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Factors Influencing Invasion of Giant Reed (*Arundo donax*) in Riparian Ecosystems of Mediterranean-type Climate Regions

A dissertation submitted in partial satisfaction of the
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by

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DEDICATION

I dedicate this dissertation to my parents
Mary Lou Coffman
and
Glenn Norman Coffman
Without their constant love and support over the years
this dissertation would not have been possible.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

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ABSTRACT OF THE DISSERTATION

Factors Influencing Invasion of Giant Reed (*Arundo donax*) in Riparian Ecosystems of Mediterranean-type Climate Regions

by

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Doctor of Philosophy in Environmental Health Sciences
University of California, Los Angeles, 2007
Professor Richard F. Ambrose, Chair

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 my dissertation is that the current abundance of nutrients, water, light, and fire in riparian ecosystems of Mediterranean-type climate promotes *A. donax* invasion. A two-year field experiment in a riparian ecosystem on the Santa Clara River in California showed that *A. donax* produced greater biomass than native species under high soil moisture, light, and nutrient levels, and its biomas-s in monoculture was much greater than most species and treatment levels. However, results suggest that high resource levels and this new plant functional group in these riparian ecosystems, rather than superior resource competition, promote *A. donax*'s competitive exclusion of native riparian species. 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 NO_3-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 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.

CHAPTER 1 -

INTRODUCTION

Invasion of riparian ecosystems by the alien plant giant reed, *Arundo donax* L., is one of the most serious threats to rivers in Mediterranean-type climate regions worldwide. *Arundo donax* has successfully invaded many rivers in these regions, forming extensive monocultures and altering physical and biological processes. In California, infestations of *A. donax* are known to increase risks of flooding, create unnatural fire hazards, outcompeting indigenous riparian species for scarce water resources, and reduce the value of riparian habitat for most wildlife (Dudley and Collins 1995, Bell 1997, DiTomaso 1998, Dudley 2000). Although introduced several hundred years ago to southern California, rapid expansion of *A. donax* in natural riparian ecosystems appears to have occurred in the last 35 years (Bell 1997).

Researchers have suggested that natural and human disturbances, which are prevalent in Mediterranean-type climate regions such as California, are primary factors contributing to the extensive distribution of *A. donax* along rivers in these areas (Rieger and Kreager 1989, Bell 1997). Large winter floods occur naturally every few years and remove riparian plants from floodplains, thereby creating open substrates for recolonization. Pieces of *A. donax* (rhizomes and culms) are dispersed downstream during flooding and establish vegetatively wherever they are deposited (Else 1996, Else and Zedler 1996). However, natural disturbance along rivers is not a new phenomenon in Mediterranean-type climates; river systems have long been dynamic components of the landscape in these regions (Mount 1995). Most physical human disturbance of rivers and their watersheds dates back to human settlement of these regions (Mount 1995, Rundel et al. 1998), which occurred much earlier than the onset of *A. donax* invasion. Therefore, other factors must contribute to the relatively recent success of this plant's invasion.

More recently, humans have altered riparian ecosystem processes by increasing nutrient delivery from adjacent land use practices, importing water for the ever-growing population, exporting water for agriculture, removing mature riparian vegetation for development, and increasing fire frequency in adjacent shrubland communities. I investigated the influence of these factors on invasion of rivers by *A. donax* in southern California. I hypothesized that increased nutrient, water, and light availability, as well as the introduction of fire into riparian ecosystems, has contributed to successful *A. donax* invasion in Mediterranean-type climate regions.

BACKGROUND

Throughout history, man has embraced the idea of cultivating exotic plants and animals worldwide for agricultural, aesthetic, and other purposes. However, moving biological organisms has created a human-induced breakdown of biogeographical barriers to species dispersal and many species that evolved separately are now living together (D'Antonio and Vitousek 1992, Richardson et al. 2000). As far back as 1958, Charles Elton wrote of the terrific dislocations in nature that mixing different organisms from various parts of the world would cause (Elton 1958). Despite his warning, consequences of these introductions of plants and animals had not been fully recognized until recently.

The problem of plant introductions[1] and resulting invasions[2] in Mediterranean-type climate regions has received considerable attention because these regions provide ideal climactic conditions for plant growth (Drake et al. 1989, D'Antonio and Dudley 1993). In California, plant invasions have occurred in many natural ecosystems, including grasslands, woodlands, wetlands, coastal dunes, salt marshes, and riparian areas (Kruger et al. 1989, Rejmanek 1989, Rejmanek et al. 1991). Aquatic ecosystems such as rivers and wetlands are among the world's most heavily invaded systems (Mooney et al. 1986, Kruger et al. 1989, Pysek and Prach 1994, Alpert et al. 2000, Rundel 2000). Natural and altered disturbance regimes and anthropogenic enhancement of nutrients are thought to contribute to success of plant invasion in rivers (Crawley 1986, Ashton and Mitchell 1989, Drake et al. 1989, Hobbs 1989, Hobbs and Huenneke 1992, Alpert et al. 2000).

Riparian ecosystems occupy a unique area in the landscape; as ecotones between aquatic and terrestrial ecosystems, they have naturally high species diversity, a diverse array of biological and physical processes, and a mosaic of vegetation types and structural components due to natural disturbance regimes (Gregory et al. 1991, Malanson 1993, Naiman and Decamps 1997). Natural dynamic disturbance regimes of river and stream systems in Mediterranean-type climates likely promote the spread of invasive plant species through these systems. For example, intense but infrequent winter flooding

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[1] Introduction implies human transport of a plant across a major geographic barrier.

[2] Invasion refers to an introduced plant that produces reproductive offspring in areas distant from the origin of its introduction (>100m in <50 years). Richardson et al. (2000) suggested several barriers to plant introduction, naturalization, and invasion by including geographic, environmental (local), reproductive, dispersal, environmental (disturbed habitats), and environmental (natural habitats).

scours stream corridors and exposes vast areas of sandy floodplain, channels, and terraces (Gasith and Resh 1999), rendering them vulnerable to disturbance colonizers, which are primarily invasive, weedy plants. Weedy plants are able to establish and grow quickly in these open disturbed areas, often out-competing the indigenous riparian plant species for light, water, and nutrients (Baker 1974).

Historically, riparian plant communities in Mediterranean-type climates have been particularly impacted by human perturbations due to the ephemeral and braided nature of the river systems in which they are found (Mount 1995). Since early human settlement of these areas, humans have dammed, channelized, mined, rerouted, diverted, and developed floodplains of rivers, resulting in great losses and degradation of associated riparian plant communities (Palmer 1993, Mount 1995). These alterations to river systems have left riparian plant communities susceptible to plant invasions by weedy species. Rapid expansion of urban and agricultural development into these regions in the last century has resulted in habitat fragmentation, reduction in biological diversity, and altered distribution of resources in these areas (i.e., water and nutrients) (Aschmann 1991, Palmer 1993). These anthropogenic land-use changes have created conditions that allow for large-scale plant invasion of remaining natural ecosystems (D'Antonio and Dudley 1993).

Arundo donax *Invasion*

Currently, one of the greatest invasive threats to the highly modified river ecosystems of Mediterranean-type climate regions is a tall bamboo-like member of the grass family (Poaceae), giant reed (*Arundo donax* L.). *Arundo donax* appears to be of a broad southern Eurasian origin, extending from Southeast Asia to the Mediterranean Basin, although the precise extent of its native distribution is unclear (Perdue 1958, Zohary 1962, Hickman 1993). The relatively high diversity of herbivores associated with *A. donax* in the Mediterranean Basin compared to other areas where it grows suggests plant-animal co-evolution in that region (Kirk et al. 2003), but *A. donax* might have a broader indigenous range. Introduced to other areas primarily for building materials, erosion control, and windbreaks, it is now successfully established in freshwater systems in tropical to temperate climates worldwide (Polunin and Huxley 1987). In the U.S., *A. donax* has become especially widespread in riparian ecosystems in California's Mediterranean-type climate (Fischer et al. 1978). Although *A. donax* is thought to have been introduced to southern California for building materials and erosion control as early as the 1700s, and it was abundant along the Los Angeles River in the 1820s (Robbins et al. 1951), its widespread expansion in riparian ecosystems appears to be recent (Bell 1997). Currently, *A. donax* infests almost every stream and river system in coastal southern California (Gaffney 2002) (Figure 1). Based on spatial data analyses, researchers estimate more than 1,500 acres of *A. donax* infestations occur throughout rivers in southern California, although only approximately one-third of the riparian areas in coastal southern California have been surveyed (Casanova et al. unpublished data). A comprehensive survey is in progress to verify coverage of *A. donax* infestations in the field throughout all streams and rivers in southern California (Giessow pers. comm.).

Although *A. donax* produces a long plume-like inflorescence with no viable seeds in California (Johnson et al. 2006), *A. donax* spreads rapidly downstream when small pieces of the plant break off, land on bare, moist substrates, and begin to grow (Else 1996, Else and Zedler 1996, Bell 1997, Boose and Holt 1999, Decruyenaere and Holt 2005). Growing at an extremely high rate (4–10 cm per day under optimal conditions) and during all times of the year, *A. donax* quickly establishes on unvegetated or sparsely vegetated soil and grows taller than 2-4 m after only a few months and may eventually reach up to 8 m (Perdue 1958). Singh et al. (1997) suggested that *A. donax* thrives in a variety of soil types in its indigenous range in India. Under greenhouse conditions, rhizomes of *A. donax* rooted successfully during all months of the year and both rhizomes and stem fragments established under various temperatures, moisture conditions, and soil types (Boose and Holt 1999, Decruyenaere and Holt 2001). It then expands outward in area via its large rhizome or via layering (adventitious sprouting of stem tips in contact with the ground), crowding and even displacing indigenous shrubs, herbs, grasses, and eventually even trees, under elevated light, soil moisture, and nutrient conditions, (Boland 2006, Decruyenaere pers. comm.). Wang (1998) suggested that nutrient loading contributes to *A. donax* invasion, and several authors have proposed that fire might promote *A. donax* invasion because this species can respond more quickly to fire than natives (Bell 1994, DiTomaso 1998). In this manner, *A. donax* forms extensive stands or monocultures in riparian ecosystems along the floodplains and terraces of southern California's river and stream systems.

Impacts of Invasion

Infestations of *A. donax* have created serious physical and biological problems along rivers in southern California. Where it grows extensively along floodplains, *A.*

donax acts as a transformer species; it causes physical obstructions to natural water flow, thereby increasing the risk of flooding to adjacent lands. During large floods *A. donax* increases stream roughness, creates debris dams at bridge crossings, and causes bank erosion and instability (DiTomaso 1998). As the aboveground biomass dries in the hot, dry summer months that characterize Mediterranean-type climates, *A. donax* creates an unnatural fire hazard where moisture-rich riparian corridors used to form natural barriers to fire (Scott 1994, Rundel and Gustafson 2005). Water loss due to high evapotranspiration (ET) of *A. donax* reduces already scarce water resources in Mediterranean-type climate regions. Based on transpiration rates of rice (another C3 species thought to have similar transpiration rates), Iverson (1994) estimated that *A. donax* uses three times more water than native riparian species. Studies using a variety of methods indicate that ET of *A. donax* (1.2–7.5 m/year) may be much higher than that of native riparian vegetation such as *Salix* spp., *Populus* spp. (1.0–3.3 m/year) and mixed riparian communities of arid and Mediterranean-type climates (0.11–1.6 m/year) (Zimmerman 1999, Hendrickson and McGaugh 2005, Shafroth et al. 2005, Abichandani 2007, Coffman in press). Abichandani (2007) showed that *A. donax* infestations may transpire 6 to 110 times more (up to 18,206 kg m^{-2} $year^{-1}$) than native vegetation.

Arundo donax has very little known value as a wildlife habitat in California (Bell 1997, Kisner 2004) compared to the dominant native vegetation (Bell 1994, Herrera and Dudley 2003). Its stems and leaves contain an array of inorganic noxious chemicals (Jackson and Nunez 1964) that reduce herbivory by most native insects and grazers. Due to its dense clonal growth form, it physically restricts indigenous wildlife passage, yet many animals depend on the riparian corridor and river floodplain for foraging, nesting, and cover (Kisner 2004). Like other invasive plants, *A. donax* appears to have negative impacts on indigenous plant and animal biodiversity through the loss of suitable habitat and competition with indigenous species (Czech and Krausman 1997). In addition, *A. donax* threatens river ecosystem sustainability via its impacts on natural river processes, such as lowering of the groundwater table, decreased surface water levels in streams, creating the potential for unnatural and extremely hot fires, and loss of plant and animal biodiversity.

Control of* Arundo donax *in California

Because of the numerous impacts of *A. donax* infestations on rivers, streams, and adjacent property, large-scale *A. donax* control efforts have been initiated throughout California since 1990 by several multi-agency organizations. For example, Team Arundo, a forum of local, state, federal, and private organizations dedicated to the control of *A. donax*, was formed in 1992 and leads control efforts along the Santa Ana River in southern California, where invasion has been a problem since 1969 (SAWPA 2007). In 2001, the Santa Ana River contained approximately 10,000 acres of *A. donax*-infested riparian habitat; Team Arundo is currently removing *A. donax* along this river on a watershed-scale. Formed in 1996, the Team Arundo del Norte partnership was modeled after the original Team Arundo and leads control and eradication efforts in Central and Northern California, where *A. donax* has more recently invaded (Team Arundo del Norte 2007).

Many local organizations also work on *A. donax* control at the county and watershed levels. For example, the Ventura County Arundo Task Force, led by the Ventura County Resource Conservation District, conducted a pilot removal project on the Ventura River in 2003 and plans to continue long-term watershed-wide eradication of *A. donax* in all major watersheds in Ventura County starting with the Santa Clara River. In the Malibu Creek watershed, the Resource Conservation District of the Santa Monica Mountains and Mountain Conservation Trust conducted an *A. donax* eradication project on 5.2 miles of the stream. Also, *A. donax* eradication is being used for compensatory riparian and wetland mitigation in California (Stein 1998). However, controversy continues over *A. donax* removal and herbicide use associated with its removal in the Topanga Canyon watershed (Topanga Online 2007).

Eradication of *A. donax* from watersheds in Mediterranean-type climates is an important initial step in restoration and long-term sustainability of riparian ecosystems. Various mechanical and hand-clearing techniques have been successful in removing small areas of *A. donax* infestations throughout California. Several researchers are investigating the ecophysiology of *A. donax* (e.g., relative growth rates and critical nitrogen content) to determine the most effective time to apply glyphosate-containing herbicides to kill the rhizomes of these plants (Spencer et al. 2005, Wijte et al. 2005). Research on biocontrol agents is underway; however, the U.S. Food and Drug Administration (USFDA) has not approved any yet. Based on the mechanisms by which it spreads and colonizes, *A. donax* removal efforts are primarily concentrated along higher riparian terraces, locations where it is less likely to reinvade (Coffman et al. 2004).

Removal from floodplain locations requires development of watershed-scale removal plans and permits that specify removal from the upstream most infestation working downstream. However, Boland (2006) proposed an inside-out approach for *A. donax* removal (i.e., conduct treatments first inside and then outside the flood zone) due to his documentation of the importance of layering. Researchers believe that revegetation of riparian areas with native plant species after *A. donax* removal is essential in preventing infestations of other weedy species. However, long-term eradication of *A. donax* from rivers and streams in Mediterranean-type climate regions may not be completely successful without knowledge of understanding how to manage the factors that contribute to its invasion and proper management of those factors.

***Riparian Ecosystem Restoration and* Arundo donax**

Degradation of ecosystem processes and functions by man-made physical and biological alterations threatens river systems worldwide (Naiman and Decamps 1997). River restoration projects have increased exponentially since 1995 and are being conducted across the U.S. to improve water quality, enhance in-stream and riparian habitat quality, re-establish fish passage, and provide bank stabilization (Bernhardt et al. 2005). Current watershed-level river and stream restoration efforts in California include removal of dams for fish passage, elimination of levees to allow for more natural channel migrating and meandering, releases of water from dams to simulate natural flooding, implementation of policies to reduce pollutants, and revegetation of natural riparian ecosystems. However, regardless of the restoration goal or activity, restoration success will depend on control of *A. donax* in the streams that it infests. For example, removing a dam with upstream *A. donax* infestations without implementing control programs first would result in widespread dispersal of this species. Understanding the relationship between nutrient levels found in rivers, the sources of these nutrients, and *A. donax* versus native riparian species growth will help watershed managers formulate more realistic nutrient reduction policies and implementation plans. Understanding water use by *A. donax* compared to native riparian plants is critical to justifying funding of removal efforts due to its presumed high use of water in arid regions where water is limited (Abichandani 2007).

Watershed managers, restoration planners, *A. donax* eradication groups, conservation organizations, and many others require scientifically based management recommendations to control expansion of and remove *A. donax* effectively. Knowledge of how factors such as nutrient levels, water, light, and fire contribute to growth and invasion of *A. donax* is essential to long-term, large-scale control. However, little is know about the *A. donax* invasion process related to the factors. In this dissertation, I address the influence of water, nutrients, light, and fire on the *A. donax* invasion process. My aim was to provide valuable information about *A. donax* invasion and long-term restoration of riparian ecosystems in California and other Mediterranean-type climate regions.

***Influence of Water, Nutrients, Light, and Fire on Invasion by* Arundo donax**

Water Availability

Mediterranean-type climate regions are characterized by wet winters and warm, dry summers that regulate natural ecosystems processes. Many rivers and streams in these regions are intermittent (i.e., with loosing and gaining reaches) or ephemeral because of wetting and drying periods (Gasith and Resh 1999) and underlying geology (Malanson 1993). Ever-increasing population pressure in these regions has created intense competition for water, resulting in serious alterations to water quantity and quality in rivers and streams (Gasith and Resh 1999). The city of Los Angeles, for example, imports 88% of its water to supply water for drinking, agricultural irrigation, and industrial uses (Hazy 2006). This imported water is discharged into natural water bodies after use, in many cases with degraded water quality, thereby increasing flow in many streams and creating perennial systems. Groundwater abstracted for agricultural irrigation and rural residential uses adjacent to rivers may decrease flow.

Increased water quantity in stream systems of Mediterranean-type climates may promote growth of invasive species such as *A. donax*. Although *A. donax* reportedly can tolerate a wide variety of ecological conditions, it thrives in areas with high soil moisture such as along canals, ditches, and stream banks (Perdue 1958, Rezk and Edany 1979). Much higher transpiration of *A. donax* compared to native riparian plants such as *Salix* spp. and *Populus* spp. and mixed riparian communities typical of arid and Mediterranean-type climates may give it an advantage where water is abundant (Zimmerman 1999, Hendrickson and McGaugh 2005, Shafroth et al. 2005, Abichandani 2007). I hypothesized that *A. donax* would have a competitive advantage over those native species found to uptake water at a lower rates in river floodplains and terraces that receive increased water inputs from anthropogenic sources.

In riparian ecosystems in which water tables are lowered due to groundwater extraction or along naturally loosing reaches (i.e., river reaches that contribute water to the groundwater supply), the scenario is more complicated. The presence of sustained high soil moisture or near-surface shallow groundwater during the growing season is important for establishment of most species, although both *A. donax* (Perdue 1958) and *Bacharris salicifolia* are known to establish under very low soil moisture conditions. Once established, rooting depth, distribution, and structure relative to soil moisture and groundwater likely play a large role in growth and competition between *A. donax* and native species. *Salix* spp., *Populus* spp., *B. salicifolia*, and other woody riparian species are phreatophytes with adaptations to low soil moisture conditions; their roots follow the receding soil moisture and can use water from depths of up to 30 m (Robinson 1958). *Arundo donax* is a perennial grass with roots that can only reach ~3 m below the soil surface.

Nutrient Loading

During the twentieth century, nutrient inputs to river systems worldwide increased dramatically due primarily to expanding agricultural practices and municipal sewage discharge (Rundel et al. 1983, Tilman et al. 2000, Nicola 2003, FAOUN 2004). Follett and Hatfield (2001) reported groundwater nitrate concentrations under agricultural systems in the U.S. to be as high as 30mg/L in 2001, which is much higher than the EPA drinking water standards [less than 10ppm (mg/L)]. Southern California is no exception; agricultural activities and their associated nutrient inputs are widespread along river systems of southern California (Mount 1995, Pedersen 2001). Other important anthropogenic and natural sources of N and P that likely contribute to nutrient loading in river systems include: atmospheric N; manure from animal feedlots and corrals; fertilizer applied to lawns; leaky septic tanks; oxidation of organic materials; and the increased abundance of symbiotic N-fixing plants (Verhoeven et al. 1996, USEPA 1999).

Composition and increase in use of fertilizer has led to extensive nutrient loading of river systems, with mainly nitrogen (N) and phosphorus (P) (Nicola 2003). Global fertilizer use has increased more than fourfold, from 31.2 million tons in 1961 to 137.7 million tons in 2001 (FAO 2004). Total global nitrogen fertilization is expected to increase by 12.9% during the next 15 years and 23.7% in the next thirty years (FAOUN 2004). By 2050, Tilman et al. (2000) predicted that the global rates of nitrogen and phosphorus fertilization will be 2.5 times and 2.4 times, respectively, that of current levels. In the U.S., annual fertilizer use in agricultural areas has increased from 24.9 in 1959 to 53 million tons in 2001 and continues to increase (FAOUN 2004). Currently, nitrogen fertilizers represent about 55% of all fertilizer uses, followed by phosphate at 26%. In the U.S., the average percent of nitrogen, the main constituent in commercial fertilizers, has risen from 11% in 1959 to 22.7% in 2001 (FAOUN 2004).

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). Excess N and P from fertilizers used in agriculture, golf courses, and residential lawns, as well as treated wastewater effluent, have contributed to nutrient loading in rivers across the U.S. (USEPA 1999). Nutrient enrichment and the dynamics of riparian ecosystems in agricultural landscapes in the eastern U.S. and Western Europe have been well studied (Peterjohn and Correll 1984, Gilliam 1994, Hill 1996, Bennett et al. 2005). However, limited information exists about these processes in Mediterranean-type climates such as southern California (Kim 2003, Robinson et al. 2005).

The effects of increased nutrient levels on plant composition and invasion may be even more profound in streams of Mediterranean-type climate regions compared to other regions of the world because they have naturally low levels of nitrogen and phosphorous (Day 1983, diCastri 1991, Dallman 1998). Plant species that are restricted to non-fertile sites generally respond less to nutrient addition or nutrient supply than do the same species from more fertile soils (Chapin et al. 1986). Hellmers et al. (1955) reported that the nitrogen-limiting conditions found in chaparral communities in southern California also exist in riparian ecosystems; thus, excess nitrogen from adjacent land use practices might promote *A. donax* growth and invasion in riparian ecosystems of southern California and other Mediterranean-type climate regions (Wang 1998). A demographic study of *A. donax* in southern California indicated that *A. donax* tends to spread radially or invade under nutrient-rich conditions, and it ceases spreading and establishes relatively dense clumps under nutrient-poor conditions (Decruyenaere and Holt 2001, Decruyenaere pers. comm. October 5, 2001). Preliminary results of another study indicate that *A. donax* biomass is greater than that of *Salix laevigata* under conditions of no nitrogen (0 g/m^2 N) and high levels of nitrogen addition (12–14 g/m^2 N) (Dudley unpublished data), whereas *S. laevigata* grows larger than *A. donax* at nutrient addition levels of 4g/m^2. Seasonal drought conditions confine nutrient availability to wetter times of the year and to areas with perennially high soil moisture retention regardless of nutrient inputs, potentially influencing invasion dynamics.

Excess nitrogen and phosphorus contained in surface and shallow groundwater are transported from land use activities to adjacent river ecosystems (Schlosser and Karr 1981, Correll 1984, Correll et al. 1992, Triska et al. 1994, Rodda 1995, Basnyat et al. 1999). Although the quantity of N and P in the shallow groundwater and soil is important to plant productivity, only certain constituents of N and P are readily available to plants. Plants absorb and assimilate both NO_3^- and NH_4^+ most readily. Nitrogen found in the form of NO_3^- and NH_4^+ in fertilizer and wastewater is water-soluble and moves quickly through soils in the shallow groundwater between agricultural practices, wastewater treatment plants, and adjacent river systems. Widely known as the primary productivity-enhancing nutrient, N assimilation and metabolism is complex and under genetic control (Duncan 1994). Although not addressed in this study, atmospheric N in the form of air pollution is a growing source of this nutrient for plants (Verhoeven et al. 1996). Because plant species vary in their ability to uptake atmospheric N through their stomata (Stark 1994), this anthropogenic source should be examined further.

Phosphorus is an insoluble mineral that readily adsorbs to soil particles, which are then transported to river systems through overland runoff and soil erosion. Required for many metabolic processes, P is absorbed rapidly into plant roots but requires active uptake due to steep concentration gradients between the soil solution and plant roots (Shuman 1994). Plants can uptake P only when dissolved in water as ortho-phosphates or poly-phosphates, and the rate of uptake is highly pH-dependent (optimal uptake at pH 6.5) (Shuman 1994).

The majority of water and minerals absorbed by plants enters through the root system. The ability of plants to assimilate nutrients available in the surrounding soil and groundwater depends on the development of an extensive root system and on rooting structure (Kozlowski et al. 1991). Root morphology and architecture differ between monocots, such as *A. donax,* and dicots like *Salix laevigata* (Taiz and Zeiger 1991). The physiological strategies of both plants differ greatly due to their inherent structure. *A. donax* roots are fibrous and tend to be shallower than those of *S. laevigata*, which has a taproot that can extend 30 m or more to groundwater. Thus, *A. donax* may utilize nutrients in the upper soil profile and shallower groundwater compared to phreatophytes like *S. laevigata* from loosing stream reaches in which groundwater is deep.

The supply of N and P in the soil and the availability of these nutrients to plants in the soil medium can vary greatly based on soil grain size and pH (Metz et al. 1966). Variability in soil grain size leads to variability in soil moisture content, which in turn affects rates of both nutrient diffusion transport and biological activity. Soil grain size has a strong influence on water and nutrient retention in soils: Coarser soil grain sizes 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. Mineral ions are either adsorbed onto the surface of soil particles or exist in soil solution. The cation NH_4^+ may be found dissolved in water or associated with aerobic soils in which it oxidizes quickly into NO_2^- and NO_3^- (nitrification) or reacts with other components in the soil to form ammonium salts. Because NO_2^- and NO_3^- are highly soluble in water due to their negative charge, concentrations of these nutrients in the soil water solution tend to be lower in well-drained coarser grained soils. Conversely, negative charges on the soil particle surface promote adsorption of mineral cations such as phosphate, which bind readily to clay particles (containing aluminum or iron) and are not easily lost to groundwater or available to plants.

Light Availability

Light availability influences plant invasion in many ecosystems, due to both vegetation removal and direct effects of shading by invasive species (Crawley 1987, D'Antonio and Vitousek 1992, Yamashita et al. 2000, Meekins and McCarthy 2001, Fargione and Tilman 2002). Reduction in light availability may act as a barrier to invasion in both disturbed and natural habitats (Richardson et al. 2000). Plant species vary greatly in the amount of light they require for colonization and optimal growth (Treshow 1970, Menges and Waller 1983). Although the specific light requirements of *A. donax* and the dominant riparian plant species in California are not well known (Braatne et al. 1996), D'Antonio and Vitousek (1992) reported that invasive grass species prevent establishment and growth of woody species by shading them. Dudley (1998) suggested that monocultures (large infestations) of *A. donax* limit native riparian plant recruitment through light reduction, but the mechanisms behind this phenomenon are still unknown (Dudley 1998). Furthermore, light limitations can promote strong belowground competition between species (Schenk 2006).

Occurrence of Fire

Wildfires ignited by man at unnatural and dangerous times of the year burn rapidly through riparian corridors infested with *A. donax* and may help spread fires across watersheds and along riparian corridors. Historically, dense biomass that accumulated over a period of 30–50 years or more in chaparral communities of California and shrublands in other Mediterranean-type climate regions caused fires to ignite (Minnich 1983, Keeley et al. 1999, Keeley and Fotheringham 2001, 2005). Although fire was once a natural part of shrubland ecosystems in many Mediterranean-type climate regions, large riparian ecosystems provided natural firebreaks because native vegetation retained foliar water that resisted ignition (Bell 1994). Lightning was the primary cause of wildfires, especially during the summer and fall under dry, low humidity conditions (Naveh 1975, Keeley 1982, Keeley et al. 1999). Currently, however, most wildfires in these areas are anthropogenic in origin (Rugen 1987, D'Antonio and Vitousek 1992, Keeley et al. 1999). For example, all 14 concurrent fires in southern California in October 2003 (739,597 acres burned) resulted from human activities (Keeley and Fotheringham 2005).

Fire suppression and, more recently, controlled burning of wildland vegetation are techniques used in the twentieth century to manage vegetation and to avoid wildfires (Kozlowski et al. 1991). However, when enough fuel accumulates due to changes in vegetation type (i.e., native shrublands and perennial grasslands in California have changed to Mediterranean annual grasslands) or a decrease in fire frequency in a region, fires are easily started.

Invasion of annual grass species has been linked to altered fire regimes in rangelands, deserts, and wildlands of California and the Western U.S. (D'Antonio and Vitousek 1992, D'Antonio 2000, Brooks 2002, Brooks et al. 2004, Keeley 2004, Keeley and Fotheringham 2005). *Arundo donax* may pose a more extensive problem in riparian ecosystems due to its perennial growth form (the large volume of biomass produced) and its rapid recovery after fire. Several accounts suggest that infestations of giant reed have increased fuel load as well as fire frequency and intensity along riparian corridors (Rieger and Kreager 1989, Bell 1994, Scott 1994, Dukes and Mooney 2004).

Natural, healthy riparian areas historically have acted as firebreaks primarily because native vegetation has high leaf moisture content (i.e., contains enough water to have low flammability) when fires typically occur in summer and fall. However, the October 2003 wildfire along the Santa Clara River clearly has shown that when natural riparian habitats are infested with *A. donax*, fires spread readily through this historically fire-hardy habitat (Coffman in press). For example, during the Simi/Verdale fire, the fire jumped across Highway 126 and the Santa Clara River through a section of the river densely invaded by *A. donax*, and from there made its way rapidly up and down the riparian corridor on either side of the river (estimated 5 miles per hour) (see Chapter 4). The fire then spread from the riparian corridor to the shrublands on the other side of the river and burned the Santa Suzanna Mountains, including the Simi Hills in the Calleguas Creek watershed to the south. This process was observed in several other locations along the Santa Clara River where shrublands were located close to the river floodplains and terraces (observation by G. Coffman and S. Hedrick 2003). In this way, fire spread rapidly up and down river corridors through large patches of *A. donax*, especially along terraces where *A. donax* was very dry and provided more fuel than natural vegetation.

Although no scientific evidence exists, a few authors have suggested that fire in riparian ecosystems may increase the ability of *A. donax* to invade natural riparian systems (Rieger and Kreager 1989, Bell 1994, Scott 1994). The large quantity of highly flammable biomass produced by *A. donax*, and its rhizomes immediate growth response compared to native riparian species following fire contributes to its invasion success. Bell (1994) suggested that invasion of riparian ecosystems by *A. donax* is changing these systems from primarily flood-defined to fire-defined systems. Riparian ecosystems infested by *A. donax* that are adjacent to fire-prone shrublands in southern California appear to be on a trajectory towards an invasive plant-fire regime (Brooks et al. 2004).

ORGANIZATION OF DISSERTATION

My dissertation research focused on investigating the influence of nutrients, water, light, and fire on *A. donax* invasion of riparian ecosystems in Mediterranean-type climate regions. My main hypothesis is that increased nutrient, water, and light availability caused by anthropogenic sources in river systems throughout southern California have promoted invasion by *A. donax*. To test this hypothesis, I conducted three main studies employing two study approaches. First, I conducted a large-scale field experiment, located along a riparian terrace of the Santa Clara River in southern California, to test competition between *A. donax* and three native plant species for water, nutrient, and light availability. In a second watershed-scale observational field study, I investigated the influence of nutrients from various land use types and fluvial geomorphic locations on *A. donax* invasion of riparian ecosystems along several coastal rivers in southern California. In my third study, I examined the role of fire in promoting *A. donax* invasion of riparian terraces of the Santa Clara River. Following this Introduction chapter, each of these three studies will be described in chapters 1–3. The final chapter (Conclusions Chapter) of the dissertation presents conclusions and management implications based on these studies.

FIGURES

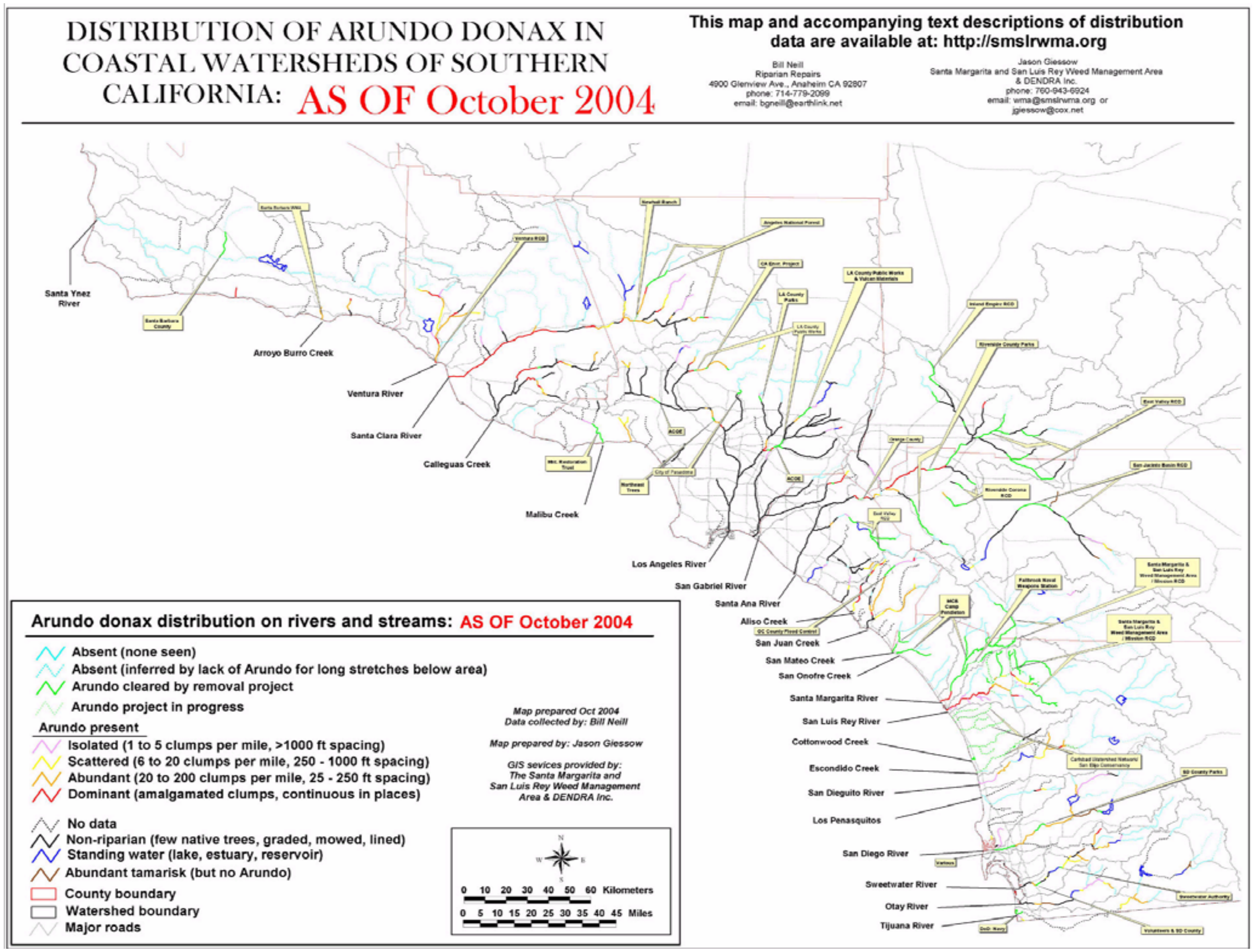

Figure 1. Distribution of *A. donax* throughout streams and rivers of Southern California (Used by the permission of Jason Giessow and Bill Neill, http://smslrwma.org/invasives/Arundo/ADRegionalMap.html).

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CHAPTER 2 -

EFFECTS OF WATER, NUTRIENT, AND LIGHT AVAILABILITY ON COMPETITION BETWEEN *ARUNDO DONAX*, A LARGE INVASIVE GRASS, AND NATIVE RIPARIAN SPECIES

Abstract: Invasion by alien plant species is currently one of the greatest threats to biodiversity and natural functioning of many ecosystems worldwide. Superior resource competition by alien grass species has been shown as the fundamental mechanism for invasion in many ecosystems. In this study, I tested the hypothesis that superior competition for soil moisture, light, and nutrient availability promotes invasion of a large bamboo-like grass, *Arundo donax* L., in riparian ecosystems. I established a large-scale field experiment with several competition plant groupings (mixed and single-species groupings), soil moisture, light, and nutrient treatments in a riparian ecosystem in southern California. I planted 168 four-plant groupings in 12 blocks perpendicular to shallow groundwater flow in a full factorial randomized block design. Effects of treatments on survivorship and aboveground biomass of *A. donax* were compared to native *Baccharis salicifolia*, *Salix laevigata*, and *Populus balsamifera* ssp. *trichocarpa*. Percent survivorship was high for all species (97.8% overall) and did not differ significantly for *A. donax* between treatments. Results show *A. donax* only suppressed one native species (*P. balsamifera* ssp. *trichocarpa*) under the most stressful environmental conditions. Competition from *B. salicifolia* and *S. laevigata* had a strong negative effect on *A. donax* biomass under high soil moisture, light, and nutrients.

Furthermore, *B. salicifolia* was facilitated by *A. donax* in half of the conditions tested. Despite negative effects of competition, *A. donax* produced a much higher biomass than native species under high soil moisture, light, and nutrient levels, and *A. donax* biomass in monoculture was much higher than all species within all treatment levels. Results suggest that high resource levels and the clonal growth form, not superior resource competition by the invasive *A. donax*, promote observed preemptive competitive exclusion of native riparian species. Its unique morphology and physiology, absent in this system before its introduction, allows *A. donax* to readily displace natives in many resource levels. *Arundo donax* appears to be a super invader, able to outperform native woody riparian species in almost every resource scenario tested.

Key Words: *Arundo donax, Salix laevigata*, *Populus balsamifera* ssp. *trichocarpa*, *Baccharis salicifolia*, giant reed, invasive species, alien, competition, nutrients, nitrogen, light, soil moisture, riparian, rivers, Mediterranean-type climate

INTRODUCTION

Invasion of natural ecosystems by alien plant species is a widespread phenomenon known to result in significant losses to biodiversity and impacts to ecosystem functioning (Elton 1958, Mooney and Drake 1986, Ramakrishnan and Vitousek 1989, D'Antonio and Vitousek 1992, Vitousek et al. 1996). Aquatic ecosystems such as rivers and wetlands are among the world's most heavily invaded systems (Mooney et al. 1986, Kruger et al. 1989, Pysek and Prach 1994, Alpert et al. 2000, Rundel 2000). Altered disturbance regimes, low stress environmental conditions, and anthropogenic enhancement of nutrients are thought to contribute to success of plant invasion in rivers and wetlands (Ashton and Mitchell 1989, Hobbs 1989, Hobbs and Huenneke 1992, Alpert et al. 2000). However, mechanisms by which invasive plant species exclude native plant species and dominate natural vegetation in these ecosystems are not well understood, yet are essential for developing effective control and restoration plans (Dudley 1998, Minchinton et al. 2006).

Superior interspecific competition between native and introduced species for water, light, and nutrient resources plays a critical role in plant invasion in many terrestrial ecosystems (D'Antonio and Vitousek 1992, Gordon and Rice 2000, Booth et al. 2003, Suding et al. 2004, White and Holt 2005, Richardson 2006). In the California grassland ecosystem, superior resource competition by Mediterranean annual grasses for water (Hamilton et al. 1999, Coleman and Levine 2007) and nutrients (Kolb et al. 2002) has been found to contribute to the almost total exclusion of native perennial bunchgrasses (D'Antonio and Vitousek 1992). Recent work by a number of authors has revealed the relative importance of various resources and levels of each resource in this invasion process (Kolb and Alpert 2003, Corbin and D'Antonio 2004b, Thomsen et al. 2006). A few experimental studies in river and wetland ecosystems have demonstrated superior resource competition by invasive plants for either nutrients (Green and Galatowitsch 2002, Minchinton and Bertness 2003) or water (Sher and Marshall 2003), but no studies have examined effects of multiple resources simultaneously (i.e., various levels of water, light, and nutrients). Furthermore, controversy exists over the relative importance of competition in stressful, infertile versus productive ecosystems (Grime 1979, Tilman 1988, Goldberg and Novoplansky 1997, Alpert et al. 2000). Experimental studies addressing competitive interactions between invasive and native plants under multiple resources conditions (water, light, and nutrients) are needed to help elucidate the invasion process and aid in restoration of invaded ecosystems.

In the last half of the twentieth century, a tall bamboo-like member of the grass family (Poaceae), giant reed (*Arundo donax* L.), has become one of the most successful weedy riparian invaders in arid and Mediterranean-type climates worldwide (Bell 1997, Dudley 1998, Boose and Holt 1999). *Arundo donax* appears to be of a broad southern Eurasian origin, extending from Southeast Asia to the Mediterranean Basin, although the precise extent of its native distribution is unclear (Perdue 1958, Zohary 1962, Hickman 1993). Introduced extensively to other areas primarily for building materials, erosion control, and windbreaks, it is now successfully established in freshwater systems in tropical to temperate climates worldwide (Perdue 1958, Crampton 1974, Polunin and Huxley 1987, Hickman 1993, Sharma et al. 1998). Although the seeds are usually sterile

(Johnson et al. 2006), *A. donax* is dispersed downstream when pieces of culm or rhizome 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). From these pieces, the plant grows at an extremely fast rate (up to 10 cm per day under optimal conditions), quickly establishing on exposed or sparsely vegetated soil and growing to more than 8 m in height after only a few months (Perdue 1958, Rieger and Kreager 1989, Bell 1994). Once established, *A. donax* expands outward in area by clonal propagation, displacing indigenous shrubs, herbs and grasses, and eventually even trees (Decruyenaere and Holt 2001). In this manner, *A. donax* forms extensive stands or monocultures in riparian ecosystems.

In Mediterranean-type climates, *A. donax* infestations have become especially devastating to riparian ecosystems, creating significant physical and biological impacts on natural river functioning and sustainability (Rieger and Kreager 1989, Bell 1997, DiTomaso 1998, Rundel 2003). High magnitude winter floods characteristic of many arid climates help distribute *A. donax* downstream, where it successfully establishes on a diverse array of substrates (Rieger and Kreager 1989, Else 1996, Else and Zedler 1996) much like the native riparian species in these systems. However, mechanisms of *A. donax* invasion in natural riparian ecosystems have been largely unexplored. Researchers have suggested that high resource levels and superior resource competition with native riparian plants (i.e., for elevated water, nutrients, and light availability) may promote invasion of *A. donax* in riparian ecosystems of southern California (Bell 1997, Wang 1998, Rundel 2003, Coffman et al. 2004), yet no experimental evidence of resource competition by *A. donax* exists to support this hypothesis. Mechanisms that promote invasion of *A. donax* under various resource conditions in riparian ecosystems are essential to its control and restoration of these systems.

In this study, I examined the role of competition between *A. donax* and native species under varying resource scenarios found in riparian ecosystems in the plant invasion process. I predicted that aboveground biomass of native riparian plant species would be suppressed by high productivity of *A. donax* in high soil moisture, light and nutrient treatments, while under more stressful (and lower) resource conditions competitive interactions would favor native species which have evolved under these conditions (Alpert et al. 2000, Daehler 2003). Where *A. donax* establishes with native riparian plants in high resource conditions, growth rate will be high but competition from native plants for soil moisture and nutrients will be high as well. Differing habit, phenology, and rooting depth of *A. donax* (clonal) and native riparian species (phreatophytes) play a key role under these conditions (Fargione and Tilman 2005).

Physiological integration among culms and their spatial arrangement may provide *A. donax* with a competitive advantage over native woody riparian trees and shrubs (Gough et al. 2002). The clonal growth form of *A. donax* enables it to grow horizontally, preemptively acquiring space from competitors and to average out surrounding heterogeneity in soil resources (Decruyenaere and Holt 2005). Although *A. donax* has a much shallower rooting depth than native riparian phreatophytes, *S. laevigata* and *P. balsamifera* spp. *trichocarpa*, root depth of these plants should remain relatively shallow and density low when resources are abundant (Schade and Lewis 2006, Schenk 2006)

(See Chapter 3; Figure 9). Thus, substantial overlap in the density of root mass between species may result in stronger competition under these conditions. Depending on density (Gough et al. 2002) and native species competing, these conditions may lead to either successful competitive exclusion of all or some native species by *A. donax*. In high stress and low resource conditions, naturally found along rivers in Mediterranean-type climates, *A. donax* may avoid competition with native plants due to differential rooting depths; native phreatophytes will develop deeper roots than *A. donax* when soil moisture and nutrients are scarce.

I hypothesized that superior resource competition in high soil moisture, light, and nutrient regimes has promoted invasion of *A. donax* throughout rivers in Mediterranean-type climates. I investigated *A. donax* competition with several common native woody riparian plant species under various soil moisture, nutrient, and light levels in a large-scale field experiment in southern California. Plant survivorship and aboveground biomass of each species in intraspecific compared to interspecific competition groupings were analyzed. This experimental design allowed me to investigate the role of varying resource conditions thought to be most fundamental to competitive exclusion of indigenous riparian plants by *A. donax* using a natural, controlled approach.

METHODS

Study Site

The field experiment site was located on a private ranch on the south side of the Santa Clara River between Santa Paula and Fillmore, Ventura County, California (34.36° N, 118.99° W) (Figure 2). The 187 km long Santa Clara River and its tributaries drain a

4,185 square km watershed, the second largest coastal watershed in southern California. Prior to its clearing for agriculture, the riparian terrace in which the field experiment was established was once dominated by large riparian trees such as black cottonwood (*Populus* (L.) *balsamifera* ssp. *trichocarpa* Torrey & A. Gray) and red willow (*Salix laevigata* Bebb). A mixture of smaller trees and shrubs likely comprised the understory layer, including arroyo willow (*Salix lasiolepis* Benth.), mulefat [*Baccharis salicifolia* (Ruiz Lopez & Pavon) Pers.], and blue elderberry (*Sambucus mexicana* C. Presl.).

The experiment ran for two growing seasons, from December 2002 to December 2004. In October 2002, I began construction of the 0.5-hectare field experiment on a riparian terrace between agricultural fields and the river. Based on measurements of groundwater depth taken from a grid of borings throughout the experimental area, I found that shallow groundwater flowed in a southeast to northwest direction from the agricultural fields through the field experiment toward the river. Rows (or blocks) of plant groupings within the field experiment were located perpendicular to the direction of shallow groundwater flow to accommodate variance due to differing hydrology (Figure 3).

Baseline soil grain size (soil texture) and nutrient status were determined in Summer 2002, before construction of the experiment began to help in final placement of experimental groupings and treatments. The western side of the experimental area was primarily composed of a shallow horizon (soil surface to 26–66 cm) of sandy loam, silt loam, and loam with a deep horizon of fine sand and coarser sand below (to 171–199 cm and deeper). The eastern side of the experiment contained mostly loam (and silt loam) in the top horizon (soil surface to 44–102 cm), loam and silt loam in a middle horizon, and sand in the lowest horizon (below 138–216 cm). Soil moisture was consistently higher on the eastern side of the experiment than the western side due to soil grain size composition and topography.

I conducted baseline soil nutrient analyses on 18 soil samples collected from 0–30 cm depth systematically throughout the experiment. In spring 2003, pre-fertilization soil nutrient levels in the experimental study area mean soil nitrate (5.2 ± 1.7 ppm) and phosphate (11.1 ± 1.1 ppm) levels were comparable to concentrations found in soil along similar riparian terraces along the Santa Clara River (see Chapter 3). Average soil pH (7.69 ± 0.02) did not differ markedly throughout the experimental site.

Study Species

Arundo donax is a robust, perennial, bamboo-like member of the Poaceae (grass) family that was introduced and is now widespread throughout the floodplains and terraces of rivers in California and other warm, temperate climates worldwide (Perdue 1958, Crampton 1974). It has erect stout (yet hollow) culms that are 1–4 cm thick and 2–8 m in height. Culms branch to form 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 (Crampton 1974, Hickman 1993). *Arundo donax* reproduces vegetatively through a network of large, thick rhizomes that grow horizontally just below the ground surface. Under some conditions it produces a large (3–6 dm) terminal plume-like inflorescence (panicles) at the end of the growing season (Faber and Holland 1992, Hickman 1993).

I selected three native riparian plant species commonly found on terraces of rivers in southern California to use in the experiment: *Salix laevigata* (red willow) *Populus balsamifera* (black cottonwood) ssp. *trichocarpa*, and *Baccharis salicifolia* (mulefat). *Salix laevigata* is a riparian tree that can grow as tall as 15 m and is a member of the Salicaceae. Dominant in both floodplains and terraces along rivers in southern California, *S. laevigata* can be identified by its dark, deeply furrowed bark on mature trees and lanceolate leaves, which are shiny on the top and glaucous beneath. Also a member of Salicaceae, *P. balsamifera* ssp. *trichocarpa* grows to a height of 30 m in alluvial plains along rivers in southern California. *Populus balsamifera* ssp. *trichocarpa* trees can be identified by their broad crown and bicolored ovate leaves with acute tips, which are dark green on the top and glaucous underneath (Faber and Holland 1992, Hickman 1993). *Baccharis salicifolia* is the dominant shrub found throughout floodplains and terraces of streams and rivers in southern California. A member of the Asteraceae, *B. salicifolia* usually grows to a height of less than 4 m. Its long linear to lanceolate leaves resemble willow leaves, but they typically have three principal veins that extend the entire length of the leaf and are coarsely serrated (Faber and Holland 1992, Hickman 1993). In addition, *B. salicifolia* shrubs produce a rounded panicle of white simple compound dioecious flowers.

Experimental Design

This field experiment was organized as a full factorial randomized block design to minimize variation due to heterogeneous soil and shallow groundwater conditions found within the site. A total of 288 plant groupings (four plants per grouping) were organized in 12 blocks (rows) of 24 groups each perpendicular to the general flow of shallow groundwater hydrology (Figure 3). Blocks of plant groupings were placed 4 m apart and plant groupings within blocks were placed 3 m apart. 756 cuttings of riparian trees (1 m long by approximately 2–3 cm in diameter) and 396 rhizomes of *A. donax* (200–400 g) were planted approximately 0.75 m apart in square configurations. Native riparian species cuttings were planted in December 2002, and *A. donax* rhizomes were planted in March 2003. Multiple levels of three resource treatments and competition treatment were applied randomly to plant groupings along rows before planting, including soil moisture (high and low), light (high and low), and nutrient additions (high and none). To simplify the interpretation and presentation of results, the 96 low-nutrient treatment plant groupings in the experiment are not included in the analyses.

I used two competition groupings (two-species and one-species groupings) in the experiment to compare interspecific versus intraspecific competitive interactions (Table 1). The two-species groupings, referred to as 'mixed species grouping' consisted of two *A. donax* plants and two plants of a single native species. Like species were planted diagonally across from each other in the mixed species groupings. One species-groupings, or monocultures, contained four plants of only one species per grouping. (The 36 four-species groupings in the experiment were not included in this study.) In this experiment, the criterion for existence of an interspecific competitive interaction was evidence of significantly different biomass in mixed plant groupings compared to monocultures. If mean biomass of a species was lower when grown with another species compared to in monoculture, an interspecific competitive interaction was present. An interspecific interaction was deemed positive (facilitation) when the mean biomass of a species was higher in mixed species groupings compared to its biomass when grown in monoculture.

Two soil moisture treatments occurred naturally; the western half of the experiment contained soils that were better drained (referred to as low soil moisture), whereas the eastern half of the experiment retained higher soil moisture throughout the year (high soil moisture). To simulate natural establishment conditions, I did not apply artificial irrigation.

In Spring 2003, I built shade structures over half of the experiment to simulate shading by a mature riparian canopy and test the effects of light availability. The two light treatments consisted of full sun (referred to as high light) and 80% shade (low light). I used 80% black shade cloth on six shade structures (total dimensions were 200 feet x 10 feet x 15 feet high) that were erected along rows in two large blocks of the experiment to minimize the shade effect onto non-shaded rows. One block (three rows) was placed over the high soil moisture portion (northeast) and one block (three rows) was placed over the low soil moisture portion (southwest) (Figure 3). I applied nutrient treatments to designated plant groupings twice a year: a fertilized “high N” treatment and “no N” treatment control in which only water was added. Granular ammonium-nitrate fertilizer (N-P-K, 34-0-0) was used as the source of added nitrogen and was mixed with 2 gallons of water before application. High nitrogen treatments (100 g N/m^2/year or 56 g N/plant/year) were added to one-half of the plant groupings to simulate row crop fertilization levels adjacent to riparian areas. I applied half of the nutrient treatments at the beginning of the growing season and the remainder at the peak of the growing season; this timing of fertilization application is similar to that used in agricultural practices in the area. Each plant in the no fertilizer treatment received 2 gallons of water at each of the two application periods.

Sampling Methods

I monitored soil moisture to characterize the soil water content throughout the experimental site using 14 soil moisture probes (20 cm ECH$_2$O Dielectric Aquameter sensors by Decagon Devices, Inc.), which I installed systematically throughout the experiment in the summer of 2004 (Figure 3). I placed 10 soil moisture probes in a soil horizon (between 60–80 cm from the soil surface) located roughly in the middle of the root system for most plants. The other four probes were placed in a shallower soil horizon (from 30–50 cm) to measure soil moisture in the area in which the cuttings were initially planted. I measured soil moisture content of these probes weekly from July 2004 to September 2005.

Annual mean soil moisture content (60–80 cm below ground surface) on the eastern side (Mean ± SE = 38.5% ± 0.5) of the experiment was significantly higher than on the western side (33.2% ± 1.0) during the 2004–2005 water year (one-way analysis of variance results: $F_{(1,383)} = 23.583$; $P < 0.001$). The shallower soil horizon (30–50 cm below the ground surface) in which cuttings were established exhibited a similar trend; soil moisture was 42.1% ± 0.4 on the eastern side and 37.8% ± 0.5 on the western side (one-way analysis of variance results: $F_{(1,166)} = 47.686$; $P < 0.001$). Mean soil moisture content fluctuated throughout the year but was consistently higher on the eastern side than the western side (Figure 4). Although soil moisture probes were not installed until the end of the second growing season (Summer 2004), trends observed during 2004-2005 were likely similar or more pronounced in 2003-2004 due to lower annual precipitation. Thus, the eastern side was designated as the high soil moisture treatment and the western side as the low soil moisture treatment.

I measured plant survivorship at three time periods: 1) survivorship of planted cuttings in spring 2003, 2) plant survivorship at the end of 2003, and 3) plant survivorship at the end of 2004. A few cuttings and rhizomes that did not grow initially were replanted in spring 2003 and the replacement plant establishment success was included in the 2003 and 2004 percent survivorship results.

Biomass Estimation

The aboveground biomass of all plants in the field experiment was estimated over the two-year study period (2003 to 2004). I used non-destructive dimensional analyses to estimate aboveground biomass dry weight of plants in the experiment so that I would interfere as little as possible with plant growth and other measurements taken throughout the course of the study period (Whittaker 1961, 1965, Whittaker and Marks 1975, Sharifi et al. 1982, Spencer et al. 2006). Compartments of aboveground biomass measured included: branches, main trunk (cutting), leaves, flowers, and seeds of native species, and culms, leaves, and ramets of *A. donax*. Regression models were created using the basal diameter measurements to predict biomass of all compartments (except main trunks) of each plant. All data were natural log transformed in the regression models. Trunk biomass (the aboveground portion of the original cutting) of native species was estimated by dividing the trunk volume (cm^3) by the density (cm^3/g) of a sample of wood of that particular species. Trunk volume was calculated using average diameter and length of the cutting in the equation for cylinder volume ($V = \pi r^2 h$).

At the end of each growing season (2003 and 2004), branches/culms were cut, basal diameter measured, biomass oven-dried, leaves separated from branches/culms, and biomass weighed separately. I collected a total of 320 branch/culm aboveground biomass samples in 2003 and 400 samples in 2004 for the dimensional analysis biomass estimation. In 2003, 20 branches/culms from the range of branch diameters present for each of the four species were harvested from monoculture competition groupings in each of the experimental quadrants (SE, NE, NW, SW – two soil moisture and two light levels) (20 x 4 x 4 = 320) (Figure 3). In addition, 20 second-year *A. donax* culms were collected in each experimental quadrant in 2004 (total of 80 culms). Only fully mature *A. donax* culms were sampled.

Regression equations for branch/culm basal diameter versus corresponding dry aboveground biomass samples were calculated for each species in each of the four soil moisture-light treatment combinations (16 for 2003 and 20 for 2004). Regression models for aboveground biomass were very highly significant for all species under various combinations of soil moisture and light treatments in 2003 and 2004 ($r^2 = 0.770–0.996$, $P < 0.001$) (see Appendix 2-1 for model equations). Therefore, I used these equations to estimate aboveground biomass for all plants within the field experiment.

At the end of the 2003 and 2004 growing seasons, I measured basal diameters (10 cm from the trunk of riparian plants or 10 cm above the ground surface for *A. donax*) of each branch or culm growing from the original cutting. Only culms that were > 60% of mature height were measured. To calculate total biomass of each plant at the end of each growing season, I used the basal diameter of each branch/culm of an individual plant in the corresponding regression equation for that species and treatment and totaled the resulting biomass for all branches/culms. Trunk biomass estimates were added to total biomass for each native riparian plant.

Statistical Analyses

Descriptive statistics were performed on soil moisture and plant survivorship measurements. I conducted one-way ANOVAs on soil moisture content to validate high and low soil moisture treatments and establishment of plant species between the first and second growing season, with Tukey's post-hoc test for pair-wise comparisons of means.

The competition experiment was organized in a full multifactorial design in which combinations of four fixed factors (Model 1) were crossed with each other. Four-way analysis of variance (ANOVA) tests were used to analyze effects of various combinations of four factors (independent variables) on total aboveground biomass data (standing stock) collected at the end of the second growing season (dependent or response variables) (Systat Statistical Program [Version 10]). The four independent variables were competition plant groupings, soil moisture, light, and nutrient addition treatments. Data were analyzed for main effects of individual factors and interactions between factors. ANOVA F-tests were performed to evaluate a priori contrasts between means of grouping variables and levels in multifactor ANOVA results. Probability plots were examined to test for normality of data and to identify any data that required transformation. Because soil moisture and percent survivorship data were normally distributed, data transformation was unnecessary. All biomass 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.

RESULTS

Establishment

Plant establishment success between installation in winter 2002–2003 and the end of the growing season in 2004 was very high for all species. Cutting survivorship in spring 2003 was 97.7% for all plants. Total plant survivorship at the end of 2003 and 2004 was 98.4% and 97.8%, respectively, and slightly higher than cutting survivorship due to replanting of unsuccessful cuttings. Soil moisture, nutrient, and light treatments had no effect on *A. donax*, *S. laevigata*, or *B. salicifolia* survivorship (See Appendix 2-2 for analyses of species and resource treatment effects). However, establishment success of *P. balsamifera* ssp. *trichocarpa* at the end of the first growing season (2003) was significantly lower within the high soil moisture treatment than in any other species and soil moisture treatment combination. Percent survivorship did not decrease significantly during the two-year establishment period ($F_{(1,158)} = 0.485$; $P = 0.487$). Therefore, I considered plants fully established by the end of the first growing season (2003) and evaluated competitive interactions at the end of the second growing season (2004).

Biomass Production

Arundo donax biomass was higher than native plant species biomass under nearly all soil moisture, light, and nutrient conditions at the end of the second growing season. In fact, the mean biomass of *A. donax* in monoculture under high soil moisture, light and nutrient conditions was 2–34 times that of all native species under all conditions tested [range = 0.46 kg (SE 0.30–0.68) to 7.03 kg (SE 6.41–7.72)] (Figure 5). In high soil moisture, light, and nutrient conditions, monocultures of *A. donax* exhibited a significantly higher mean biomass [17.05 kg (SE 15.98–18.20)] than any native plant species under these conditions [2.63 kg (SE 2.24–3.10) to 4.21 kg (SE 3.69–4.80)] (Figure 6). Despite negative competitive interactions with *B. salicifolia* and *S. laevigata* under high resource conditions (high soil moisture, light, and nutrients), mean biomass of *A. donax* was nearly double that of *S. laevigata* and 20 percent higher than *B. salicifolia* in mixed groupings (Figure 5). Biomass of *A. donax* grown in monoculture was almost six times that of *P. balsamifera* spp. *trichocarpa* in high resource conditions. Facilitation by *P. balsamifera* spp. *trichocarpa* contributed to an even higher mean biomass of *A. donax* in the 2-species mixed grouping compared to monoculture in similar experimental conditions. *Arundo donax* biomass was consistently higher than that of most native species in other soil moisture, light, and nutrient treatments, however differences between biomass of *A. donax* and native species were not as great.

Biomass of *A. donax* grown under high soil moisture, light, and nutrient conditions was much higher than when grown under any other experimental condition (Figure 5 and Figure 6). Although native plant species show similar trends, differences in mean biomass between these treatment conditions were much less than for *A. donax*. Under high resource conditions, mean biomass of *A. donax* was highest in monoculture [17.05 kg (SE 15.98–18.20)] and lowest in the low soil moisture-high light and high soil moisture-low light treatments (Figure 6). Of the native species grown in monoculture, *B. salicifolia* yielded the highest mean biomass [4.20 kg (SE 3.69–4.80)] in the high soil moisture, light, and nutrient treatment, but this was only one-quarter of the maximum biomass produced by *A. donax*. The lowest native species biomass in monoculture was produced by *P. balsamifera* spp. *trichocarpa* in the low soil moisture, light, and nutrient treatment [0.53 kg (SE 0.46–0.60)], more than 30 times lower than *A. donax* biomass in high resource conditions.

The 4-way ANOVA for aboveground biomass of all species by factors of plant grouping, soil moisture, light, and nutrients resulted in two 3-way interactions (Table 2). The plant grouping x soil moisture x light interaction was difficult to interpret but significance was mainly due to lower *S. laevigata* biomass than other species in low soil moisture-high light treatments as well as numerous significant competition interactions mentioned below. The significant soil moisture x light x nutrients interaction was explained by higher biomass in high soil moisture-high light than any other combination of these factors and levels.

Resource Competition

When I compared mean aboveground biomass by species in mixed groupings versus monocultures, effects of competition between *A. donax* and native plants varied significantly by species and resource treatment levels. *Arundo donax* was a superior resource competitor to only one native plant, *P. balsamifera* spp. *trichocarpa*, under only one of the conditions tested. Under the most stressful experimental conditions of low soil moisture, full sun, and no nutrient additions, *A. donax* competition had a negative effect on *P. balsamifera* spp. *trichocarpa* biomass (Table 3). Under these conditions, *P. balsamifera* spp. *trichocarpa* obtained the lowest biomass of all native species [0.46 kg (SE 0.30–0.68)] (Figure 5). The 4-way ANOVA of *P. balsamifera* spp. *trichocarpa* biomass resulted in a significant 3-way interaction (plant grouping x light x nutrients) due to this competitive interaction (Table 3). In high resource conditions (high soil moisture, light, and nutrients), there was a suggestion of *A. donax* facilitation by *P. balsamifera* spp. *trichocarpa*, with *A. donax* biomass being 30% greater in the mixed species grouping with *P. balsamifera* spp. *trichocarpa* [22.95 kg (SE 20.13–26.16)] than in monoculture [17.05 kg (SE 15.98–18.20)], but this difference was not statistically significant. A significant negative effect of competition with *P. balsamifera* spp. *trichocarpa* was detected under high soil moisture, low light, and high nutrient levels, conditions in which *A. donax* was least productive [1.38 kg (SE 1.03–1.85)]. Significant 3-way interactions (plant grouping x light x nutrients and soil moisture x light x nutrients) in the 4-way ANOVA of *A. donax* biomass were found (Table 3). The plant grouping x light x nutrients interaction was due to facilitation of *A. donax* by *P. balsamifera* spp. *trichocarpa* under high soil moisture, light, and nutrients. Much higher biomass in high soil moisture-high light treatments than in all other treatments was the primary cause of the significant soil moisture x light x nutrients interaction.

When grown with *A. donax* in the mixed species grouping compared to in monoculture, *S. laevigata* exhibited no significant competitive interactions with *A. donax* regardless of resource levels. Although competitive effects were not significant, the trend throughout various combinations of treatments, especially under low soil moisture conditions, indicated slight facilitation of *S. laevigata* by *A. donax* (Figure 5). Two-way interactions (soil moisture x light and soil moisture x nutrients) were significant for *S. laevigata* biomass in the 4-way ANOVA (Table 4) due to differing trends among levels in these factors. The soil moisture x light interaction was significant due to lower biomass in high light-low soil moisture compared to the low light-low soil moisture treatments, and the significant soil moisture x nutrient interaction was caused primarily by higher biomass in high nutrient-high soil moisture treatments compared to low nutrient-high soil moisture treatments. *Arundo donax* aboveground biomass was significantly higher (roughly twice as high) in monoculture compared to in the 2-species grouping when grown with *S. laevigata* in the high soil moisture, light, and nutrient treatment (Figure 5). Results of the 4-way ANOVA indicate significant 2-way interactions between soil moisture and light as well as between light and nutrients. The soil moisture x light interaction was significant because in the shade biomass was similar with regard to soil moisture; however, biomass was significantly higher in full sun-high soil moisture compared to full sun-low soil moisture (Table 4). The significant light x nutrient interaction resulted from higher biomass in full sun-high nutrient treatment compared to full sun-no nutrient treatment.

When grown in the mixed species grouping compared to in monoculture, *A. donax* facilitated growth of *B. salicifolia* in half of the treatment combinations (Figure 5). When *B. salicifolia* was grown with *A. donax*, its mean aboveground biomass was almost two-fold higher on average than when grow in monoculture. In the 4-way ANOVA of *B. salicifolia* aboveground biomass, the 4-way interaction was significant (Table 5) due to the presence of strong facilitation effects on half of the treatment combinations and no significant effects on the other half. In contrast, *A. donax* biomass was suppressed by competition with *B. salicifolia* under high soil moisture, light, and nutrient conditions; its biomass was two times higher in monoculture [17.05 kg (SE 15.98–18.20)] than in the mixed grouping containing *A. donax* and *B. salicifolia* [8.74 kg (SE 6.55–1.17)]. Higher mean aboveground biomass of *A. donax* monocultures in high soil moisture-full sun treatments than in any other combination of treatments as well as the competitive suppression of *A. donax* by *B. salicifolia* (Figure 5) yielded a significant 3-way interaction between plant grouping, soil moisture, and light in the 4-way ANOVA (Table 5).

DISCUSSION

In this study, I experimentally investigated competition between a particularly invasive bamboo-like grass species and three native woody riparian species under varying multiple-resource conditions that are found in natural riparian ecosystems. Superior interspecific competitive interactions between native and introduced species for water, light, and nutrient resources are critical in the plant invasion process in many ecosystems (D'Antonio and Vitousek 1992, Hamilton et al. 1999, Gordon and Rice 2000, Green and Galatowitsch 2002, Booth et al. 2003, Kolb and Alpert 2003, Sher and Marshall 2003, Suding et al. 2004, White and Holt 2005, Minchinton et al. 2006, Richardson 2006, Coleman and Levine 2007). Preemptive as well as interspecific competition for resources between plant species has been well documented in many ecosystems (Connell 1983, Schoener 1983, Tilman 1987, Goldberg and Barton 1992, Daehler 2003). Evidence of several positive, negative, and non-significant competitive interactions between species was observed in the experiment, but interactions were different than predicted. Surprisingly, results indicated only one negative competitive interaction of *A. donax* on a native riparian plant, although its biomass was higher than almost all native plants in almost every experimental condition tested during the length of this study. Competitive interactions between these species may change over time and should be studied over a longer time span.

Competition

The only instance in which *A. donax* outcompeted a native plant species for resources was under the most stressful experimental conditions tested (low soil moisture, high light, and no nutrient addition levels). Under these conditions, competition with *A. donax* resulted in lower *P. balsamifera* ssp. *trichocarpa* biomass than found in monoculture. In fact, the mean aboveground biomass of *P. balsamifera* ssp. *trichocarpa* under these conditions was lower than in any other combination of resource levels. It seems likely that exploitative competition (competition for limiting resources) for soil moisture and available nutrients accounts for this negative effect of competition, since *A. donax* did not grow large enough to shade out *P. balsamifera* ssp. *trichocarpa* by preemptive (competition for space) or overgrowth (one species grows over another, blocking light or depriving other species of a limiting resource) competition (Schoener 1983). This finding does not concur with Grime's hypothesis that resource competition is relatively unimportant for plants in unproductive or stressful environments due to the low biomass produced and corresponding low resource depletion (Grime 1977, 1979). According to Tilman (1988) however, competition occurs across productivity gradients and plants compete strongly under low resource conditions for belowground resources, mainly nutrients and water. Alpert et al. (2000) asserted that environmental stress may shift the competitive balance between invasive and native plants; mainly invasive plants take advantage of high resource availability compared to natives and low resource availability tends to cause low invasibility. However, I found that *A. donax* grew much more rapidly than all three native species under nearly all treatment conditions and suppressed one native species under low resource conditions.

Despite these hypotheses and predictions, invasive-native competitive interactions in conditions of high environmental stress are not well understood and experimental results vary by species and ecosystem. In grasslands of the western U.S., low nitrogen levels were found to have no effect on competitive ability of invasive annual grasses (Kolb and Alpert 2003, Lowe et al. 2003, Thomsen et al. 2006) or an invasive herb (*Centaurea diffusa*) on native grassland species. An invasive perennial grass (*Phalaris arundinacea*) suppressed native aboveground and belowground biomass in a wetland sedge meadow at low nitrate levels (Green and Galatowitsch 2002), yet lower phosphorus levels decreased *C. diffusa* competitive advantage over native species (Suding et al.

2004). Lowered water availability had no effect on competitive interactions between an invasive grass compared to a native grass in a Canadian mixed-grass prairie; however, low water availability was found to favor a small invasive tree, *Tamarix ramosissima*, in a floodplain of the Mojave Desert (Cleverly et al. 1997). Only one published experiment has examined competitive interactions under stressful conditions similar to my study with low soil moisture, high light, and low soil nutrients. The non-native annual grass (*Lolium multiflorum*) outcompeted a native perennial grass (*Hordeum brachyantherum*) at all resource levels when germinated simultaneously (Kolb et al. 2002). No studies showed increase in (or higher) competitive ability of invasive species relative to native species in stressful conditions of low nutrients, low water, and/or high light availability (Alpert et al. 2000). My experiment demonstrates that resource competition between invasive and native species may be highly species-specific under stressful environmental conditions. Differences in physiology of competing species, including variation in soil moisture and associated nutrient use, phenology, and differing rooting depth, may be important in mediating competitive interactions between *A. donax* and native woody riparian species (Reynolds and Pacala 1993, Fargione and Tilman 2005, Schenk 2006).

Although specific light requirements of *A. donax* and dominant riparian plant species in California are not well known (Braatne et al. 1996), invasive grass species are known to prevent woody species establishment and growth by shading them (D'Antonio and Vitousek 1992). Under conditions of high soil moisture and nutrient levels but low light, such as those found in mature riparian forests along streams in California, *A. donax* biomass was lower when grown with *P. balsamifera* spp. *trichocarpa* compared to in monoculture. Light limitations can promote strong belowground competition between species (Schenk 2006). Although not measured in this study, similarities in rooting depth and higher growth rate of roots versus shoots of *P. balsamifera* spp. *trichocarpa* (Braatne et al. 1996, Pregitzer and Friend 1996) compared to *A. donax* in these conditions may help explain suppression of *A. donax*. *Populus balsamifera* spp. *trichocarpa* develops a shallow, lateral root system primarily with occasional sinker roots (similar to a taproot) (Pregitzer and Friend 1996). Nonetheless, this finding was surprising given the documented shade-intolerance of riparian *Populus* spp. (Walters and Reich 2000, Portsmuth and Niinemets 2007), but competitive effects might differ if grown from seed due to high light germination requirements (Braatne et al. 1996). Conservation and restoration of structurally diverse mature riparian forest, including *P. balsamifera* spp. *trichocarpa*, may help suppress *A. donax* invasion where high water and nutrient conditions prevail.

Competition with both *S. laevigata* and *B. salicifolia* reduced *A. donax* biomass by half when grown together in mixed groupings in high soil moisture, light and nutrient conditions. Suppression of *A. donax* biomass by native trees in these high resource conditions was an unexpected result. I predicted *A. donax* would competitively suppress and exclude natives under high resource availability following Goldberg and Novoplanksy’s (1997) two-phase resource dynamics hypothesis and Tilman’s resource competition hypothesis (Tilman 1982, 1988). Native plant preemptive competition may be responsible for negative effects on *A. donax* biomass, since water, light, and nutrient resources were abundant. Although biomass of these two natives was much lower than the *A. donax* they suppressed, their woody phenology (upward, wide branching growth habit) may have restricted *A. donax* from expanding horizontally in all directions as it does naturally when grown alone or with other *A. donax* individuals. After the first year of growth upward, *A. donax* adds biomass by growing outward in a clonal manner. It appears that *S. laevigata* and *B. salicifolia* were able to limit its growth outward toward them somewhat (although not totally). Close observation of *A. donax* removed after the experiment indicated that individual clones planted in monoculture (four individuals) grow laterally in all directions intertwining with other *A. donax* individuals.

Facilitation

The role of positive interspecific competition for multiple resources in the invasion process has been relatively unexplored, but potentially of considerable importance in explaining mechanisms of riparian ecosystems invasion. Most examples of invasive plant species exerting competitive exclusion on native species have focused on and demonstrated negative competitive effects varying only one resource condition. However, the importance of facilitation in plant community organization and structure and its role in ameliorating harsh physical environments have been elucidated recently (Bertness and Callaway 1994, Bruno et al. 2003). Several examples of positive competitive interactions, or facilitation, between invasive and native plant species have been documented (Maron and Connors 1996, Green and Galatowitsch 2001, Rodriguez 2006).

Direct positive interactions, including facilitation, between native and invasive species has been overlooked until recently (Bertness and Callaway 1994, Rodriguez

2006). In California coastal prairie, Maron and Connors (1996) demonstrated that the native bush lupine shrub (*Lupinus arboreus*) facilitates an invasive annual grass (*Bromus diandrus*) invasion through fertilizing of the surrounding soil by nitrogen fixing and deposition of nitrogen-rich litter. I found only one study exhibiting facilitation of a native plant species by an invasive plant species; evidence of weak facilitative effects of an invasive wetland monocot (*Typha* x *glauca*) on native sedge meadow community were documented under the highest nitrate levels applied (Green and Galatowitsch 2001). However, the authors admit that *T.* x *glauca* did not appear to be well established during the short duration (4-months) of the experiment and this likely effected results. I discovered that the invasive *A. donax* facilitated the native *B. salicifolia* under half of the conditions tested; *B. salicifolia* exhibited much higher biomass when grown with *A. donax* than when grown in monoculture. In three out of four treatments tested, facilitation of the native *B. salicifolia* was detected under high soil moisture, high light, or low nutrient conditions. Similar but weaker trends in facilitation of *S. laevigata* by *A. donax* were observed.

Plant facilitation may be a particularly common characteristic in harsh physical environments in which primary space-holders buffer neighbors from potentially limiting stresses (Bertness and Callaway 1994, Bruno et al. 2003, Rodriguez 2006). Introduction of novel habitats or physical structure provided by an invasive species can alter abiotic conditions that enable native species to survive (Rodriguez 2006). Although both plants occupy roughly the same rooting zone especially in the first few years under high soil moisture conditions, *A. donax* may ameliorate stressful conditions for *B. salicifolia*. For example, *A. donax* may draw down high soil water content in the surrounding rooting zone in very high soil moisture levels or decrease high salinity levels, conditions that have been shown to limit *B. salicifolia* growth otherwise (Vandersande et al. 2001). Since *A. donax* is functionally unique compared to the native phreatophyte *S. laevigata* and slight facilitation was detected under almost all growing conditions, novel facilitation by *A. donax* could provide a new habitat structure for *S. laevigata* as well. Mechanisms responsible for this type of facilitative interaction should be addressed in future research. Finally, facilitation of *B. salicifolia* and *S. laevigata* by *A. donax* may be only present in paired species groupings or when surrounded by *A. donax* and absent or not as important in naturally diverse riparian communities due to more complex interspecific relationships with other species.

High Resource Levels and Competitive Exclusion

Contrary to my prediction, I found that *A. donax* did not exhibit superior resource competition or competitive exclusion of natives under high resource levels during the time period of my experiment. *Arundo donax* exhibits competitive exclusion of native species in riparian ecosystems in Mediterranean-type climates under most resource conditions, especially in high water, light, and nutrient levels. Although most competition experiments are 2 years or less in duration (Goldberg and Barton 1992), exclusion of native plant species by *A. donax* by resource competition was not observed due likely to the short duration of this study.

Arundo donax demonstrated inferior resource competition ability in almost all conditions, was suppressed by both a native tree and shrub in high resource conditions, and even facilitated the native shrub *B. salicifolia* in half of the treatments. Despite these disadvantages, *A. donax* was still much more productive in high soil moisture, light, and nutrients compared to the native plants and under other experimental conditions. *Arundo donax* appears to be on a trajectory to competitive exclusion of natives when resource availability is high (high soil moisture, light, and nutrient levels) regardless of its inferior resource competitive ability.

Results of resource competition experiments between invaders and native species vary considerably by resource level (Alpert et al. 2000), but most invaders benefited from elevated nutrient and water conditions. In a review of invader versus native plant species performance, invaders exhibited either universal superior competitive performance or superior performance in high nutrient conditions in two-thirds of the studies examined, but under low resource conditions native species usually outperformed invaders (Daehler 2003). Daehler (2003) concluded from his evaluation that relative performance of invasive compared to native species may shift in high resource conditions; increased resource availability combined with altered disturbance regimes, not universal performance advantages, often increase performance of invasive relative to native species. High biomass production of *A. donax* compared to native species in high resource conditions revealed in this study supports Daehler's hypothesis.

Invasion Mechanisms in Varying Resource Conditions

Results of this study suggest that mechanisms of *A. donax* invasion in riparian ecosystems may vary depending on availability for multiple resources and competition from native species. When resources are abundant (high soil moisture, light, and nutrients) and no competition from native species exists, high allocation to photosynthetic tissue, high growth rate, and phenology of *A. donax* allow it to accumulate biomass faster than natives and eventually competitively exclude natives in these areas. In this study, *A. donax* monocultures grew exceptionally well under high soil moisture, nutrient, and light conditions, producing between four to six times more biomass than other native species under these optimal conditions. Several other invasive versus native plant comparative studies in wetlands have reported similar trends in clonal plant performance under conditions of high resource availability (Green and Galatowitsch 2001, Svengsouk and Mitsch 2001, Green and Galatowitsch 2002).

When resources are abundant, Tilman (1988) suggested differences in growth rates between species are due to a greater allocation of growth to photosynthetic tissues compared to non-photosynthetic roots, seeds, and branches/trunk. In contrast, plants that allocate to more non-photosynthetic tissues are favored in resource limiting environments (Tilman 1988). All *A. donax* biomass produced in the first year of growth, both leaves and culms, contains photosynthetic tissue (Sharma et al. 1998, Decruyenaere and Holt 2001), whereas *B. salicifolia*, *S. laevigata*, and *P. balsamifera* ssp. *trichocarpa* allocate a significant percentage of their biomass to non-photosynthetic trunks, branches, roots, and reproductive parts. *Arundo donax* has an extremely high growth rate, with shoot elongation of up to 10 cm per day and a relative growth rate of 0.13 g $g^{-1}day^{-1}$ under optimal conditions (Perdue 1958, Else 1996, Bell 1997, DiTomaso 1998, Spencer et al. 2005). At the end of two growing seasons, the mean height of *A. donax* throughout the experiment was 4.01 m (SE ± 0.04) and ranged from 0.64–7.84m. On average native riparian species grown from cuttings attained much lower heights than *A. donax* after two years growth [*P. balsamifera* ssp. *trichocarpa* = 2.71 m (SE ± 0.03); *S. laevigata* = 2.75 m (SE ± 0.05); *B. salicifolia* = 2.94 m (SE ± 0.03)] or when grown from seedlings. Seedlings of native species such as *P. balsamifera* ssp. *trichocarpa* are known to reach only 5–60 cm after two years (Braatne et al. 1996). Furthermore, Decruyenaere and Holt (2005) documented year-round growth of *A. donax* and recruitment of new culms in sites with high nitrogen levels in southern California.

High resource conditions appear optimal for competitive exclusion of natives by *A. donax*. However, *A. donax* exhibited higher biomass production than either *S. laevigata* or *P. balsamifera* ssp. *trichocarpa* in most other treatments and greatest differences between *A. donax* and native species were seen in low soil moisture treatments. This evidence of plant plasticity (ability of a plant to thrive under all resource availability levels) may contribute to *A. donax* invasibility (Rezk and Edany 1979, Claridge and Franklin 2002) in other resource conditions, as is often the case with other invaders (Daehler 2003). When resource levels are lower, soil resource availability for *A. donax* versus riparian species is likely more distinctly partitioned (niche differences greater) and interspecific competition is avoided. Fargione and Tilman (2005) attributed coexistence of two prairie bunchgrasses to niche differences of phenology and rooting depth. Phreatophyte adaptations to resource limitation, such as greater root:shoot allocation (Vandersande et al. 2001, Schade and Lewis 2006) and deep tap roots (Tilman 1988) provide *A. donax* almost exclusive use of soil moisture and nutrients in shallow soil horizons. Interspecific competition between *A. donax* and native phreatophytes may only be important when native aboveground biomass is extremely low and thus rooting depths are similar. For example, evidence of negative competitive effects of *A. donax* on native plants was only found in the most stressful environmental conditions (low soil moisture, light, and nutrients); competition from *A. donax* reduced *P. balsamifera* spp. *trichocarpa* biomass to the lowest values found in the experiment. Native woody riparian plants were not found to have a competitive advantage in low resource conditions as predicted (Tilman 1988) or shown in other studies (Alpert et al. 2000, Daehler 2003).

Arundo donax appears to be a "super invader", outperforming three common native species under high as well as low resource conditions (Daehler 2003) due to its unique morphology and physiology in riparian ecosystems of Mediterranean-type climates. However, the competitive ability of *A. donax* is strongest under high resource conditions. Strong novel facilitation of *B. salicifolia* (and week facilitation of *S. laevigata*) by *A. donax* in several resource conditions and competition from *P. balsamifera* spp. *trichocarpa* in high soil moisture-low light-high nutrient conditions may partially combat this invasion, but further study is required. Community-level competition experiments are needed to identify any indirect competitive interactions and verify the magnitude of pairwise or individual-level competitive interactions found in this study. Also, competitive interactions and productivity are likely to change over time and should be studied over a longer-time frame to validate invasion predictions.

CONCLUSIONS

This experiment demonstrated the absence of competitive advantages for resource use by a highly invasive grass, *A. donax*. Under high resource levels, *A. donax* is extremely productive, but is slightly suppressed by two native species. Nonetheless, it still obtains a higher biomass than all native plant species under these conditions. Relatively high plant plasticity allows *A. donax* to obtain a higher biomass than natives under lower resource level conditions as well. The unique morphology and physiology of *A. donax* compared to native woody riparian species enable *A. donax* to dominate the aboveground biomass under most environmental conditions. Under high resource levels, *A. donax* appears to be on a trajectory of competitive exclusion despite little observed resource competition with two common native species.

The results of this study have broad application to managing *A. donax* in rivers and wetlands worldwide, especially in areas where high soil moisture, elevated nutrients, and disturbance (high light availability) all exist. In arid and Mediterranean-type climates with naturally low soil nutrients (Pettijohn 1975, Day 1983, diCastri 1991, Dallman 1998) and groundwater levels, dense urbanization and intense agricultural practices have elevated both nutrient and water levels in streams (Hazy 2006). Both the natural dynamic flood regime characteristic of these climates and anthropogenic enhancement of water, nutrients, and light levels have created the ideal conditions for invasion of river and stream systems by *A. donax* (see Chapter 3).

If we continue to create or promote high resource conditions in riparian ecosystems, invasion of *A. donax* will continue and may eventually lead to its expanded dominance in riparian ecosystems. Displacement of native riparian species by *A. donax* will only continue to lead to decreased biodiversity, altered ecosystem functioning, loss of wildlife habitat, and changes in natural flood and fire (Bell 1997, DiTomaso 1998, Dudley 2000).

My findings will help organizations working on riparian habitat conservation and restoration predict locations where it is most invasive and least invasive, contributing to successful control of this invasive species. Large-scale restoration projects (levee and dam removal) need to consider the effects of these restoration actions on the potential spread of fast growing invasive plants like *A. donax. Arundo donax* will be most invasive in high soil moisture, nutrient and light levels and most difficult to manage or remove. These conditions are commonly found along urbanized or agricultural river floodplains after large storms and along interfaces between high nutrient land use practices (agricultural fields) and riparian ecosystems (see Chapter 3). Areas exhibiting the most stressful environmental conditions (low soil moisture, low nutrients, high light, and competition from native species) will have the lowest risk of *A. donax* invasion. *Arundo donax* control efforts should focus in these stressful environments, such as dry reaches of rivers or ephemeral streams where *B. salicifolia* and other native species are established along with *A. donax*.

Knowledge of the effects of environmental conditions on *A. donax* growth provides valuable insight into the timing and selection of management techniques in *A. donax* control projects. Active revegetation with natives after *A. donax* removal is recommended in areas with high soil moisture and nutrients. However, *B. salicifolia* planting may be lower priority because it naturally colonizes riparian ecosystems. Active revegetation may also be effective in the low soil moisture, low nutrients, and full sun conditions found in many arid stream systems; under such condition in this study, *B. salicifolia* had a higher biomass and was facilitated by *A. donax*.. Because plants are more susceptible to herbicide treatments when carbohydrates are translocated from aboveground to belowground organs, *A. donax* in low soil moisture and full sun conditions may require treatment earlier in the growing season than those growing along streams with high water availability (Spencer et al. 2005).

Long-term control of invasive species such as *A. donax* in natural ecosystems may require management of resource levels that promote invasion to reduce growth and competition. Manipulation of resource availability in favor of a given native (desired) species may create a competitive advantage and a barrier to reinvasion (Blumenthal et al. 2003, Corbin and D'Antonio 2004a, Suding et al. 2004, Prober et al. 2005, Perry and Galatowitsch 2006). Watershed management organizations should consider reducing nutrient levels from urban runoff and excess treated wastewater released into rivers to reduce growth and invasion by *A. donax*. Suppression of *A. donax* via competition from several native species under high soil moisture and low light conditions has implications for riparian forest conservation and restoration efforts aimed at controlling *A. donax*, but further research is needed to verify these finding over a longer time frame. Conservation and restoration of structurally and species diverse riparian forests may help to suppress and reduce *A. donax* invasion in areas of high soil moisture.

TABLES

Table 1. Plant distribution in competition plant groupings (four plants per grouping) used in the field experiment.

Competition grouping treatment	**Plant species (number of species per grouping)**			
	Arundo donax	***Baccharis salicifolia***	***Salix laevigata***	***Populus balsamifera* ssp. *trichocarpa***
2-species grouping	2	2		
	2		2	
	2			2
1-species grouping (monoculture)	4			
		4		
			4	
				4

Table 2. Four-way ANOVA significance table for aboveground biomass (total biomass at end of 2004 growing season) by factors of competition groupings [2-species mixed grouping of *A. donax* and one native riparian species (*S. laevigata*, *P. balsamifera* ssp. *trichocarpa*, and *B. salicifolia)* and monocultures groupings)], soil moisture (high and low), and light (high and low), and nutrients (high and none). Significant results are reported in bold.

Factors and interactions	Mean aboveground biomass
Plant grouping	**$F_{(9,560)}$ = 33.384, $P < 0.001$*****
Soil moisture	**$F_{(1,560)}$ = 145.772, $P < 0.001$*****
Light	**$F_{(1,560)}$ = 26.615, $P < 0.001$*****
Nutrients	**$F_{(1,560)}$ = 16.339, $P < 0.001$*****
Plant grouping x soil moisture	**$F_{(9,560)}$ = 1.917, $P = 0.047$***
Plant grouping x light	**$F_{(9,560)}$ = 3.633, $P < 0.001$*****
Plant grouping x nutrients	$F_{(9,560)}$ = 1.100, $P = 0.361$
Soil moisture x light	**$F_{(1,560)}$ = 81.422, $P < 0.001$*****
Soil moisture x nutrients	$F_{(1,560)}$ = 3.365, $P = 0.067$
Light x nutrients	**$F_{(1,560)}$ = 5.593, $P = 0.018$***
Plant grouping x soil moisture x light	**$F_{(9,560)}$ = 2.974, $P = 0.002$****
Plant grouping x soil moisture x nutrients	$F_{(9,560)}$ = 1.124, $P = 0.343$
Plant grouping x light x nutrients	$F_{(9,560)}$ = 1.789, $P = 0.067$
Soil moisture x light x nutrients	**$F_{(1,560)}$ = 4.689, $P = 0.031$***
Plant grouping x soil moisture x light x nutrients	$F_{(9,560)}$ = 0.694, $P = 0.715$
r^2	0.581

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

Table 3. Four-way ANOVA significance table for mean aboveground biomass (total biomass at end of 2004 growing season) of *A. donax* and *P. balsamifera* ssp. *trichocarpa* by factors of plant groupings (2-species mixed grouping and monocultures), soil moisture (high and low), light (high and low), and nutrients (high and none). Significant results are reported in bold.

Factors and interactions	*A. donax*	*P. balsamifera* ssp. *trichocarpa*
Plant grouping	$F_{(1,122)} = 1.789, P = 0.184$	$F_{(1,115)} = 0.053, P = 0.819$
Soil moisture	$\mathbf{F_{(1,122)} = 35.445, P < 0.001***}$	$\mathbf{F_{(1,115)} = 63.190, P < 0.001***}$
Light	$\mathbf{F_{(1,122)} = 36.561, P < 0.001***}$	$\mathbf{F_{(1,115)} = 4.094, P = 0.045*}$
Nutrients	$\mathbf{F_{(1,122)} = 7.682, P = 0.006**}$	$\mathbf{F_{(1,115)} = 6.966, P = 0.009**}$
Plant grouping x soil moisture	$F_{(1,122)} = 1.027, P = 0.313$	$F_{(1,115)} = 0.900, P = 0.345$
Plant grouping x light	$F_{(1,122)} = 2.118, P = 0.148$	$F_{(1,115)} = 2.340, P = 0.129$
Plant grouping x nutrients	$F_{(1,122)} = 0.881, P = 0.350$	$F_{(1,115)} = 1.017, P = 0.315$
Soil moisture x light	$\mathbf{F_{(1,122)} = 87.616, P < 0.001***}$	$\mathbf{F_{(1,115)} = 5.376, P = 0.022*}$
Soil moisture x nutrients	$F_{(1,122)} = 1.838, P = 0.178$	$F_{(1,115)} = 0.068, P = 0.795$
Light x nutrients	$\mathbf{F_{(1,122)} = 12.246, P = 0.001***}$	$F_{(1,115)} = 0.061, P = 0.805$
Plant grouping x soil moisture x light	$F_{(1,122)} = 1.024, P = 0.314$	$F_{(1,115)} = 0.241, P = 0.624$
Plant grouping x soil moisture x nutrients	$F_{(1,122)} = 0.706, P = 0.402$	$F_{(1,115)} = 0.165, P = 0.686$
Plant grouping x light x nutrients	$\mathbf{F_{(1,122)} = 4.564, P = 0.035*}$	$\mathbf{F_{(1,115)} = 5.022, P = 0.027*}$
Soil moisture x light x nutrients	$\mathbf{F_{(1,122)} = 8.449, P = 0.004**}$	$F_{(1,115)} = 0.369, P = 0.545$
Plant grouping x soil moisture x light x nutrients	$F_{(1,122)} = 0.242, P = 0.623$	$F_{(1,115)} = 0.265, P = 0.608$
r^2	0.646	0.457

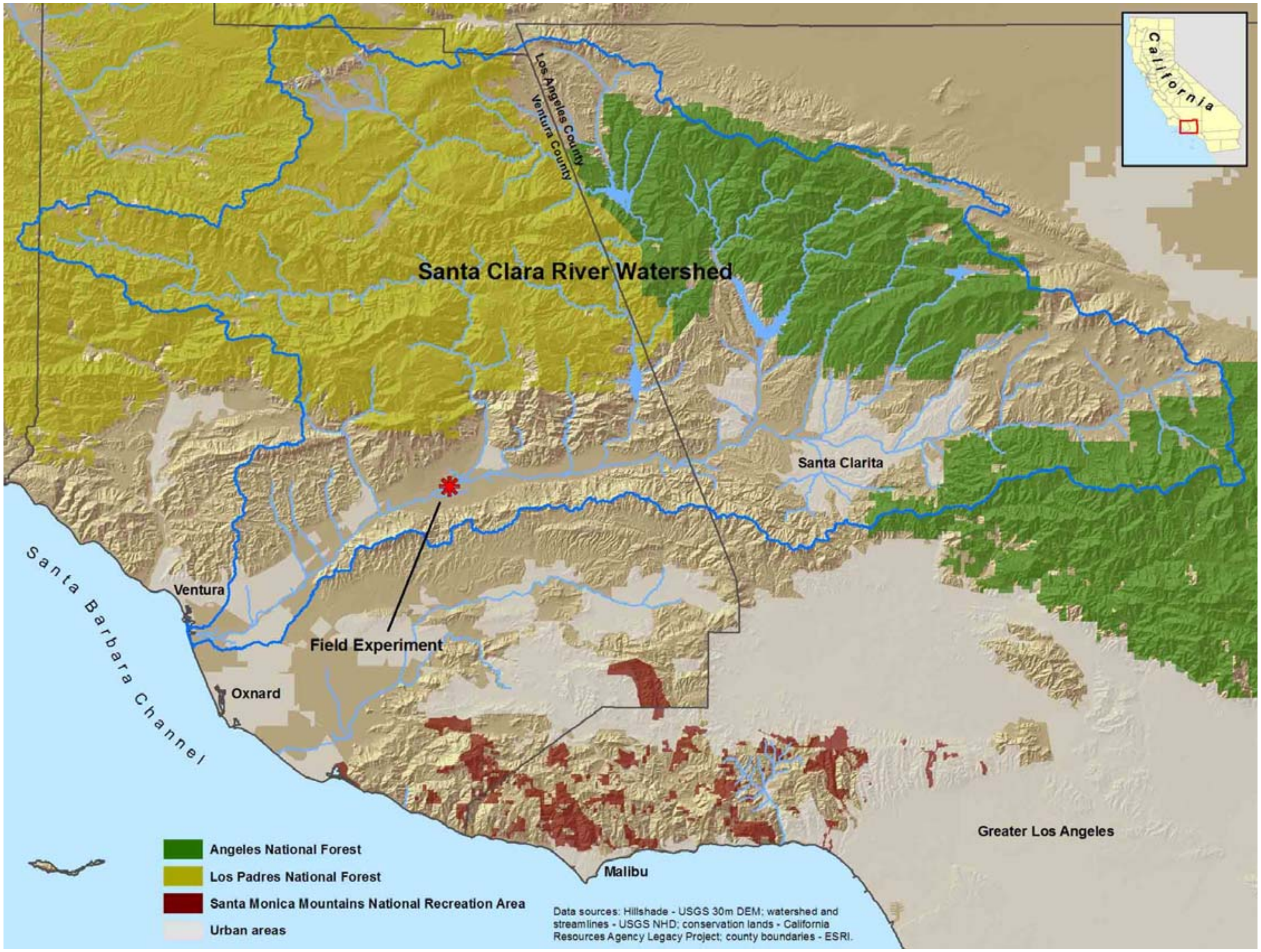
Table 4. Four-way ANOVA significance table for mean aboveground biomass (total biomass at end of 2004 growing season) of *A. donax* and *S. laevigata* by factors of plant groupings (2-species mixed grouping and monocultures), soil moisture (high and low), light (high and low), and nutrients (high and none). Significant results are reported in bold.

Factors and interactions	***A. donax***	***S. laevigata***
Plant grouping	$F_{(1,122)}$ = 0.034, P = 0.854	**$F_{(1,120)}$ = 5.348, P = 0.022***
Soil moisture	**$F_{(1,122)}$ = 52.395, P < 0.001*****	**$F_{(1,120)}$ = 21.523, P < 0.001*****
Light	**$F_{(1,122)}$ = 23.905, P < 0.001*****	$F_{(1,120)}$ = 1.303, P = 0.256
Nutrients	$F_{(1,122)}$ = 0.873, P = 0.352	$F_{(1,120)}$ = 0.636, P = 0.427
Plant grouping x soil moisture	$F_{(1,122)}$ = 1.364, P = 0.245	$F_{(1,120)}$ = 0.076, P = 0.783
Plant grouping x light	$F_{(1,122)}$ = 0.423, P = 0.516	$F_{(1,120)}$ = 0.084, P = 0.772
Plant grouping x nutrients	$F_{(1,122)}$ = 1.631, P = 0.204	$F_{(1,120)}$ = 1.076, P = 0.302
Soil moisture x light	**$F_{(1,122)}$ = 73.333, P < 0.001*****	**$F_{(1,120)}$ = 5.427, P = 0.022***
Soil moisture x nutrients	$F_{(1,122)}$ = 0.477, P = 0.491	**$F_{(1,120)}$ = 4.416, P = 0.038***
Light x nutrients	**$F_{(1,122)}$ = 4.349, P = 0.039***	$F_{(1,120)}$ = 0.904, P = 0.344
Plant grouping x soil moisture x light	$F_{(1,122)}$ = 2.279, P = 0.134	$F_{(1,120)}$ = 0.918, P = 0.340
Plant grouping x soil moisture x nutrients	$F_{(1,122)}$ = 3.837, P = 0.052	$F_{(1,120)}$ = 0.514, P = 0.475
Plant grouping x light x nutrients	$F_{(1,122)}$ = 0.194, P = 0.660	$F_{(1,120)}$ = 0.407, P = 0.525
Soil moisture x light x nutrients	$F_{(1,122)}$ = 3.866, P = 0.052	$F_{(1,120)}$ = 0.060, P = 0.808
Plant grouping x soil moisture x light x nutrients	$F_{(1,122)}$ = 0.897, P = 0.345	$F_{(1,120)}$ = 0.013, P = 0.908
r^2	0.652	0.310

Table 5. Four-way ANOVA significance table for mean aboveground biomass (total biomass at end of 2004 growing season) of *A. donax* and *B. salicifolia* by factors of plant groupings (2-species mixed grouping and monocultures), soil moisture (high and low), light (high and low), and nutrients (high and none). Significant results are reported in bold.

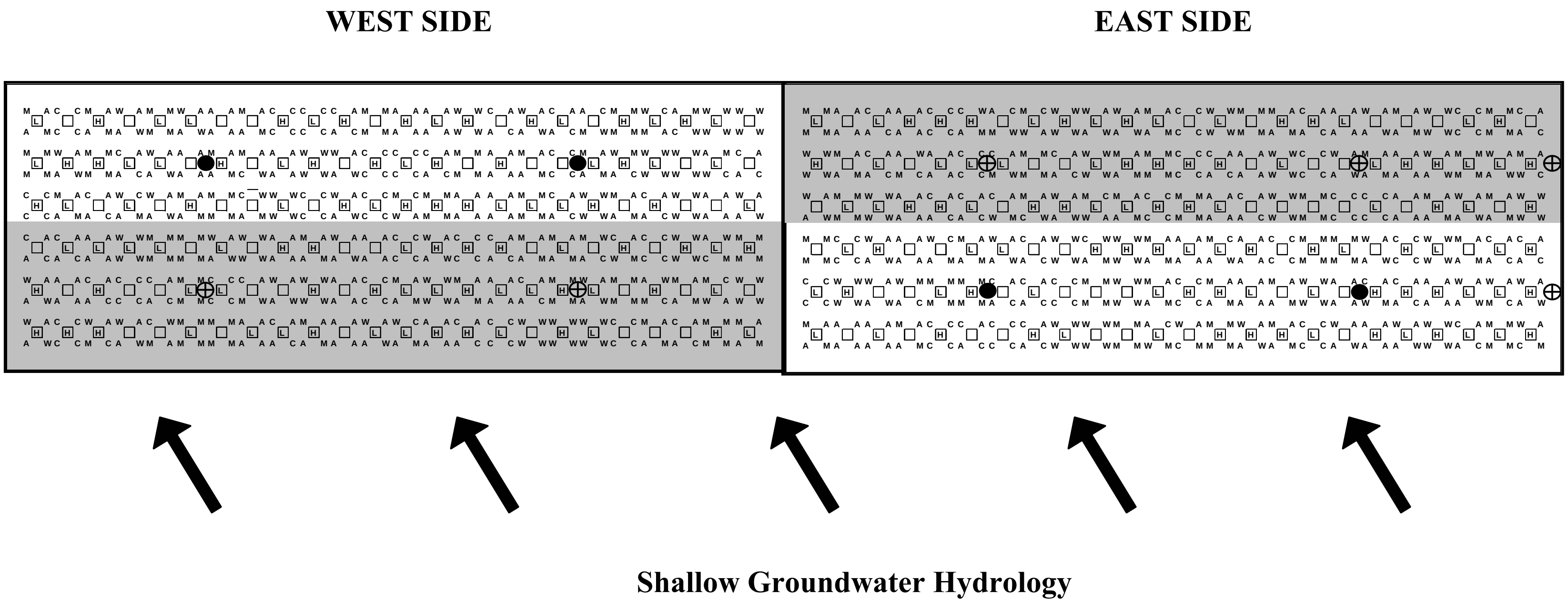
Factors and interactions	*A. donax*	*B. salicifolia*
Plant grouping	**$F_{(1,125)}$ = 4.715, P = 0.032***	**$F_{(1,128)}$ = 21.950, P < 0.001*******
Soil moisture	**$F_{(1,125)}$ = 56.410, P < 0.001*******	**$F_{(1,128)}$ = 27.082, P < 0.001*******
Light	**$F_{(1,125)}$ = 18.760, P < 0.001*******	**$F_{(1,128)}$ = 32.204, P < 0.001*******
Nutrients	**$F_{(1,125)}$ = 14.659, P < 0.001*******	$F_{(1,128)}$ = 3.708, P = 0.056
Plant grouping x soil moisture	$F_{(1,125)}$ = 0.483, P = 0.488	$F_{(1,128)}$ = 1.033, P = 0.311
Plant grouping x light	$F_{(1,125)}$ = 1.159, P = 0.284	$F_{(1,128)}$ = 3.079, P = 0.082
Plant grouping x nutrients	$F_{(1,125)}$ = 2.789, P = 0.097	**$F_{(1,128)}$ = 5.154, P = 0.025***
Soil moisture x light	**$F_{(1,125)}$ = 55.937, P < 0.001*******	**$F_{(1,128)}$ = 16.483, P < 0.001*******
Soil moisture x nutrients	$F_{(1,125)}$ = 2.668, P = 0.105	$F_{(1,128)}$ = 0.009, P = 0.925
Light x nutrients	$F_{(1,125)}$ = 0.801, P = 0.373	$F_{(1,128)}$ = 0.093, P = 0.761
Plant grouping x soil moisture x light	**$F_{(1,125)}$ = 5.539, P = 0.020***	$F_{(1,128)}$ = 0.488, P = 0.486
Plant grouping x soil moisture x nutrients	$F_{(1,125)}$ = 0.908, P = 0.342	**$F_{(1,128)}$ = 5.346, P = 0.022***
Plant grouping x light x nutrients	$F_{(1,125)}$ = 0.505, P = 0.479	$F_{(1,128)}$ = 0.548, P = 0.460
Soil moisture x light x nutrients	$F_{(1,125)}$ = 2.519, P = 0.115	$F_{(1,128)}$ = 2.638, P = 0.107
Plant grouping x soil moisture x light x nutrients	$F_{(1,125)}$ = 1.579, P = 0.211	**$F_{(1,128)}$ = 6.267, P = 0.014***
r^2	0.633	0.496

FIGURES



Data sources: Hillshade - USGS 30m DEM; watershed and streamlines - USGS NHD; conservation lands - California Resources Agency Legacy Project; county boundaries - ESRI.

Figure 2. Location of field experiment study site, Santa Clara River Watershed, Ventura County, California.



Legend:

A = Arundo (*Arundo donax)*
C = Black cottonwood (*Populus balsamifera ssp. trichocarpa*)
M = Mulefat (*Baccharis salicifolia*)
W = Red willow (*Salix laevigata*)
H = High N fertilizer treatment
L = Low N fertilizer treatment
N = No N fertilizer treatment
▨ = 80% shade treatment and plant grouping
● = Soil moisture monitoring stations (deep only)
⊕ = Soil moisture monitoring stations (shallow and deep)

Figure 3. Field experiment planting and sampling layout.

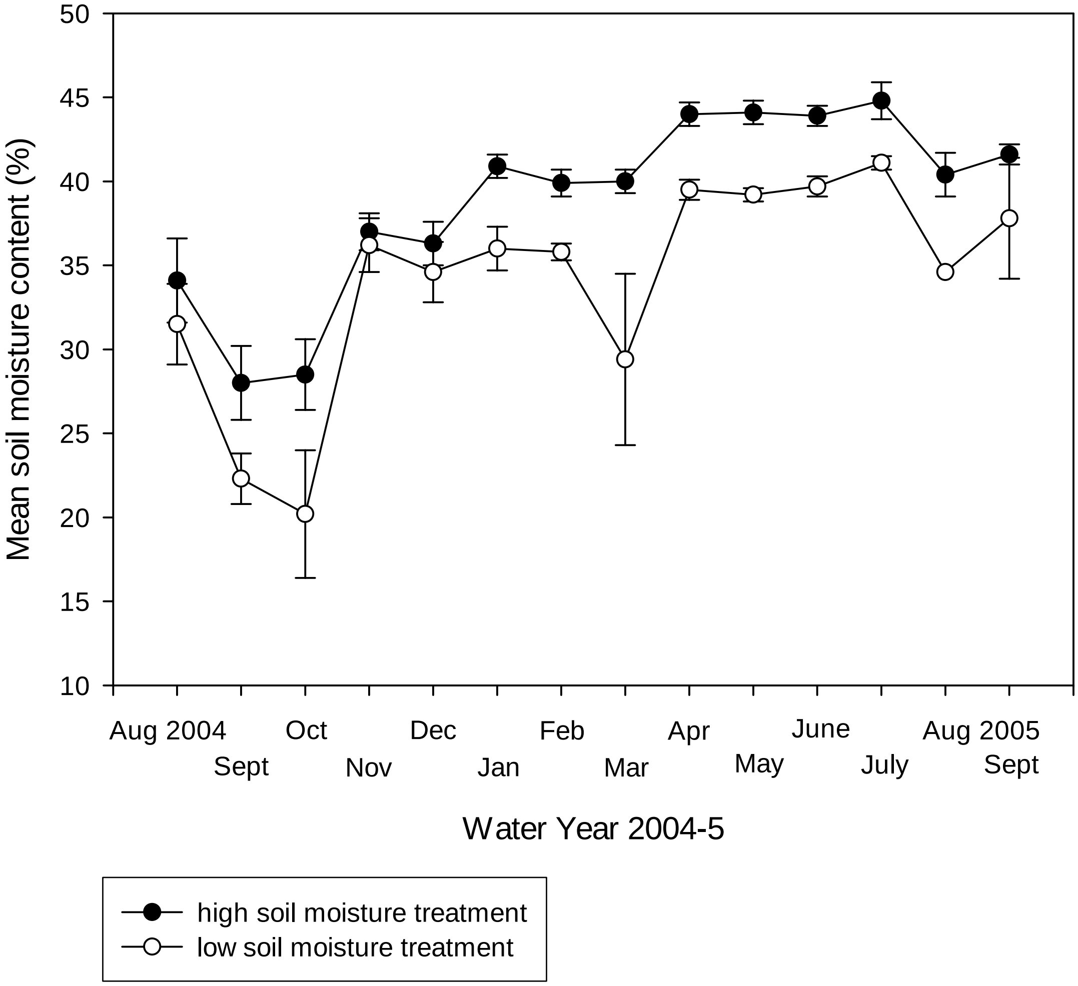


Figure 4. Mean monthly soil moisture content (percent) at 60–80 cm depth in the east and west sides of the experiment (high and low soil moisture treatments).

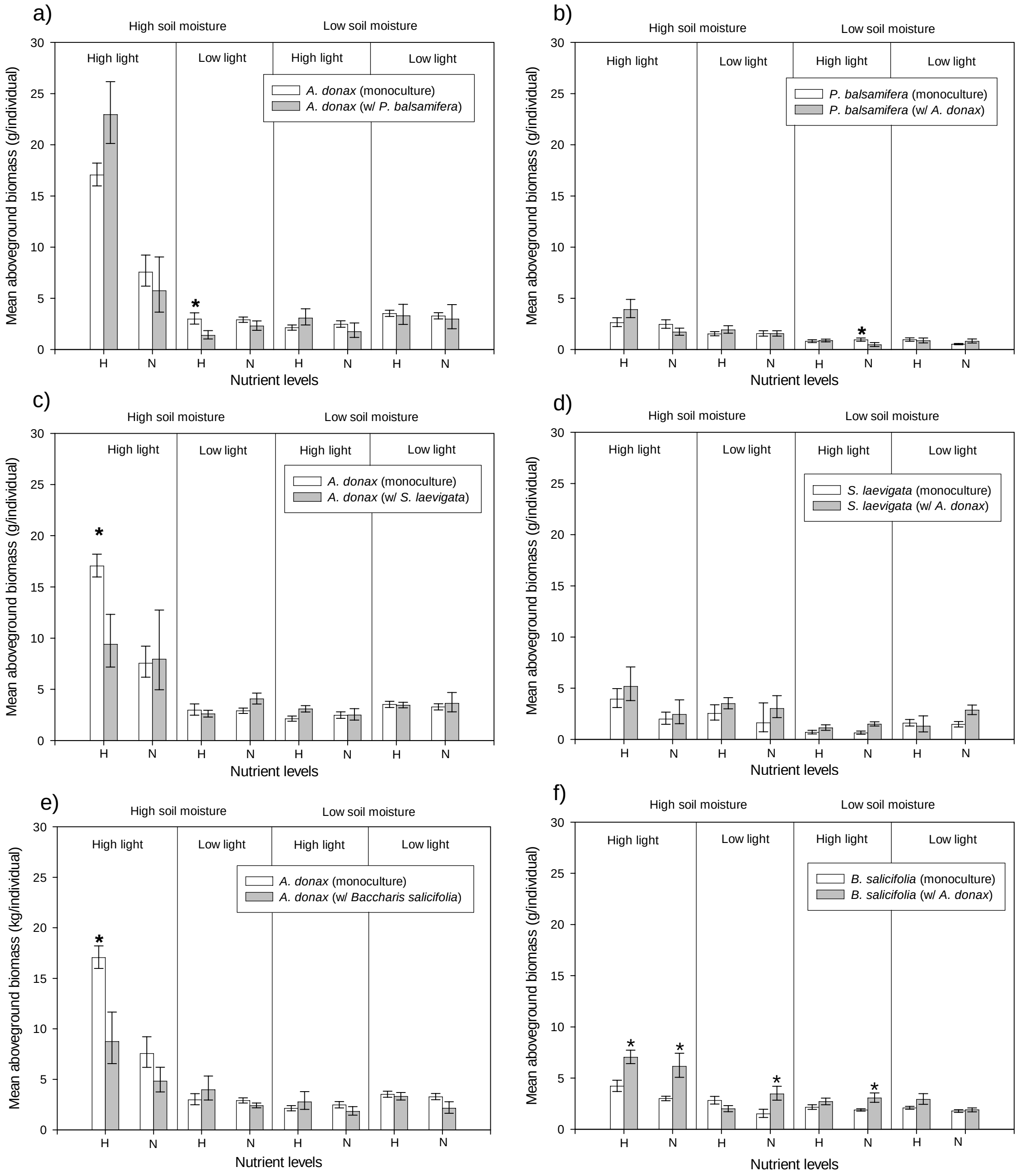


Figure 5. Mean aboveground biomass (± SE represented by error bars) of plants grown in monoculture compared to with a single competitor in the field experiment at the end of the 2004 growing season. Graphs show competitive effects by species pairings: a) *A. donax* by *P. balsamifera* spp. *trichocarpa*, b) *P. balsamifera* spp. *trichocarpa* by *A. donax*, c) *A. donax* by *S. laevigata*, d) *S. laevigata* by *A. donax*, e) *A. donax* by *B. salicifolia*, and f) *B. salicifolia* by *A. donax*. Asterisks denote results of post-hoc hypothesis tests (comparison of means) between plant groupings within similar treatments, with significance recognized at α <0.05.

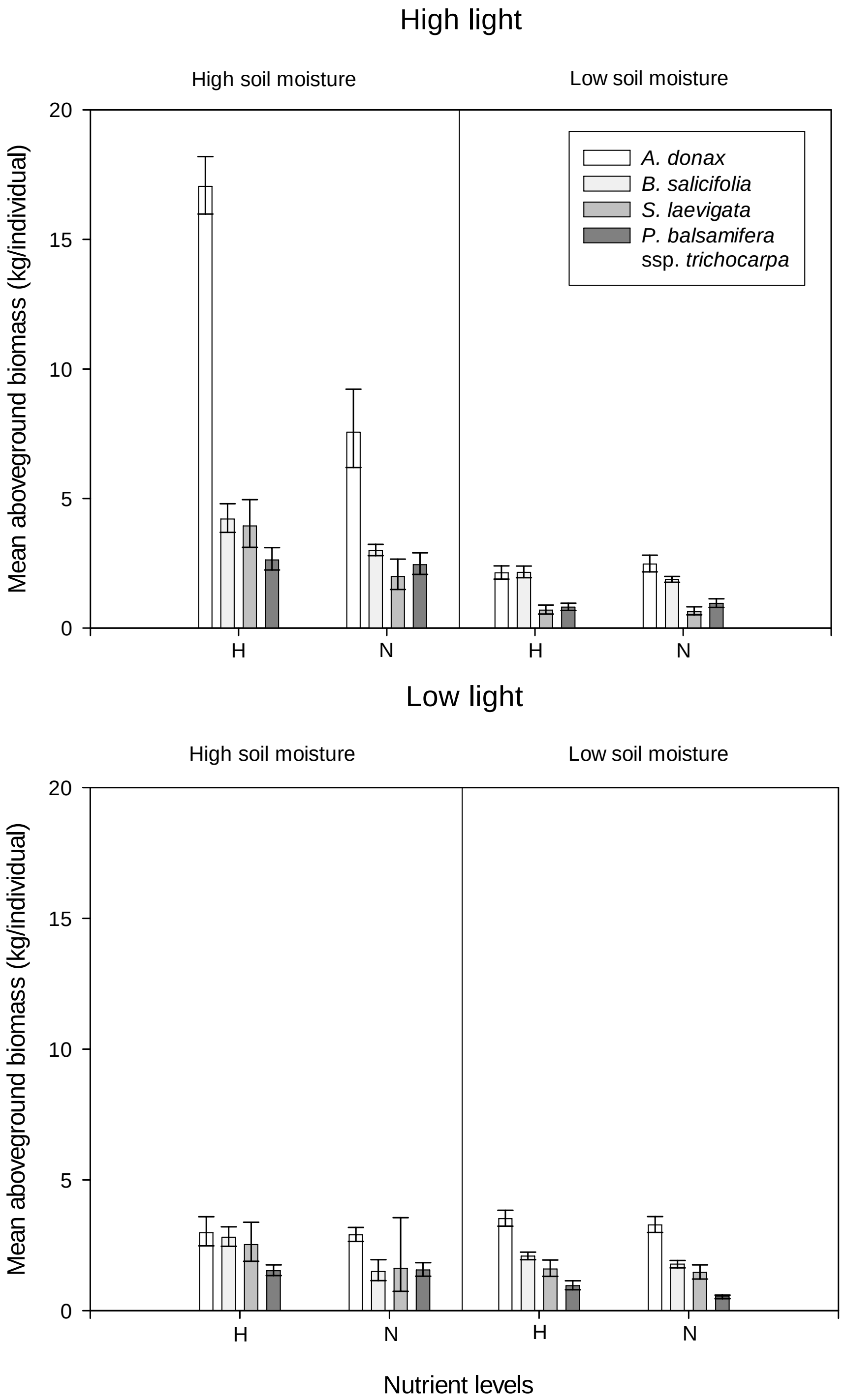


Figure 6. Mean aboveground biomass (± SE represented by error bars) of all plants grown in monoculture in the field experiment at the end of the 2004 growing season by species, soil moisture, nutrient, and light factors. Graphs are grouped by high light (a) and low light growing conditions (b).

APPENDICES

APPENDIX 2-1

BIOMASS REGRESSION EQUATIONS

Figure 1. Regression equations for *A. donax*, *Baccharis salicifolia*, *Salix laevigata*, and *Populus balsamifera* ssp. *trichocarpa* used to predict aboveground biomass of all plants under various soil moisture and light treatments in the field experiment in 2003. Equations ($y = b_1x_1 + c$) were based on aboveground biomass (g) of sample culms/branches (dependent variable or y), a regression coefficient (b_1), basal diameter (mm) of sample culms/branches (independent variable or x_1), and a constant (y-intercept or c). All data were ln transformed. All regressions were significant.

	High soil moisture						**Low soil moisture**					
	Full sun			**80% shade**			**Full sun**			**80% shade**		
Plant species	**b**	**c**	**r^2**	**b**	**c**	**r^2**	**b**	**c**	**r^2**	**b**	**c**	**r^2**
A. donax *(< 1 year)*	1.878	-0.197	0.906	3.097	-3.192	0.936	1.142	0.794	0.425	2.086	-0.760	0.923
B. salicifolia	2.287	-1.502	0.969	2.503	-2.110	0.995	2.455	-2.101	0.989	2.402	-1.905	0.969
S. laevigata	2.172	-1.023	0.989	2.173	-1.042	0.985	2.130	-1.248	0.979	2.335	-1.421	0.992
P. balsamifera* ssp. *trichocarpa	2.273	-1.037	0.993	2.256	-1.150	0.993	2.092	-1.266	0.982	2.210	-1.127	0.933

Table 2. Regression equations for *A. donax*, *Baccharis salicifolia*, *Salix laevigata*, and *Populus balsamifera* ssp. *trichocarpa* used to predict aboveground biomass of all plants under various soil moisture and light treatments in the field experiment in 2004. Equations ($y = b_1x_1 + c$) were based on aboveground biomass (g) of sample culms/branches (dependent variable or y), a regression coefficient (b_1), basal diameter (mm) of sample culms/branches (independent variable or x_1), and a constant (y-intercept or c). All data were ln transformed.

	High soil moisture						**Low soil moisture**					
	Full sun			**80% shade**			**Full sun**			**80% shade**		
Plant species	**b**	**c**	**r^2**	**b**	**c**	**r^2**	**b**	**c**	**r^2**	**b**	**c**	**r^2**
A. donax *(< 1 year)*	2.516	-1.744	0.980	1.609	0.770	0.908	1.864	-0.020	0.956	1.634	0.686	0.891
A. *donax* (> 1 year)	2.636	-1.910	0.971	2.301	-0.918	0.895	2.316	-1.290	0.936	2.856	-2.336	0.947
B. salicifolia	2.625	-2.132	0.995	2.511	-1.869	0.994	2.657	-2.314	0.993	2.658	-2.302	0.994
S. laevigata	2.195	-0.983	0.993	2.305	-1.228	0.990	2.295	-1.358	0.988	2.321	-1.337	0.995
P. balsamifera* ssp. *trichocarpa	2.408	-1.352	0.993	2.413	-1.498	0.996	2.306	-1.285	0.992	2.353	-1.445	0.993

APPENDIX 2-2

PLANT SURVIVORSHIP IN FIELD EXPERIMENT

METHODS

Sampling Methods

I measured plant survivorship at three time periods: 1) survivorship of planted cuttings in March 2003, 2) plant survivorship at the end of 2003, and 3) plant survivorship at the end of 2004. A few cuttings (14) and rhizomes (9) that did not grow initially were replanted in spring 2003. 2003 and 2004 percent survivorship results represented the establishment success for all initial and replacement cuttings.

Statistical Analyses

Descriptive statistics were performed on plant survivorship measurements. Four-way ANOVAs (all combinations of competition groupings, soil moisture, light, and nutrient factors and levels) were performed on percent survivorship data for three time periods (cuttings and at the end of the two growing seasons) to determine treatment effects during the plant establishment period. Percent plant survivorship measured at the end of 2003 and 2004 was compared in the two-way ANOVA (year x competition grouping). The 36 four-species groupings and 96 low nutrient treatments plant groupings in the experiment were not included in these statistical analyses.

RESULTS

The four-way ANOVA (species x soil moisture x nutrients x light) for percent survivorship yielded no significant main effects or interactions for cuttings and plants at the end of the 2004 growing season (Table 1), yet resulted in one two-way interaction between species and soil moisture for plant survivorship at the end of 2003 growing season (Table 1). Only five plants (0.8% of plants in groupings analyzed) did not survive the second growing season. First year plant survivorship of *P. balsamifera* ssp. *trichocarpa* was significantly lower within the high soil moisture treatment than in any other species and soil moisture treatment combination (Figure 1).

Table 1. Four-way ANOVA significance table for percent plant survivorship during establishment by factors of species from one-species and two-species groupings combined (*Arundo donax* and three native riparian species, *Salix laevigata*, *Populus balsamifera* ssp. *trichocarpa*, and *Baccharis salicifolia*), soil moisture (high and low), nutrient additions (high and none), and light (high and low). Results are for three time periods: 1) cutting survivorship (March 2003), 2) plant survivorship at end of 2003, and 3) plant survivorship at end of 2004. Significant results are in bold.

Factors and interactions	**Cuttings**	**2003**	**2004**
Species	$F_{(3,48)} = 1.821, P = 0.156$	$F_{(3,48)} = 2.352, P = 0.084$	$F_{(3,48)} = 2.523, P = 0.069$
Soil moisture	$F_{(1,48)} = 1.346, P = 0.252$	$F_{(1,48)} = 4.029, P = 0.050$	$F_{(1,48)} = 1.858, P = 0.179$
Nutrients	$F_{(1,48)} = 0.050, P = 0.824$	$F_{(1,48)} = 0.042, P = 0.839$	$F_{(1,48)} = 0.046, P = 0.831$
Light	$F_{(1,48)} = 1.625, P = 0.208$	$F_{(1,48)} = 0.855, P = 0.360$	$F_{(1,48)} = 0.170, P = 0.682$
Species x soil moisture	$F_{(3,48)} = 1.456, P = 0.238$	**$F_{(3,48)} = 3.628, P = 0.019$***	$F_{(3,48)} = 2.100, P = 0.113$
Species x nutrients	$F_{(3,48)} = 0.398, P = 0.755$	$F_{(3,48)} = 0.513, P = 0.675$	$F_{(3,48)} = 0.723, P = 0.543$
Species x light	$F_{(3,48)} = 0.400, P = 0.754$	$F_{(3,48)} = 1.197, P = 0.321$	$F_{(3,48)} = 0.412, P = 0.745$
Soil moisture x nutrients	$F_{(1,48)} = 0.361, P = 0.551$	$F_{(1,48)} = 0.490, P = 0.487$	$F_{(1,48)} = 1.018, P = 0.318$
Soil moisture x light	$F_{(1,48)} = 0.022, P = 0.884$	$F_{(1,48)} = 0.000, P = 0.984$	$F_{(1,48)} = 1.455, P = 0.234$
Nutrients x light	$F_{(1,48)} = 0.624, P = 0.434$	$F_{(1,48)} = 0.001, P = 0.980$	$F_{(1,48)} = 0.138, P = 0.712$
Species x soil moisture x nutrients	$F_{(3,48)} = 0.124, P = 0.946$	$F_{(3,48)} = 0.265, P = 0.850$	$F_{(3,48)} = 1.266, P = 0.296$
Species x soil moisture x light	$F_{(3,48)} = 2.431, P = 0.077$	$F_{(3,48)} = 1.253, P = 0.301$	$F_{(3,48)} = 1.543, P = 0.215$
Species x nutrients x light	$F_{(3,48)} = 1.193, P = 0.322$	$F_{(3,48)} = 2.046, P = 0.120$	$F_{(3,48)} = 0.921, P = 0.438$
Soil moisture x nutrients x light	$F_{(1,48)} = 0.111, P = 0.740$	$F_{(1,48)} = 0.772, P = 0.384$	$F_{(1,48)} = 1.359, P = 0.249$
Species x soil moisture x nutrients x light	$F_{(3,48)} = 2.212, P = 0.099$	$F_{(3,48)} = 2.104, P = 0.112$	$F_{(3,48)} = 2.431, P = 0.077$
r^2	0.428	0.490	0.457

* = $0.05 \geq P > 0.01$ = significant; ** = $0.01 \geq P > 0.001$ = highly significant; *** = $P \leq 0.001$ = very highly significant.

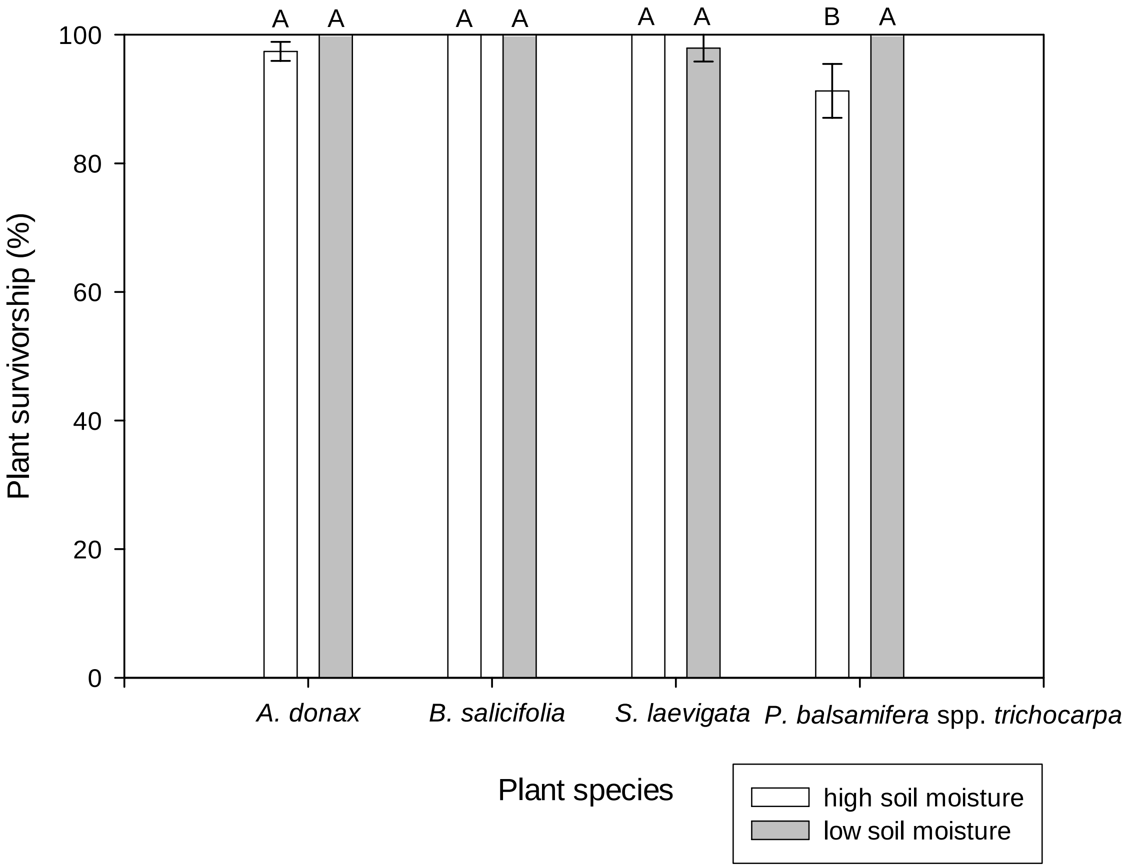


Figure 1. Effects of soil moisture availability on percent plant survivorship of *A. donax* compared to three native riparian plant species at the end of the first growing season (fall 2003) based on the four-way ANOVA (competition x soil moisture x nutrients x light). Letters denote results of post-hoc hypothesis tests (comparison of means) between individual treatments within each graph only, with significance recognized at $\alpha < 0.05$.

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CHAPTER 3 -

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.). I 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. I 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 NO_3-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*.

Key Words: Arundo donax, giant reed, invasive species, alien species, nutrients, nutrient loading, nitrogen, phosphorus, land use, riparian, Mediterranean-type climate, watershed, rivers

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, I 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, diCastri 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. I 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, I 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.

METHODS

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 7). 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 km^2, 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 8). 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 km^2, 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 8). 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 km^2, 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 8).

To fully test my hypothesis that riparian ecosystems in developed watersheds were invaded due to increased nutrient supply from anthropogenic inputs, I 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 my hypothesis. However to establish reference conditions, I 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). I 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, I assumed similar levels of atmospheric N dry deposition among watersheds (Lu et al. unpublished data).

Study Design and Sampling Locations

I 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 6; Figure 8). 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 m^2. 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. I 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 m^2), and (3) the dominant component of the vegetation (> 100 m^2), 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 9) (See Appendix 3-1 for site locations).

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 (NO_3-N/ppm), ammonia-N (NH_4-N/ppm), orthophosphate (PO_4-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 NO_3-N and NH_4-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 PO_4-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 NH_4-N, NO_3-N + NO_2-N, PO_4-P, total Kjeldahl nitrogen (TKN), total N (total N = TKN + NO_3-N + NO_2-N), and pH by Fruit Growers Environmental Laboratories in Santa Paula, California. NH_4-N (4500NH3H), NO_3-N + NO_2-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 PO_4-P (Olsen P Methods 300.0 and 4500) were analyzed per *Methods for Chemical Analysis of Water and Wastes* (USEPA 1983).

Statistical Analyses

In this study, I 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.

I 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). I 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 NO_3-N and PO_4-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 $\log_{10}$ base transformed. Raw data were used for leaf tissue N and K and shallow groundwater PO_4-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.

RESULTS

Naturally Occurring Nutrient Levels

I 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 7). However, NO_3-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 (NO_3-N:PO_4-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 8). 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)].

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 9). 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 10a). 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 10). 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 NO_3-N + NO_2-N concentration in the shallow groundwater (Table 9). 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 ($F_{(2,50)} = 3.866$; $P = 0.027$). NO_3-N + NO_2-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 10b). The one-way ANOVA for NO_3-N + NO_2-N concentrations by watershed was very highly significant (Table 10). Shallow groundwater NO_3-N + NO_2-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 NH_4-N levels found in floodplains (Table 9). Significantly higher mean NH_4-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 10d and e). Large infestations adjacent to open space on Calleguas Creek contained higher shallow groundwater NH_4-N levels than many other combinations of factors. However, the one-way ANOVA by watershed indicated that levels of NH_4-N in shallow groundwater did not differ significantly between reference watersheds and any of the main study watersheds (Table 10).

Reference watersheds contained an average of 0.26 mg/L (SE 0.21–0.33) NH_4-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 PO_4-P in the three-way ANOVA (Table 9). The watershed with the highest proportion of total anthropogenic land cover, Calleguas Creek, contained the highest shallow groundwater PO_4-P concentrations (Figure 8). Orthophosphate concentrations in the shallow groundwater were significantly higher along Calleguas Creek (2.67 ± SE 0.38 mg/L) than Santa Clara River (0.64 ± SE 0.10 mg/L). The one-way ANOVA for shallow groundwater PO_4-P levels by watershed was also very highly significant (Table 10). Shallow groundwater PO_4-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 10). Calleguas Creek and the Santa Clara River had significantly more acidic shallow groundwater than did Topanga Canyon and the reference watersheds.

Soils Nutrients and Grain Size

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 9). 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, NH_4-N and NO_3-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 11).

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 PO_4-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, PO_4-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 9); 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 ± SE

0.003%). NO_3-N levels in the soil varied significantly by all factors (all main effects significant). The mean content of NO_3-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 ± 0.4 ppm) and open space (1.4 ppm, SE 1.1–1.8 ppm) contained significantly higher levels of NO_3-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 NO_3-N soil levels (1.6 ± SE 0.4 ppm and 1.5 ppm, 1.1 –1.8 ppm, respectively) then non-infested areas (0.8 ppm, SE 0.7–1.1 ppm). Levels of NH_4-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 PO_4-P levels found in floodplain soils was significant (Table 9). In most cases, levels of soil PO_4-P were higher in Calleguas Creek than along the Santa Clara River (Figure 12). Levels of PO_4-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 PO_4-P levels than small or non-infested floodplains next to open space along the Santa Clara River.

Soil NO_3-N and PO_4-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 13a and c). Soil nutrient levels did not differ significantly along floodplains, with the exception of lower PO_4-P levels adjacent to residential compared to agricultural land uses (Figure 13d). However, soil associated with the deeper-rooted *S. laevigata* from non-infested riparian terraces contained significantly higher NO_3-N and PO_4-P concentrations than soil associated with either *A. donax* infestation stage (Figure 13a and c). Soil PO_4-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 13d). Terrace sites adjacent to anthropogenic land uses had significantly higher soil PO_4-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 PO_4-P adjacent to agricultural versus open space land use (Figure 13e).

One-way ANOVAs for mean soil NO_3-N and PO_4-P content by watershed were very highly significant (Table 10). Mean NO_3-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 PO_4-P content than soils along the Santa Clara River or Topanga Canyon.

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 11). Percent silt + clay content was significantly higher on terraces verses floodplains in non-infested sites and small infestations of *A. donax* (Figure 13b). 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 11). 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.

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 11 and Figure 14). 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, NO_3-N + NO_2-N, and NH_4-N) in the shallow groundwater (Figure 14). 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 NO_3-N + NO_2-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 PO_4-P levels were highly significant in floodplains, but were not found between *A. donax* leaves and shallow groundwater PO_4-P levels. A strong positive relationship was found between *A. donax* leaf N content and soil NO_3-N on riparian terraces (Figure 11). Also, *A. donax* leaf N content indicated a positive relationship with both soil total N and NH_4-N on terraces and NO_3-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 PO_4-P concentrations in terrace or floodplain locations.

Leaf tissue Nutrients

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 9). 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 15a). 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 11). Mean leaf tissue N content was higher in sites adjacent to agricultural (2.54 ± SE 0.08%) and residential (2.64 ± SE 0.08%) land uses compared to open space (2.21 ± SE 0.09%). Large *A. donax* infestations (2.59 ± SE 0.07%) contained significantly higher mean leaf tissue N than small infestations (2.36 ± 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 ± SE 0.06%, n = 62) than in small infestations (2.38 ± 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 10). 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.

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 9). 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 11).

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 10). *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.

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 9). 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 15b). 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 11). 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 ± SE 0.07%, n = 62) than in small infestations (2.55 ± 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 10). 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.

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 8). 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 8). 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 8). 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.

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. I 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, my 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).

Natural Nutrient Levels

Naturally occuring 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, diCastri 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 my 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 my reference watersheds were within the range of levels (slightly nutrient-rich) found in adjacent shrubland ecosystems of California (Day 1983, diCastri 1991) (Table 2). The young sedimentary geology of my 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).

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 my 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 ≤ 14:1 (molar ratio 31:1) indicate N limiting conditions and ratios ≥ 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.

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 NH_4-N, NO_3-N, and NO_2-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.

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, my 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, NO_3-N + NO_2-N, NH_4-N, and PO_4-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 PO_4-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 NO_3-N + NO_2-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).

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 NH_4-N in floodplain locations. Although NO_3-N and PO_4-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 PO_4-P levels were higher adjacent to both agriculture and residential land use than next to open space.

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. NO_3-N and PO_4-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 PO_4-P on terraces compared to floodplains.

Degree of Infestation

Riparian ecosystems infested by *A. donax* contained higher NO_3-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 NO_3-N and PO_4-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 9). 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.

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 NO_3-N and PO_4-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 9). 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 NO_3-N and PO_4-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 9). 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.

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 NO_3-N in the soil, whereas *S. laevigata* showed a significant positive response to only NO_3-N + NO_2-N and PO_4-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.

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, NO_3-N, and NH_4-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*. My 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.

TABLES

Table 6. 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 *A. donax* infestation	3	3	3
Number of replicates	5–6	5	5
TOTAL	93	45	30

Table 7. Natural and anthropogenic soil and shallow groundwater nutrient levels (means ± SE).

	Shrubland Ecosystems[3]			**Streams draining undeveloped basins in U.S. (median)**[4]	**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 ± 0.002	0.095 (0.088–0.103)
NO_3-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)	-	-	-	-
PO_4-P (ppm)	-	-	-	-	7.2 (6.1–8.6)	5.9 ± 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)	-
NO_3-N (mg/L)	-	-	-	0.087	0.13 (0.11–0.16)[3]	0.40 (0.34–0.46)	-
NH_4-N (mg/L)	-	-	-	0.02	0.26 (0.21–0.33)	0.37 (0.33–0.40)	-
PO_4-P (mg/L)	-	-	-	0.01	0.53 (± 0.03)	1.39 (± 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

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[3] Shrubland ecosystem soil nutrient data for 5 Mediterranean-type climate regions (Day 1983).
[4] Clark et al. 2000
[3] Values are NO_3-N + NO_2-N for reference and study watersheds.

Table 8. 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 ± SE) and results of one-way ANOVAs by watershed.

	Reference Watersheds	**Topanga Canyon**	**Santa Clara River**	**Calleguas Creek**	**All Study Watersheds**	**Significance values**[5]
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 (*S. laevigata*)	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 (*A. donax*)	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 (*S. laevigata*)	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 (*A. donax*)	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 ≥ P > 0.01 = significant

** = 0.01 ≥ P > 0.001 = highly significant

*** = P ≤ 0.001 = very highly significant

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[5] No terrace data used in this analysis

Table 9. Three-way ANOVA significance table for shallow groundwater, soil, and leaf tissue nutrients by watershed (Santa Clara River[6], Calleguas Creek), land use (agricultural, residential, open space) and degree of infestation (none, small, large).

	Factors						
Nutrient analyte	**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)[7]	**$F_{(1,74)} = 5.474$; $P = 0.022$***	**$F_{(2,74)} = 3.630$; $P = 0.031$***	$F_{(2,74)} = 1.639$; $P = 0.201$	**$F_{(2,74)} = 3.848$; $P = 0.026$***	$F_{(2,74)} = 0.323$; $P = 0.725$	$F_{(4,74)} = 1.030$; $P = 0.398$	$F_{(4,74)} = 0.981$; $P = 0.423$
NO_3-N + NO_2-N (mg/L)	**$F_{(1,74)} = 18.788$; $P < 0.001$*****	$F_{(2,74)} = 1.559$; $P = 0.217$	$F_{(2,74)} = 0.168$; $P = 0.846$	$F_{(2,74)} = 2.969$; $P = 0.057$	$F_{(2,74)} = 1.520$; $P = 0.225$	$F_{(4,74)} = 0.897$; $P = 0.470$	$F_{(4,74)} = 1.725$; $P = 0.154$
NH_4-N (mg/L)	**$F_{(1,74)} = 5.553$; $P = 0.021$***	**$F_{(2,74)} = 5.466$; $P = 0.006$****	**$F_{(2,74)} = 3.552$; $P = 0.034$***	**$F_{(2,74)} = 10.340$; $P < 0.001$*****	**$F_{(2,74)} = 3.510$; $P = 0.035$***	$F_{(4,74)} = 1.044$; $P = 0.390$	**$F_{(4,74)} = 3.266$; $P = 0.016$***
PO_4 (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	$F_{(1,74)} = 3.768$; $P = 0.056$	$F_{(2,74)} = 2.638$; $P = 0.078$	$F_{(2,74)} = 0.036$; $P = 0.964$	$F_{(2,74)} = 1.283$; $P = 0.283$	$F_{(2,74)} = 1.317$; $P = 0.274$	$F_{(4,74)} = 0.176$; $P = 0.950$	$F_{(2,74)} = 0.948$; $P = 0.441$
Soil[8]							
Total N (%)	**$F_{(1,73)} = 3.987$; $P = 0.050$***	$F_{(2,73)} = 0.859$; $P = 0.428$	$F_{(2,73)} = 0.002$; $P = 0.998$	$F_{(2,73)} = 0.241$; $P = 0.787$	$F_{(2,73)} = 0.931$; $P = 0.399$	$F_{(4,73)} = 1.313$; $P = 0.273$	$F_{(4,74)} = 2.071$; $P = 0.093$
NO_3-N (ppm)	**$F_{(1,73)} = 28.540$; $P < 0.001$*****	**$F_{(2,73)} = 3.578$; $P = 0.033$***	**$F_{(2,73)} = 3.566$; $P = 0.033$***	$F_{(2,73)} = 0.544$; $P = 0.583$	$F_{(2,73)} = 1.983$; $P = 0.145$	$F_{(4,73)} = 1.771$; $P = 0.144$	$F_{(4,73)} = 0.390$; $P = 0.815$
NH_4-N (ppm)	**$F_{(1,73)} = 22.267$; $P < 0.001$*****	$F_{(2,73)} = 2.286$; $P = 0.109$	$F_{(2,73)} = 0.347$; $P = 0.708$	$F_{(2,73)} = 2.340$; $P = 0.103$	$F_{(2,73)} = 1.750$; $P = 0.181$	$F_{(4,73)} = 0.871$; $P = 0.485$	$F_{(4,73)} = 1.340$; $P = 0.263$
PO_4 (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: * = $0.05 \geq P > 0.01$ = significant, ** = $0.01 \geq P > 0.001$ = highly significant, *** = $P \leq 0.001$ = very highly significant

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[6] No terrace data used in this analysis.

[7] All data log base 10 transformed except raw data were used for groundwater PO_4 and pH; and plant total N and K.

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

Table 9 (continued). Three-way ANOVA significance table for shallow groundwater, soil, and leaf tissue nutrients by watershed (Santa Clara River[9], Calleguas Creek), land use (agricultural, residential, open space), degree of infestation (none, small, large).

	Factors						
Nutrient analyte	**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**
***Arundo donax* 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: * = $0.05 \geq P > 0.01$ = significant, ** = $0.01 \geq P > 0.001$ = highly significant, *** = $P \leq 0.001$ = very highly significant

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[9] No terrace data used in this analysis.

Table 10. 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.

	Mean (± SE)				
Nutrient analyte	**Reference sites**	**Topanga Canyon**	**Santa Clara River**	**Calleguas Creek**	**Significance values**[10]
Shallow Groundwater Nutrients					
Total N (mg/L)[11]	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*****
NO_3-N + NO_2-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*****
NH_4-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
PO_4 (mg/L)[12]	0.53 ± 0.03	0.66 ± 0.09	0.64 ± 0.10	2.67 ± 0.38	**$F_{(3,128)}$ = 16.664; P < 0.001*****
pH	7.75 ± 0.09	7.80 ± 0.06	7.39 ± 0.05	7.25 ± 0.05	**$F_{(3,128)}$ = 20.847; P < 0.001*****
Soil Nutrients and Grain Size[13]					
NO_3-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*****
PO_4-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 (%) (*Salix laevigata)*	1.78 ± 0.15	1.87 ± 0.13	2.40 ± 0.12	2.27 ± 0.10	**$F_{(3,47)}$ = 6.113; P = 0.001*****
Total N (%) (*Arundo donax*)	No Data	2.19 ± 0.10	2.50 ± 0.08	2.88 ± 0.10	**$F_{(2,78)}$ = 11.982; P < 0.001*****
Total P (%) (*Salix laevigata)*	0.14 ± 0.01	0.13 (0.125-0.134)	0.16 (0.147-0.164)	0.19 ± 0.01	**$F_{(3,47)}$ = 8.595; P < 0.001*****
Total P (%) (*Arundo donax*)	No Data	0.17 ± 0.008	0.17 ± 0.006	0.19 (0.184-0.193)	**$F_{(2,78)}$ = 4.364; P = 0.016***
Total K (%) (*Salix laevigata)*	1.25 ± 0.17	1.33 ± 0.06	1.44 ± 0.07	1.41 ± 0.07	$F_{(3,47)}$ = 0.860; P = 0.469
Total K (%) (*Arundo donax*)	No Data	2.49 ± 0.10	2.73 ± 0.07	2.49 ± 0.09	**$F_{(2,78)}$ = 3.172; P = 0.047***

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

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[10] No terrace data used in this analysis.

[11] All data log base 10 transformed except those noted otherwise.

[12] Raw data were used for groundwater PO_4 and pH; and plant total N and K.

[13] Percent silt + clay (square root transformed) was used as a covariate

Table 11. 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.

	Factors						
Nutrient analyte	**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**
Soil[14]							
NO_3-N (ppm)[15]	**$F_{(2,84)} = 5.101$; $P = 0.008$***	**$F_{(1,84)} = 51.453$; $P < 0.001$*******	$F_{(2,84)} = 2.662$; $P = 0.076$	$F_{(2,84)} = 3.643$; $P = 0.030$	$F_{(4,84)} = 1.661$; $P = 0.167$	**$F_{(2,84)} = 4.626$; $P = 0.012$***	$F_{(4,84)} = 1.636$; $P = 0.173$
PO_4-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 (%)[16]	**$F_{(2,60)} = 6.029$; $P = 0.004$******	$F_{(1,60)} = 0.862$; $P = 0.357$	**$F_{(1,60)} = 5.876$; $P = 0.018$***	$F_{(2,60)} = 2.572$; $P = 0.085$	$F_{(2,60)} = 0.109$; $P = 0.897$	$F_{(1,60)} = 0.964$; $P = 0.330$	$F_{(2,60)} = 0.239$; $P = 0.788$
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: * = $0.05 \geq P > 0.01$ = significant, ** = $0.01 \geq P > 0.001$ = highly significant*** = $P \leq 0.001$ = very highly significant

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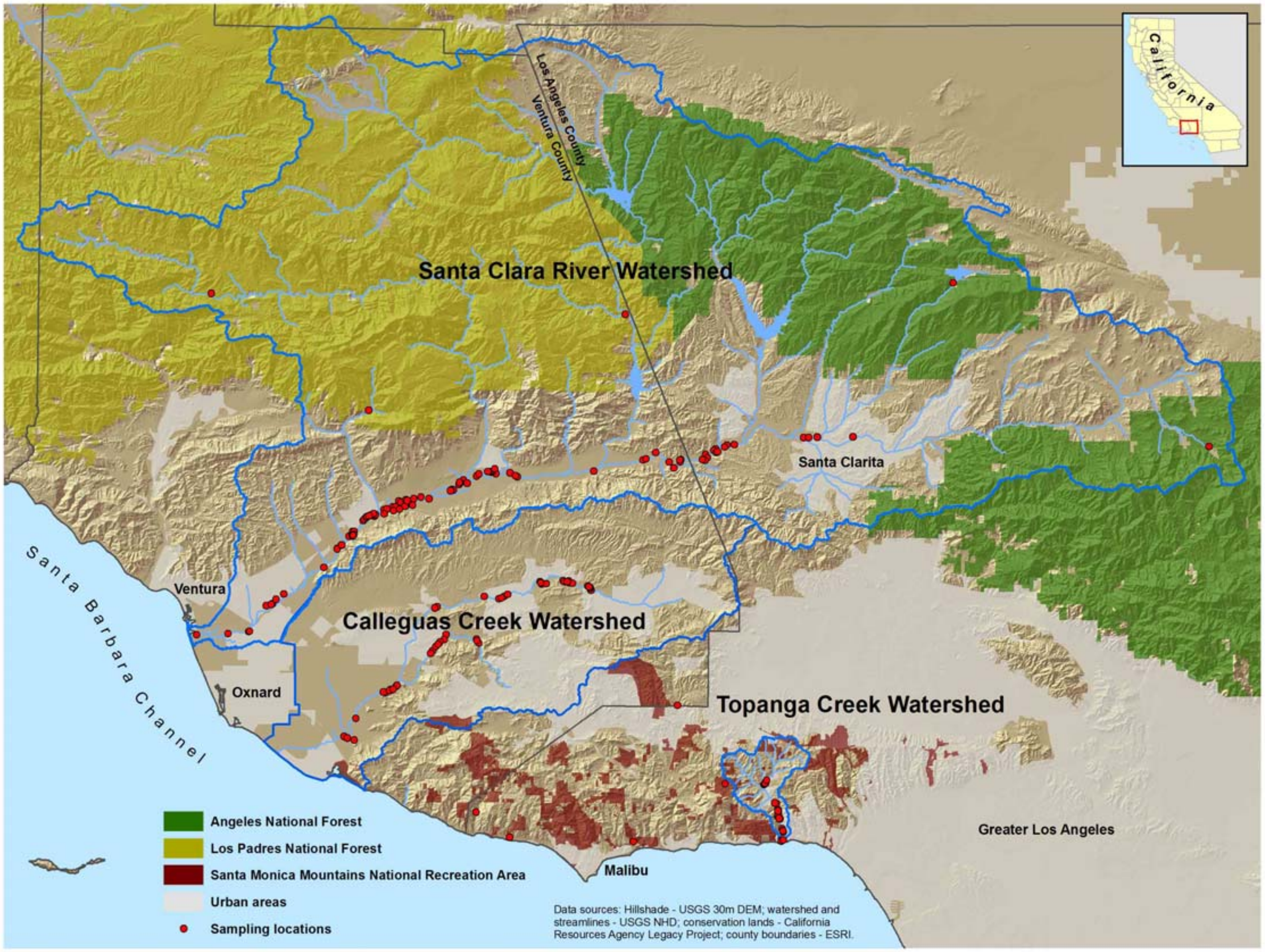
[14] Percent silt + clay (square root transformed) used as a covariate for all soil nutrients.

[15] Soil nutrient data and pH were $\log_{10}$ base transformed.

[16] Raw data was used for leaf tissue total N and K. Leaf tissue total P was $\log_{10}$ base transformed.

FIGURES



Data sources: Hillshade - USGS 30m DEM; watershed and streamlines - USGS NHD; conservation lands - California Resources Agency Legacy Project; county boundaries - ESRI.

Figure 7. The three study watersheds in Ventura and Los Angeles Counties, California.

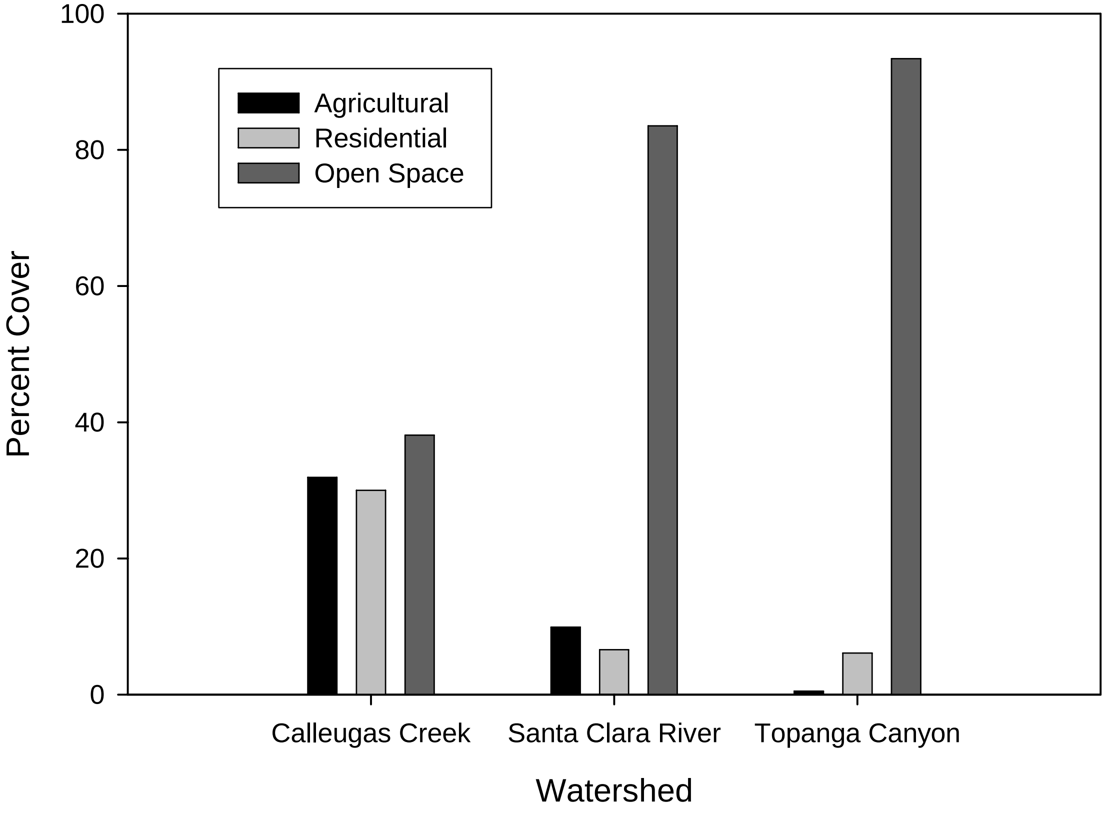


Figure 8. Distribution of land use type within the three studied watersheds.

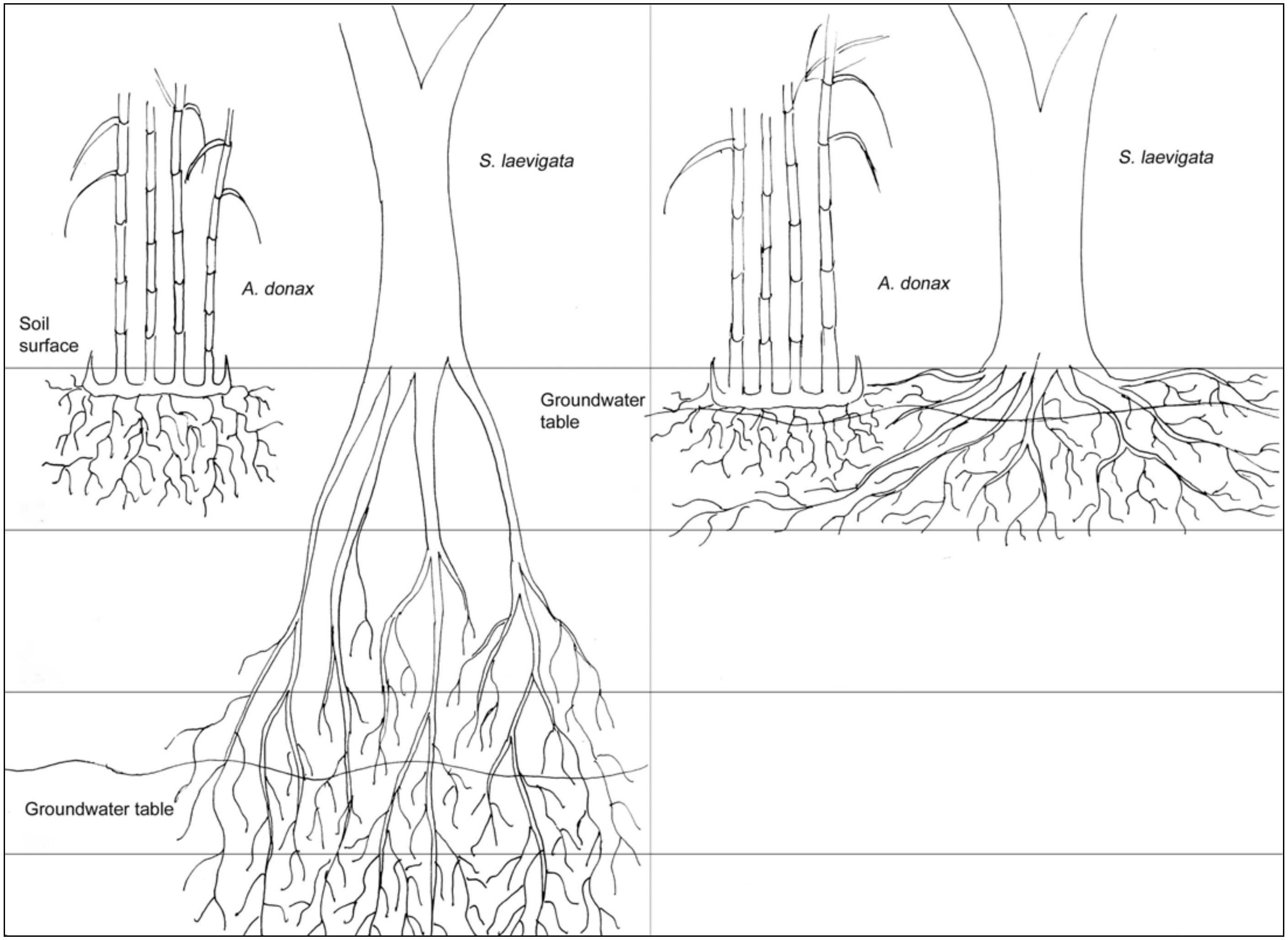


Figure 9. Diagram of *A. donax* and *S. laevigata* rooting depths and distribution in a) deep and b) shallow groundwater table conditions.

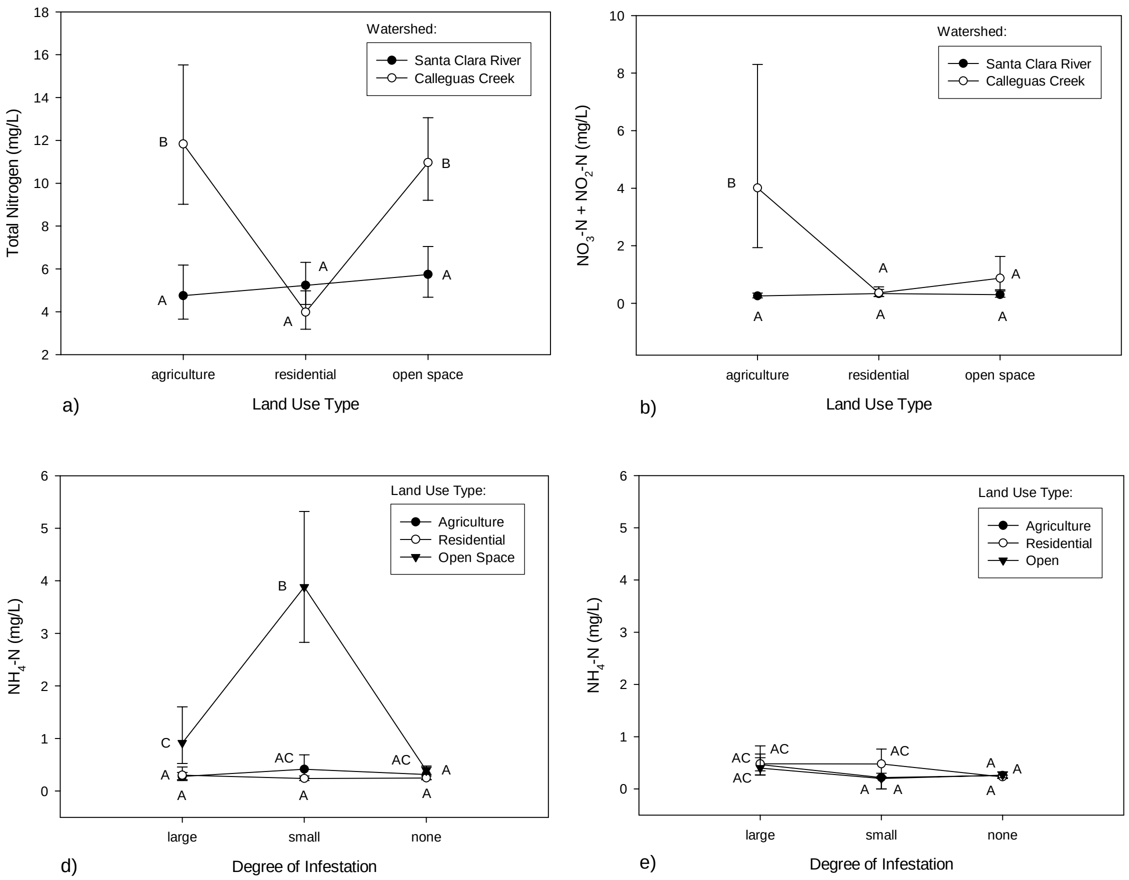


Figure 10. Interaction plots for 3-way ANOVA of shallow groundwater nutrients by watershed (Santa Clara River and Calleguas Creek only) x land use (A = agricultural, R = residential, and O = open space) x degree of infestation (N = none, S = small, and L = large). Plots include two-way interaction plots for shallow groundwater a) total N, and b) NO_3-N + NO_2-N (small infestation data removed), and three-way interaction plots for shallow groundwater NH_4-N in c) Calleguas Creek and d) Santa Clara River.

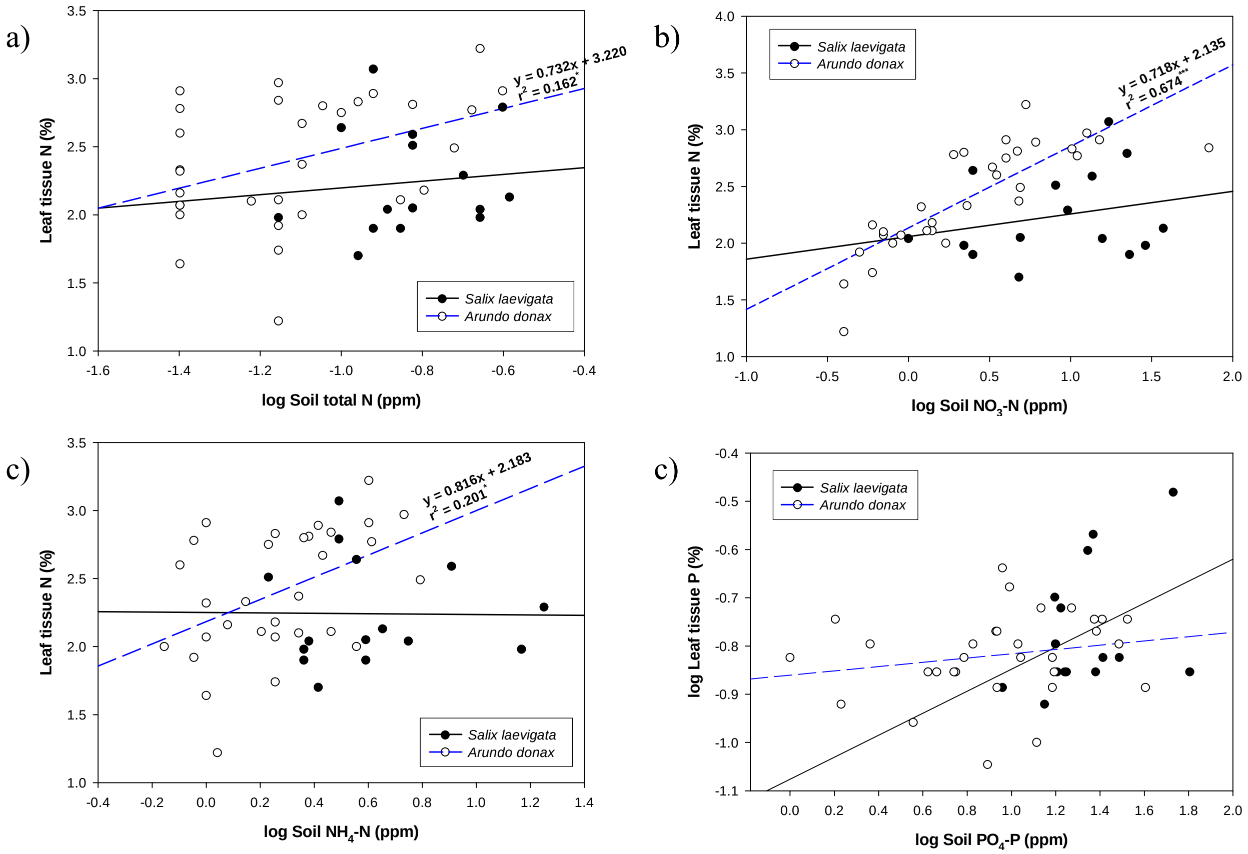


Figure 11. Linear regression relationships between shallow groundwater and soil nutrients (independent variable) found in terrace sites and associated leaf tissue nutrients (response variable) of target plants by plant species. Only Santa Clara River data was used. Equations were only included for significant relationships. Leaf tissue N/P and soil (a) total N, (b) NO$_3$-N, (c) NH$_4$-N, and (d) PO$_4$-P.

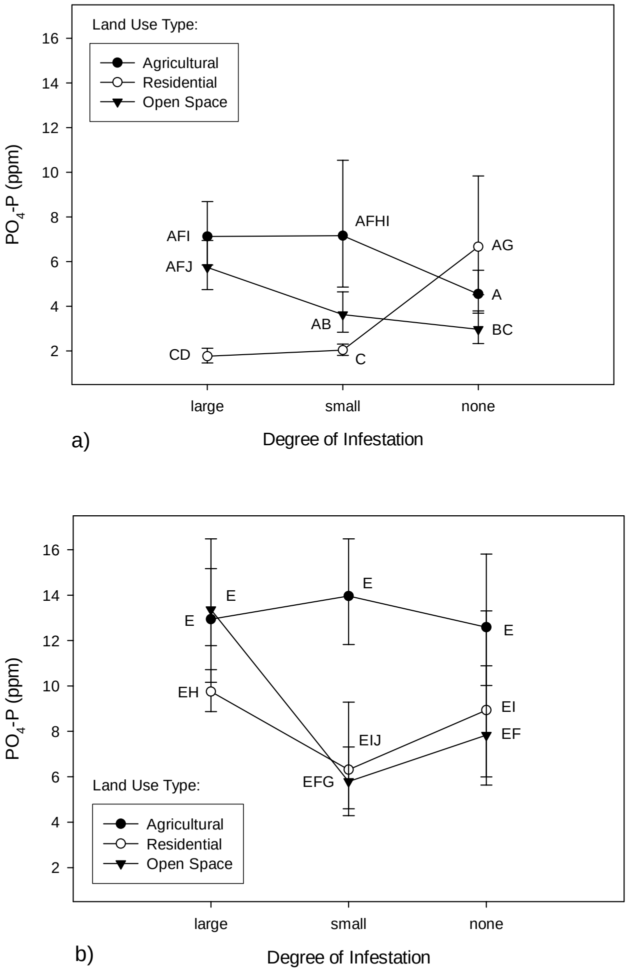


Figure 12. Interaction plots for 3-way ANOVA of soil nutrients by watershed (Santa Clara River and Calleguas Creek only) x land use (A = agricultural, R = residential and O = open space) x degree of infestation (N = none, S = small, and L = large). Plots show the three-way interaction for soil PO_4-P in a) Santa Clara River and b) Calleguas Creek.

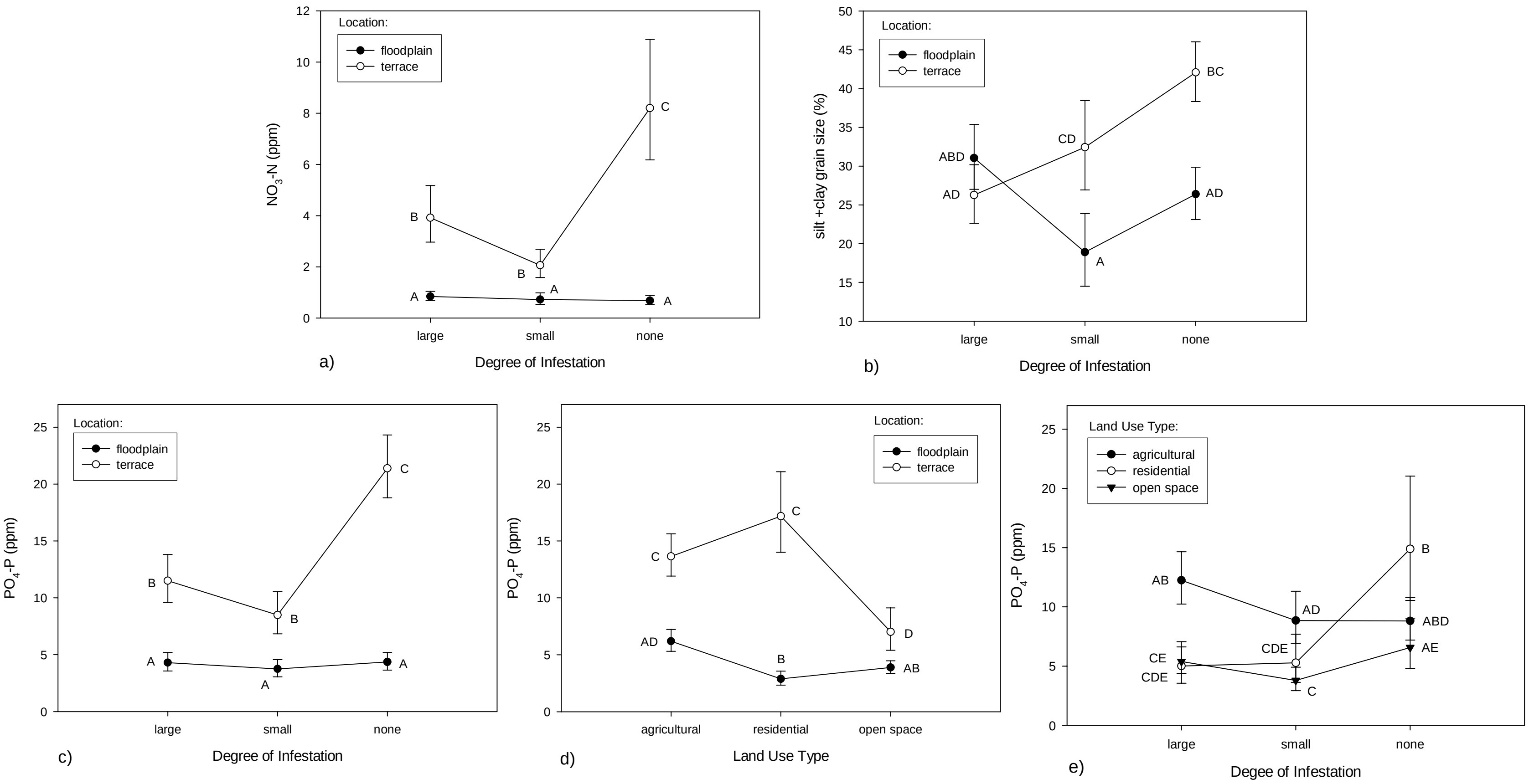


Figure 13. Interaction plots for 3-way ANOVA of soil nutrients and grain size for land use (A = agricultural, R = residential, and O = open space) x degree of infestation (N = none, S = small, and L = large) x fluvial geomorphic location (terrace and floodplain) for Santa Clara River only. Plots include 2-way interactions of a) soil NO_3-N and b) silt + clay and 3-way interaction of soil PO_4-P (c, d, and e).

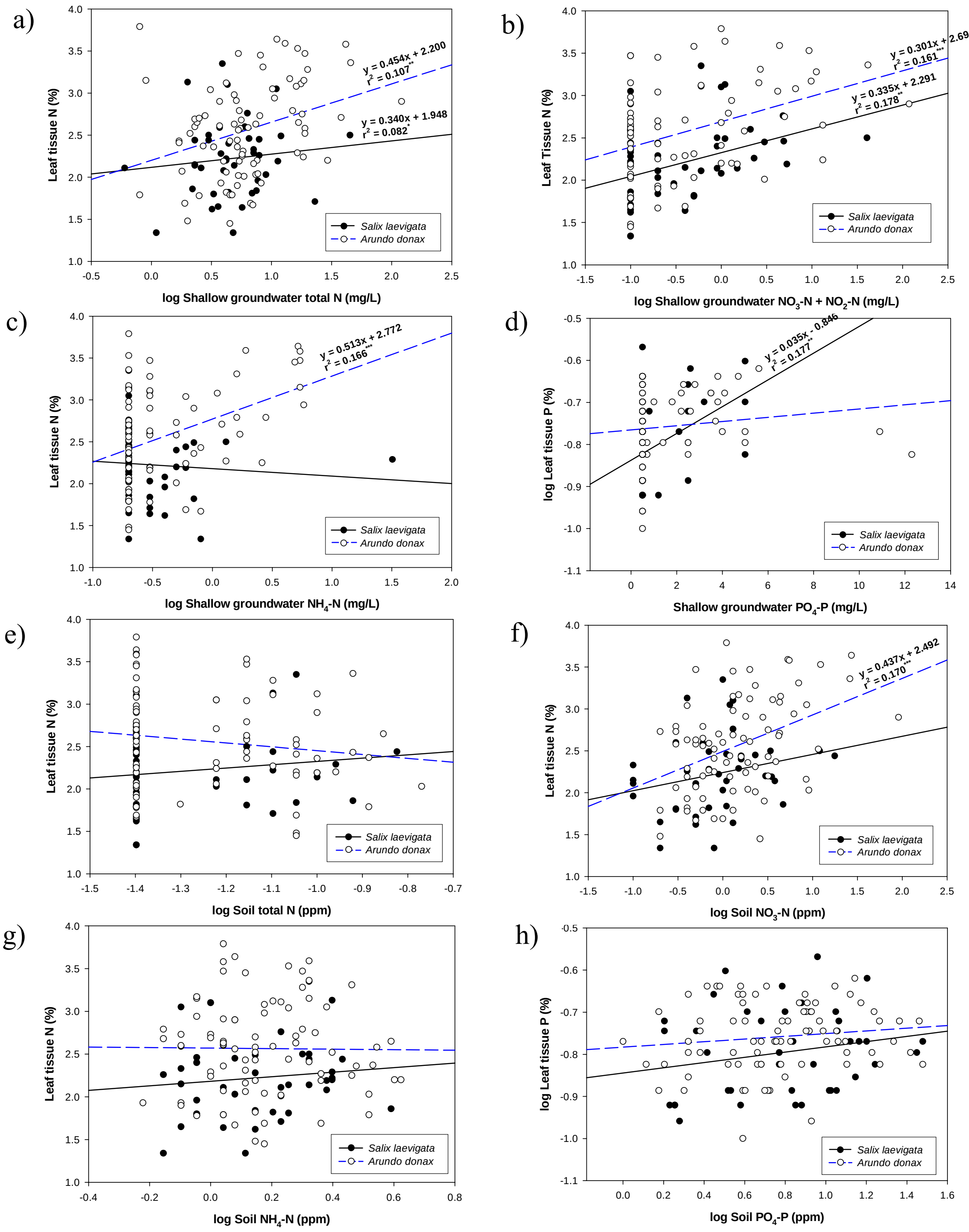


Figure 14. Linear regression relationships between shallow groundwater and soil nutrients (independent variable) found in floodplain sites and associated leaf tissue nutrients (response variable) of target plants by plant species. Equations were only included for significant relationships. Leaf tissue N/P and soil (a) total N, (b) NO_3-N, (c) NH_4-N, and (d) PO_4-P. Leaf tissue N/P and shallow groundwater (e) total N, (f) NO_3-N + NO_2-N, (g) NH_4-N, and (h) PO_4-P.

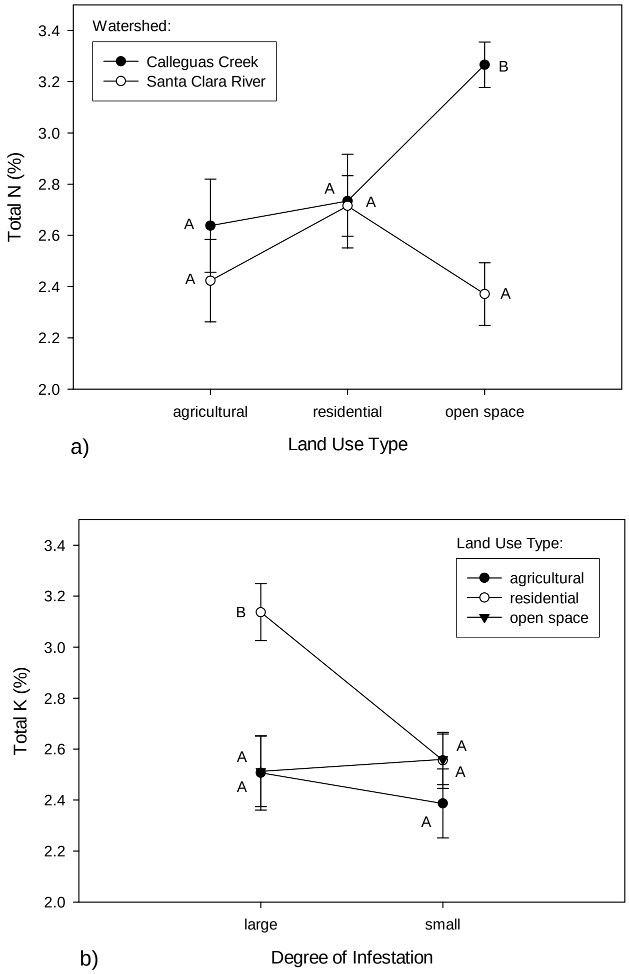


Figure 15. Interaction plots for 3-way ANOVA of *A. donax* leaf tissue nutrients by watershed (Santa Clara River and Calleguas Creek only) x land use (A = agricultural, R = residential, O = open space) x degree of infestation (S = small, L = large). Plots illustrate the two-way interaction for a) leaf tissue N and b) leaf tissue K.

APPENDIX

APPENDIX 3-1

TABLE 1. SAMPLING LOCATIONS

Site ID[17]	Latitude (degrees)	Longitude (degrees)
Calleguas Creek		
CAFL1	34.18181797	-119.03227547
CAFL2	34.18522848	-119.02564312
CAFL3	34.26126039	-118.97952396
CAFL4	34.26026671	-118.98207734
CAFL5	34.27144197	-118.92569614
CAFN1	34.13669625	-119.08521188
CAFN2	34.15400296	-119.07143463
CAFN3	34.17924422	-119.03796569
CAFN4	34.23487474	-118.96908212
CAFN5	34.18599115	-119.02471977
CAFS1	34.13507461	-119.08160741
CAFS2	34.13344902	-119.07335250
CAFS3	34.17960581	-119.04052360
CAFS4	34.21919798	-118.98473675
CAFS5	34.22309129	-118.98073481
COFL1	34.18100023	-119.03332044
COFL2	34.28386898	-118.85975520
COFL3	34.28732609	-118.83532254
COFL4	34.28502903	-118.82843195
COFL5	34.23055504	-118.93391920
COFN1	34.18210127	-119.02929805
COFN2	34.28435823	-118.85500057
COFN3	34.28635279	-118.83322028
COFN4	34.28214583	-118.80707444
COFN5	34.22688327	-118.93127832
COFS1	34.28637156	-118.83378790
COFS2	34.28705938	-118.82914742
COFS3	34.28464581	-118.82491607
COFS4	34.28645848	-118.83080796
COFS5	34.22922341	-118.93361712

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[17] First character stands for watershed (S = Santa Clara River; C = Calleguas Creek; T = Topanga Cayon); Second character stands for land use (A = agricultural; O = open space; R = residential); Third character stands for fluvial geomorphic location (F = floodplain; T = terrace); Fourth character stands for degree of infestation (L = large infestation; S = small infestation; N = no infestation); and number stands for replicate.

TABLE 1 (continued). SAMPLING LOCATIONS

Site ID[18]	Latitude (degrees)	Longitude (degrees)
CRFL1	34.26952092	-118.90881867
CRFL2	34.27168974	-118.90275277
CRFL3	34.27363845	-118.89887664
CRFL4	34.28602137	-118.86197255
CRFL5	34.27015417	-118.90565316
CRFN1	34.27816652	-118.80317417
CRFN2	34.28010098	-118.80417497
CRFN3	34.28114930	-118.80471577
CRFN4	34.23009370	-118.97145169
CRFN5	34.28538610	-118.86089791
CRFS1	34.21678056	-118.98688914
CRFS2	34.22753965	-118.97609828
CRFS3	34.28504504	-118.86083965
CRFS4	34.28149489	-118.80560375
CRFS5	34.22546622	-118.97838193
Santa Clara River		
SAFL1	34.31599656	-119.09517872
SAFL2	34.38832736	-118.93290969
SAFL3	34.37853578	-118.95602329
SAFL4	34.35348068	-119.04170327
SAFL5	34.38983082	-118.89746865
SAFL6	34.40303776	-118.74487334
SAFN1	34.38109352	-118.95231379
SAFN2	34.38252431	-118.95086406
SAFN3	34.38010991	-118.95468604
SAFN4	34.38622895	-118.88881040
SAFN5	34.41809141	-118.64794627
SAFS1	34.38650915	-118.93600730
SAFS2	34.38889540	-118.91346602
SAFS3	34.37347672	-118.96392172
SAFS4	34.38713193	-118.89121969
SAFS5	34.40141788	-118.71480217
SATL1	34.37955360	-118.94674502

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[18] First character stands for watershed (S = Santa Clara River; C = Calleguas Creek; T = Topanga Cayon); Second character stands for land use (A = agricultural; O = open space; R = residential); Third character stands for fluvial geomorphic location (F = floodplain; T = terrace); Fourth character stands for degree of infestation (L = large infestation; S = small infestation; N = no infestation); and number stands for replicate.

TABLE 1 (continued). SAMPLING LOCATIONS

Site ID[19]	Latitude (degrees)	Longitude (degrees)
SATL2	34.37299149	-118.96207594
SATL3	34.36193652	-119.02509629
SATL4	34.33253070	-119.07771637
SATL5	34.40404988	-118.74102739
SATLD1	34.23179138	-119.25541925
SATLD2	34.34685814	-119.05269706
SATLD3	34.36438361	-118.99051289
SATLD4	34.23333733	-119.21936131
SATLD5	34.32794371	-119.08172417
SATN1	34.41422937	-118.66145672
SATN2	34.40875657	-118.67276156
SATN3	34.36076590	-119.02292772
SATN4	34.41591941	-118.65056385
SATN5	34.40360916	-118.70071513
SATS1	34.37267943	-118.96522050
SATS2	34.38859608	-118.93302837
SATS3	34.38028551	-118.95542398
SATS4	34.40124856	-118.70185146
SATS5	34.39195890	-118.80118028
SATSD1	34.41272029	-118.66298717
SATSD2	34.37248522	-118.96579332
SATSD3	34.41051199	-118.66039256
SATSD4	34.41148815	-118.65905279
SATSD5	34.40319082	-118.70229227
SOFL1	34.35990047	-119.01475981
SOFL2	34.35719647	-119.01773538
SOFL3	34.36599487	-118.99932973
SOFL4	34.36452552	-119.00776427
SOFL5	34.39567518	-118.70910885
SOFN1	34.32881568	-119.07774386
SOFN2	34.31887373	-119.09080865
SOFN3	34.33239022	-119.07561427
SOFN4	34.35490100	-119.02514490

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[19] First character stands for watershed (S = Santa Clara River; C = Calleguas Creek; T = Topanga Cayon); Second character stands for land use (A = agricultural; O = open space; R = residential); Third character stands for fluvial geomorphic location (F = floodplain; T = terrace); Fourth character stands for degree of infestation (L = large infestation; S = small infestation; N = no infestation); and number stands for replicate.

TABLE 1 (continued). SAMPLING LOCATIONS

Site ID[20]	Latitude (degrees)	Longitude (degrees)
SOFN5	34.35635107	-119.03155874
SOFN6	34.40588200	-118.67016896
SOFS1	34.31559457	-119.09520957
SOFS2	34.31924572	-119.09028830
SOFS3	34.35645919	-119.02864812
SOFS4	34.35424478	-119.03863080
SOFS5	34.35664217	-119.01821039
SOTL1	34.32809450	-119.07738880
SOTL2	34.32945983	-119.07627577
SOTL3	34.34939501	-119.04156798
SOTL4	34.35409910	-119.02377773
SOTL5	34.41041409	-118.73012722
SOTN1	34.36328583	-119.01684833
SOTN2	34.35810691	-119.00888879
SOTN3	34.41841671	-118.63987014
SOTN4	34.40295386	-118.67300430
SOTN5	34.42674807	-118.50331075
SOTS1	34.32863555	-119.07692595
SOTS2	34.35231283	-119.03071065
SOTS3	34.36246751	-119.01539817
SOTS4	34.40365333	-118.67624148
SOTS5	34.29775595	-119.11061701
SRFL1	34.34551662	-119.06320377
SRFL2	34.34638943	-119.06159009
SRFL3	34.34678681	-119.06052181
SRFL4	34.34727757	-119.05925003
SRFL5	34.34763791	-119.05837077
SRFN1	34.39021530	-118.91872273
SRFN2	34.39055946	-118.92006811
SRFN3	34.39047094	-118.92058108
SRFN4	34.34850996	-119.05502697
SRFN5	34.34279946	-119.06580761
SRFS1	34.34842966	-119.05599014

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[20] First character stands for watershed (S = Santa Clara River; C = Calleguas Creek; T = Topanga Cayon); Second character stands for land use (A = agricultural; O = open space; R = residential); Third character stands for fluvial geomorphic location (F = floodplain; T = terrace); Fourth character stands for degree of infestation (L = large infestation; S = small infestation; N = no infestation); and number stands for replicate.

TABLE 1 (continued). SAMPLING LOCATIONS

Site ID[21]	Latitude (degrees)	Longitude (degrees)
SRFS2	34.34434206	-119.06444111
SRFS3	34.34619077	-119.06199317
SRFS4	34.34843880	-119.05402014
SRFS5	34.34869981	-119.05140314
SRTL1	34.34955376	-119.05358260
SRTL2	34.26270140	-119.16888054
SRTL3	34.27168856	-119.15589622
SRTL4	34.34653955	-119.06151641
SRTL5	34.23558016	-119.19549652
SRTL6	34.42552071	-118.56015748
SRTN1	34.39073430	-118.92195504
SRTN2	34.39069558	-118.92312767
SRTN3	34.26057022	-119.17577449
SRTN4	34.26676621	-119.16454090
SRTN5	34.42593033	-118.54444083
SRTS1	34.26179976	-119.17029432
SRTS2	34.34747539	-119.05919303
SRTS3	34.23591485	-119.19486805
SRTS4	34.42548039	-118.55383988
SRTS5	34.39371038	-118.91472976
Topanga Canyon		
TOFL1	34.06384511	-118.58723690
TOFL2	34.06142517	-118.58494202
TOFL3	34.05183099	-118.58190827
TOFL4	34.06960465	-118.58714193
TOFL5	34.06604201	-118.58649661
TOFN1	34.04854679	-118.58064923
TOFN2	34.06349609	-118.58599612
TOFN3	34.05022988	-118.58104510
TOFN4	34.06934339	-118.58688243
TOFN5	34.07574029	-118.58923590
TOFS1	34.04960300	-118.58127845
TOFS2	34.06511346	-118.58651371

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[21] First character stands for watershed (S = Santa Clara River; C = Calleguas Creek; T = Topanga Cayon); Second character stands for land use (A = agricultural; O = open space; R = residential); Third character stands for fluvial geomorphic location (F = floodplain; T = terrace); Fourth character stands for degree of infestation (L = large infestation; S = small infestation; N = no infestation); and number stands for replicate.

TABLE 1 (continued). SAMPLING LOCATIONS

Site ID[22]	Latitude (degrees)	Longitude (degrees)
TOFS3	34.06168367	-118.58562925
TOFS4	34.06894994	-118.58698418
TOFS5	34.07637094	-118.59061053
TRFL1	34.04108514	-118.58094972
TRFL2	34.04112973	-118.58058594
TRFL3	34.04087928	-118.58260598
TRFL4	34.04068482	-118.58244010
TRFL5	34.03998594	-118.58274286
TRFN1	34.09726543	-118.60056496
TRFN2	34.09518739	-118.60157046
TRFN3	34.09382936	-118.60303125
TRFN4	34.09431375	-118.60276169
TRFN5	34.09441508	-118.60242583
TRFS1	34.09592609	-118.60095137
TRFS2	34.09501355	-118.60170339
TRFS3	34.09789693	-118.60000195
TRFS4	34.04005618	-118.58304461
TRFS5	34.04103183	-118.58065979
Reference Sites		
Agua Blanca	34.54197845	-118.76600772
Aliso Canyon	34.41807398	-118.09363894
Arroyo Sequit	34.06579390	-118.93263468
Bouquet Canyon	34.57381133	-118.38870624
Cold Creek	34.09425859	-118.64799891
Lachusa Creek	34.04172728	-118.89414808
Las Virgenes Creek	34.16885342	-118.70297916
Solstice Canyon	34.03844903	-118.75221346
Sespe Creek	34.55823516	-119.24346691
Santa Paula Creek	34.44816727	-119.06068350

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[22] First character stands for watershed (S = Santa Clara River; C = Calleguas Creek; T = Topanga Cayon); Second character stands for land use (A = agricultural; O = open space; R = residential); Third character stands for fluvial geomorphic location (F = floodplain; T = terrace); Fourth character stands for degree of infestation (L = large infestation; S = small infestation; N = no infestation); and number stands for replicate.

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CHAPTER 4 -

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. I 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 NH_4-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.

Key Words: *Arundo donax,* wildfire, giant reed, invasive species, alien species, competition, nitrogen, riparian, Mediterranean-type climate, rivers, soil nutrients

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 a 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, I compared growth and recolonization of *A. donax* to that of native plant species in riparian ecosystems burned in a southern California wildfire. I 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.

METHODS

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 16). The 187 km-long Santa Clara River and its tributaries drain a 4,185 km^2 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.).

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. I 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). I 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. I monitored recolonization of all sites from November 2003-October 2004 (Figure 16) (see Appendix 4-1 for study site locations and descriptions). The 14 study sites were approximately 600 m^2 (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.

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*, I 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.

Sampling methods

I 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. I 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 m^2 quadrants place 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 $1m^2$ quadrants (placed randomly each time) within all 14 study sites. I 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, I 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. I calculated mean shoot elongation rate (cm d^{-1}) for each species using data from the permanently marked individuals.

I 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). I 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 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.

I 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).

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

Mean productivity (kg m^{-2} year^{-1}) for each species was calculated at approximately 1 year post-fire. I 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). I 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 (NO_3-N - ppm), ammonia-N (NH_4-N - ppm), and orthophosphate (PO_4-P - ppm). Total N in the soil was determined by the combustion gas analyzer method (Method 972.43) (Hofer 2003, Knepel 2003). Concentrations of NO_3-N and NH_4-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 PO_4-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).

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 (NH_4-N, NO_3-N, and phosphate in ppm).

I 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. I 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 NH_4-N, and NO_3-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.

RESULTS

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 12). Percent cover of *A. donax* was much higher than native plant cover both before and after the study sites were burned (Figure 17). 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 17). 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.

Post-fire density

The two-way ANOVA (plant type x time period) of plant density revealed a significant two-way interaction (Table 12). 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 18). 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 ± SE 3.2 stems m^{-2}) was an order of magnitude greater than that of native species (1.4 ± SE 0.4 stems m^{-2}) within the burned riparian ecosystems sampled.

Post-fire shoot length

Post-fire resprout timing and shoot length over time differed significantly between *A. donax* and the native plants studied (Figure 19). *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) 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 12). 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 19).

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 20 and Figure 21). 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 13). 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 13). The mean RGR of *A. donax* was much greater initially (first three months) than that of the native plant species (Figure 21). *Arundo donax* mean RGR was extremely high (0.094 ± 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).

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 22). 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.

Soil nutrients

Mean pre- and post-fire soil nutrient levels surrounding *A. donax* compared to native plants differed significantly (Figure 23; Table 14). Mean soil nutrient levels (NH_4-N, NO_3-N, and PO_4-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 NH_4-N and PO_4-P concentrations were more than twice as high in the soil adjacent to *A. donax* plants compared to native plant species.

DISCUSSION

In this study, I 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 maintain 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).

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, *Artemesia 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 lead to dominance by the invader.

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.

Mechanisms of Invasion

I 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 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.

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 Mediterreanean-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).

TABLES

Table 12. 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	$F_{(1,80)} = 0.006$; $P = 0.937$	$F_{(5,852)} = 2.850$; $P = 0.015$*	$F_{(8,3231)} = 21.295$; $P < 0.001$***
r^2	0.626	0.287	0.591

* = $0.05 \geq P > 0.01$ = significant; ** = $0.01 \geq P > 0.001$ = highly significant; *** = $P \leq 0.001$ = very highly significant

Table 13. Two-way ANOVA of shoot elongation rate (cm d^{-1}) and relative growth rate (RGR; g g^{-1}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 14. Two-way ANOVA of soil nutrients (NH_4-N, NO_3-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. NH_4-N and NO_3-N were ln transformed.

Factors and interactions	**NH_4-N (ppm)**	**NO_3-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*
r^2	0.555	0.255	0.394

FIGURES

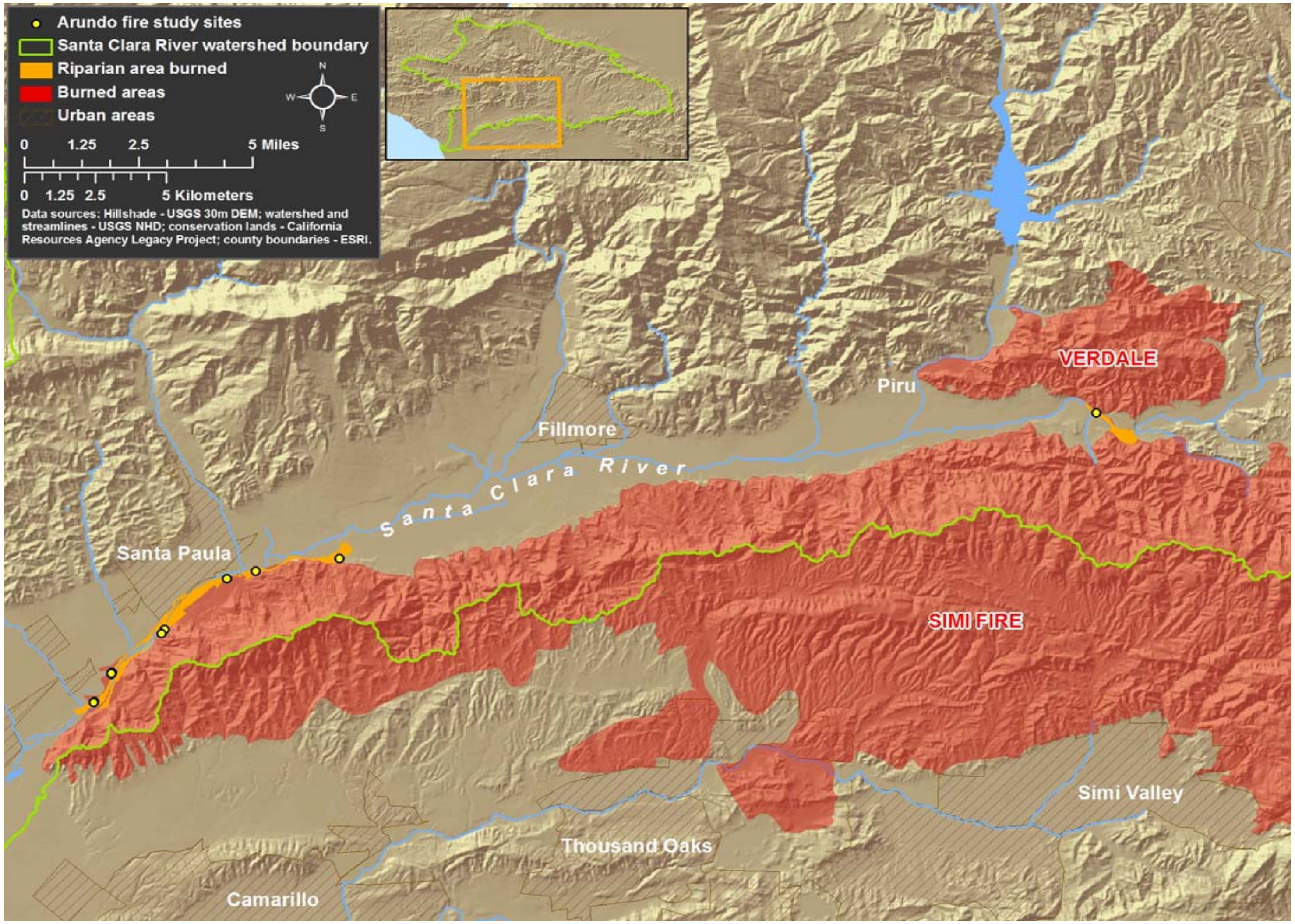

Figure 16. Location of study sites in riparian terraces of the Santa Clara River, Ventura County, California.

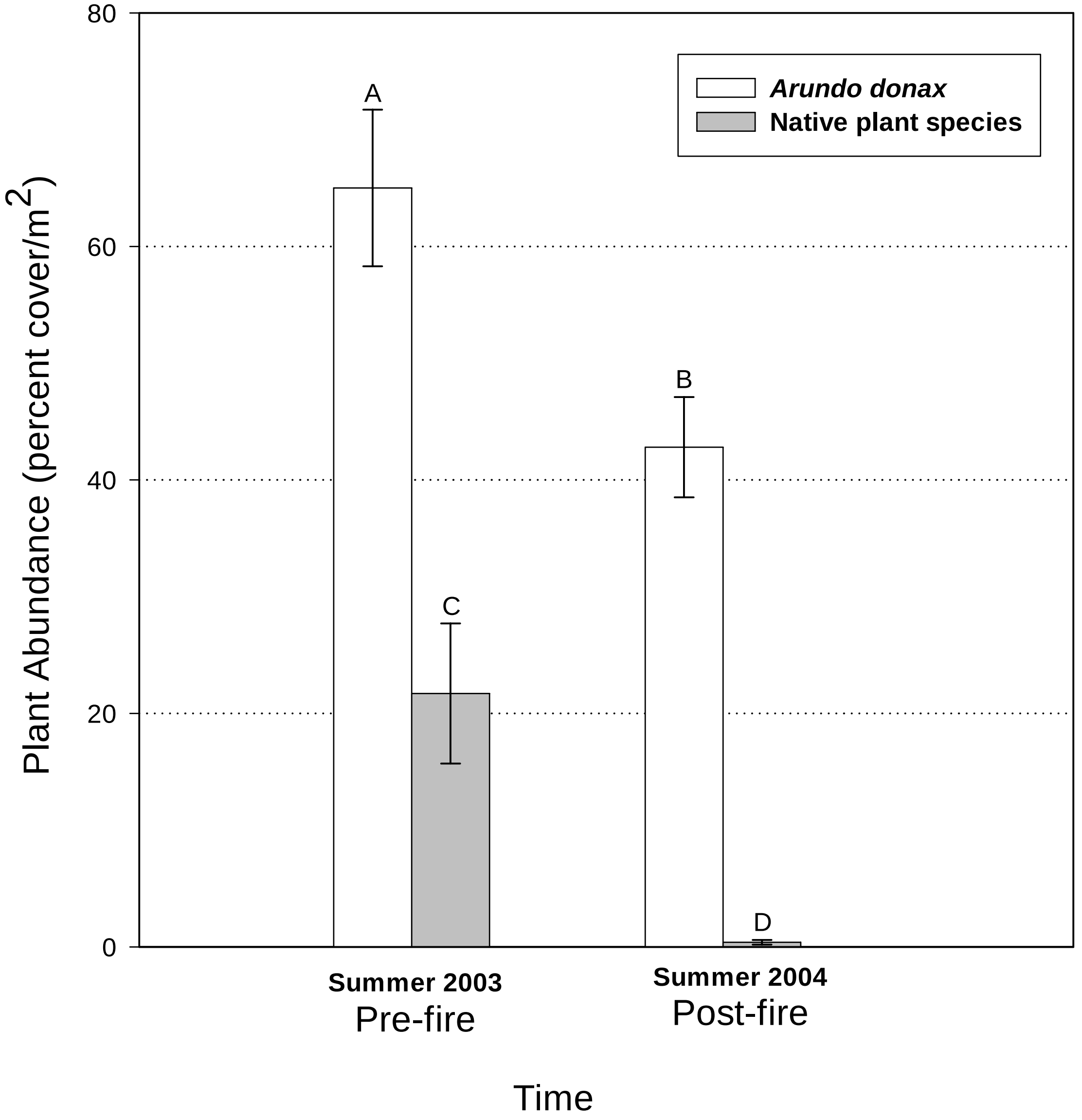

Figure 17. Abundance of *A. donax* compared to native riparian plant species before the October 2003 wildfire (summer 2003) and a year later. Letters denote results of post-hoc hypothesis tests (comparison of means) with significance recognized at $\alpha < 0.05$.

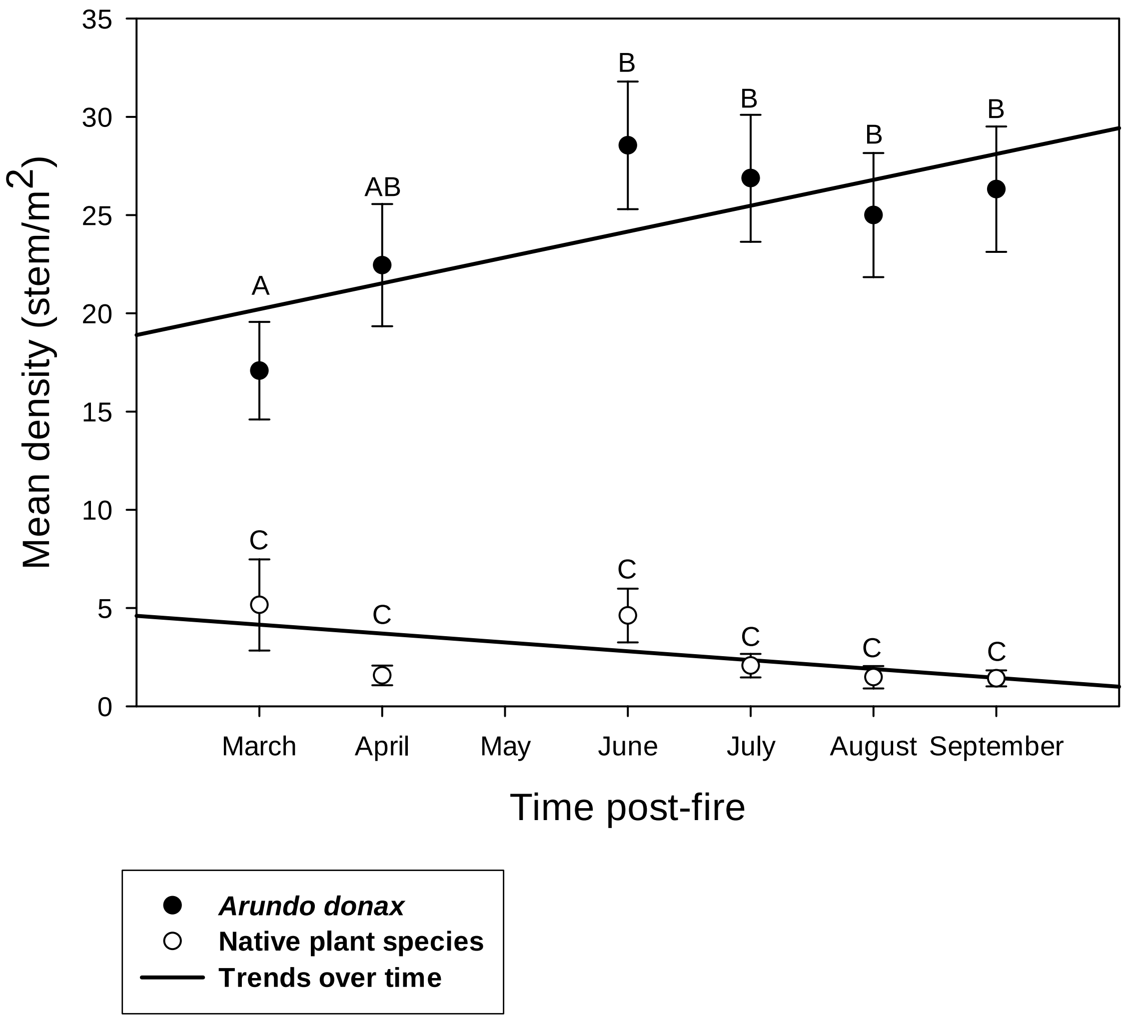

Figure 18. Mean density of *A. donax* versus native plants after the October 2003 wildfire. Regression lines illustrate trends over time. Letters denote results of post-hoc hypothesis tests (comparison of means) with significance recognized at α < 0.05.

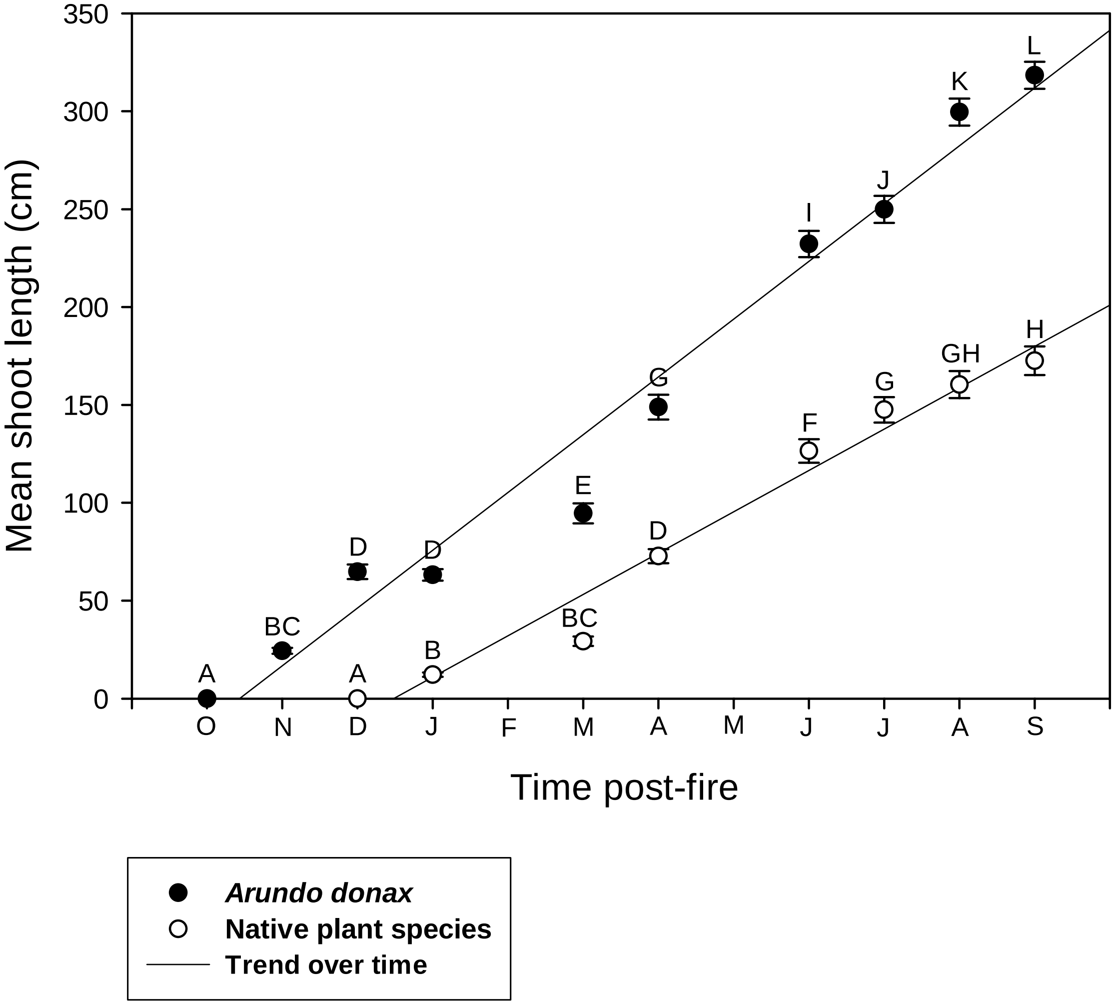

Figure 19. Monthly mean shoot length of *A. donax* compared to native plant species for a year following the October 2003 wildfires. Regression lines illustrate trends over time. Letters denote results of post-hoc hypothesis tests (comparison of means) with significance recognized at $\alpha < 0.05$.

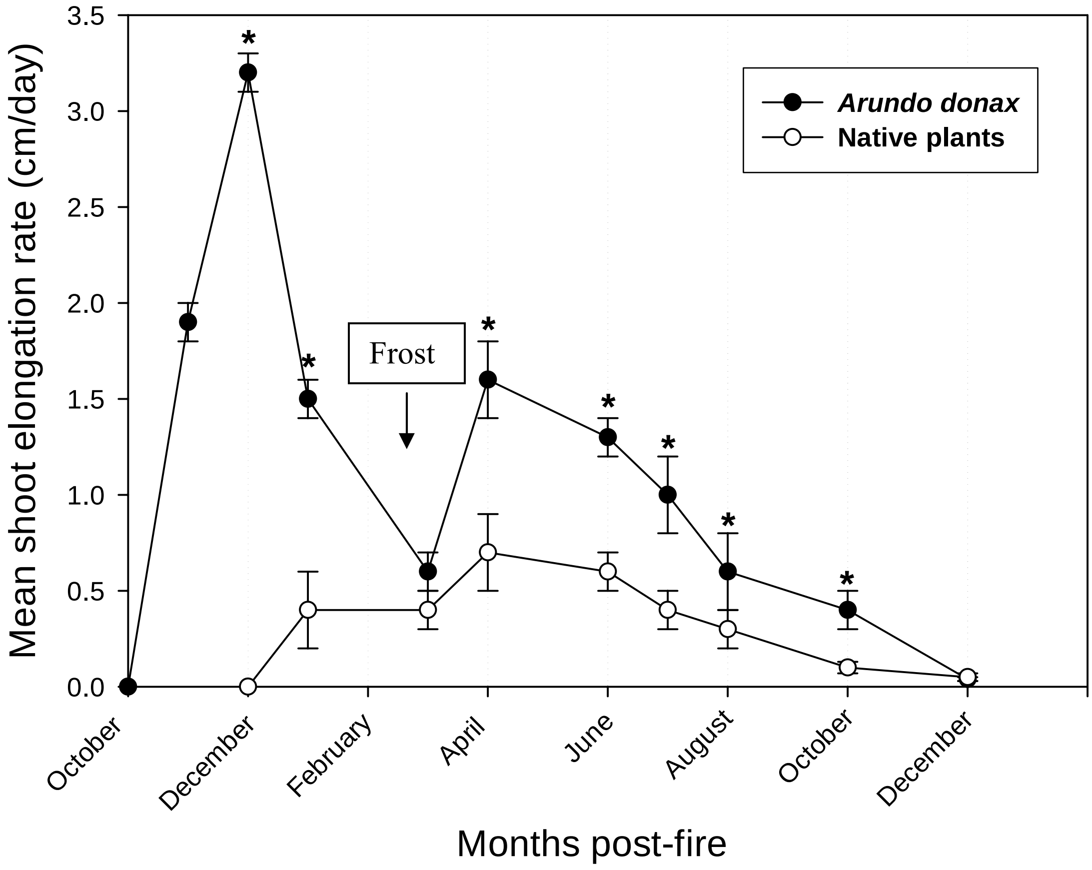

Figure 20. Mean monthly shoot elongation rates of *A. donax* compared to native plants after being burned in the October 25, 2003 wildfire. Asterisks denote significant differences in means between *A. donax* and native plants at each time period based on results of post-hoc hypothesis tests (comparison of means) with significance recognized at $\alpha < 0.05$.

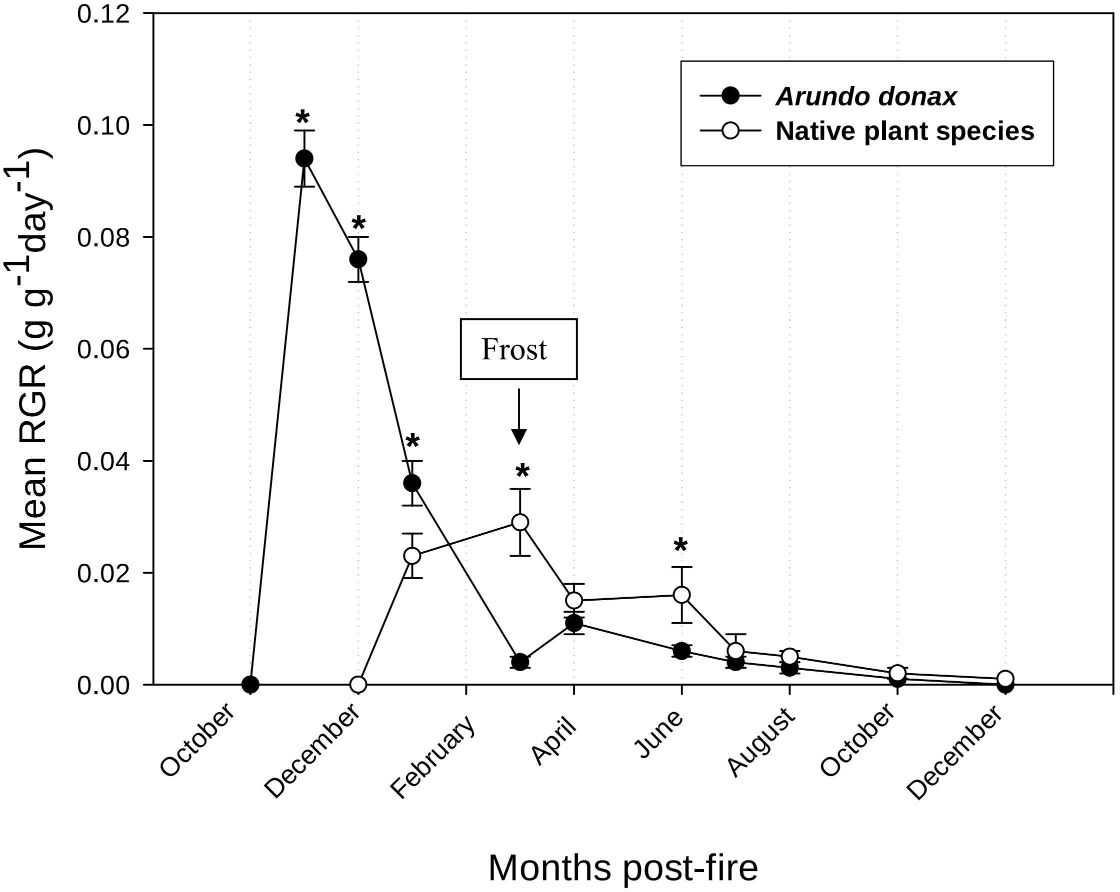

Figure 21. Relative growth rate of *A. donax* compared to native plant species. Asterisks denote significant differences in means between A. donax and native plants at each time period based on results of post-hoc hypothesis tests (comparison of means) with significance recognized at $\alpha < 0.05$.

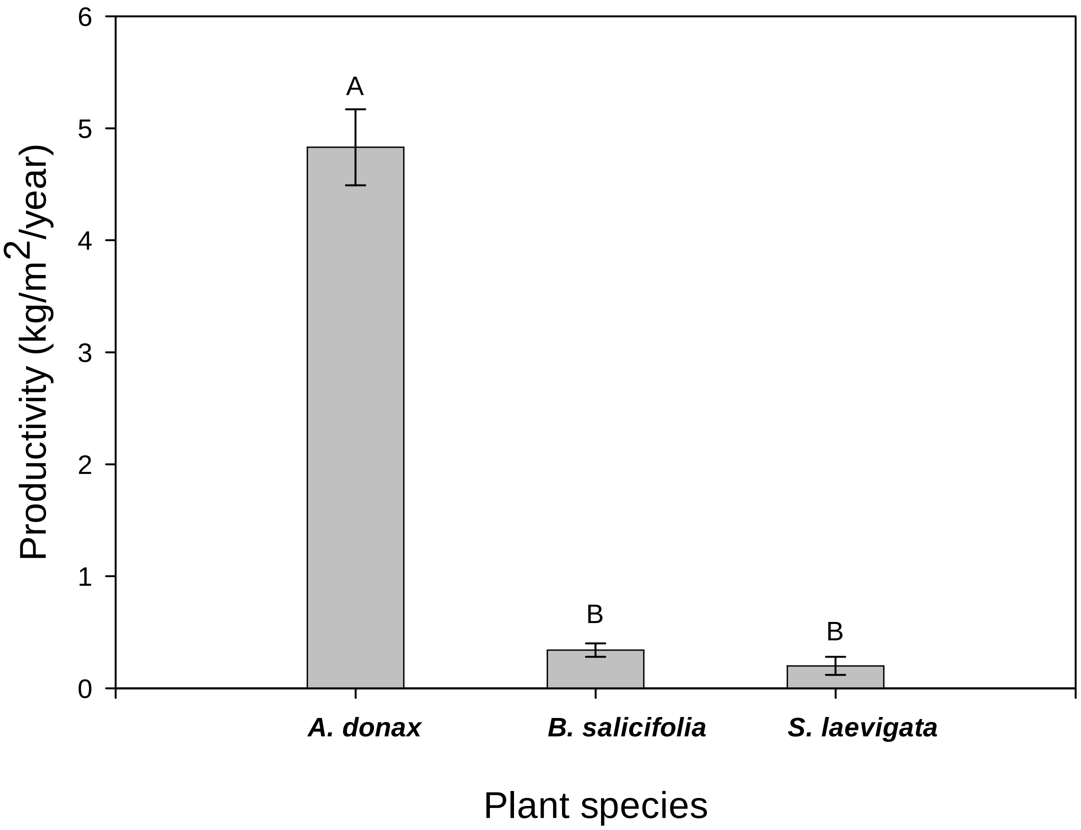

Figure 22. Mean productivity (kg/m^2/year) of *A. donax* compared to native plant species in burned sites. Letters denote results of post-hoc hypothesis tests (comparison of means) with significance recognized at $\alpha < 0.05$.

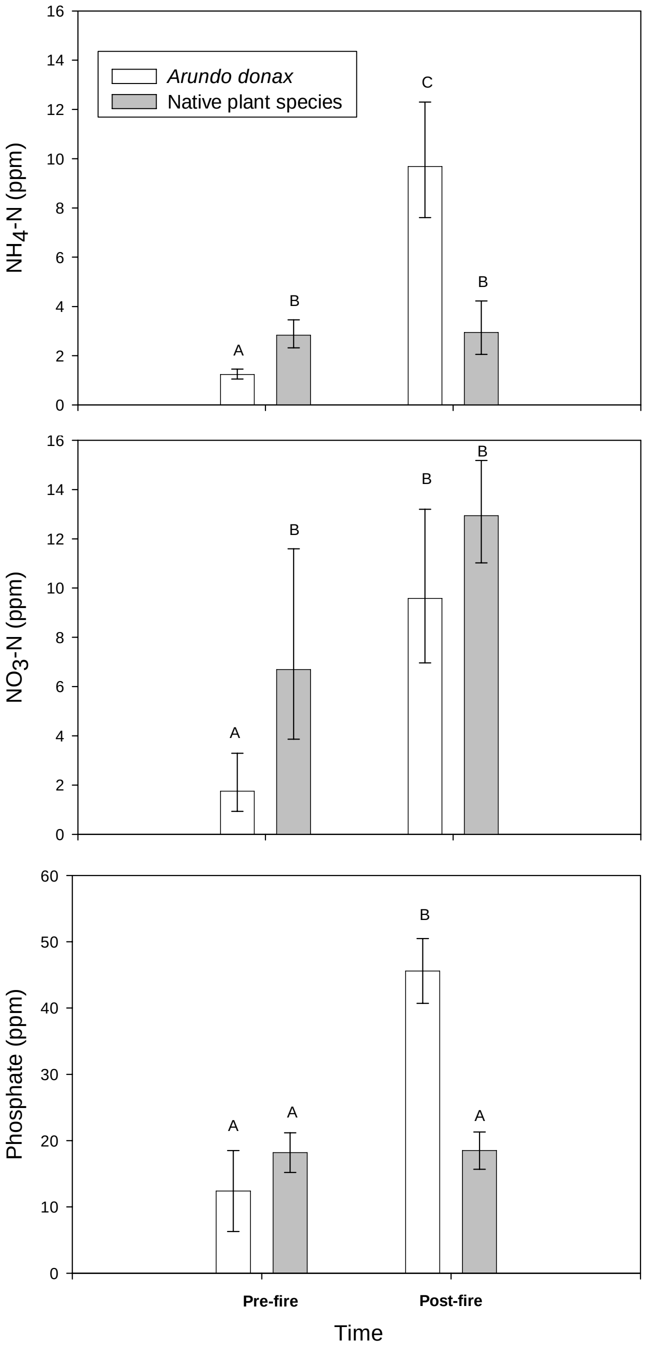

Figure 23. Pre- and post-fire mean nutrient levels of soil adjacent to *A. donax* compared to soil next to native plants. Letters denote results of post-hoc hypothesis tests (comparison of means) with significance recognized at $\alpha < 0.05$.

APPENDIX

APPENDIX 4-1

SAMPLING LOCATIONS

Site No.	Location Description	Latitude	Longitude	Pre-Fire Data Available
1	Near Piru, along Hwy 126 where fire spread to riparian corridor, on right bank of river terrace	34.41°	118.73°	Yes
2	East of Santa Paula and off of Peck Road, on left bank of river terrace	34.33°	119.08°	Yes
3	East of Santa Paula and off of Peck Road, on left bank of high river terrace	34.33°	119.08°	Yes
4	Just Downstream of 12th Street Bridge in Santa Paula, on left bank of river terrace under large coastal live oaks	34.35°	119.05°	Yes
5	Approximately 2 miles east of Santa Paula along South Mountain Road, on left bank of river terrace	34.35°	119.02°	Yes
6	Approximately 1 mile east of Santa Paula along South Mountain Road, on left bank of river terrace under mature willow trees	34.35°	119.04°	Yes
7	Southwest of Santa Paula, east of Mission Rock Road, on right bank of river terrace	34.31°	119.10°	No
8	Southwest of Santa Paula, east of Mission Rock Road, on right bank of river terrace	34.31°	119.10°	No
9	Southwest of Santa Paula, east of Mission Rock Road, on right bank of river terrace	34.31°	119.10°	No
10	Southwest of Santa Paula, east of Mission Rock Road, on right bank of river terrace	34.31°	119.10°	No
11	Southwest of Santa Paula, west of Mission Rock Road, on right bank of river terrace	34.30°	119.10°	No
12	Southwest of Santa Paula, west of Mission Rock Road, on right bank of river terrace	34.30°	119.10°	No
13	Southwest of Santa Paula, west of Mission Rock Road, on right bank of river terrace	34.30°	119.10°	No
14	Southwest of Santa Paula, west of Mission Rock Road, on right bank of river terrace	34.30°	119.10°	No

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CHAPTER 5 -

CONCLUSIONS

FACTORS INFLUENCING *ARUNDO DONAX* INVASION

I found that the role of all four factors that I investigated in my dissertation were critical to the *A. donax* invasion process, but varied in importance based on quantity and availability to plants. My results show that nutrient enrichment in riparian ecosystems due to increased urban and agricultural land use development plays an important role in *A. donax* expansion in the past half century. *Arundo donax* dominated experimental high soil moisture and nutrient treatments in full sun, indicating that the combination of elevated water quantity, decreased quality and light is key to its invasion success especially where disturbance levels are high. Fire appeared to have the greatest effect on *A. donax* invasion; it promotes rapid expansion of *A. donax* infestations near fire-prone shrublands and dominates the vegetation only months after burned.

Nutrient Availability

Anthropogenic nutrient enrichment has been linked to invasion of natural ecosystems worldwide (Kolb et al. 2002, Booth et al. 2003, Brooks 2003, Kolb and Alpert 2003, Suding et al. 2004), but little is known about the role of nutrients in promoting invasion in riparian ecosystems in Mediterranean-type climates (Wang 1998). I explored the influence of anthropogenic nutrient enrichment on the invasion of riparian ecosystems by *A. donax* in southern California. My field study results suggest that N (nitrogen) limiting conditions may occur naturally in riparian ecosystems in this geologically young landscape but that anthropogenic nutrient inputs have elevated groundwater N:P ratios and may provide invasive species with an advantage where N enrichment of soils and groundwater occurs. In my study area, elevated levels of N in shallow groundwater and soils of floodplains were associated with adjacent land use and with watersheds with higher anthropogenic nutrient inputs. Floodplains with both large and small *A. donax* infestations contained higher soil NO_3-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 those of native red willow (*Salix laevigata* Bebb.) collected from 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.

Interspecific competition between native and introduced species for nutrients, water, and light availability plays a critical role in plant invasion in many terrestrial ecosystems worldwide (D'Antonio and Vitousek 1992, Gordon and Rice 2000, Booth et al. 2003, Suding et al. 2004, White and Holt 2005, Richardson 2006). Experimental studies in river and wetland ecosystems have demonstrated superior resource competition by invasive plants for nutrients (Green and Galatowitsch 2002, Minchinton and Bertness 2003). My experimental findings suggest that higher nutrient levels may benefit *A. donax* more than native species, although response to competition for nutrients varies by species groupings. *Arundo donax* exhibited a positive response to high nutrient additions, but primarily under high soil moisture and light levels, and these effects were much greater in monocultures of *A. donax* (see Chapter 2, Figure 6). Both *S. laevigata* and *B. salicifolia* responded positively to high nutrient treatments under similar conditions, but the effects were of much lower magnitude than those of *A. donax*. When *A. donax* was grown in competition with *P. balsamifera* spp. *trichocarpa*, responses to high nutrient treatments were greater for both species compared to the effects when they were grown in monoculture. However, when grown in competition with either *S. laevigata* and *B. salicifolia* effects of nutrient addition on *A. donax* were decreased; thus, competition from *B. salicifolia* and *S. laevigata* had a strong negative effect on *A. donax* biomass under high soil moisture, light, and nutrient conditions.

Water Availability

In this dissertation, I hypothesized that high soil moisture levels may promote invasion by *A. donax*. Although *A. donax* tolerates a wide variety of ecological conditions, it reportedly thrives in areas with high soil moisture, such as along canals, ditches, and stream banks (Perdue 1958, Rezk and Edany 1979). Preliminary data analyses (Stillwater Sciences, unpublished spatial data) indicate that a higher percentage of *A. donax* is associated with areas of rising groundwater, compared to other drier areas in riparian ecosystems along the Santa Clara River. In addition, increased water quantity in stream systems of Mediterranean-type climates caused by anthropogenic inputs may contribute to higher than natural soil moisture availability. My field experiment showed that *A. donax* produced the highest biomass under high soil moisture conditions, especially when light and nutrient levels were also high (see Chapter 2; Figure 5). Although competition with *A. donax* did not suppress native plant species aboveground biomass under these high resource conditions during the time frame of the study, its biomass was much higher than those of all three native plant species studied.

Along naturally loosing stream reaches (i.e., river reaches that contribute water to the groundwater supply) in southern California or in riparian ecosystems with water tables lowered by groundwater extraction, invasion by *A. donax* appears to be diminished by lower water availability. However, growth of all native riparian species as well as *A. donax* appears to be lower than under higher water availability; all four species exhibited much lower biomass under low soil moisture versus high soil moisture conditions in my field experiment (see Chapter 2). The presence of sustained high soil moisture or near-surface shallow groundwater during the growing season may important for establishment of most riparian species (especially *Populus* spp. seedlings) (Braatne et al. 1996, Stella et al. 2006), although *A. donax* is known to establish under very low soil moisture conditions (Perdue 1958) and *B. salicifolia* grown from cuttings also had a high rate of survival in low soil moisture conditions in my field experiment (See Appendix 2-2). However, in years with prolonged wet winters all species may establish successfully, even in areas where soil type does not normally sustain high moisture levels. Once established, rooting depth, distribution, and structure relative to soil moisture and depth to groundwater likely play a larger role in growth of and competition between *A. donax* and native species (see Chapter 2, Figure 9). *Salix* spp., *Populus* spp., *B. salicifolia*, and other woody riparian species are phreatophytes with adaptations to low soil moisture conditions; their roots follow the receding soil moisture during establishment and can use water from depths of up to 30 m (Robinson 1958). In contrast, *A. donax* is a perennial grass with roots that can only reach ~3 m below the soil surface based on my field observations. Evidence from my field experiment indicates that all plants grow much more slowly under low compared to high soil moisture conditions, but the higher biomass of *A. donax* under all conditions may only decrease the rate of expansion in drier riparian ecosystems.

Light Availability

Light availability influences plant invasion in many ecosystems, due to both vegetation removal and direct effects of shading by invasive species (Crawley 1987, D'Antonio and Vitousek 1992, Yamashita et al. 2000, Meekins and McCarthy 2001, Fargione and Tilman 2002). Reduction in light availability may act as a barrier to invasion in both disturbed and natural habitats (Richardson et al. 2000), because plant species vary greatly in the amount of light they require for colonization and optimal growth (Treshow 1970, Menges and Waller 1983). Light availability varies greatly according to time and space along rivers in Mediterranean-type climates; the natural dynamic disturbance regime within these rivers creates large open areas after flooding and mature riparian forests create light limiting environments on high terraces. I experimentally investigated the effects of varying light levels on *A. donax* growth (in combination with nutrients and soil moisture factors) and competition with three native plant species. Light availability did not affect initial plant establishment of woody species (or *A. donax*) in this experiment, as was documented by D'Antonio and Vitousek

(1992) for other invasive grass species (see Appendix 2-2). In general, biomass of *A. donax* and native plant species was lower under low light conditions when soil moisture was not limiting (see Chapter 3, Figure 5). However, *A. donax* biomass was much higher than that of native species in low light and low soil moisture conditions but similar in high soil moisture conditions. Only one negative effect of competition was observed under conditions of low light (and high soil moisture): *A. donax* biomass was significantly lower when grown with *P. balsamifera* spp. *trichocarpa* compared to monoculture. Thus, light reduction does not appear to be an effective barrier to initial *A. donax* invasion in riparian ecosystems in Mediterranean-type climates. Dudley (1998) suggested that monotypic stands of *A. donax* limit native riparian plant recruitment through light reduction. Further investigation is needed to determine the effects of *A. donax* infestations on recruitment of native plant species in later stages of the invasion process.

Occurrence of Fire

Although healthy riparian ecosystems function as natural barriers to wildfire (Radtke et al. 1981, Dudley 1998, Rundel 2000, 2003), 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. Due to its immediate regrowth after the fire and its high growth rate compared to that of native riparian plants, *A. donax* dominated these burned riparian ecosystems within a few months after the fire and comprised 99% of the vegetative 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 greater and productivity was 14–24 times higher than density and productivity of native plants. Elevated soil nutrient levels post-fire may have contributed to *A. donax*'s high post-fire growth rate, which was similar to post-fire growth observed for chaparral resprouters after fire (Zedler et al. 1983). The large amounts of *A. donax* biomass that replaced native woody species after the wildfire have increased the susceptibility of riparian ecosystems along the Santa Clara River to fire, creating an invasive plant-fire regime cycle similar to those described by D'Antonio and Vitousek (1992) and Brooks et al. (2004). Wildfire not only promotes dominance of *A. donax* in riparian ecosystems but also alters vital ecosystem processes and increases the risk that fire will spread to surrounding shrublands, towns, and agricultural areas.

ARUNDO DONAX **INVASION ECOLOGY**

Based on my research findings and available literature, I propose three *A. donax* invasion scenarios and associated conceptual invasion trajectories. I extrapolated invasion scenarios and trajectories from my two-year field experiment based on results of my two field studies, other *A. donax* invasion research, and my personal field observations. Proposed conceptual invasion trajectories represent general degree of infestation (abundance of *A. donax*) over time depending on variation in amount and timing in factors (and levels) investigated in my research: water, nutrient, light, and fire. Invasion scenarios include: *A. donax* growing alone in monocultures (scenario1), *A. donax* growing with native plants from the onset of establishment (scenario 2), and *A. donax* growing under a mature riparian forest canopy (scenario 3).

Invasion Scenario 1

According to experimental results and field observations, *A. donax* expansion is most rapid where it grows alone in large monotypic stands (Figure 24). Results of my field experiment show that after two years, *A. donax* biomass was highest when it was grown by itself in monoculture then when grown with any other species (see Chapter 3, Figure 4). *Arundo donax* (and native riparian plant) biomass was relatively low under the low resource conditions (low water and nutrient availability) that naturally exist in the riparian ecosystems found in many floodplains as well as high terraces in Mediterranean-type climates (Figure 24). However, I predict that a rapid *A. donax* invasion trajectory will occur where naturally high soil moisture, nutrient, and light conditions prevail or are added to the system, such as in floodplains in highly urbanized watersheds or high terraces next to agricultural areas (see Chapters 2 and 3). Several studies have shown a similar increased response of invasive, clonal plant species to addition of nutrients and light in a variety of ecosystems (Aerts and Berendese 1988, Bobbink et al. 1988, Green and Galatowitsch 2002, Maurer and Zedler 2002). Maurer and Zedler (2002) reported that rapid expansion of *Phalaris arundinacea*, another clonal grass species, into wetlands throughout North America was likely due to clonal subsidy, morphological plasticity, and high nutrient availability. When fire burns through large, continuous *A. donax* infestations on riparian terraces where high resource conditions are prevalent, *A. donax* reinvades on an even steeper trajectory (Figure 24; also Coffman unpublished data and Chapter 4). Results of my fire study showed that *A. donax* dominated burned riparian ecosystems (i.e., via high regrowth from rhizomes) within a few months after a large fire and reached 99% in aerial cover one year later (see Chapter 4). Regardless of resource level or combination of resources added, *A. donax* expansion is most rapid when it grows alone in monotypic stands.

Invasion Scenario 2

Where *A. donax* begins (at time 0) to grow with native plants on bare substrates after a large disturbance, a more gradual but similar invasion trajectory to Scenario 1 may be found regardless of resources added (Figure 24). Results of my field experiment show that in low resource conditions *A. donax* aboveground biomass was slightly lower when grown with *B. salicifolia* compared to in monoculture, possibly due to early shading by this native species (see Chapter 2; Figure 5). Although *A. donax* only suppressed one native species (*P. balsamifera* ssp. *trichocarpa*) under naturally low resource conditions, its biomass was 2–3 times higher than that of either native tree. Under high soil moisture, nutrient, and light conditions, competition from *B. salicifolia* and *S. laevigata* had negative effects on *A. donax* biomass. Despite some suppression by these native species, however, *A. donax* had a higher biomass than that of all native plant species examined. In a similar field competition experiment, Booth et al. (2003) showed that a native clonal perennial grass (*Elymus elymoides*) suppressed an annual invasive grass (*Bromus tectorum*) in high soil moisture and nutrient conditions, thereby facilitating recruitment of a native shrub (*Artemesia tridentata*). When fire is introduced to riparian terraces infested with *A. donax* and a mix of native riparian plants, fire intensity is likely decreased due to higher leaf water content of natives (Brooks et al. 2004). However, the invasion trajectory in this type of mixed community is probably only slightly lower than that of large *A. donax* infestations (Scenario 1) due to immediate resprouting and much higher growth rates of *A. donax* compared to native plants after fire (Figure 24). However, this invasion trajectory will vary between Scenario 1 and 3 depending on length of time from establishment to fire.

Invasion Scenario 3

An invasion trajectory similar to Scenario 2 (low water and nutrient availability) occurs when *A. donax* establishes under a mature riparian canopy regardless of soil moisture or nutrient levels (Figure 24). In my field experiment, under low light but high water and nutrient availability conditions *A. donax* biomass was slightly lower than it was where all resource conditions were low, but the biomass of native plant species was slightly higher. Competition with *Populus balsamifera* ssp. *trichocarpa* saplings that establish concurrently may suppress *A. donax* growth, but only under high soil moisture and nutrient levels. Thus, the incline of the trajectory may be slightly lower when water and nutrients are added due to the different responses of *A. donax* and native plant species found under these experimental conditions. When fire enters riparian ecosystems containing a mature riparian canopy infested by an understory of *A. donax*, a crown fire may spread through these areas due to an unnatural ladder effect: *A. donax* provides a large quantity of flammable material that transfers fire vertically to large riparian trees under which it grows (Brooks et al. 2004). The post-fire invasion trajectory is initially gradual due to competition from resprouts, but most of these resprouts will eventually die (according to field observations; Coffman unpublished data), and the trajectory then increases in steepness.

MANAGEMENT IMPLICATIONS

Arundo donax *removal effort priorities*

Millions of dollars have been spent to remove *A. donax* infestations of riparian ecosystems throughout California (Katagi et al. 2002). Due to the lack of understanding of *A. donax* ecology, however, decisions regarding prioritization of removal areas and removal techniques often have to be made in the absence of sufficient scientific information. After analyzing my own research results and the current body of literature available on *A. donax*, I propose the following management strategies, which incorporate the most current understanding of the *A. donax* invasion process, to most effectively and efficiently address this problem. I recommend that *A. donax* control efforts should be placed where ecological benefits are the greatest and associated removal effort the lowest.

1. Remove *A. donax* under mature riparian forests, especially adjacent to fire-prone shrublands. The highest priority location for *A. donax* control is within mature riparian forests adjacent to shrublands. My research suggests that removal in these areas creates the greatest environmental benefit, because these areas have the highest risk of further damage if removal is conducted and threat of reinfestation is lowest (i.e., where removal effort is long-lasting). *Arundo donax* may reinfest areas that are flooded occasionally but not completely scoured (e.g., higher terraces), especially where water and nutrient levels are high. In these locations, mature riparian forests may facilitate invasion by physically trapping propagules after flooding (Dudley pers. comm.). Although my research shows that *A. donax* does not grow as rapidly in low light conditions compared to high light conditions when high levels of water and nutrients are present (see Chapter 2), my field observations suggest that the understory of mature riparian forests can be invaded by *A. donax* after large floods; the invasion trajectory just may be more protracted. When these mature riparian forests become heavily invaded, areas near fire-prone shrublands are highly susceptible to fire. The large, dry biomass produced by *A. donax* in these areas carries fires (i.e., ladder effect) through canopies of these once-natural firebreaks, burning across and along river systems. These areas should be targeted for high priority removal due to the subsequent threat of an invasive plant-fire cycle and the lasting damage caused, the complete loss of mature riparian forests.

2. Remove the largest *A. donax* propagule source. Another *A. donax* removal priority should be to target areas containing the largest source of propagules to curtail the distribution of *A. donax*, thereby working to control it in the initial phase of the invasion process. Due to its clonal growth form, dominant asexual reproduction, and flood-driven dispersal mechanisms, the largest *A. donax* infestations will produce the highest quantity of vegetative propagules. My research suggests that the largest infestations are most prevalent in riparian ecosystems that are within highly urbanized watersheds, located adjacent to agricultural and residential land uses, and in areas that have burned in both southern California and the Western Cape region of South Africa. Large infestations in areas most frequently scoured by winter flooding contain the largest potential source of propagules.

Prioritization of removal in riparian ecosystems with the lowest likelihood of reinfestation has been suggested (i.e., areas outside the flood zone) (Coffman et al. 2004).

In general, my research findings suggest that *A. donax* is least likely to invade open substrates or recently scoured areas in which resources levels are low (i.e., low soil moisture and nutrient availability) and where native plants have established at the same time. Further investigation of the relationship between frequency of rhizome establishment and *A. donax* abundance in various locations after flood events is necessary to validate this recommendation. Riparian ecosystems downstream of large propagule sources along active floodplains are most likely to be reinfested and removal in these areas should be given lowest priority. Results of my studies suggest that *A. donax* is most likely to invade open (i.e., very low native vegetation cover) or recently scoured areas in which resources levels area high (i.e., high soil moisture and nutrient availability). These areas often are found next to agricultural land uses and areas exposed to wastewater treatment discharge from residential land use (see Chapter 3) (Neely and Baker 1989).

I recommend that more effort should be placed where ecological benefits are the greatest and associated removal costs the lowest. Natural biological and physical processes in riparian ecosystems that are heavily invaded by *A. donax* are usually already degraded. Although removal efforts may slightly reduce propagule abundance, net ecological benefits from removing *A. donax* in these areas may be much lower than in areas less invaded. My research suggests that removal of *A. donax* in locations within riparian forests adjacent to fire-prone shrublands, watersheds with low nutrient inputs, and watersheds with little *A. donax* abundance will result in the greatest ecological benefit. Furthermore, a considerable amount of money and effort is involved in removal of large infestations.

3. Control *A. donax* on a watershed scale. Here I suggest several watershed-scale *A. donax* control strategies given the natural dynamic flood regime in streams of Mediterranean-type climate regions and the widespread anthropogenic resource inputs that are not easily altered. *Arundo donax* should be removed from low nutrient input watersheds where infestations are small or area of infestation is localized; the highest probability of eradication success at the lowest cost is possible in these locations. However, watershed-scale long-term control of *A. donax* in natural riparian ecosystems may require management of resource levels that promote invasion to reduce growth and competition. Manipulation of resource availability in favor of a given native (desired) species has been proposed to create a competitive advantage and a barrier to reinvasion (Blumenthal et al. 2003, Corbin and D'Antonio 2004, Suding et al. 2004, Prober et al. 2005, Perry and Galatowitsch 2006). Results of my studies suggest that reduction of nutrient inputs in urbanized watersheds may slow invasion of *A. donax* but likely will not alone prevent its eventual spread.

Several researchers suggest that *A. donax* should be removed from the most frequently inundated floodplains only using a top-down directional approach (Bell 1997, Coffman et al. 2004). Removal of *A. donax* on higher terraces may not necessarily need to proceed in this downstream manner because reinfestation is much less likely. However, one study suggests that layering (i.e., rooting from nodes) is an important *A. donax* invasion mechanism in streams of southern California and, thus, an inside-out approach is required (Boland 2006). I suggest that both approaches are necessary depending on the flooding dynamics of the stream, infestation size and distribution, and fluvial geomorphic location of the infestation. Because removal of large areas of *A. donax* is very costly, the ideal time to remove it from a heavily infested watershed may be immediately after a very large flood event (i.e., 100-year flood) that removes most of the vegetation, resulting in much easier access to much reduced quantities of *A. donax* biomass.

4. Revegetation after removal may not help resist or suppress *A. donax*. The management literature recommends revegetation of riparian systems with native species after removal of invasive species, including *A. donax*, to resist further invasion (Sonoma Ecology Center 1999, County of Ventura Planning Division 2006). Resistance to invasion may be achieved if natives obtain a much higher biomass than *A. donax* and suppress it when competing for resources. However, results of my two-year competition field experiment suggest that this is rarely the case; *A. donax* had a significantly higher biomass than almost all native plant species under all resource levels and only minimal suppression by native plants was documented under a few conditions tested (see Chapter 2). Results of my competition field experiment indicate that *B. salicifolia* may increase in biomass when grown with *A. donax*, although it never obtained a significantly higher biomass than *A. donax* under any condition. Longer studies are needed to validate these findings, although it appears that revegetation will not resist reinvasion without implementation of appropriate *A. donax* maintenance. However, active revegetation after *A. donax* removal should help initiate restoration of riparian ecosystem functioning if *A. donax* removal is conducted in the appropriate location and diligent maintenance is implemented.

FIGURES

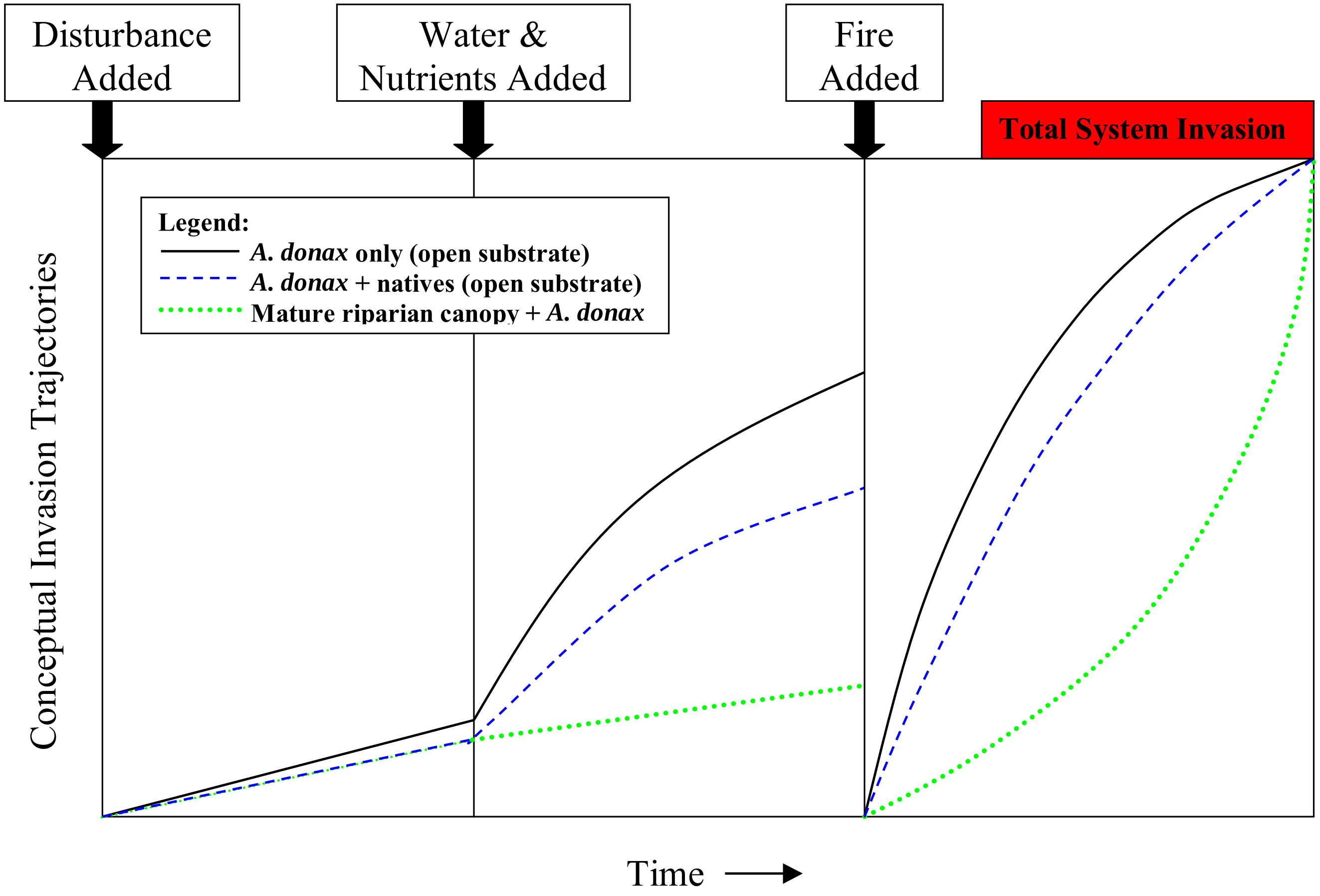

Figure 24. Conceptual *Arundo donax* invasion trajectories over time. Trajectories represent three invasion trends beginning after a large disturbance, including invasion where *A. donax* grows in monotypic stands, where it begins to grow at the same time as native riparian plants, and where it grows underneath a mature riparian forest canopy. The first panel shows invasion under low resource levels, conditions found throughout natural riparian ecosystems in California. When water and nutrients are added to riparian ecosystems, trajectories increase (panel 2). Panel 3 illustrates the steep invasion trajectories that occur when fire is introduced to riparian ecosystems where *A. donax* is already present.

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