of *Phragmites australis* in a coastal marsh. *Ecological Applications* 13:1400-1416.
- Minnich, R. A. 1983. Fire mosaics in Southern California and Northern Baja California. *Science* 219:1287-1294.
- Mooney, H. A., S. P. Hamburg, and J. A. Drake. 1986. The invasion of plants and animals into California. Pages 250-272 in H. A. Mooney and J. A. Drake, editors. *The Ecology of Biological Invasions of North America and Hawaii*. Springer-Verlag, New York.
- Mount, J. F. 1995. *California Rivers and Streams: the Conflict Between Fluvial Process and Land Use*. University of California Press, Berkeley, California.
- Naveh, Z. 1975. The evolutionary significance of fire in the Mediterranean region. *Vegetatio* 29:199-208.
- Nicola, N. 2003. Fertilized to death. *Nature* 425:894-895.
- NOAA. 2000. Southern Coastal California Land Cover/Land Use. http://www.csc.noaa.gov/crs/lca/ca_so2000.html. Coastal Services Center. Charleston, South Carolina. *in*.
- Olsen, S. R., and L. E. Sommers. 1982. Phosphorus. Pages 403-430 in A. L. Page, editor. *Methods of Soil Analysis: Part 2. Chemical and Microbiological Properties*. ASA Monograph Number 9.
- Padgett, P. E., E. B. Allen, A. Bytnerowicz, and R. A. Minich. 1999. Changes in soil inorganic nitrogen as related to atmospheric nitrogenous pollutants in southern California. *Atmospheric Environment* 33:769-781.
- Palmer, T. 1993. *California's Threatened Environment: Restoring the Dream*. Island Press, Washington, D.C.
- Perdue, R. E. 1958. *Arundo donax* - source of musical reeds and industrial cellulose. *Economic Botany* 12:157-172.
- Peterjohn, W. T., and D. L. Correll. 1984. Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. *Ecology* 65:1466-1475.
- Pettijohn, F. J. 1975. *Sedimentary Rocks*, 3rd edition. Harper & Row Publishers, New York, New York, 628 pp.
- Phillips, W. S. 1963. Depth of roots in soil. *Ecology* 44:424-429.

- Polunin, O., and A. Huxley. 1987. *Flowers of the Mediterranean*. Hogarth Press, London.
- Prokopy, W. R. 1995. Phosphorus in 0.5 M Sodium Bicarbonate Soil Extracts. QuikChem Method 12-115-01-1-B. Lachat Instruments, Milwaukee, Wisconsin.
- Pysek, P., and K. Prach. 1994. How important are rivers for supporting plant invasions? Pages 19-26 in L. C. de Waal, L. E. Child, P. M. Wade, and J. H. Brock, editors. *Ecology and Management of Invasive Riverside Plants*. Wiley & Sons, New York.
- Randall, J. M., M. Rejmanek, and J. C. Hunter. 1998. Characteristics of the exotic flora of California. *Fremontia* 26:3-12.
- Redfield, A. C. 1958. The biological control of chemical factors in the environment. *American Scientist* 46:205-221.
- Richardson, D. M., P. Pysek, M. Rejmanek, M. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization and invasion of alien plants: Concepts and definitions. *Diversity and Distributions* 6:93-107.
- Rieger, J. P., and D. A. Kreager. 1989. Giant reed (*Arundo donax*): A climax community of the riparian zone. Pages 222-225 in D. L. Abell, editor. *Proceedings of the California Riparian Systems Conference: Protection, Management, and Restoration for the 1990s*. USDA Forest Service Gen. Tech. Rep. PSW-110, Berkeley, California.
- Robbins, W. W., M. K. Bellue, and W. S. Ball. 1951. *Weeds of California*. California Department of Agriculture, Sacramento, California.
- Robinson, T. H., A. Leydecker, A. A. Keller, and J. M. Melack. 2005. Steps towards modeling nutrient export in coastal California streams with a Mediterranean climate. *Agricultural Water Management* 77:144-158.
- Robinson, T. W. 1958. *Phreatophytes*. U.S. Geological Survey Water-Supply Paper 1423. U.S. Government Printing Office, Washington, D.C.
- Rodda, H. J. E. 1995. Modeling nitrate leaching at the catchment scale. Pages 49-63 in I. D. L. Foster, A. M. Gurnell, and B. W. Webb, editors. *Sediment and Water Quality in River Catchments*. John Wiley & Sons Ltd., New York.
- Romanya, J., P. Casals, and V. R. Vallejo. 2001. Short-term effects of fire on soil nitrogen availability in Mediterranean grasslands and shrublands growing in old fields. *Forest Ecology and Management* 147:39-53.
- Rugen, F. J. 1987. *Fires in Ventura County: 1871-1879*. Ventura County Historical Museum (docent class).
- Rundel, P. W. 1998. Landscape disturbance in Mediterranean-type ecosystems: An overview. Pages 3-22 in P. W. Rundel, G. Montenegro, and F.M. Jaksic, editors.

Landscape Disturbance and Biodiversity in Mediterranean-Type Ecosystems. Ecological Studies 136. Springer-Verlag, Berlin.

- Rundel, P. W. 2000. Alien species in the flora and vegetation of the Santa Monica Mountains, CA: Patterns, processes, and management implications. Pages 145-152 in J. E. Keeley, M. Baer-Keeley, and C. J. Fotheringham, editors. 2nd Interface Between Ecology and Land Development in California. U.S. Geological Survey Open-File Report 00-62.
- Rundel, P. W. 2003. Invasive species. Pages 4-11 in A. E. Carlson and A. M. Winer, editors. Southern California Environmental Report Card 2003. UCLA Institute of the Environment.
- Rundel, P. W., G. C. Bate, A. B. Low, P. C. Miller, P. Miller, and D. T. Mitchell. 1983. Nutrient cycling processes. Pages 19-32 in J. A. Day, editor. Mineral Nutrients in Mediterranean Ecosystems. South African National Scientific Programmes Report No 71, Hermanus, South Africa.
- Rundel, P. W., and R. Gustafson. 2005. Introduction to the Plant Life of Southern California: Coast to Foothills. University of California Press, Berkeley, California.
- Rundel, P. W., and D. J. Parsons. 1980. Nutrient changes in two chaparral shrubs along a fire induced age gradient. *American Journal of Botany* 67:51-58.
- Rundel, P. W., and D. J. Parsons. 1984. Post-fire uptake of nutrients by diverse ephemeral herbs in chamise chaparral. *Oecologia* 61:285-288.
- Russell, S. 1963. Plant Root Systems. McGraw-Hill, New York.
- Sah, R. N., and R. O. Miller. 1992. Spontaneous reaction for acid dissolution of biological tissues in closed vessels. *Analytical Chemistry* 64:230-233.
- Samuels, I., and R. S. Knight. 2003. Assessing the risk for increased invasion of the giant reed, *Arundo donax*, in South Africa. *South African Journal of Botany* 69:224-268.
- Schlosser, I. J., and J. R. Karr. 1981. Riparian vegetation and channel morphology impact on spatial patterns of water quality in agricultural watersheds. *Environmental Management*. 5:233-243.
- Scott, G. 1994. Fire threat from *Arundo donax*. Pages 17-18 in N. E. Jackson, P. Frandsen, and S. Douthit, editors. November 1993 *Arundo donax* Workshop Proceedings, Ontario, California.
- Sharifi, M. R., E. T. Nilsen, and P. W. Rundel. 1982. Biomass and net primary production of *Prosopis glandulosa* (Fabaceae) in the Sonoran Desert of California. *American Journal of Botany* 69:760-767.

- Sharma, K. P., S. P. S. Kushwaha, and B. Gopal. 1998. A comparative study of stand structure and standing crops of two wetland species, *Arundo donax* and *Phragmites karka*, and primary production in *Arundo donax* with observations on the effect of clipping. *Tropical Ecology* 39:3-14.
- Sheldrick, B. H., and C. Wang. 1993. Particle-size distribution. Pages 499-511 in M. R. Carter, editor. *Soil Sampling and Methods of Analysis*. Canadian Society of Soil Science. Lewis Publishers, Ann Arbor, Michigan.
- Spencer, D. F., G. G. Ksander, and L. D. Whitehand. 2005. Spatial and temporal variation in RGR and leaf quality of a clonal riparian plant: *Arundo donax*. *Aquatic Botany* 81:27-36.
- Spencer, D. F., P. S. Liow, W. K. Chan, G. G. Ksander, and K. D. Getsinger. 2006. Estimating *Arundo donax* shoot biomass. *Aquatic Botany* 84:272-276.
- Stark, J. M. 1994. Causes of soil nutrient heterogeneity at different scales. in M. M. Caldwell and R. W. Pearcy, editors. *Exploitation of Environmental Heterogeneity by Plants*. Academic Press, Inc., San Diego, California.
- Stella, J. C., J. J. Battles, B. K. Orr, and J. R. McBride. 2006. Synchrony of seed dispersal hydrology and local climate in a semi-arid river reach in California. *Ecosystems* 9:1200-1214.
- Suding, K. N., K. D. LeJeune, and T. R. Seastedt. 2004. Competitive impacts and responses of an invasive weed: dependencies on nitrogen and phosphorus availability. *Oecologia* 141:526-535.
- Svengsouk, L. J., and W. J. Mitsch. 2001. Dynamics of mixtures of *Typha latifolia* and *Schoenoplectus tabernaemontani* in nutrient-enrichment wetland experiments. *American Midland Naturalist* 145:309-324.
- Taiz, L., and E. Zeiger. 1991. *Plant Physiology*. The Benjamin/Cummings Publishing Company, Inc., New York.
- Thomas, C. M., and S. D. Davis. 1989. Recovery patterns of three chaparral shrub species after wildfire. *Oecologia* 80:309-320.
- Tilman, D. 1988. *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, New Jersey.
- Tripler, C. E., S. S. Kaushal, G. E. Likens, and M. T. Walter. 2006. Patterns in potassium dynamics in forest ecosystems. *Ecology Letters* 9:451-466.
- Triska, F. J., A. P. Jackman, J. H. Duff, and R. J. Avanzino. 1994. Ammonium sorption to channel and riparian sediments: A transient storage pool for dissolved inorganic nitrogen. *Biogeochemistry* 26:67-83.

- USDA. 1954. pH reading of saturated soil paste. Pages 102 *in* L. A. Richards, editor. Diagnosis and Improvement of Saline and Alkali Soils. USDA Agricultural Handbook 60. U.S. Government Printing Office, Washington, D.C.
- USEPA. 1983. Methods for Chemical Analysis of Water and Wastes. Environmental Protection Agency, Analytical Quality Control Laboratory, Cincinnati, Ohio.
- USEPA. 1999. Protocol for Developing Nutrient TMDLs. EPA 841-B-99-007, U.S. Environmental Protection Agency, Office of Water, Washington, DC.
- Verhoeven, J. T. A., W. Koerselman, and A. F. M. Meuleman. 1996. Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: relations with atmospheric inputs and management regimes. *Trends in Ecology and Evolution* 11:494-497.
- Vitousek, P. M. 1996. Nutrient limitation and soil development: experimental test of a biogeochemical theory. *Bulletin of the Ecological Society of America* (1996 Annual Combined Meeting, Providence, RI. 10-14 August 1996):461.
- Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. *American Scientist* 84:468-478.
- Walker, T. W., and J. K. Syers. 1976. The fate of phosphorus during pedogenesis. *Geoderma* 15:1-19.
- Wang, A. 1998. Groundwater nitrate levels as promoters of *Arundo donax* invasion. Pages 720 *in* T. Dudley and K. Kennedy, editors. Environmental Science: Policy and Practice. Proceedings, Senior Research Seminar, Environmental Sciences Group Major - UGIS, University of California, Berkeley.
- Warrick, J. A., L. Washburn, M. A. Brzezinski, and D. A. Siegel. 2005. Nutrient contributions to the Santa Barbara Channel, California, from ephemeral Santa Clara River. *Estuarine, Coastal and Shelf Science* 62:559-574.
- Whisenant, S. G. 1990. Changing Fire Frequencies on Idaho's Snake River Plains: Ecological and Management Implications. Logan, Utah. U.S. Department of Agriculture, Forest Service, Intermountain Research Center. General Technical Report INT-276.
- Whittaker, R. H. 1961. Estimation of net primary production of forest and shrub communities. *Ecology* 41:177-180.
- Whittaker, R. H. 1965. Branch dimensions and estimation of branch production. *Ecology* 46:365-370.
- Whittaker, R. H., and P. L. Marks. 1975. Methods of assessing terrestrial productivity. Pages 55-118 *in* H. Lieth and R. H. Whittaker, editors. Primary Productivity of the Biosphere. Springer-Verlag, New York.

- Wijte, A. H. B. M., T. Mizutani, E. R. Motamed, M. L. Merryfield, D. E. Miller, and D. E. Alexander. 2005. Temperature and endogenous factors cause seasonal patterns in rooting by stem fragments of the invasive giant reed, *Arundo donax* (Poaceae). *International Journal of Plant Sciences* 166:507-517.
- Williams, A. E., L. J. Lund, J. A. Johnson, and Z. L. Kabala. 1998. Natural and anthropogenic nitrate contamination of groundwater in a rural community, California. *Environmental Science Technology* 32:32-39.
- Zedler, P. H., C. R. Gautier, and G. S. McMaster. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. *Ecology* 64:809-818.

TABLES

Table 1. Number and distribution of sampling locations in three study watersheds.

	Santa Clara River	Calleguas Creek	Topanga Canyon
Land use type	3	3	2 (no agricultural)
Floodplain/terrace	2	1 (no terrace)	1 (no terrace)
Degree of <i>A. donax</i> infestation	3	3	3
Number of replicates	5–6	5	5
TOTAL	93	45	30

Table 2. Natural and anthropogenic soil and shallow groundwater nutrient levels (means \pm SE).

	Shrubland Ecosystems ¹			Streams draining undeveloped basins in U.S. (median) ²	Riparian Ecosystems		
	Nutrient-poor; strongly-leached; oligotrophic	Nutrient-rich; moderately-leached; mesotrophic	Agriculturally-rich; weakly-leached; eutrophic		Reference watersheds (mean)	All study watersheds (mean)	
					Floodplains	Floodplains	Terraces
Soil							
Total N (%)	< 0.12 (CA: 0.03–0.12)	0.12–0.30 (CA: 0.12–0.21)	> 0.30	-	0.13 (0.11–0.16)	0.056 \pm 0.002	0.095 (0.088–0.103)
NO₃-N (ppm)	-	-	-	-	1.3 (0.9–2.0)	1.2 (1.1–1.4)	3.8 (3.2–4.5)
Total P (%)	< 0.022	0.022–0.06 (CA: 0.022–0.06)	0.06 (CA: 0.06–0.082)	-	-	-	-
PO₄-P (ppm)	-	-	-	-	7.2 (6.1–8.6)	5.9 \pm 0.4	12.2 (10.8–13.7)
Shallow groundwater							
Total N (mg/L)	-	-	-	0.26	1.11 (0.87–1.43)	5.74 (5.30–6.22)	-
NO₃-N (mg/L)	-	-	-	0.087	0.13 (0.11–0.16) ³	0.40 (0.34–0.46)	-
NH₄-N (mg/L)	-	-	-	0.02	0.26 (0.21–0.33)	0.37 (0.33–0.40)	-
PO₄-P (mg/L)	-	-	-	0.01	0.53 (\pm 0.03)	1.39 (\pm 1.22–1.56)	-
N:P (molar)	-	-	-	19.2:1	2.4:1 (2.0:1–3.0:1)	4.4:1 (3.9:1–5.0:1)	-

Legend: CA = nutrient levels found in California SE = standard error

¹ Shrubland ecosystem soil nutrient data for 5 Mediterranean-type climate regions (Day 1983).

² Clark et al. 2000

³ Values are NO₃-N + NO₂-N for reference and study watersheds.

Table 3. N:P and N:K ratios (on a mass basis) of *Salix laevigata* and *Arundo donax* leaf tissue and associated shallow groundwater (molar ratio) along floodplains of study watersheds (mean \pm SE) and results of one-way ANOVAs by watershed.

	Reference Watersheds	Topanga Canyon	Santa Clara River	Calleguas Creek	All Study Watersheds	Significance values ³
N:P						
Shallow groundwater	2.4:1 (2.0:1–3.0:1)	2.7:1 (2.3:1–3.2:1)	4.7:1 (3.9:1–5.7:1)	5.7:1 (4.4:1–7.5:1)	4.4:1 (3.9:1–5.0:1)	$F_{(3,128)} = 2.385$; $P = 0.072$
Leaf tissue (<i>S. laevigata</i>)	12.1:1 (11.5–12.8)	14.2:1 (13.5–14.9)	15.2:1 (14.4–16.1)	11.8:1 (11.2–12.7)	13.7:1 (13.2–14.1)	$F_{(3,47)} = 5.250$; $P = 0.003^{**}$
Leaf tissue (<i>A. donax</i>)	ND	13.3:1 (13.0-13.6)	14.9:1 (14.5-15.3)	13.8:1 (13.4-14.3)	14.4:1 (14.1-14.6)	$F_{(2,78)} = 6.289$; $P = 0.003^{**}$
N:K						
Leaf tissue (<i>S. laevigata</i>)	1.5:1 (1.4–1.6)	1.4:1 (1.3–1.5)	1.7:1 (1.6–1.8)	1.6:1 (1.5–1.7)	1.6:1 (1.5–1.6)	$F_{(3,47)} = 1.015$; $P = 0.356$
Leaf tissue (<i>A. donax</i>)	ND	0.9:1 (0.86-0.93)	0.9:1 (0.88-0.94)	1.2:1 (1.10–1.22)	1.0:1 (0.96–1.02)	$F_{(2,78)} = 12.109$; $P < 0.001^{***}$

Legend:

SE = standard error

ND = no data since no *A. donax* in reference watersheds

* = $0.05 \geq P > 0.01$ = significant

** = $0.01 \geq P > 0.001$ = highly significant

*** = $P \leq 0.001$ = very highly significant

³ No terrace data used in this analysis

Table 4. Three-way ANOVA significance table for shallow groundwater, soil, and leaf tissue nutrients by watershed (Santa Clara River⁴, Calleguas Creek), land use (agricultural, residential, open space) and degree of infestation (none, small, large).

Nutrient analyte	Factors						
	Watershed	Land use	Degree of infestation	Watershed x land use	Watershed x degree of infestation	Land use x degree of infestation	Watershed x land use x degree of infestation
Shallow Groundwater							
Total N (mg/L)⁵	F_(1,74) = 5.474; P = 0.022*	F_(2,74) = 3.630; P = 0.031*	F _(2,74) = 1.639; P = 0.201	F_(2,74) = 3.848; P = 0.026*	F _(2,74) = 0.323; P = 0.725	F _(4,74) = 1.030; P = 0.398	F _(4,74) = 0.981; P = 0.423
NO₃-N + NO₂-N (mg/L)	F_(1,74) = 18.788; P < 0.001***	F _(2,74) = 1.559; P = 0.217	F _(2,74) = 0.168; P = 0.846	F _(2,74) = 2.969; P = 0.057	F _(2,74) = 1.520; P = 0.225	F _(4,74) = 0.897; P = 0.470	F _(4,74) = 1.725; P = 0.154
NH₄-N (mg/L)	F_(1,74) = 5.553; P = 0.021*	F_(2,74) = 5.466; P = 0.006**	F_(2,74) = 3.552; P = 0.034*	F_(2,74) = 10.340; P < 0.001***	F_(2,74) = 3.510; P = 0.035*	F _(4,74) = 1.044; P = 0.390	F_(4,74) = 3.266; P = 0.016*
PO₄ (mg/L)	F_(1,74) = 28.012; P < 0.001***	F _(2,74) = 0.160; P = 0.852	F _(2,74) = 1.276; P = 0.285	F _(2,74) = 0.383; P = 0.683	F _(2,74) = 2.201; P = 0.118	F _(4,74) = 0.948; P = 0.441	F _(4,74) = 0.982; P = 0.423
pH	F _(1,74) = 3.768; P = 0.056	F _(2,74) = 2.638; P = 0.078	F _(2,74) = 0.036; P = 0.964	F _(2,74) = 1.283; P = 0.283	F _(2,74) = 1.317; P = 0.274	F _(4,74) = 0.176; P = 0.950	F _(2,74) = 0.948; P = 0.441
Soil⁶							
Total N (%)	F_(1,73) = 3.987; P = 0.050*	F _(2,73) = 0.859; P = 0.428	F _(2,73) = 0.002; P = 0.998	F _(2,73) = 0.241; P = 0.787	F _(2,73) = 0.931; P = 0.399	F _(4,73) = 1.313; P = 0.273	F _(4,74) = 2.071; P = 0.093
NO₃-N (ppm)	F_(1,73) = 28.540; P < 0.001***	F_(2,73) = 3.578; P = 0.033*	F_(2,73) = 3.566; P = 0.033*	F _(2,73) = 0.544; P = 0.583	F _(2,73) = 1.983; P = 0.145	F _(4,73) = 1.771; P = 0.144	F _(4,73) = 0.390; P = 0.815
NH₄-N (ppm)	F_(1,73) = 22.267; P < 0.001***	F _(2,73) = 2.286; P = 0.109	F _(2,73) = 0.347; P = 0.708	F _(2,73) = 2.340; P = 0.103	F _(2,73) = 1.750; P = 0.181	F _(4,73) = 0.871; P = 0.485	F _(4,73) = 1.340; P = 0.263
PO₄ (ppm)	F_(1,73) = 102.353; P < 0.001***	F_(2,73) = 14.664; P < 0.001***	F _(2,73) = 0.027; P = 0.974	F_(2,73) = 3.162; P = 0.048*	F _(2,73) = 1.708; P = 0.188	F_(4,73) = 5.517; P = 0.001***	F_(4,73) = 3.259; P = 0.016*

Legend: * = 0.05 ≥ P > 0.01 = significant, ** = 0.01 ≥ P > 0.001 = highly significant, *** = P ≤ 0.001 = very highly significant

⁴ No terrace data used in this analysis.

⁵ All data log base 10 transformed except raw data were used for groundwater PO₄ and pH; and plant total N and K.

⁶ Percent silt + clay (square root transformed) used as a covariate (significant for all soil nutrient analytes)

Table 4 (continued). Three-way ANOVA significance table for shallow groundwater, soil, and leaf tissue nutrients by watershed (Santa Clara River⁷, Calleguas Creek), land use (agricultural, residential, open space), degree of infestation (none, small, large).

Nutrient analyte	Factors						
	Watershed	Land use	Degree of infestation	Watershed x land use	Watershed x degree of infestation	Land use x degree of infestation	Watershed x land use x degree of infestation
<i>Arundo donax</i> Leaf Tissue							
Total N (%)	F_(1,49) = 10.511; P = 0.002**	F _(2,49) = 2.223; P = 0.119	F_(1,49) = 5.081; P = 0.029*	F_(2,49) = 4.974; P = 0.011*	F _(1,49) = 0.088; P = 0.522	F _(2,49) = 0.799; P = 0.456	F _(2,49) = 0.771; P = 0.468
Total P (%)	F_(1,49) = 7.947; P = 0.007**	F _(2,49) = 2.424; P = 0.099	F _(1,49) = 0.425; P = 0.517	F _(2,49) = 1.927; P = 0.156	F _(1,49) = 0.071; P = 0.792	F _(2,49) = 0.535; P = 0.589	F _(2,49) = 0.254; P = 0.777
Total K (%)	F_(1,49) = 5.651; P = 0.021*	F_(2,49) = 5.713; P = 0.006**	F_(1,49) = 4.528; P = 0.038*	F _(2,49) = 0.315; P = 0.731	F _(1,49) = 0.040; P = 0.843	F_(2,49) = 3.386; P = 0.042*	F _(2,49) = 0.234; P = 0.793

Legend: * = 0.05 ≥ P > 0.01 = significant, ** = 0.01 ≥ P > 0.001 = highly significant, *** = P ≤ 0.001 = very highly significant

⁷ No terrace data used in this analysis.

Table 5. Mean concentrations of shallow groundwater, soil, and leaf tissue nutrients and soil grain size in floodplains and results of the one-way ANOVA by watershed factor.

Nutrient analyte	Mean (\pm SE)				Significance values ⁸
	Reference sites	Topanga Canyon	Santa Clara River	Calleguas Creek	
Shallow Groundwater Nutrients					
Total N (mg/L)⁹	1.11 (0.87–1.43)	4.03 (3.68–4.41)	5.22 (4.60–5.93)	8.02 (6.92–9.29)	F_(3,128) = 16.119; P < 0.001***
NO₃-N + NO₂-N (mg/L)	0.14 (0.11–0.16)	0.17 (0.14–0.19)	0.27 (0.23–0.32)	1.08 (0.80–1.46)	F_(3,128) = 14.711; P < 0.001***
NH₄-N (mg/L)	0.26 (0.21–0.33)	0.33 (0.27–0.40)	0.31 (0.28–0.35)	0.46 (0.39–0.54)	F _(3,128) = 1.710; P = 0.168
PO₄ (mg/L)¹⁰	0.53 \pm 0.03	0.66 \pm 0.09	0.64 \pm 0.10	2.67 \pm 0.38	F_(3,128) = 16.664; P < 0.001***
pH	7.75 \pm 0.09	7.80 \pm 0.06	7.39 \pm 0.05	7.25 \pm 0.05	F_(3,128) = 20.847; P < 0.001***
Soil Nutrients and Grain Size¹¹					
NO₃-N (ppm)	1.33 (0.89–1.98)	1.11 (0.91–1.36)	0.75 (0.65–0.87)	2.13 (1.75–2.60)	F_(3,127) = 9.047; P < 0.001***
PO₄-P (ppm)	7.23 (6.10–8.57)	4.84 (4.27–5.50)	4.14 (3.72–4.60)	9.71 (8.85–10.64)	F_(3,12) = 23.592; P < 0.001***
silt + clay (%)	20.1 (17.4–22.9)	12.8 (11.6–14.0)	25.3 (22.9–27.9)	11.18 (9.9–12.5)	F_(3,128) = 13.510; P < 0.001***
Leaf Tissue Nutrients					
Total N (%) (<i>Salix laevigata</i>)	1.78 \pm 0.15	1.87 \pm 0.13	2.40 \pm 0.12	2.27 \pm 0.10	F_(3,47) = 6.113; P = 0.001***
Total N (%) (<i>Arundo donax</i>)	No Data	2.19 \pm 0.10	2.50 \pm 0.08	2.88 \pm 0.10	F_(2,78) = 11.982; P < 0.001***
Total P (%) (<i>Salix laevigata</i>)	0.14 \pm 0.01	0.13 (0.125–0.134)	0.16 (0.147–0.164)	0.19 \pm 0.01	F_(3,47) = 8.595; P < 0.001***
Total P (%) (<i>Arundo donax</i>)	No Data	0.17 \pm 0.008	0.17 \pm 0.006	0.19 (0.184–0.193)	F_(2,78) = 4.364; P = 0.016*
Total K (%) (<i>Salix laevigata</i>)	1.25 \pm 0.17	1.33 \pm 0.06	1.44 \pm 0.07	1.41 \pm 0.07	F _(3,47) = 0.860; P = 0.469
Total K (%) (<i>Arundo donax</i>)	No Data	2.49 \pm 0.10	2.73 \pm 0.07	2.49 \pm 0.09	F_(2,78) = 3.172; P = 0.047*

Legend: * = 0.05 \geq P > 0.01 = significant, ** = 0.01 \geq P > 0.001 = highly significant*** = P \leq 0.001 = very highly significant
SE = standard error

⁸ No terrace data used in this analysis.

⁹ All data log base 10 transformed except those noted otherwise.

¹⁰ Raw data were used for groundwater PO₄ and pH; and plant total N and K.

¹¹ Percent silt + clay (square root transformed) was used as a covariate

Table 6. Three-way ANOVA significance table for soil and leaf tissue nutrients by land use (agricultural, residential, and open space), fluvial geomorphic location (terrace and floodplain), and degree of infestation (none, small, and large). Analyses were only conducted on Santa Clara River sites. Only *A. donax* from small and large infestations (levels) were used in leaf tissue ANOVAs.

Nutrient analyte	Factors						
	Land use	Fluvial geomorphic location	Degree of infestation	Land use x fluvial geomorphic location	Land use x degree of infestation	Location x degree of infestation	Land use x location x degree of infestation
Soil¹²							
NO₃-N (ppm)¹³	F_(2,84) = 5.101; P = 0.008*	F_(1,84) = 51.453; P < 0.001***	F _(2,84) = 2.662; P = 0.076	F _(2,84) = 3.643; P = 0.030	F _(4,84) = 1.661; P = 0.167	F_(2,84) = 4.626; P = 0.012*	F _(4,84) = 1.636; P = 0.173
PO₄-P (ppm)	F_(2,84) = 8.081; P = 0.001***	F_(1,84) = 60.137; P < 0.001***	F_(2,84) = 4.613; P = 0.013*	F_(2,84) = 12.129; P < 0.001***	F_(4,84) = 4.507; P = 0.002**	F_(2,84) = 3.689; P = 0.029*	F_(2,84) = 3.205; P = 0.017*
Silt + Clay (%)	F _(2,85) = 1.772; P = 0.176	F_(1,85) = 4.343; P = 0.040*	F _(2,85) = 1.517; P = 0.225	F _(2,85) = 0.593; P = 0.555	F _(4,85) = 0.865; P = 0.488	F_(2,85) = 3.206; P = 0.045*	F _(4,85) = 0.343; P = 0.848
pH	F_(2,85) = 9.685; P < 0.001***	F _(1,85) = 0.297; P = 0.587	F _(2,85) = 0.970; P = 0.383	F _(2,85) = 2.366; P = 0.100	F _(4,85) = 0.991; P = 0.417	F _(2,85) = 1.738; P = 0.182	F _(4,85) = 1.144; P = 0.341
Arundo donax Leaf Tissue							
Total N (%)¹⁴	F_(2,60) = 6.029; P = 0.004**	F _(1,60) = 0.862; P = 0.357	F_(1,60) = 5.876; P = 0.018*	F _(2,60) = 2.572; P = 0.085	F _(2,60) = 0.109; P = 0.897	F _(1,60) = 0.964; P = 0.330	F _(2,60) = 0.239; P = 0.788
Total P (%)	F _(2,60) = 1.009; P = 0.371	F _(1,60) = 3.015; P = 0.088	F _(1,60) = 2.425; P = 0.125	F _(2,60) = 1.172; P = 0.317	F _(2,60) = 0.174; P = 0.841	F _(1,60) = 1.481; P = 0.228	F _(2,60) = 0.508; P = 0.604
Total K (%)	F _(2,60) = 0.587; P = 0.559	F _(1,60) = 1.637; P = 0.206	F_(1,60) = 9.909; P = 0.003**	F _(2,60) = 2.775; P = 0.070	F _(2,60) = 1.012; P = 0.370	F _(1,60) = 1.198; P = 0.278	F _(2,60) = 2.879; P = 0.064

Legend: * = 0.05 ≥ P > 0.01 = significant, ** = 0.01 ≥ P > 0.001 = highly significant*** = P ≤ 0.001 = very highly significant

¹² Percent silt + clay (square root transformed) used as a covariate for all soil nutrients.

¹³ Soil nutrient data and pH were log₁₀ base transformed.

¹⁴ Raw data was used for leaf tissue total N and K. Leaf tissue total P was log₁₀ base transformed.

Table 7. Two-way ANOVA of plant abundance (% cover), density (stems m⁻²), and shoot height (cm) by factors of plant type (*A. donax* and native plant species) and pre- and post-fire time periods.

Factors and interactions	Plant abundance	Density	Height (shoot elongation)
Plant type	F _(1,80) = 59.123; P < 0.001***	F _(1,852) = 322.769; P < 0.001***	F _(1,3231) = 819.299; P < 0.001***
Time period	F _(1,80) = 15.166; P < 0.001***	F _(5,852) = 1.700; P = 0.132	F _(8,3231) = 442.074; P < 0.001***
Plant type x time period	F _(1,80) = 0.006; P = 0.937	F _(5,852) = 2.850; P = 0.015*	F _(8,3231) = 21.295; P < 0.001***
r²	0.626	0.287	0.591

* = 0.05 ≥ P > 0.01 = significant; ** = 0.01 ≥ P > 0.001 = highly significant; *** = P ≤ 0.001 = very highly significant

Table 8. Two-way ANOVA of shoot elongation rate (cm d^{-1}) and relative growth rate (RGR; $\text{g g}^{-1}\text{day}^{-1}$) by factors of plant type (*A. donax* and native plant species) and month post-fire (12 months).

Factors and interactions	Shoot elongation rate	RGR
Plant type	$F_{(9,319)} = 16.178; P < 0.001^{***}$	$F_{(9,315)} = 44.146; P < 0.001^{***}$
Month post-fire	$F_{(1,319)} = 76.481; P < 0.001^{***}$	$F_{(1,315)} = 81.154; P < 0.001^{***}$
Plant type x month post-fire	$F_{(9,319)} = 6.845; P < 0.001^{***}$	$F_{(9,315)} = 55.397; P < 0.001^{***}$
r^2	0.556	0.762

Table 9. Two-way ANOVA of soil nutrients (NH₄-N, NO₃-N, and P) by factors of plant type (*A. donax* and native plant species) and pre- and post-fire time periods. Soil grain size (% silt + clay) was used as a covariate. NH₄-N and NO₃-N were ln transformed.

Factors and interactions	NH₄-N (ppm)	NO₃-N (ppm)	P (ppm)
Plant type	F _(2,44) = 2.002; P = 0.164	F _(2,44) = 0.612; P = 0.438	F _(2,44) = 3.021; P = 0.089
Time period	F _(1,44) = 8.125; P = 0.001***	F _(1,44) = 2.670; P = 0.080	F _(1,44) = 6.002; P = 0.005**
Plant type x time period	F _(2,44) = 5.459; P = 0.008**	F _(2,44) = 2.268; P = 0.115	F _(2,44) = 2.224; P = 0.120
Silt + clay	F _(1,44) = 11.737; P = 0.001***	F _(1,44) = 2.710; P = 0.107	F _(1,44) = 5.803; P = 0.020*
r²	0.555	0.255	0.394

FIGURES

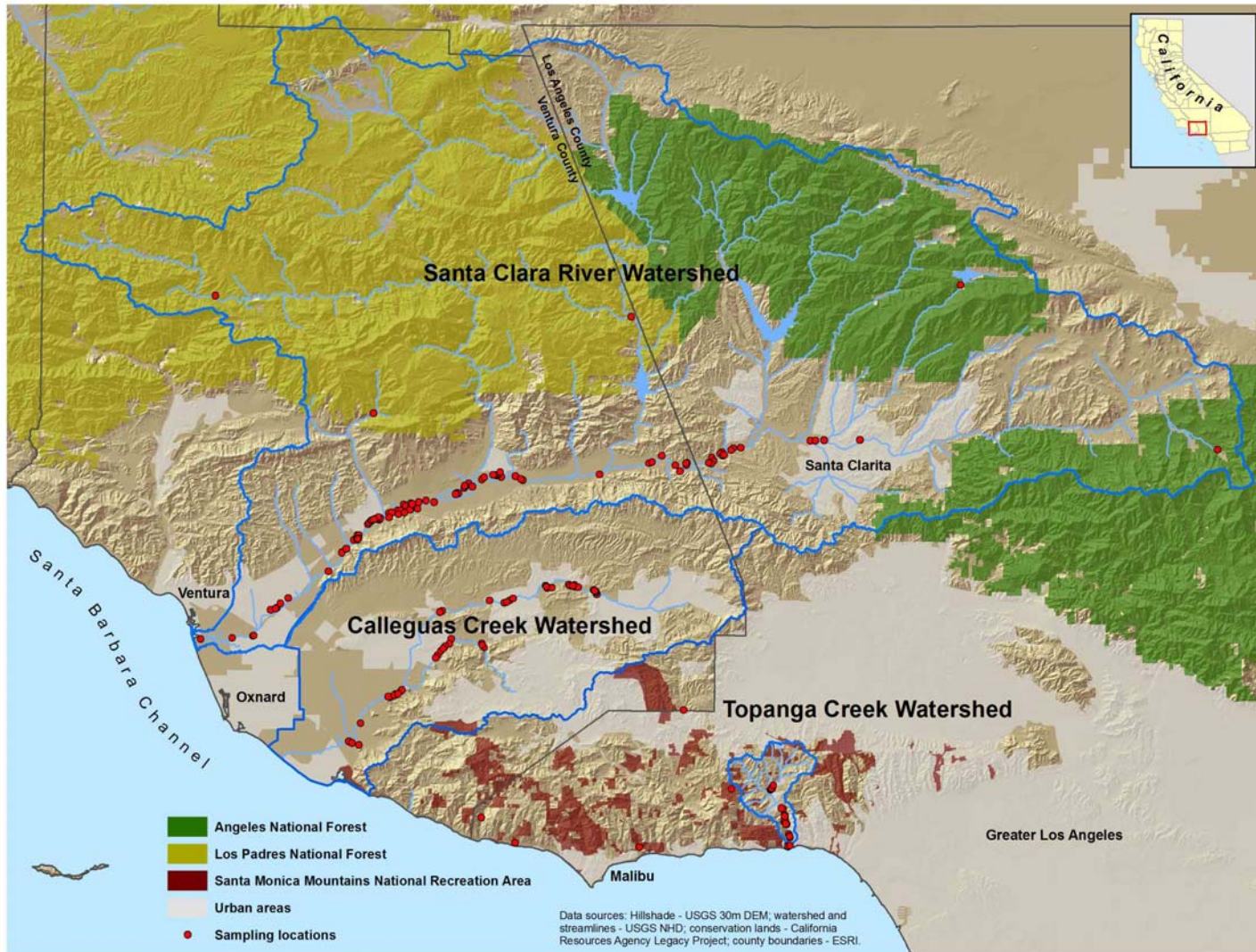


Figure 1. The three study watersheds in Ventura and Los Angeles Counties, California.

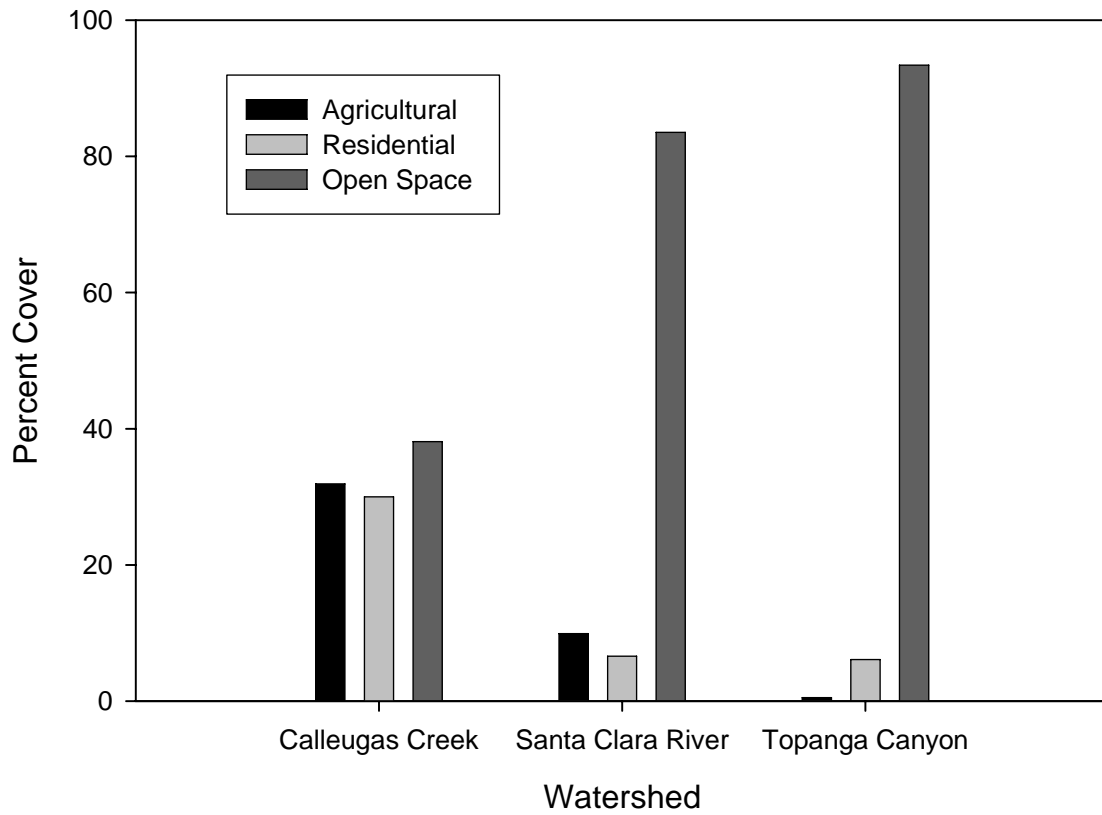


Figure 2. Distribution of land use type within the three studied watersheds.

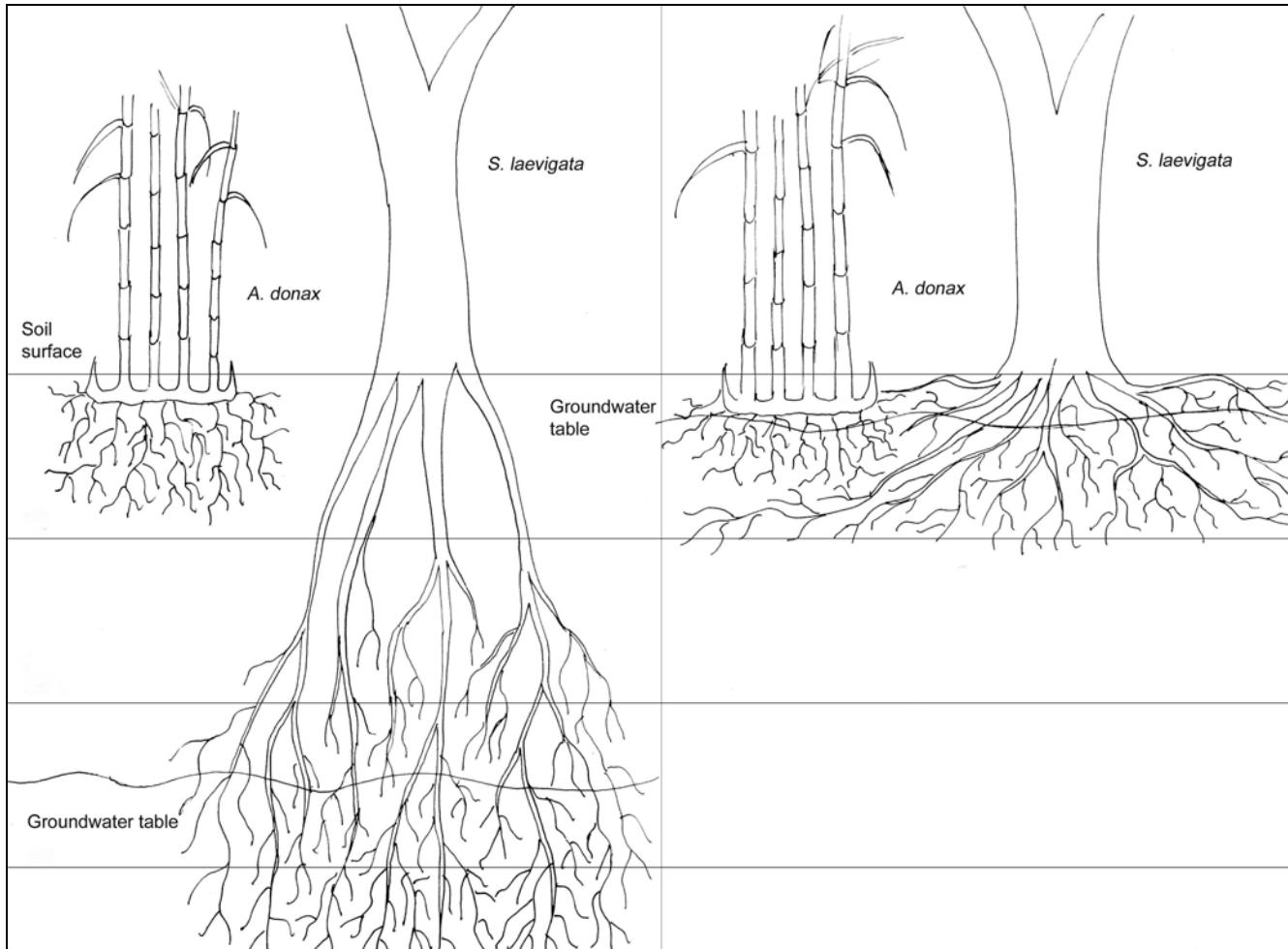


Figure 3. Diagram of *A. donax* and *S. laevigata* rooting depths and distribution in a) deep and b) shallow groundwater table conditions.

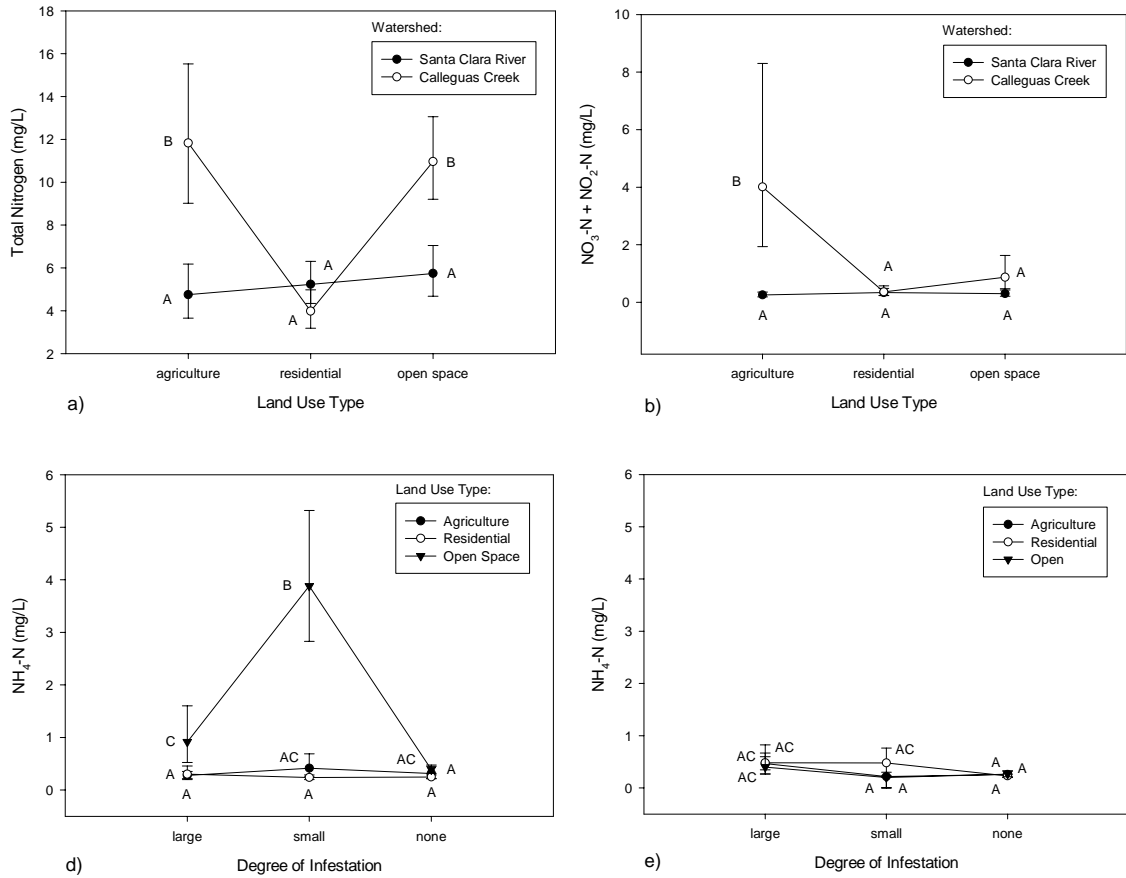


Figure 4. Interaction plots for 3-way ANOVA of shallow groundwater nutrients by watershed (Santa Clara River and Calleguas Creek only) x land use (A = agricultural, R = residential, and O = open space) x degree of infestation (N = none, S = small, and L = large). Plots include two-way interaction plots for shallow groundwater a) total N, and b) NO₃-N + NO₂-N (small infestation data removed), and three-way interaction plots for shallow groundwater NH₄-N in c) Calleguas Creek and d) Santa Clara River.

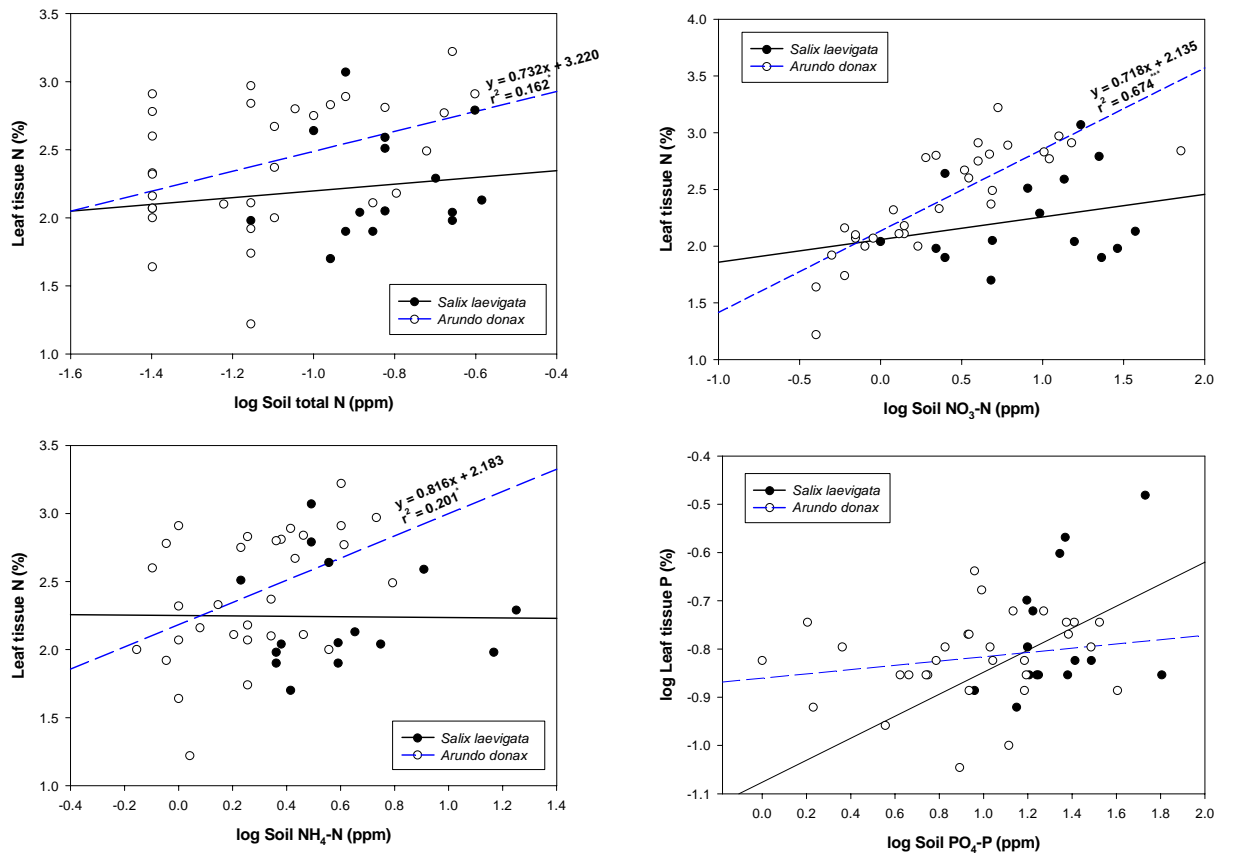


Figure 5. Linear regression relationships between shallow groundwater and soil nutrients (independent variable) found in terrace sites and associated leaf tissue nutrients (response variable) of target plants by plant species. Only Santa Clara River data was used. Equations were only included for significant relationships. Leaf tissue N/P and soil (a) total N, (b) NO₃-N, (c) NH₄-N, and (d) PO₄-P.

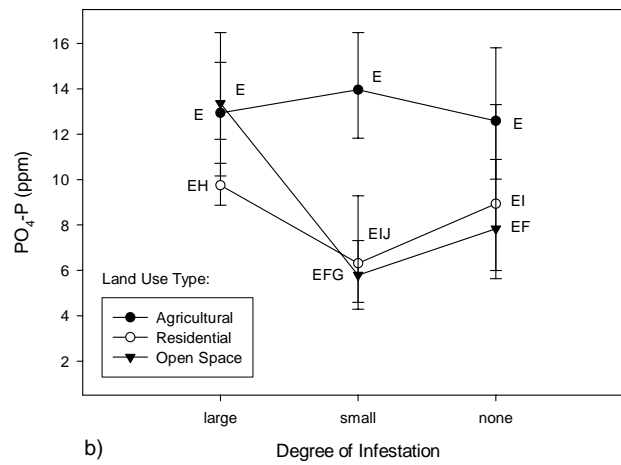
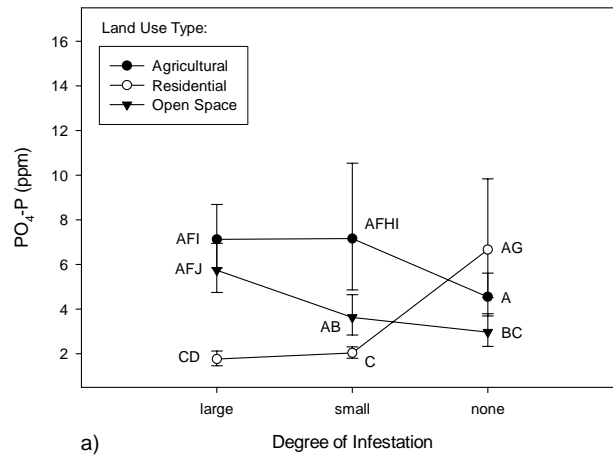


Figure 6. Interaction plots for 3-way ANOVA of soil nutrients by watershed (Santa Clara River and Calleguas Creek only) x land use (A = agricultural, R = residential and O = open space) x degree of infestation (N = none, S = small, and L = large). Plots show the three-way interaction for soil PO₄-P in a) Santa Clara River and b) Calleguas Creek.

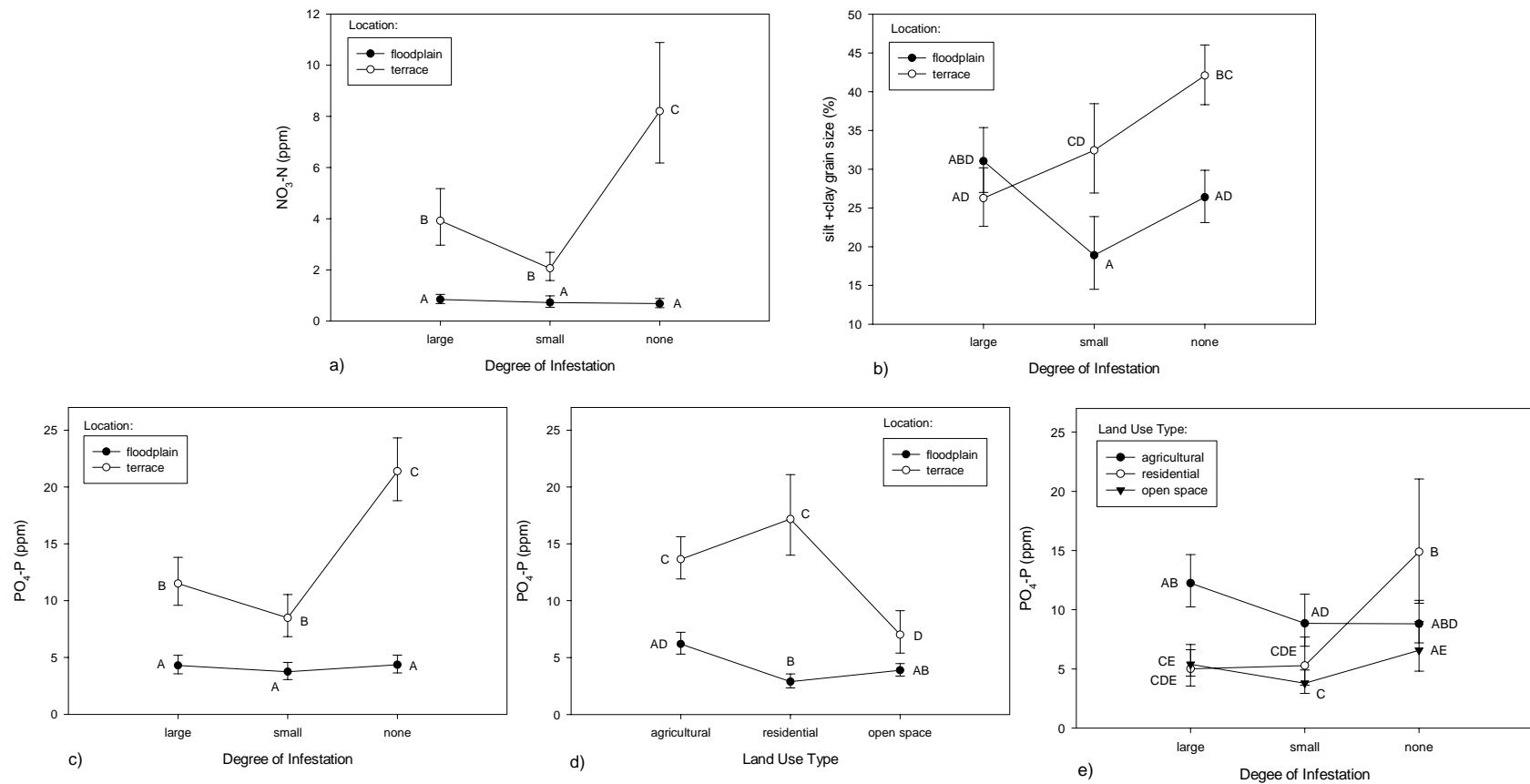


Figure 7. Interaction plots for 3-way ANOVA of soil nutrients and grain size for land use (A = agricultural, R = residential, and O = open space) x degree of infestation (N = none, S = small, and L = large) x fluvial geomorphic location (terrace and floodplain) for Santa Clara River only. Plots include 2-way interactions of a) soil $\text{NO}_3\text{-N}$ and b) silt + clay and 3-way interaction of soil $\text{PO}_4\text{-P}$ (c, d, and e).

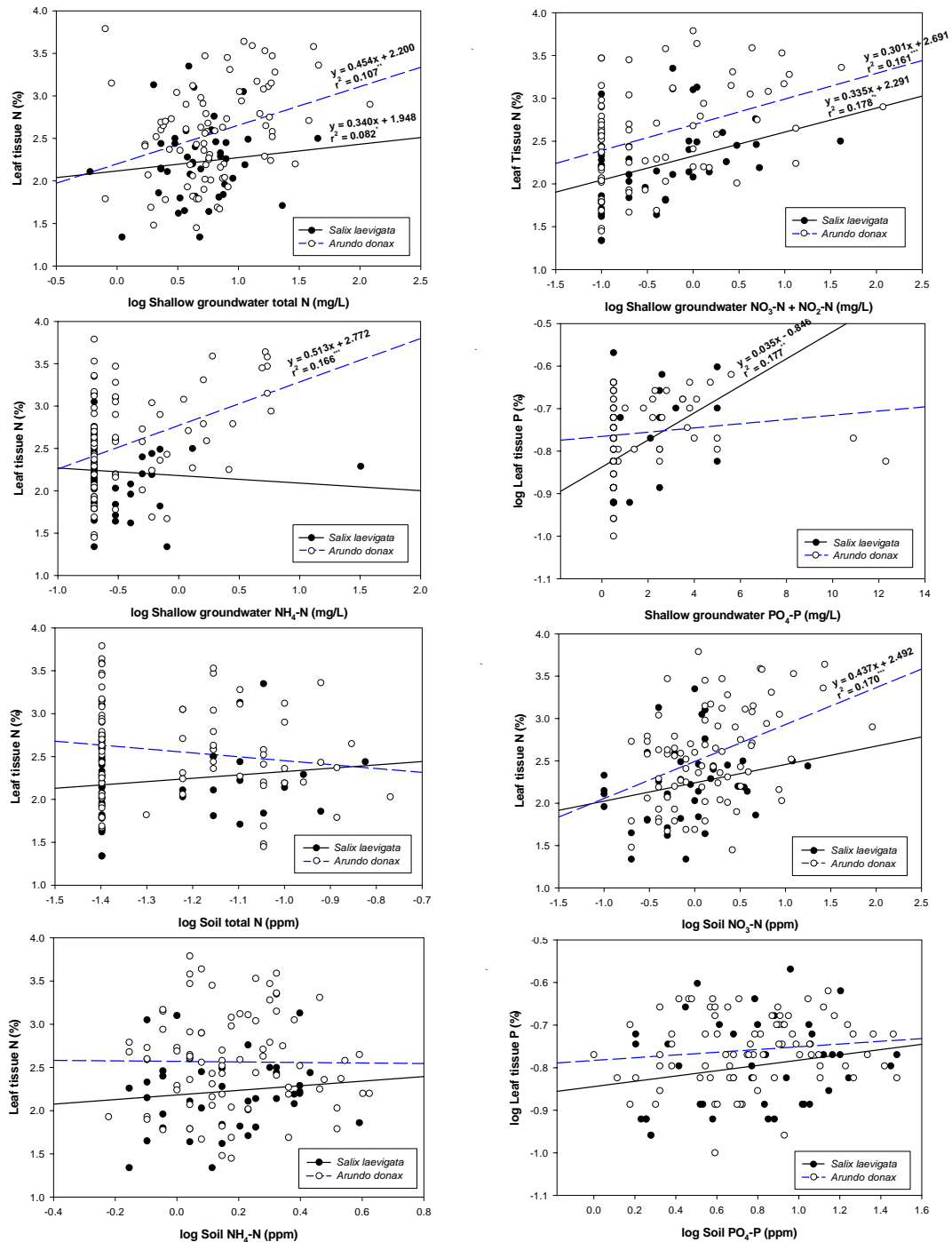


Figure 8. Linear regression relationships between shallow groundwater and soil nutrients (independent variable) found in floodplain sites and associated leaf tissue nutrients (response variable) of target plants by plant species. Equations were only included for significant relationships. Leaf tissue N/P and soil (a) total N, (b) NO₃-N, (c) NH₄-N, and (d) PO₄-P. Leaf tissue N/P and shallow groundwater (e) total N, (f) NO₃-N + NO₂-N, (g) NH₄-N, and (h) PO₄-P.

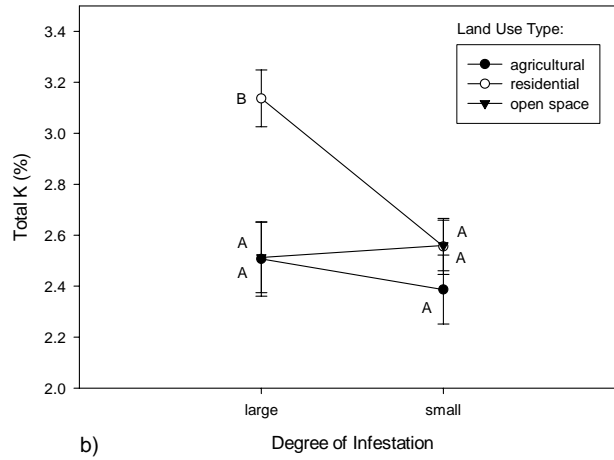
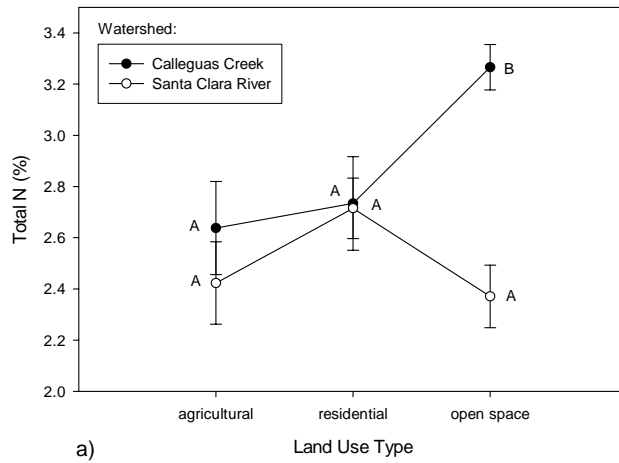


Figure 9. Interaction plots for 3-way ANOVA of *A. donax* leaf tissue nutrients by watershed (Santa Clara River and Calleguas Creek only) x land use (A = agricultural, R = residential, O = open space) x degree of infestation (S = small, L = large). Plots illustrate the two-way interaction for a) leaf tissue N and b) leaf tissue K.

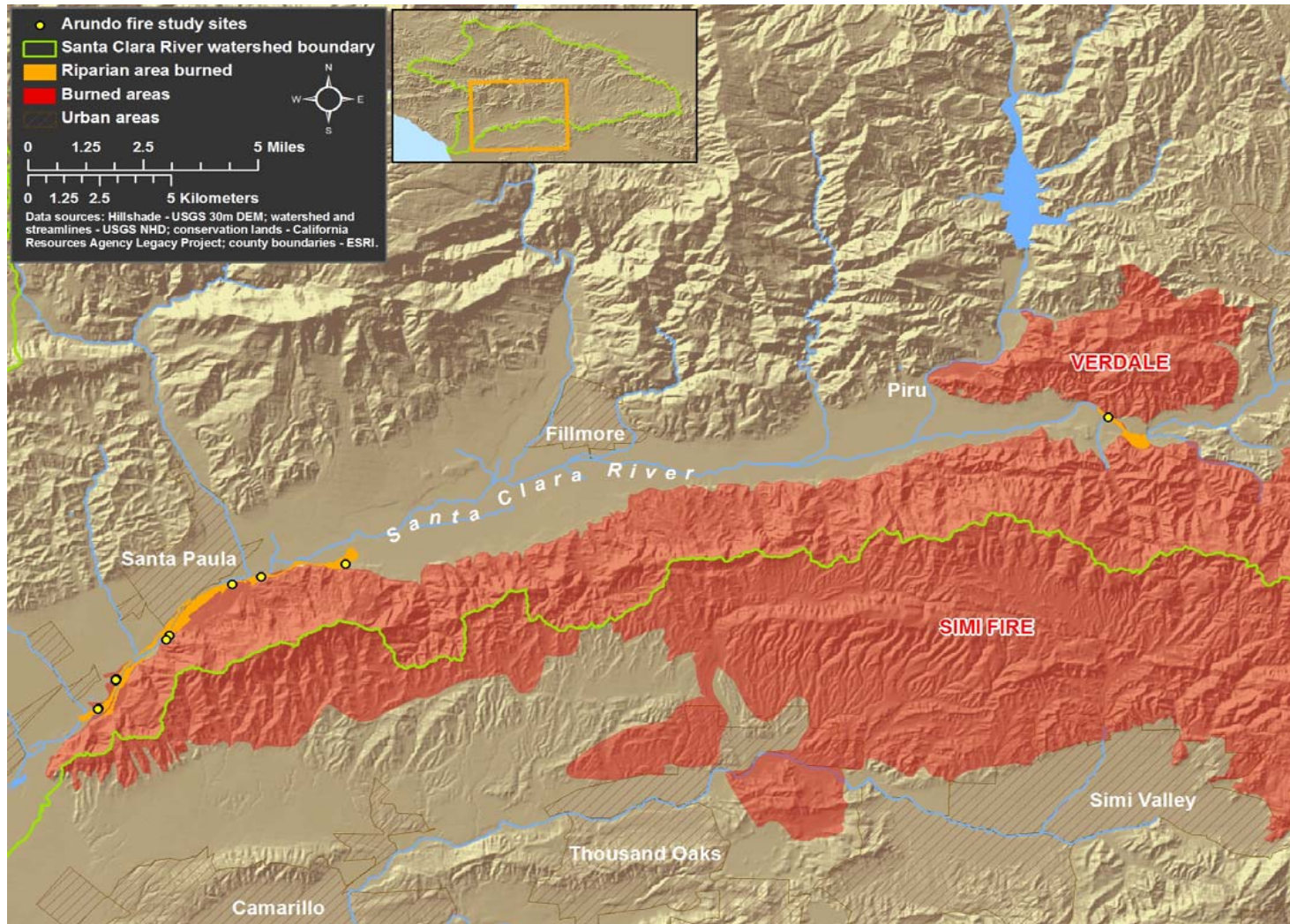


Figure 10. Location of study sites in riparian terraces of the Santa Clara River, Ventura County, California.

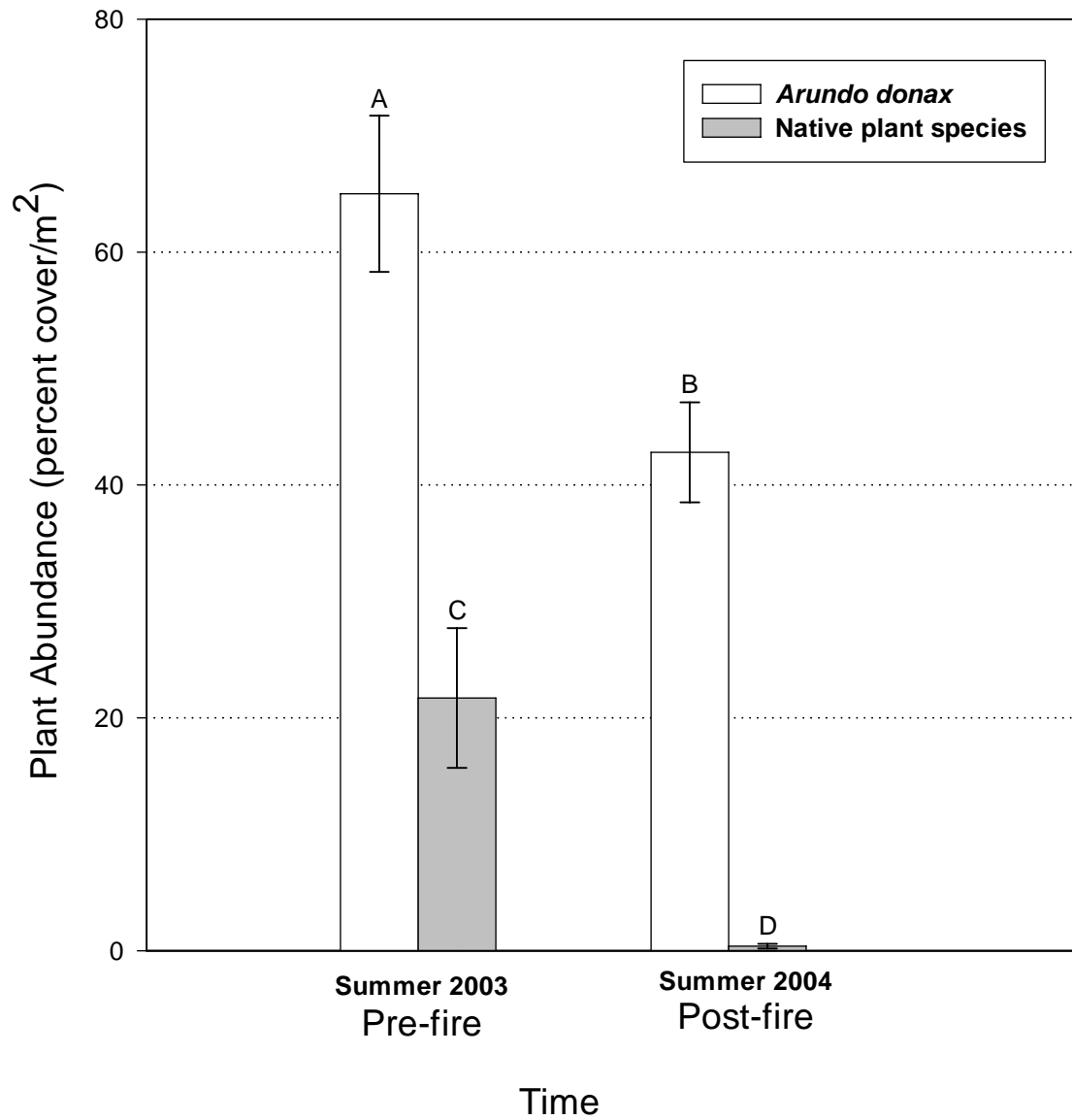


Figure 11. Abundance of *A. donax* compared to native riparian plant species before the October 2003 wildfire (summer 2003) and a year later. Letters denote results of post-hoc hypothesis tests (comparison of means) with significance recognized at $\alpha < 0.05$.

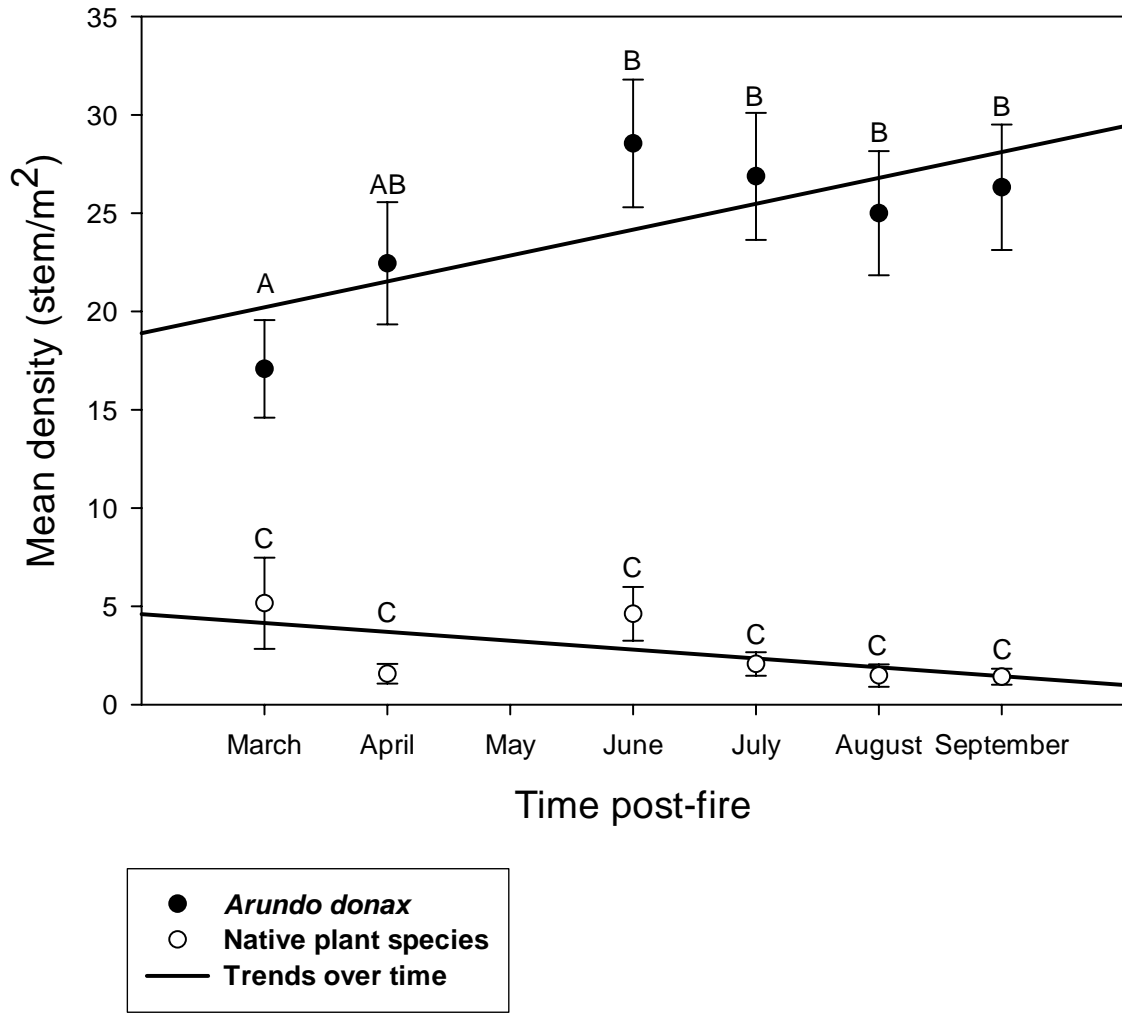


Figure 12. Mean density of *A. donax* versus native plants after the October 2003 wildfire. Regression lines illustrate trends over time. Letters denote results of post-hoc hypothesis tests (comparison of means) with significance recognized at $\alpha < 0.05$.

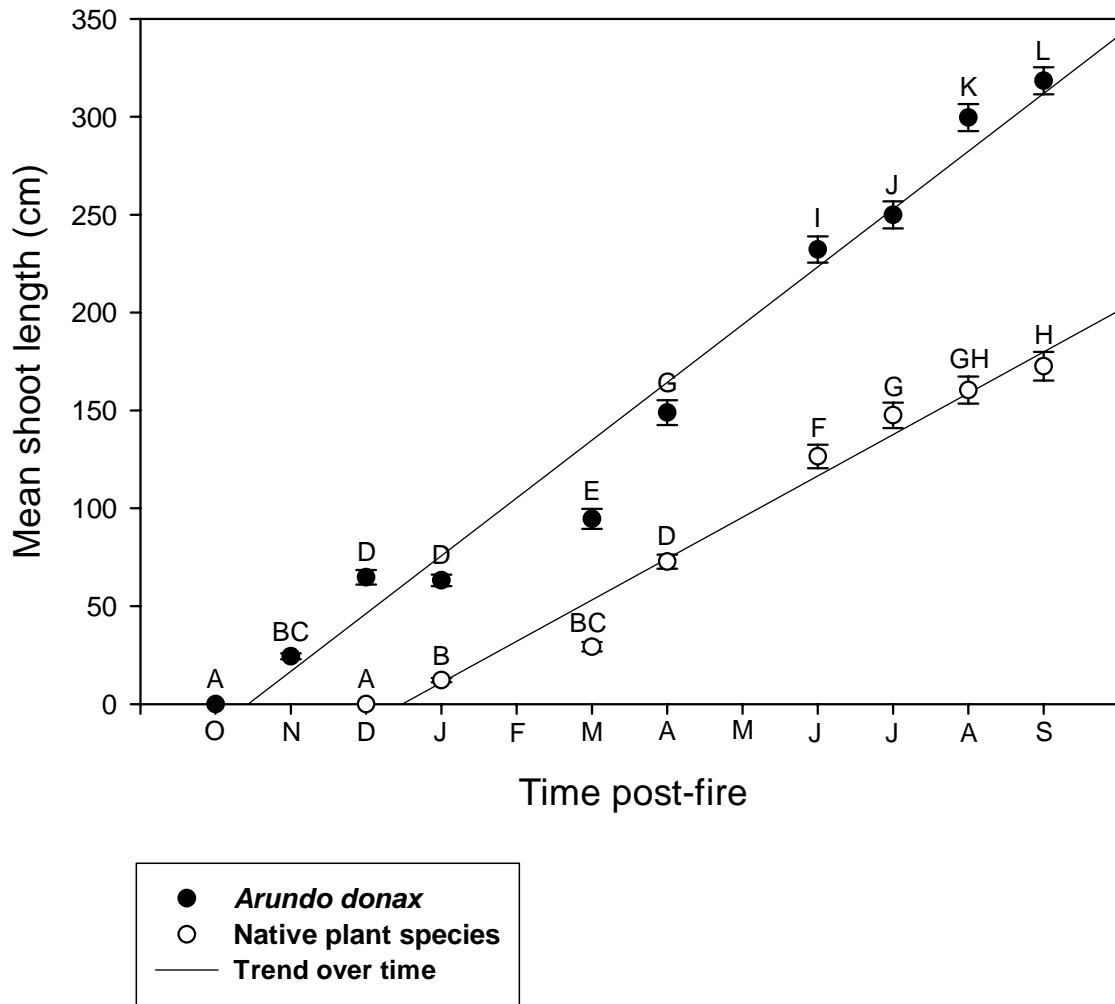


Figure 13. Monthly mean shoot length of *A. donax* compared to native plant species for a year following the October 2003 wildfires. Regression lines illustrate trends over time. Letters denote results of post-hoc hypothesis tests (comparison of means) with significance recognized at $\alpha < 0.05$.

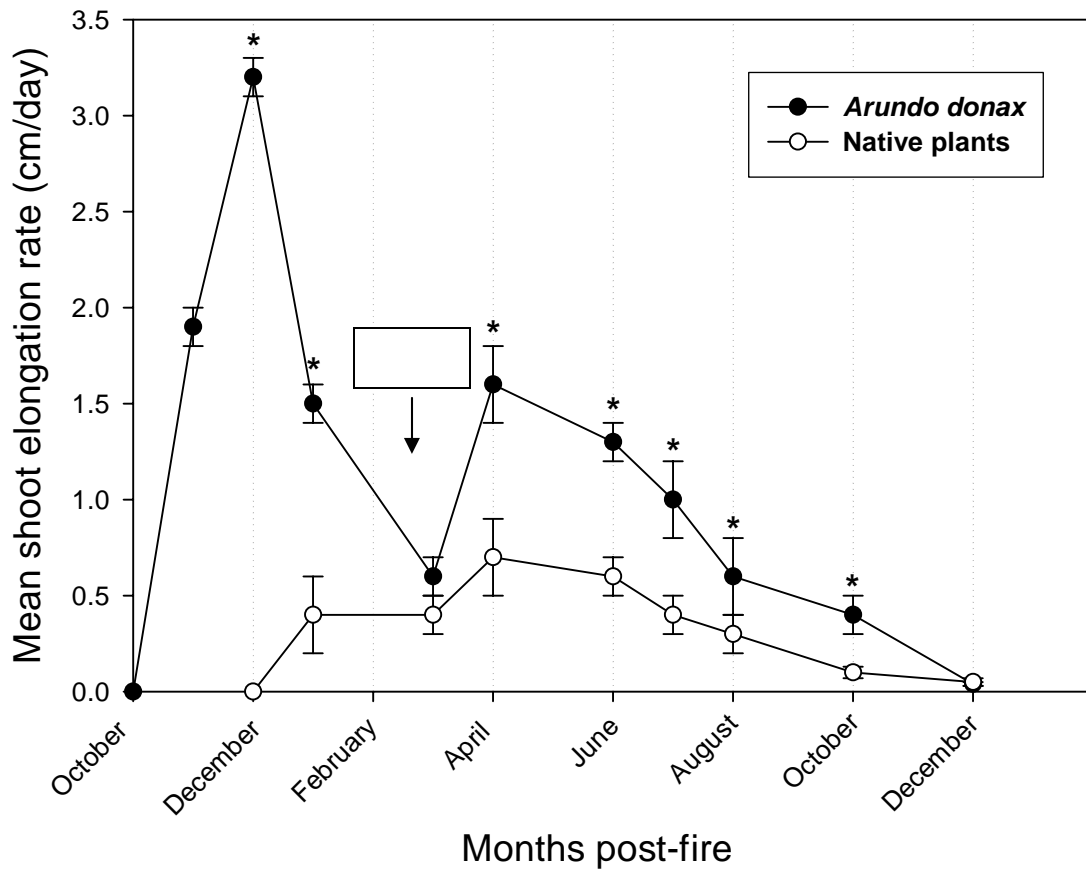


Figure 14. Mean monthly shoot elongation rates of *A. donax* compared to native plants after being burned in the October 25, 2003 wildfire. Asterisks denote significant differences in means between *A. donax* and native plants at each time period based on results of post-hoc hypothesis tests (comparison of means) with significance recognized at $\alpha < 0.05$.

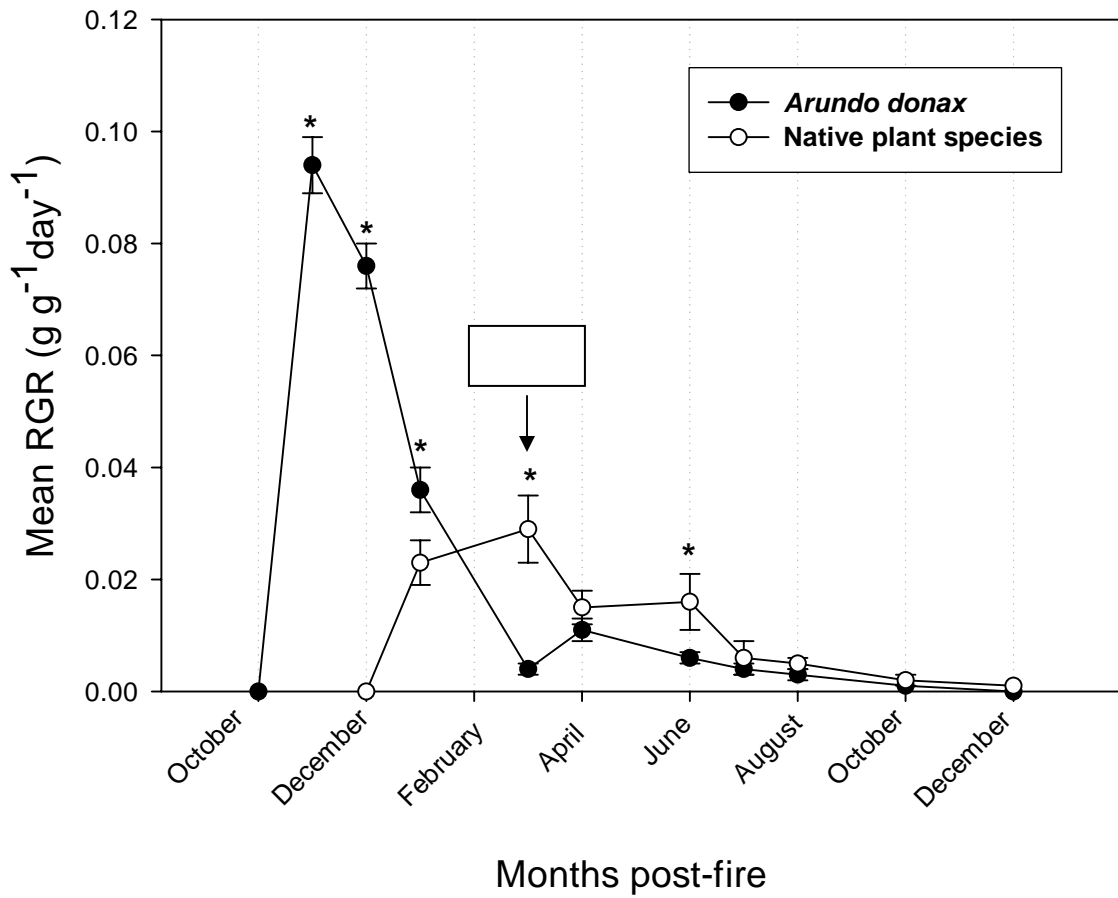


Figure 15. Relative growth rate of *A. donax* compared to native plant species. Asterisks denote significant differences in means between *A. donax* and native plants at each time period based on results of post-hoc hypothesis tests (comparison of means) with significance recognized at $\alpha < 0.05$.

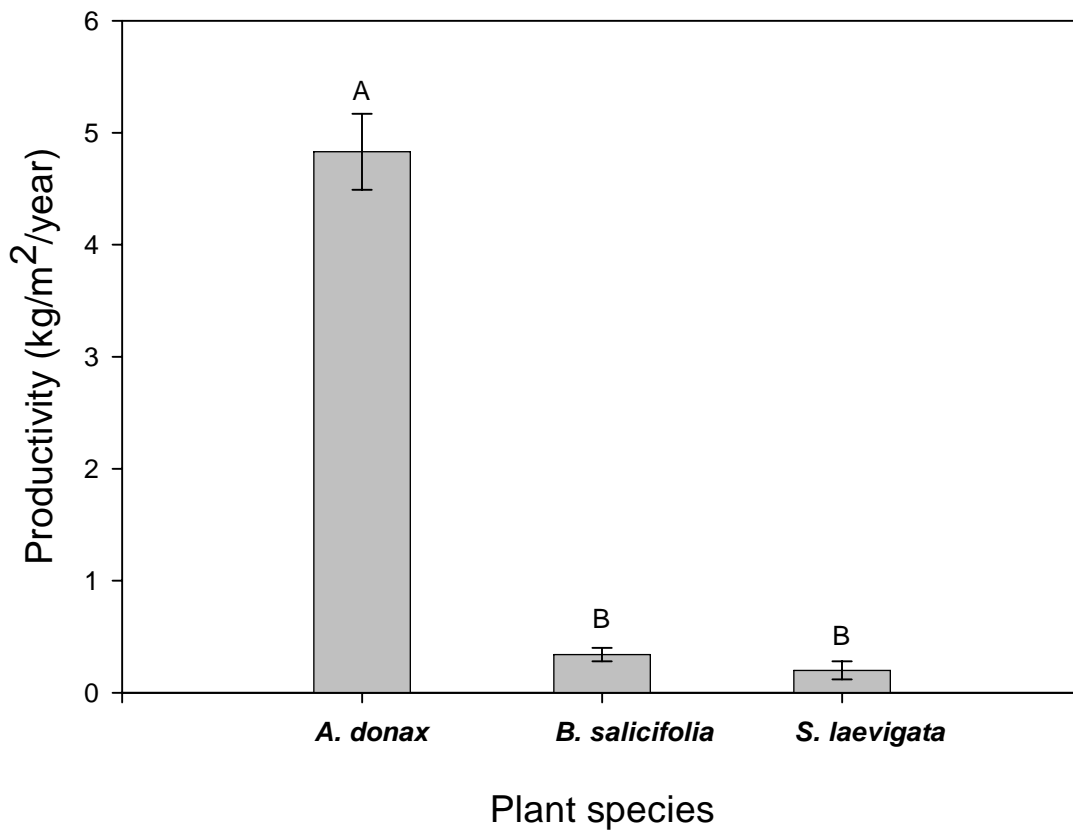


Figure 16. Mean productivity (kg/m²/year) of *A. donax* compared to native plant species in burned sites. Letters denote results of post-hoc hypothesis tests (comparison of means) with significance recognized at $\alpha < 0.05$.

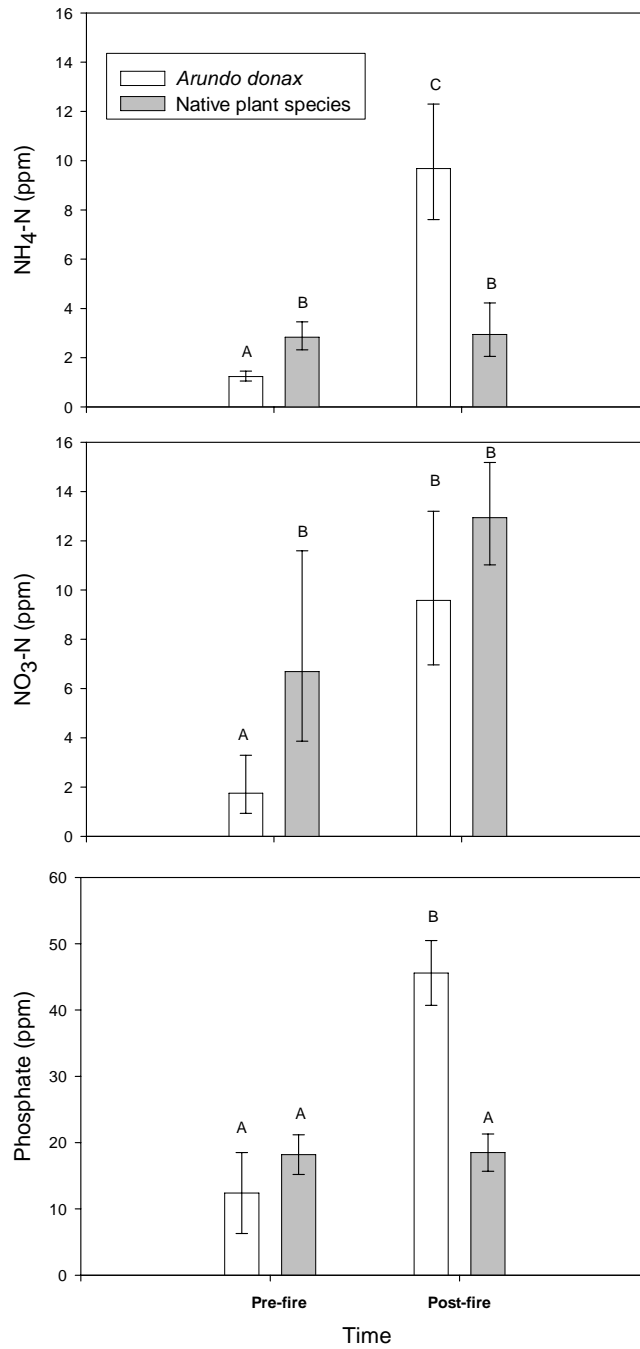


Figure 17. Pre- and post-fire mean nutrient levels of soil adjacent to *A. donax* compared to soil next to native plants. Letters denote results of post-hoc hypothesis tests (comparison of means) with significance recognized at $\alpha < 0.05$.

LIST OF PUBLICATIONS

- Coffman, G.C. 2007. Factors Influencing Invasion of Giant Reed (*Arundo donax*) in Riparian Ecosystems of Mediterranean-type Climate Regions. Ph.D. Dissertation, University of California, Los Angeles.
- Coffman, G. C. in press. Giant reed (*Arundo donax*) invasion: Effects on streams and water resources. Encyclopedia of Water Science.
- Coffman, G. C., R. F. Ambrose, and P. W. Rundel. 2004. Invasion of *Arundo donax* in river systems of Mediterranean climates: causes, impacts and management strategies. Pages 138 (full text on cd) in M. Arianoutsou and V. P. Papanastasis, editors. 10th International Conference on Mediterranean Climate Ecosystems. Millpress, Rhodes, Greece.