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The Role of Native Riparian Vegetation in Resisting Invasion by Giant Reed, *Arundo donax*

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Plant Biology

by

Kai Thomas Palenscar

December 2012

Dissertation Committee:
  Dr. Jodie S. Holt, Chairperson
  Dr. Edith B. Allen
  Dr. Louis S. Santiago

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The Dissertation of Kai Thomas Palenscar is approved:

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Committee Chairperson

University of California, Riverside

ACKNOWLEDGEMENTS

It is bitter sweet to be writing this, as it means I will be ending another chapter in my life. At UC Riverside I have gained many new life friends, a new academic family, and have grown my personal family from two to three, and soon to four. An academic and professional thank you goes to the Holt Lab, including most importantly my advisor and mentor, Dr. Jodie S. Holt, followed by Dr. Rana Tayyar and Douglas Holt, and to past lab members Dr. Lynn Sweet, Polly Johnson, Sarah Otter, Dr. Lauren Quinn, Dr. Virginia White, Dwight Williams, Jacob Gray and Katie Johnson which have all provided various research support. The Allen and Santiago labs have also provided much needed research support and guidance during stressful times. I would like to thank, from the Allen lab, Dr. Edith Allen, Dr. Michael Allen, Dr. Michael Bell, Dr. Heather Schneider and Dr. Sara Jo Dickens, and from the Santiago lab, Dr. Luis Santiago and Sarah Pasquini. To the botany department and agricultural operations, I must acknowledge Robert Lennox, Eric McCullough, Jerry Sterrett, and Chuck Ferrar for their much needed help in irrigation design and weed control, and constant supply of caffeine and good conversation. To the UCR Herbarium, thank you Andrew Sanders for providing me with many hours of thoughtful discussion and critical plant identifications.

Cal-IPC Student Chapter is a student group at UCR and was cofounded in 2007 by Heather Schneider and Sara Jo Dickens. Many of the above-mentioned graduate students, including myself, took part in bringing together academics and land managers to answer wildland weed challenges. Thank you guys for all of your support, and for the

opportunity to create wildland weed manager contacts throughout California that were invaluable in my research.

Locating restoration sites for my third research chapter would not have been possible without the help provided by groups like the California Invasive Plant Council, the Inland Empire and Riverside Resource Conservation Districts, the Santa Ana Watershed Association, and individuals including James Law, Jason Giessow, Jason Casanova, John Ekhoff, Bill Winans, Bill Neill, Jutta Burger, Lynne Baker, Dustin McLain, Mike Kelly, Carvel Bass, Ben Lardiere, Kerwin Russell and many others. Thank you all! I could not have done this without you.

DEDICATION PAGE

I would like to dedicate this work to my wife Tory and my daughter Isla who bring joy to my life and have allowed me to pursue my passion, and to my parents, Tom and Bonnie Palenscar for providing me with a loving childhood and allowing me the freedom to find my own path.

ABSTRACT OF THE DISSERTATION

The Role of Native Riparian Vegetation in Resisting Invasion by Giant Reed, *Arundo donax*

by

Kai Thomas Palenscar

Doctor of Philosophy, Graduate Program in Plant Biology
University of California, Riverside, December 2012
Dr. Jodie S. Holt, Chairperson

Several decades of giant reed (*Arundo donax* L.) management in coastal riparian plant communities of southern California have provided many opportunities to observe the long-term trajectories of restoration projects. The two objectives of the current research were 1) to test if invasion resistance to *A. donax* could be achieved through native restoration, where carbon limitation through shading was the resource limitation facilitating the resistance, and 2) to determine which factors were most important in restoration success of *A. donax* removal sites. In the first objective, physiological responses of *A. donax* to shading revealed that a 94% reduction in total plant mass occurred with extreme shade (5% light), where moderate shading (65% light) was found to facilitate plant establishment. Next, a simulated restoration planting tested the effects of competitive shading from two native shrub species on *A. donax* establishment. Invasion resistance was only found with one species, mulefat (*Baccharis salicifolia*), and was positively correlated with the level of shade generated. Complete inhibition of establishment was only observed in the oldest and most densely planted competitive environments. These findings were supported in the wildland where under various native riparian competitive canopies mulefat provided the greatest invasion resistance to *A. donax* establishment. In the second objective, aged *A. donax* restoration sites (59 total), from 5 to 20 yr since invasive removal, were surveyed across southern California for restoration success. On a regional scale, active restoration provided early, dense native cover and potentially invasion resistant habitats, whereas passive restoration provided delayed native recruitment. Restoration age was positively correlated with native woody cover and negatively with exotic cover for both restoration types, and total species richness was equivalent regionally. Small passive restoration sites found close to the watercourse were most apt to recruit native species and provide successful habitat restoration. Management methods that leave viable *A. donax* rhizome fragments in Mediterranean riparian plant communities need to insure that fragments are less than 60 g to minimize invasion potential, as propagule size, especially rhizome fragments greater than 240 g, may limit the competitive effects imposed by existing or actively restored native vegetation.

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INTRODUCTION

With globalization and increased translocation of horticultural plants and other weedy species into novel regions, native plant communities have become increasingly impacted throughout the world (Elton 1958; Vitousek *et al.* 1997). Native riparian plant communities in the western United States have been severely degraded through anthropogenic activities (Shafroth *et al.* 2005) and more recently through plant invasions (Vitousek 1986; Vitousek *et al.* 1997; Wilcove *et al.* 1998; Mack *et al.* 2000; Corbin & D'Antonio 2012). From 1980 to 2007, two billion dollars were spent on projects related to river restoration and invasive species management in California (Kondolf *et al.* 2007). The susceptibility of these systems to invasion by exotic species is thought to be disproportionately high (Planty-Tabacchi *et al.* 1996; Stohlgren *et al.* 1998; Hood & Naiman 2000; Quinn, Rauterkus, & Holt 2007; Cushman & Gaffney 2010) due to frequent disturbance and dispersal via hydrochory. Exotic species can dominate both total plant richness and abundance in riparian corridors, facilitating new invasions (Pysek & Prack 1994; Zedler & Kercher 2004); therefore, these communities present a challenge for land managers.

Successful exotic invasion has been attributed to invader traits, abiotic factors and community composition (Richardson & Pysek 2006). Invasion into intact plant communities favors resource specialist species (Reinhart *et al.* 2006), whereas generalist species are most commonly found invading disturbed landscapes with limited competitive interactions (Levine *et al.* 2003; Daehler 2003). Facilitation of invasion by the competitor has also been found, allowing invasion to occur into otherwise resistant plant communities (Simberloff & Holle 1999). Once established, exotic species can alter ecosystem properties and functions to their advantage, as well as to the disadvantage of competitors, potentially creating exotic monocultures (Vitousek *et al.* 1987, 1997; Vitousek 1990; Gordon 1998; Yelenik, Stock, & Richardson 2004).

Various hypotheses have been proposed to explain mechanisms of invader success, including the enemy release hypothesis (ERH), the evolution of increased competitive ability (EICA) (Blossey & Notzold 1995), and the novel weapons hypothesis (Callaway & Ridenour 2004). These hypotheses have given insights into why certain species have come to dominate novel ecosystems as well as potential methods for managing these species through restoration design (Blumenthal, Jordan, & Svenson 2003; Sheley & Krueger-mangold 2003; D'Antonio & Thomsen 2004; Bakker & Wilson 2004; Sheley *et al.* 2006). The potential to use restoration design to limit invader success is founded in both niche complementary and sampling effect hypotheses (Loreau 2000; Loreau & Hector 2001), which state that self-assembled communities can be highly diverse and maximize resource consumption (complimentary) or composed of fewer, dominant species which have extreme trait values that can maximally utilize few resources (sampling effect). Community diversity has been shown to influence exotic invasion. Communities resistant to invasion have been linked to both high (Levine, Adler, & Yelenik 2004; Fargione & Tilman 2005) and low species diversity (Stohlgren *et al.* 1999), supporting both the complimentary and the sampling effect hypotheses.

Understanding invasion mechanisms and the development of control and restoration strategies based on ecological principles are essential for efficient management of invasive species in highly invasible systems, like the riparian plant community (Sheley & Krueger-mangold 2003; Radosevich, Holt, & Ghersa 2007; Sheley *et al.* 2010). When restoring with the specific purpose of creating an invasion resistant community, what may be more important than species diversity is restoring to fill functional trait gaps found in self-assembled native communities that could potentially be useful to the invader. Funk and co-authors (2008) found that native communities with species with functional traits similar to that of the invader were less invasible, suggesting that dominant species that consume resources required by the invader should be chosen for use in restoration projects.

Giant reed (*Arundo donax* L.) is a perennial, hydrophytic, clonal grass with C_3 metabolism (Rossa *et al.* 1998; Dudley 2000). Useful as a light building material, horticultural specimen, and source for instrumental reeds, it has followed human migration throughout the world (Perdue 1958; Bell 1997). After its intentional introduction into California from the Mediterranean region of Europe in the early 1800s (Dudley 2000; Dudley *et al.* 2008), clones now invade riparian habitats from Maryland to California (Bell 1997). Reproduction is strictly vegetative outside of its native range, and occurs from stem or rhizome fragments (Decruyenaere & Holt 2001; Quinn & Holt 2008). No viable seeds nor seedlings have been observed in the United States (Else 1996; Bell 1997; Wijte 2005; Balogh *et al.* 2012), although in its native range of Asia viable seeds have been reported (Perdue 1958). Plant division (fragmentation) likely occurs in one of two ways, naturally during flooding events or artificially by anthropogenic means (e.g., transplantation for horticulture or during invasive control)

(Bell 1997). Long distance dispersal of large, carbohydrate-rich propagules occurs most commonly via hydrochory (Decruyenaere & Holt 2001), where there is high potential for fragments to sprout new individuals successfully (Boose & Holt 1999; Khudamrongsawat *et al.* 2004; Quinn, Rauterkus, & Holt 2007; Quinn & Holt 2008). Post dispersal invasion into new environments occurs via radial vegetative patch expansion by rhizome growth or by shoot layering (Else 1996; Boland 2006; Quinn & Holt 2008). *A. donax* has a novel life form (*sensu* Vitousek 1986) in Mediterranean climates and has been defined as having a ruderal-competitive life strategy (Quinn 2006). It is also part of a unique functional group shared with common reed (*Phragmites australis* (Cav.) Steud.), termed a large-statured invasive grass (Lambert, Dudley, & Saltonstall 2010). All of these qualities benefit an organism living in a frequently flood-disturbed environment like the riparian ecosystem.

The riparian ecosystem has high temporal variability of resources due to the timing and duration of flood disturbance events. The associated riparian plant community has physiological and phenological adaptations to take advantage of these fluctuating conditions. Seed dispersal of woody species is timed to occur during the latter portion of the wet season, whereby seeds are shed directly onto moist soil for immediate germination (Shafroth *et al.* 1998). Seedling survival of the dominant phreatophytic canopy trees increases with longer durations on moist soil (Sacchi & Price 1992; Roelle & Gladwin 1999; Taylor, Smith, & Haukos 2006), where soil texture is an important factor (Bhattacharjee *et al.* 2008).

One important biotic factor influential to the survival of an individual plant is propagule size. The larger the propagule, the more resources it has available for initial growth, giving it a competitive advantage and making it less susceptible to environmental stressors (Burke & Grime 1996; Dalling & Hubbell 2002; Parciak 2002; Wulff 2012). There are, however, trade-offs that limit the benefits of larger propagules size. Dispersal distance is limited with increasing propagule size unless facilitated by animal or water, such as those conditions occurring during flood-pulse events (Junk, Bayley, & Sparks 1989; Boedeltje et al. 2004). Invasive clonal species with low or no sexual reproductive ability have become dominant within riparian ecosystems (Pysek 1997; Richardson *et al.* 2000; Cushman & Gaffney 2010). During post flood disturbance conditions *A. donax* has a competitive advantage over native species due to large rhizome propagules, enabling rapid growth under light limiting conditions (Else 1996; Decruyenaere & Holt 2005).

Riparian communities, especially urbanized waterways like in southern California, are typically not limited in soil nutrients (Decruyenaere & Holt 2005; Quinn, Rauterkus, & Holt 2007) but are light limited during secondary succession of ruderal species (Keddy, Fraser, & Wisheu 1998). Woody riparian species can be defined as ruderal due to their small seed size, need for cross-pollination, rapid growth and relatively short lifespan (Radosevich, Holt, & Ghersa 2007). The ability to form a closed canopy has been described as one mechanism whereby riparian communities can resist invasion (Pywell *et al.* 2003).

Grime (1977) defined competition as neighboring species utilizing the same environmental resource, and competitive success as successful resource capture. The “escape response” displayed by *A. donax* when shaded (Keddy, Fraser, & Wisheu 1998) suggests the potential for creating a stressful competitive environment with the ability to limit *A. donax* growth and invasion success. Previous studies have tested the competitive effects of native species on *A. donax* and found that certain species were able to retard *A. donax* growth but none conferred community resistance to invasion (Coffman 2007; Quinn & Holt 2009). Quinn and Holt (2009) found that a native evergreen shrub species negatively affected *A. donax* success within a common garden competition experiment and suggested that restoration designs should focus on species identity when considering restoring for invasive species resistance. The restoration of a system using ecologically based methods has the potential to increase project success while minimizing costs associated with long-term invasive control.

This dissertation work has been divided into three research chapters that pose questions related to determining which factors are most important in explaining *A. donax* success and failure in the context of ecosystem restoration. An additional goal for this research was to include recommendations for land managers in order to facilitate the translation of this research into land management practices. The research chapters include 1, the physiological effects of shading on *A. donax* growth; 2, the competitive effects of shading on *A. donax* growth when in a simulated restoration planting; and 3, the factors that are most important in explaining long-term restoration success in southern California. Many of the research hypotheses found in this document were able to be posed due to the work conducted in the Holt lab at the University of California, Riverside

(Boose & Holt 1999; Decruyenaere & Holt 2001, 2005; Khudamrongsawat *et al.* 2004; Quinn & Holt 2004, 2008, 2009; Quinn, Rauterkus, & Holt 2007).

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Physiological Response of Giant Reed (*Arundo donax* L.) to Environmental Factors Associated with Invasion Potential

ABSTRACT

Giant reed (*Arundo donax* L.) is an invasive hydrophytic grass found widely in coastal southern California riparian ecosystems and throughout Mediterranean climates worldwide. In order to understand mechanisms of invasion in these ecosystems, morphological and physiological responses of *A. donax* to environmental factors were examined during early growth. We conducted controlled glasshouse experiments over three consecutive spring seasons (2009-11) to quantify growth responses of *A. donax* to shading, to the interaction between shading and starting rhizome propagule size, and to the interaction between soil moisture and rhizome planting depth. Three shade levels (5, 35 or 100% PAR), five propagule sizes (30, 60, 120, 240 or 480g starting propagule mass) and four planting depth/soil moisture combinations (5 or 30 cm depth, +/- drought) were tested. Results indicated that *A. donax* growth decreased by more than 94% with increasing shade. Plants exhibited a shade avoidance growth response where they allocated resources aboveground to grow few, tall shoots with large leaves for light foraging. This decrease in stem number greatly diminished the ability of plants to store energy, as rhizome size was correlated with stem number (R^2=0.70). The moderate treatment plants (35% PAR) were found to have increased total leaf area relative to the control treatment plants (100% PAR), which provided ample carbon gain for net positive growth. No photosynthetic acclimation to low light was found in moderate treatment plants, whereas deep shade treatment plants (95% PAR) photosynthetically acclimated to

low light. When shaded, starting rhizome propagule mass was an important factor related to plant growth, where larger propagules resulted in a greater number or shoots, leaves and overall plant height than smaller propagules. The interaction between planting depth and soil moisture had no effect on overall plant growth or mass, although emergence was reduced in the deep-planted rhizomes. In the drought treatments plant survival was increased in deep-planted treatments relative to shallow-planted treatments. Two main factors may contribute to *A. donax* invasion success in Mediterranean riparian ecosystems. First, more massive rhizomes increase the productivity of *A. donax* regardless of shading level. Second, rhizome planting, simulating burial in natural systems, increases the rate of survival of *A. donax* during drought. This research provides insights into the physiological reasons why restoration techniques utilizing shrub species that produce dense canopies, may provide invasion resistance of *A. donax*. However, successful invasion may ultimately be determined by propagule mass no matter the shading capacity of the native competitor.

INTRODUCTION

Exotic ruderal weed species are generally defined as having rapid growth rates and the ability to establish in low stress and low competition environments (Grime 1977; Radosevich, Holt, & Ghersa 2007). Early growth and development in less-than-favorable environmental conditions, especially when radiant energy falls below plant metabolic needs, are dependent on stored sources of energy until morphological and physiological compensatory adjustments are made to satisfy metabolic needs (Chapin, Schulze, &

Mooney 1990; Myers & Kitajima 2007). Species identity and genetic adaptations determine the degree to which a plant can acclimate to a novel environment (Walters & Reich 2000). Invasive annual weed species have been shown to acclimate poorly to radiation-limiting environments leading to the inability to invade certain ecosystems (Pierson, Mack, & Black 1990). In environments where the most limiting resource is radiant energy, plant growth responses have been used to place plants into either shade-tolerant or shade-intolerant categories (shade avoidance) (Boardman 1977), where most plant species display some attributes of both (Mulkey 1986; Kull & Niinemets 1998; Walters 2005). Shade-tolerant species are pre-adapted to maximize carbon gain under radiation-limiting conditions and display very little morphological response to shading, especially stem elongation (Givnish 1988; Urbas & Zobel 2000). In contrast, shade-avoiding species must acclimate morphologically and physiologically in order to increase carbon gain and satisfy respiratory demands. Species having more stored energy reserves are better able to survive periods of suboptimal environmental conditions (Myers & Kitajima 2007). When radiant energy is limiting, asexual reproduction via vegetative propagules is favored over sexual reproduction, especially when survival depends on foraging for limited resources (Kanno & Seiwa 2004).

Wildland invasive weed species are commonly found in low stress and frequently flood-disturbed riparian plant communities (Planty-Tabacchi *et al.* 1996). In southern California, these communities are typically not limited in either soil nutrients or soil moisture but they can be limited in radiant energy, as ruderal species quickly form closed canopies, minimizing the amount of transmitted light to the soil surface (Keddy, Fraser,

& Wisheu 1998). The ability to form a closed canopy has been described as one mechanism by which riparian communities resist exotic invasion (Pywell *et al.* 2003; Galatowitsch & Richardson 2005). Clonal species, especially grasses, can have large stores of non-structural carbohydrates found in underground rhizomes (Chapin, Schulze, & Mooney 1990). This stored energy can facilitate invasion into highly competitive environments by shade-avoiding species (Quinn & Holt 2008).

Arundo donax L. (giant reed, Poaceae) is an invasive weed species in North America and found throughout subtropical and Mediterranean climates worldwide. It is adapted to flood disturbance with large, buoyant, water-dispersed stem and rhizome propagules (hydrochory) that can emerge and grow rapidly even within a competitive environment (Bell 1997; Boose & Holt 1999; Decruyenaere & Holt 2001; Rauterkus 2004; Wijte *et al.* 2005; Quinn 2006). *A. donax* is a tall (up to 10 m. in southern California) clonal plant that typically creates large monotypic patches of poor quality riparian habitat (Herrera & Dudley 2003) and is found throughout coastal California and non-coastal riparian areas below 500 m (Bell 1997). In California, the unique ruderal-competitive growth form of *A. donax* has likely been a major contributor to the success of this species in riparian systems (Quinn & Holt 2008; Lambert, Dudley, & Saltonstall 2010). In addition, it is adapted to fire, growing new shoots with dense foliar cover after a fire disturbance from carbohydrate reserves (Coffman 2007). These invasion mechanisms have led to the monotypic dominance of *A. donax*, creating a novel climax plant community in southern California (Rieger & Kreager 1989).

Post flood disturbance, *A. donax* has a competitive advantage over native riparian species due to faster establishment by vegetative propagules since most natives in this ecosystem reproduce sexually by small seeds (Stella *et al.* 2006). The most common *A. donax* propagules are large fragments of rhizome, and to a lesser extent stem fragments, that allow for rapid shoot elongation after dispersal, which is maximized under radiation-limited environmental conditions (Else 1996; Keddy, Fraser, & Wisheu 1998). This shade avoidance growth response has been observed (Keddy, Fraser, & Wisheu 1998), but physiological changes in proportional allocation of resources and organ development during this resource limitation phase are not well understood.

The goal of many researchers and land managers is to impart invasion resistance into habitat restoration projects (Pokorny *et al.* 2005; Funk *et al.* 2008). Within the past 30 years, many restoration projects have been completed in California with the goal of removing *A. donax* and returning lands to functioning native riparian systems. Understanding mechanisms of invasion helps land managers control this species as effectively as possible. Native species that form closed canopies have been suggested as good competitors with *A. donax* (Rauterkus 2004; Quinn 2006). The current study tests to what degree radiation limitation via shading can impact *A. donax* establishment. Additional environmental factors tested in this study include propagule size, planting depth and soil moisture, which are important for the success of species like *A. donax* that rely on hydrochory for vegetative propagule dispersal.

The following hypotheses were tested in this research:

H1. Reducing total solar radiation to levels similar to those under native vegetation limits the overall growth of *A. donax.*

H2. *A. donax* allocates resources to plant organs important for carbon fixation in response to radiation limitation.

H3. Increasing *A. donax* propagule mass increases the likelihood of successful establishment under radiation limitation.

H4. Planting depth affects *A. donax* survival and growth when combined with drought stress, where deeper-planted propagules survive longer and grow more than shallow-planted propagules when moisture is limited.

MATERIALS AND METHODS

Study System

All experiments were conducted in Riverside County, California, in a glasshouse at the University of California, Riverside (UCR). Air temperature was controlled and ranged from highs of 43.3, 47.8 and 43.3 C to lows of 11.1, 14.4 and 11.1 C for Experiments 1, 2 and 3, respectively. Irrigation was regulated with variable flow emitters where soils were irrigated daily to field capacity in each experiment, unless drought-stress was a treatment factor. The growing season was standardized among all three experiments, where all rhizomes were planted in late winter (Jan. or Feb.) of sequential years (2010-12).

Experiment 1 – Response to radiation limitation

This experiment evaluated the effect of radiation level on *A. donax* physiology and morphology. Three shading treatments were imposed, including unshaded (control), moderate, and deep shade (100, 35 and 5 percent irradiance, respectively) defined as a percentage of the glasshouse photosynthetic photon flux density (PPFD; 1310 μmol $m^{-2}s^{-1}$ measured midday May 29, 2010). The PPFD of the shading treatments were created to simulate the radiant environment below common riparian shrub species of southern California, either mature mulefat (*Baccharis salicifolia*) or sandbar willow (*Salix exigua*) canopies. To determine these values, in spring 2009 transmitted radiation was sampled repeatedly below both *B. salicifolia* and *S. exigua* canopies along the Santa Ana River (Hidden Valley Wildlife Area; Norco, CA; 33.97 N, 117.49 W) using a 1 m long leaf area sampler (SunScan Canopy Analysis System, SS1-UM-1.05, Delta-T Devices Ltd, www.delta-t.co.uk) between 10 am and 2 pm. For *B. salicifolia*, transmitted light was 130.7 +/-10.8 μmol $m^{-2}s^{-1}$ (6.5% of measured full sunlight, 2,010 μmol $m^{-2}s^{-1}$), comparable to the deep shade treatment, and *S. exigua* was 688.5 +/-54.4 μmol $m^{-2}s^{-1}$ (34.6% of measured full sunlight, 1,990 μmol $m^{-2}s^{-1}$), comparable to the moderate shade treatment.

Experimental plants were arranged in a randomized complete block design with three blocks. To minimize morning and evening structural shading all experimental plants were placed toward the center of the glasshouse structure on three separate tables. Plants were caged within 1 m^3 structures constructed from plastic tubing (1.27 cm polyvinyl chloride) that supported neutral density shade cloth (Hummert International, http://www.hummert.com). Deep shade treatments required two layers of shade cloth, where moderate treatments required only one to achieve the desired PPFD treatment conditions. These shade structures were increased in height to 2 m at one month after planting, simulating an average shrub canopy height. Shading capacity was measured within each structure with a separate LI-190 quantum photosensor (http://www.licor.com/env/products/light/terrestrial.html) to standardize treatments. The structures for the control treatment had no shade cloth.

Planting

A. donax rhizome fragments were harvested from a local source (Feb. 12, 2010) trimmed to a standard size (30+/-5 g) with one obvious bud, and held at 4 degrees C until planting (Feb. 16, 2010). Three hundred rhizomes were planted into steam-sterilized pots (10 cm) filled with UC mix #2 (Matkin & Chandler 1957) plus riparian soil inoculate. To add the microbial community associated with *A. donax* to the sterilized mix, soil inoculate was collected from the stream bank of a local river (Santa Ana River, Riverside, CA) where *A. donax* was present and held at ambient temperature prior to use. Ten grams per pot of fresh soil were added at planting. All rhizomes were planted at the same time and the middle cohort was used in the experiment to insure emergence and standardize plant age. The middle cohort was obtained by documenting plant emergence dates and using only the median aged plants for the experiment. The median emergence date was February 24, 2010. Once the experimental group was defined, plants were repotted to steam-sterilized pots (2.84 L, Feb. 25, 2010) and randomized 12 per shade structure, for a total of 108 pots. Fertilizer (Scott's slow-release Osmocote, 14-14-14) was applied to the soil surface at the time of planting at a rate of 10 g per pot and again at three-month intervals.

Measurements

Irradiance was measured continuously in each shade structure with a gallium arsenide photodiode (G1115; Hamamatsu) (Pontailler 1990), placed on 60 cm risers and leveled. The sensors were calibrated simultaneously against a factory-calibrated LI-190 quantum photosensor (Mar 13, 2010) to determine photosynthetically active radiation (PAR). Data were sampled each minute and recorded hourly as mean instantaneous PAR on a micrologger (23X; Campbell Scientific). *A. donax* growth measurements, including stem and leaf counts and maximum stem height, were recorded monthly.

During spring 2010, light-response curves (0-1500 μmol $m^{-2}s^{-1}$) were produced for plants in each treatment. The three healthiest looking plants per treatment were measured using a portable photosynthesis system (CIRAS-1; PP Systems). During planning prior to experimentation, instantaneous maximum photosynthesis (A_{max}) was measured on mature *A. donax* plants grown in full sun to develop a sampling and measurement plan. Fully expanded leaves numbered five to eight, counting fully open leaves from the shoot apex and moving down, had similar, high values of A_{max}. Subsequently in this experiment, leaf number six (+/-1 leaf) was measured unless that blade was damaged. All measurements were made between 10 am and 2 pm PST (June 9-11, 2010). Measurements were taken for each radiation level, from high to low, once leaves were fully induced and A_{max} was stable for a period of at least one minute. Intermediate radiation levels were created using neutral density screens (1,500, 970, 480, 180, 90, 20 and 0 μmol $m^{-2}s^{-1}$), which were calibrated against a LI-190 quantum photosensor (March 3, 2010).

Two destructive harvests were made at three and six months (May 18, 2009, 27 plants; and Aug. 17, 2009, 27 plants, respectively). Prior to each harvest a count was made of total shoots per plant, as well as independent measures of stem height and leaf number per shoot. Stem height was measured from the pot edge to the apical meristem of the shoot, where a sum of all stem heights for the plants equaled cumulative stem height. Leaves were only counted if they were fully open exposing the ligule. Internode measures were derived per plant as mean cumulative stem height divided by cumulative leaf number. Relative chlorophyll content was measured on all plants with a SPAD chlorophyll meter (August 6, 2010). Plant organs were divided into leaves (only leaf blade), stems (stem and leaf sheath), rhizomes and roots and dried at 69 C for 21 days. Leaf area was measured on excised leaves immediately after harvest using a leaf area meter (LI-3000; Li-Cor Biosciences). Largest basal stem diameter was measured on the largest cut stem for a plant at the soil surface with micrometer calipers. Dry tissue weights as well as other growth measures were used to assess plant growth and resource allocation, including relative growth rate ($RGR = \log W_2 - \log W_1 / d_2 - d_1$).

Due to an infestation of the arundo aphid (*Melanaphis donacis*) in the glasshouse, the pesticide pymetrozine (Endeavor©) was applied at label rate, 1.5 g/L as a fog to all plants on June 28, 2010. Plant growth appeared unchanged when comparing before and after pesticide application, but it was unknown if this affected plant photosynthesis. No studies were found on the effects of this chemical on plant photosynthesis. After harvest

2, the remainder of the unharvested plants (54 plants) was removed from the study (September 2010), as recurring infestations of the arundo aphid and overall large plant size within the shade structures led to diminished plant health.

Experiment 2 – Effect of propagule size

This experiment tested the effect of propagule size on *A. donax* establishment under radiation limitation. The location and design of the shading structures was as Experiment 1, except the moderate treatment was eliminated and the replicates were increased to five for both the control and shade treatments (100 and 5 percent PPFD, respectively). The experimental design was completely randomized with two shading treatments, five propagule sizes and three subreplicate plants per shade structure for a total of 150 plants.

Planting

A. donax rhizome fragments were harvested from a local source (Feb. 2, 2011) trimmed to standard sizes (30+/-2, 60+/-2, 120+/-3, 240+/-5 and 480+/-5 g) all with at least one obvious bud, and held at 4 C until planting (Feb. 8, 2011). Five hundred total rhizomes were planted into steam-sterilized 0.64 L or 2.84 L pots, depending on rhizome size. Experimental procedures including soil inoculate collection, standardization of plant emergence, irrigation and fertilization followed Experiment 1. Once the experimental groups were defined, plants were repotted to 5.68 L, steam-sterilized pots (Feb. 21, 2011) and randomized 15 per shade structure (150 total plants). For discussion purposes rhizome propagule size groups were labeled as group 1 (30 g), group 2 (60 g), group 3 (120 g), group 4 (240 g) and group 5 (480 g) for both of the shading treatments.

Measurements

Non-destructive *A. donax* growth measurements, including shoot and leaf counts, and stem maximum height were taken weekly starting after the first week and ending after the fourth week. From these measurements the mean internode length and RGR were calculated per treatment. Internode length was derived in the same manner as Experiment 1, but for only the tallest shoot instead of using cumulative stem and leaf counts. RGR was calculated using maximum stem height measures per plant ($RGR_{height} = \log Ht_2 - \log Ht_1 / d_2 - d_1$).

Experiment 3 – Effect of planting depth and soil moisture

This experiment tested the interaction between planting depth and drought on *A. donax* growth. The experiment was a randomized complete block design with five blocks and four treatment combinations, including 2 watering treatments (well-watered or drought), and 2 rhizome planting depths (5 or 30 cm), for a total of 20 plants. All pots were placed equidistant on one table and randomized per block. Blocks were oriented with irrigation direction.

Planting

A. donax rhizome fragments were harvested from a local source (Jan. 20, 2012) trimmed to a standard size (30+/-2 g) all with at least one obvious bud, and held at 4 C until planting (Jan. 26, 2012). Rhizomes were planted into steam-sterilized ~7 L, 50 cm deep pots. Experimental procedures including collection and use of soil inoculate, irrigation for the watered treatments and fertilization followed Experiment 1. Drought treatment plants were well-watered when planting occurred with no additional water supplemented until leaf rolling/wilting was observed in more than 50 percent of the drought treatment plants. At this time water was supplied at three timepoints via sub-basin irrigation with 0.5 L of water per plant (March 30, April 5 and April 20), simulating a deep source of soil moisture. Timepoints were chosen based upon the 50 percent criterion discussed above. Each plant had an individual sub-basin ensuring equal watering treatments per plant.

Measurements

A. donax growth measurements were taken bi-weekly for the first month and then monthly for the remainder of the experiment including counts of stems and leaves, and maximum stem height per plant. One destructive harvest was made after four months of growth (5/30/11), 40 days after the final sub-basin irrigation. The determination of when to harvest was made when all drought treatment plants were assumed to have failed. The determination of plant failure was made when all shoot tissues were desiccated and brown or when plants were observed to have no shoot growth for a period of 14 days. Plant organs and leaf area were measured as in Experiment 1.

Data Analysis

A. donax growth data from all experiments were analyzed using Analysis of variance (ANOVA) with comparisons between treatments made using Tukey's HSD post-hoc tests. For Experiment 1 an initial test comparing subreplicate plant growth data within shade structures and between blocks showed greater variation between treatments than within structures. Therefore, all plants were included in ANOVA instead of the mean of subreplicate plants in each shade structure, which increased N from 3 to 9 per treatment. The interaction between block and treatment effects was used for statistical comparisons, which includes within-greenhouse radiation variation. Harvest 1 and 2 were analyzed separately. For Experiment 2 all treatments were analyzed together and Tukey's HSD post-hoc tests include both control and shaded plants within a growth parameter variable. For Experiment 3 plants that did not emerge were excluded from analyses, which resulted in unequal sample sizes, so the blocking variable was removed from statistical analyses and the experiment was analyzed as a completely randomized design. No transformations were performed on data for ANOVA as these data met statistical assumptions for normality and homogeneity of variance. All data for continuous variables were analyzed using best-fit regression or correlation models. Models for Figures 1 thru 3 included raw data in analyses, while models for Figures 4 and 5 were made taking the mean A_{max} per irradiance level. Letters indicate significant relationships from Tukey's HSD post-hoc tests. All statistical analyses were performed using the statistical software JMP (http://www.jmp.com/).

RESULTS

Experiment 1 – Response to radiation

I subjected *A. donax* to various degrees of radiation limitation to test for plastic physiological changes in proportional allocation of resources and organ development. Parameters associated with biomass accumulation varied with measured PAR (Table 1.1). Total plant mass and relative growth rate (RGR) decreased with decreasing light availability (Table 1.1, Fig. 1.1 C). Each treatment group was significantly different from other treatments. All parts of the *A. donax* plant including the shoot (aboveground) and belowground organ systems followed this trend for both harvests. Stem mass and numbers of stems and leaves per plant were different between all treatments in harvest 2, with higher radiation treatments resulting in more massive and more numerous aboveground organs (Table 1.1). These differences were not as apparent in harvest 1 where the control and moderate treatments were not significantly different; however, they were both greater than the deep shade treatment. When comparing biomass and counts of organs, there were significant differences between treatments, which were directly related to treatment PAR.

Parameters associated with a plastic, shade avoidance response involve the allocation of resources to light capture. In both harvests *A. donax* leaf area was not different between the control and moderate treatments, with both having greater total leaf area than the deep shade treatment (Table 1.1, Fig. 1.1 A). Internode length was dependent upon the level of shading in both harvests, where the deep shade treatment had the longest internodes, followed by the moderate and then the control treatments. This trend was also observed in the tallest stem height for harvest 1 but not harvest 2. In harvest 2, the moderate treatment had taller stems than the control treatment but the deep shade treatment was not different from either the moderate or control treatments (Table 1.1). Three variables, relative chlorophyll content, largest basal stem diameter and cumulative stem height, only measured in harvest 2, were not different between the control and moderate treatments but had the lowest values in the deep shade treatment. The greater allocation of resources to aboveground growth was observed in both mid and deep shade treatments relative to the control, but the moderate treatment enabled rapid stem elongation of thick stems with high leaf surface area which was not observed in the deep shade treatment.

Other plastic responses to radiation limitation involve the proportional allocation of photosynthate within the plant. Higher radiation treatments favored the proportional allocation of root growth relative to shoot growth (R:S) in both harvests (Table 1.1, Fig. 1.1b). When comparing whole plant resource allocation there was no difference between shade treatments, where more resource was allocated to aboveground growth compared to the control treatment (Above vs. below mass, Table 1.1). Proportional allocation of photosynthate storage relative to leaf surface area (Rhizome mass / leaf area) had a nonlinear relationship with shading level, where shade treatments did not differ from each other but were lower than the control (Fig. 1.2, $R^2=0.90$, $p<0.001$). There was also a significant linear corelation between the dependent growth variables, rhizome net biomass and number of stems (Fig. 1.3, $R^2=0.70$, $p<0.001$).

Shading also affected the physiological ability of *A. donax* leaves to capture light and gain carbon. Light-response curves indicated that the deep shade treatment plants were significantly reduced in their capacity to photosynthesize at PAR levels above 480 μmol $m^{-2}s^{-1}$, relative to both the moderate and control treatment plants (Fig. 1.4). Light-response curves for the control and moderate treatment plants were not different in any part of the curve. At very low irradiance, similar to the average daytime incident irradiance plants experienced in the deep shade treatment (0 to 20 μmol $m^{-2}s^{-1}$), photosynthetic acclimation to low light was found in the deep shade treatment (Fig. 1.5).

Photosynthetic acclimation to low light was not observed in the moderate treatment plants.

Experiment 2 – Effect of propagule size

All of the data reported from this experiment were associated with non-destructive growth parameters (Table 1.2). Propagule size significantly affected the maximum shoot height, proportional allocation to stem elongation (internode length), and number of leaves and stems in the deep shade treatment plants and to a lesser extent in the control treatment plants, with larger propagules growing faster and producing more tissues than smaller propagules. Deep shade grown plants were shorter than control plants in all rhizome propagule size classes except for group 5, where they were significantly taller. Internode length was significantly increased in deep shade grown plants relative to control plants in all rhizome propagule size classes except group 1. Leaf number was significantly decreased in deep shade grown plants relative to control plants in all rhizome propagule size classes except groups 4 and 5. Total shoot number in deep shade grown plants was not different from control plants in any size classes. The relative rate of stem elongation (RGR_{height}) was not different between shading or rhizome propagule size group treatments.

Experiment 3 – Effect of planting depth and soil moisture

Rhizome propagules that were deep-planted, and thus experienced extreme radiation limitation, overall sprouted 33% less frequently than those that were shallow-planted (data not shown). However, from the plants that emerged, the deep-planted propagules were the only plants to survive drought (2 plants). Upon harvest it was found that both the shallow and deep-planted treatments each had one living rhizome fragment, with roots, that had not emerged.

Overall, plant biomass and height growth varied between watering treatments but not between planting depth treatments within a watering treatment, where well-watered plants were significantly taller and more massive than drought treatment plants (Table 1.3). One exception to this result was stem mass, where well-watered plants had more massive stems than drought treatment plants, and deep-planted well-watered plants had more massive stems than shallow planted well-watered treatment plants. Rhizome mass was significantly less in deep-planted, drought treatment plants while all other treatments were not different from one another. Root biomass varied with soil moisture as well, where well-watered plants produced more root mass than drought stressed plants, but between planting depths within a soil moisture treatment root mass did not vary. The only interaction of watering treatment and planting depth occurred for root number, where the drought-stressed deep-planted treatment had more roots than the shallow-planted treatment plants, which was not observed when plants were well-watered.

DISCUSSION

Low radiation intensity, small initial propagule size, low soil moisture and shallow planting depths were all independently shown to negatively affect the growth and potentially the long-term survival of *A. donax* in controlled glasshouse experiments. Past experimentation has shown that abiotic factors such as soil moisture and soil nutrients are important limitations to *A. donax* growth (Quinn, Rauterkus, & Holt 2007; Quinn & Holt

2008). Resource limitation can initiate plastic growth responses in plants, especially stem elongation for shade avoiding species foraging for light or root elongation for drought-stressed plants foraging for soil moisture (Smith 1982; Hutchings 1988; Hutchings & de Kroon 1994; Castillo *et al.* 2006; Padilla & Pugnaire 2007). Plastic responses in invasive species have been linked to increased success of invaders over native competitors (Daehler 2003; Reinhart *et al.* 2006; Martina & Ende 2012). In this research *A. donax* displayed morphologically plastic responses to shading including increased allocation to aboveground plant organs and decreased allocation to belowground plant organs relative to non-shaded plants, similar to what has been observed in other plant species (Smith 1982; Sultan 1995; Poorter & Nagel 2000).

Effects of limitation of radiant energy

A. donax plants in moderate shade displayed several morphologically plastic responses, including increased mean internode length and total leaf area relative to unshaded plants. These responses are suggested to be adaptive as they allow a plant to capture increased light higher in the canopy (Schmitt, McCormac, & Smith 1995; Ballare, Scopel, & Sanchez 1997). No physiologically plastic responses, such as photosynthetic acclimation to shade, were found in plants in moderate shade. Similarly, in all measured aspects of leaf physiology, including photosynthetic output and chlorophyll content, the leaves of plants in moderate shade were functionally similar to leaves of full sun grown plants.

The ability to photosynthetically acclimate to changing irradiance has been found to be advantageous for perennial invading species, including grasses, within competitive environments (Yamashita *et al.* 2000; Murchie *et al.* 2005). Deep shade grown plants in this research were acclimated at very low light intensities indicated by decreased rates of dark respiration and reduced light compensation point relative to plants grown in higher light levels. Several physiological changes could have led to this acclimation, including a proportional decrease in chlorophyll a/b ratio, changes in levels of other photosynthetic pigments, or a reduction in total cellular respiration costs, most commonly due to a reduction in the abundance of the enzyme rubisco (Bjorkman 1981; Bailey *et al.* 2001). The reduction in total leaf chlorophyll measured in deep shade plants suggested a reduction in antennae pigments and a reduced ability to harvest light. Rice is also a hydrophytic grass like *A. donax* and responds to shade with a proportional shift in abundance of total chlorophyll and rubisco and in chlorophyll a/b ratio, favoring b over a (Murchie *et al.* 2002). The magnitude of these shifts in rice decreased with increasing radiation (Murchie *et al.* 2002). Proportional alteration of chlorophyll a/b ratio is known to occur in many shade acclimated plants when either total incident light is reduced or light quality is altered (Smith 1982; Murchie & Horton 1997; Bailey *et al.* 2001). Although the ratio of chlorophyll a/b was not measured in our experiments, the relative decrease in total chlorophyll in deep shade plants indicates a loss of potential carbon gain even if the ratio of chlorophyll a/b was altered, which is opposite to what is expected in shade acclimated plants. Plants in the deep shade treatment were also respiring at a reduced rate, lowering the light compensation point and providing photosynthetic acclimation to a low light environment. This potentially enabes rapid photosynthetic induction (Hull 2012). Rapid induction is important in a competitive environment when sunflecks, and dawn light may provide a majority of total irradiance (Pfitsch & Pearcy 1989; Hull 2012). Overall, my results indicate that the stress of deep shade impacted *A. donax* growth in a manner that could inhibit successful invasion into a competitive environment of similarly shaded conditions.

A general relationship exists in clonal plants between shoot production and rhizome size indicating a conserved, potentially species specific ratio between shoot number and rhizome mass (Haslam 1969; Tappeiner *et al.* 1991; Ekstram 1995). In addition to the classic plastic shade responses discussed above fewer shoots are produced in shade (Smith 1982). In our research, shading had a proportionately negative effect on both total stem number and net rhizome mass, which increased with shading level, indicating a limited ability for shaded plants to store energy belowground. This would likely make radiation-limited plants more vulnerable to additional resource limitation or aboveground tissue damage, such as drought or grazing. Based on this research, moderately shaded plants in wildlands would be expected to succeed and invade if no other compounding factors negatively affected aboveground growth, whereas deep shade grown plants would most likely persist until either a second limiting resource caused plants to fail or a disturbance created a canopy gap, removing the resource limitation, allowing successful invasion. Little information is available on the effects of interacting environmental factors on *A. donax* success in wildlands (Quinn, Rauterkus, & Holt 2007; Quinn & Holt 2008) and further research would help to understand their impacts on invasion success.

Rhizome propagule size

Quinn & Holt (2008) found that propagule size affected *A. donax* establishment in wildlands. Our results add to these findings and show that propagule size may enhance the ability of this species to invade intact riparian plant communities. When radiation was limited, larger propagules displayed an increased shade avoidance response by producing more and taller shoots having more abundant leaves than smaller propagules. However, all plants, regardless of rhizome propagule size, attained a height comparable to that of a competitive native shrub canopy, indicating the likely successful invasion of a single resource limitation environment regardless of starting propagule size.

Riparian shrub communities in the arid western United States are composed primarily of xeric species, especially mulefat (*Baccharis salicifolia*) in southern California (Else 1996; Coffman 2007; Baldwin *et al.* 2012), with the ability to survive drying soils and potentially deplete soil moisture in excess of needs of phreatophytic tree species. This suggests that when *A. donax* plants are establishing in competition with riparian xeric shrub species and both light and soil moisture are limiting, plant success (Valladares & Pearcy 2002) and invasion potential may be decreased. In contrast, riparian phreatophytic tree communities with adequate soil moisture may inhibit *A. donax* growth but not prevent invasion since large *A. donax* rhizome propagules may increase the potential for invasion in all competition or environmental scenarios.

Planting depth

Rhizome planting depth was an important factor in *A. donax* survival especially under drought conditions. Propagules successfully sprouted from a planting depth of 30 cm, which would inhibit seed germination in most species (Stromberg *et al.* 2011), but *A. donax* is known to emerge from 25 cm in controlled conditions (Boose & Holt 1999) and a least one meter planting depth in field conditions (Else 1996). In this research *A. donax* plants emerging from 30 cm attained the same mass and had greater survival than shallow planted propagules in drought conditions. Although planting depth decreased emergence rate, the increased survival of deep-planted individuals suggested that depth of propagules may not be a deterrent to wildland establishment and invasion potential.

Due to subsoil stem growth (non-rhizome) of deep-planted individuals, root growth occurred throughout the soil column, minimizing loss of water to dry surface soils through hydraulic lift (Caldwell, Dawson, & Richards 1998; Espeleta, West, & Donovan 2004). A majority of the root development was found at depth, surrounding and below the location of the rhizome propagule (data not shown). This gave access to the simulated deep pools of soil moisture not available to shallow-planted individuals. In the wildland, during periods of drought following flood dispersal, *A. donax* survival would be expected to increase with planting depth, depending on the ability to emerge and access to deep pools of soil moisture. This suggests that exotic clonal species with rhizome propagules emerging from depth would have an advantage over native sexually reproducing species during drought periods (Stromberg *et al.* 2011), increasing the likelihood of successful invasion. However, in well-watered field conditions, deep *A. donax* plantings are predicted to be less successful due to the expense of energy needed for emergence, making them vulnerable to competition.

IMPLICATIONS FOR MANAGEMENT

Managing *A. donax* is laborious and expensive; thus, understanding which mechanisms influence invasion success is important for the long-term management of the species. This research has shown that the shade avoidance response in *A. donax* creates an opportunity for managers to control the species by restoring riparian plant communities with native species able to create dense canopies with high shading potential, such as *B. salicifolia*. Under these conditions, new *A. donax* recruits would exhaust stored energy by growing fewer taller shoots that forage for radiant energy. The production of fewer shoots minimizes the ability of the plant to store carbohydrate energy in rhizomes, making it more vulnerable to a wide array of control methods, including pruning. Foliar herbicide application is predicted to be very effective on these shaded plants as leaf surface area is proportionally high relative to rhizome mass. Management time, total herbicide application and control costs could be minimized if an integrated pest management program incorporates a native restoration aspect into the plan.

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Table 1.1. Experiment 1: Values represent *A. donax* growth parameters for harvests 1 and 2 with associated F values.

Harvest 1	Control	Sig[†2]	Mid Shade	Sig	Deep Shade	Sig	F
Daily PAR (mol m^{-2}d^{-1})	31.51 (2.8)[†1]	a	10.88 (0.5)	b	1.77 (0.5)	c	783.6***[†3]
Total plant net mass (g)	32.68 (3.3)	a	20.33 (3.3)	b	1.02 (1.2)	c	168.86***
Shoot mass (g)	17.75 (1.1)	a	14.97 (2.3)	b	5.60 (0.9)	c	95.90***
Belowground mass (g)	27.24 (3.7)	a	17.62 (1.5)	b	7.46 (0.7)	c	91.16***
Leaf mass (g)	7.44 (0.7)	a	5.97 (1.0)	b	2.32 (0.3)	c	88.51***
Rhizome mass (g)	16.87 (2.0)	a	12.52 (1.0)	b	6.94 (0.7)	c	71.65***
Root mass (g)	10.38 (2.2)	a	5.10 (0.8)	b	0.51 (0.1)	c	68.55***
RGR (g g^{-1}d^{-1})	0.014 (7.5E-4)	a	0.011 (0.001)	b	9.1E-4 (8.7E-4)	c	300.83***
R:S (g g^{-1})	0.59 (0.2)	a	0.35 (0.06)	b	0.09 (0.02)	c	36.03***
Stem mass (g)	10.26 (0.8)	a	9.00 (1.5)	a	3.28 (0.7)	b	77.74***
Stem number (count)	5.56 (1.6)	a	4.67 (0.9)	a	1.67 (0.4)	b	17.9***
Leaf number (count)	41.78 (10.7)	a	35.56 (5.3)	a	16.44 (2.4)	b	17.0***
Leaf area (cm^2)	998.88 (89.4)	a	943.02 (153.6)	a	695.28 (84.4)	b	12.66***
Internode length (cm)	2.96 (0.2)	c	4.28 (0.5)	b	7.44 (0.6)	a	136.88***
Tallest stem (cm)	47.56 (2.6)	c	67.67 (8.7)	b	106.00 (11.2)	a	70.54***
Harvest 2							
Daily PAR (mol m^{-2}d^{-1})	32.95 (3.5)	a	10.79 (1.3)	b	1.91 (0.3)	c	598.61***
Total plant net mass (g)	268.67 (28.6)	a	156.46 (23.1)	b	16.4 (2.7)	c	176.13***
Shoot mass (g)	155.28 (13.2)	a	114.57 (12.9)	b	19.80 (2.2)	c	225.13***
Belowground mass (g)	125.65 (23.7)	a	54.15 (12.4)	b	8.93 (1.1)	c	78.43***
Leaf mass (g)	59.50 (3.1)	a	44.20 (4.7)	b	7.94 (0.9)	c	328.29***
Rhizome mass (g)	75.91 (15.7)	a	31.18 (8.0)	b	7.66 (1.0)	c	63.25***
Root mass (g)	49.74 (9.6)	a	23.0 (5.1)	b	1.27 (0.2)	c	82.34***
RGR (g g^{-1}d^{-1})	0.020 (9.5E-4)	a	0.018 (0.001)	b	0.0086 (0.001)	c	152.78***
R:S (g g^{-1})	0.32 (0.07)	a	0.20 (0.04)	b	0.064 (0.01)	c	48.17***
Stem mass (g)	95.78 (11.4)	a	70.37 (9.1)	b	11.86 (1.3)	c	137.67***
Stem number (count)	9.22 (0.9)	a	7.11 (1.6)	b	2.56 (0.6)	c	19.7***
Leaf number (count)	160.78 (19.3)	a	123.89 (19.6)	b	38.56 (4.2)	c	20.3***
Leaf area (cm^2)	8651.10 (522.6)	a	7882.70 (795.0)	a	2178.40 (228.8)	b	199.52***
Internode length (cm)	5.42 (0.6)	c	7.40 (0.4)	b	8.76 (0.5)	a	52.02***
Tallest stem (cm)	157.78 (15.8)	b	190.11 (12.3)	a	172.11 (11.0)	ab	7.76**
Chlorophyll content (relative)	55.60 (2.1)	a	56.03 (1.7)	a	46.21 (2.4)	b	35.90***
Stem diameter (mm)	17.33 (3.6)	a	14.67 (1.7)	a	8.00 (0.9)	b	22.00***
Cumulative stem ht. (cm)	860.22 (62.4)	a	910.22 (122.6)	a	338.33 (46.4)	b	75.00***
Above vs. below mass (g g^{-1})	1.30 (0.2)	b	2.22 (0.3)	a	2.25 (0.3)	a	18.55***

[†1] Mean +/-95% CI in parentheses.

[†2] Letters represent significant differences between groups, Tukey HSD post-hoc tests, α = 0.05.

[†3] Level of significance is indicated by the number of stars, **p<0.01 and ***p<0.001.

Table 1.2. Experiment 2: Values indicate *A. donax* growth parameters and the associated relative growth rate, in terms of height (RGR), from two shading treatments collected prior to plant harvest. All treatments were analyzed together per variable using ANOVA. Bold text indicates significant differences between propagule size group shading treatments.

Rhizome groups[†1]	Height (cm)	Sig [†3]	Internode (cm)	Sig	Leaves (#)	Sig	Shoots (#)	Sig	RGR_{height} ($cm\ cm^{-1} d^{-1}$)	Sig
Control treatments (100% light)										
Group 1 (30g)	41.1 (7.4)[†2]	ef	5.6 (0.6)	g	**7.3 (0.8)**	**cde**	1.2 (0.2)	d	0.12 (0.01)	a
Group 2 (160g)	65.7 (14.6)	de	**7.3 (1.0)**	**fg**	**8.5 (1.3)**	**abcd**	1.7 (0.3)	d	0.12 (0.01)	a
Group 3 (120g)	78.3 (12.9)	cd	**8.4 (1.0)**	**def**	**9.2 (0.8)**	**ab**	2.3 (0.6)	bcd	0.12 (0.01)	a
Group 4 (240g)	93.5 (11.4)	bc	**9.3 (0.6)**	**cdef**	10.0 (0.9)	ab	3.1 (0.6)	abc	0.11 (0.004)	a
Group 5 (480g)	**99.9 (13.6)**	**bc**	**9.8 (0.9)**	**cde**	10.3 (1.2)	a	4.1 (1.2)	a	0.11 (0.01)	a
Shade treatments (5% light)										
Group 1 (30g)	38.4 (8.7)	f	7.6 (1.2)	efg	**4.9 (0.4)**	**f**	1.1 (0.2)	d	0.13 (0.02)	a
Group 2 (160g)	63.5 (10.1)	def	**10.4 (1.2)**	**bcd**	**6.1 (0.6)**	**ef**	1.7 (0.5)	d	0.11 (0.01)	a
Group 3 (120g)	78.9 (9.6)	cd	**11.1 (0.9)**	**bc**	**7.1 (0.5)**	**de**	1.9 (0.5)	cd	0.11 (0.01)	a
Group 4 (240g)	106.5 (20.4)	b	**12.7 (1.4)**	**b**	8.2 (0.9)	bcd	2.0 (0.4)	cd	0.12 (0.01)	a
Group 5 (480g)	**140.9 (14.3)**	**a**	**15.6 (1.5)**	**a**	9.1 (0.8)	abc	3.5 (0.8)	ab	0.11 (0.01)	a
R^2	0.64		0.68		0.54		0.43		0.10	
F	27.59***[†4]		33.44***		18.47***		11.79***		1.72	

[†1] Rhizome groups based upon initial fragment masses.

[†2] Mean +/-95% CI in parentheses.

[†3] Letters represent significant differences between groups, Tukey HSD post-hoc tests, α = 0.05.

[†4] Level of significance is indicated by the number of stars, ***p<0.001.

Table 1.3. Experiment 3: Values represent harvested *A. donax* growth parameters with associated F values. All treatments were analyzed together by parameter using ANOVA.

	Drought				Well-watered				
Parameter	5 cm[†1]	Sig [†2]	30 cm[†1]	Sig	5 cm	Sig	30 cm	Sig	F
Total plant wt. (g)	27.5 (4.7) [†4]	b	21.6 (0.4)	b	78.9 (23.0)	a	90.1 (36.7)	a	18.7***[†3]
Tallest stem (cm)	36.5 (7.6)	b	35.0 (2.5)	b	86.8 (20.7)	a	112.0 (29.3)	a	30.2***
Stem mass (g)	4.0 (0.9)	c	5.2 (0.5)	c	21.0 (6.9)	b	35.1 (18.4)	a	18.8***
Rhizome mass (g)	3.4 (2.9)	ab	0.7 (0.2)	b	11.9 (9.1)	a	12.8 (7.3)	a	5.7*
Root mass (g)	2.5 (1.1)	b	2.3 (1.0)	b	13.2 (6.6)	a	12.1 (5.5)	a	11.1***
Root Number (#)	12.5 (11.5)	c	31.0 (9.9)	b	48.8 (24.3)	ab	65.0 (31.1)	a	11.3*

[†1] Planting depth

[†2] Letters represent significant differences between groups, Tukey HSD post-hoc tests, α=0.05.

[†3] Level of significance is indicated by the number of stars, *p<0.05, **p<0.01 and ***p<0.001.

[†4] Mean +/-95% CI in parentheses.

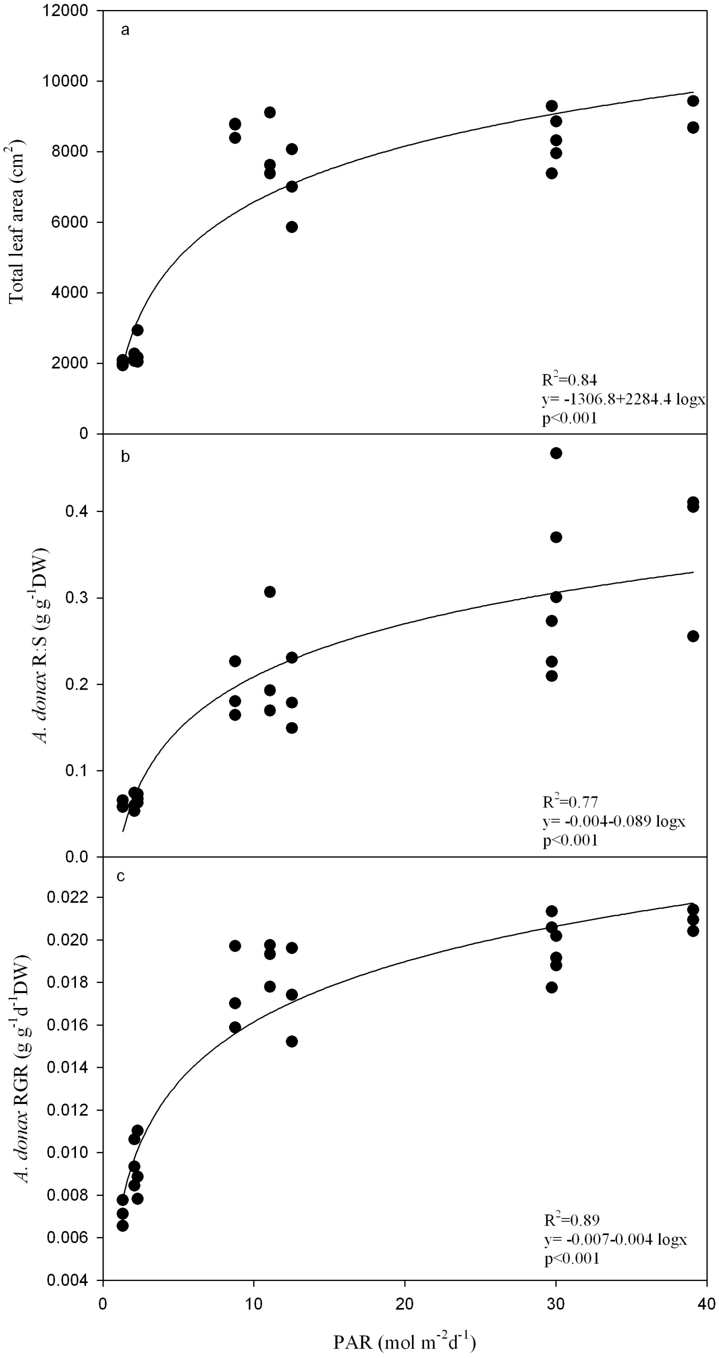

Figure 1.1. Experiment 1, harvest 2: *A. donax* plants grown in three shading treatments; 100% light (29.7-39.1 mol m^{-2}d^{-1}), 35% light (8.8-12.5 mol m^{-2}d^{-1}), and 5% light (1.3-2.3 mol m^{-2}d^{-1}). a. Total leaf area (F=133.5), b. root to shoot ratio (R:S) (F=83.9) and c. relative growth rate (RGR) (F=206.2) were best explained by logarithmic regression models.

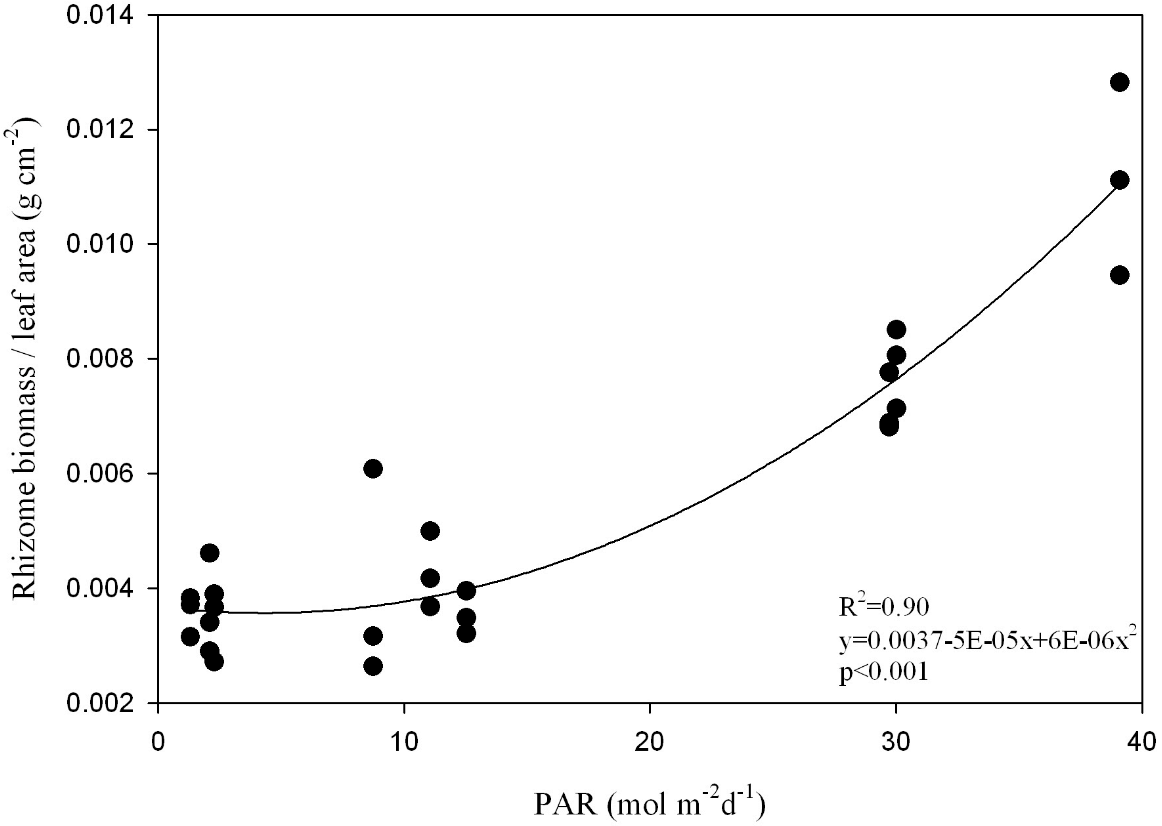

Figure 1.2. Experiment 1, harvest 2: Quadratic regression model showing the effect of shading on the proportional allocation of carbon to either storage or to maximizing leaf area for carbon dioxide aquisition in *A. donax* (F=105.5).

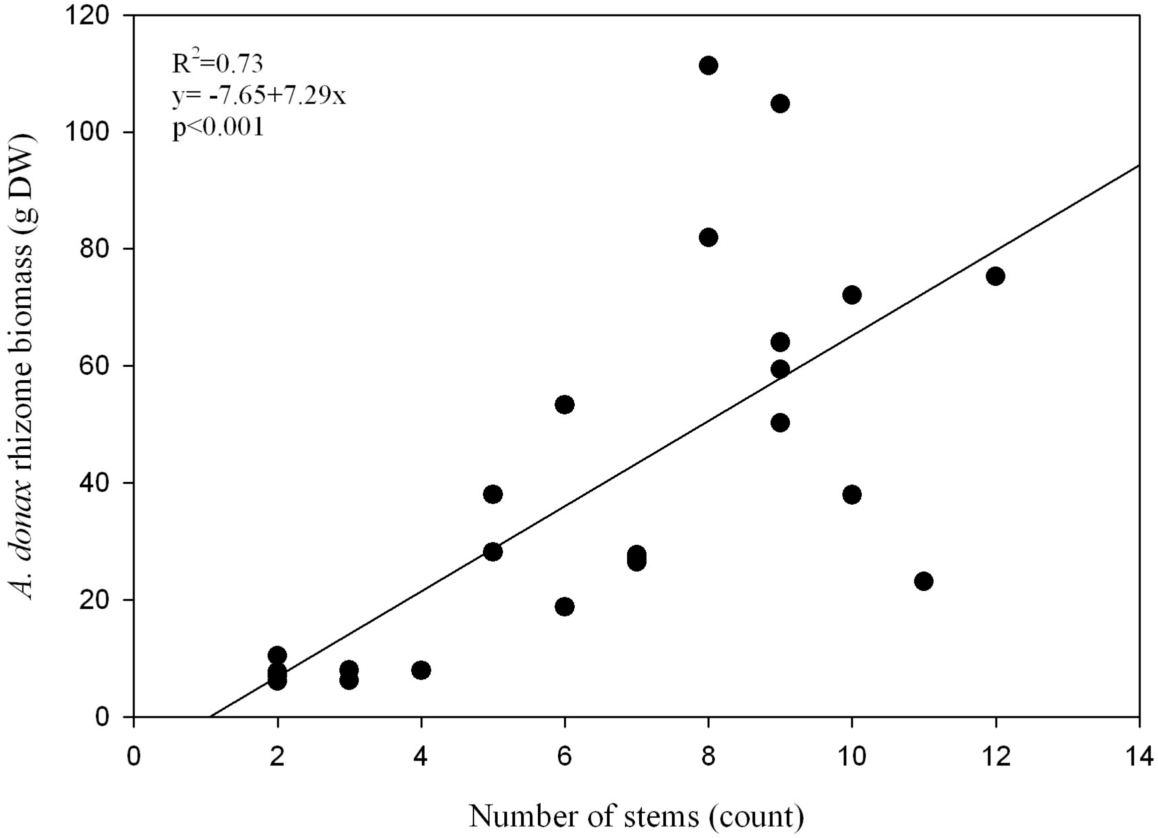

Figure 1.3. Experiment 1, harvest 2: Correlation between the total number of shoots and rhizome biomass (net) in *A. donax* (F=28.6). Plants from all treatments were included.

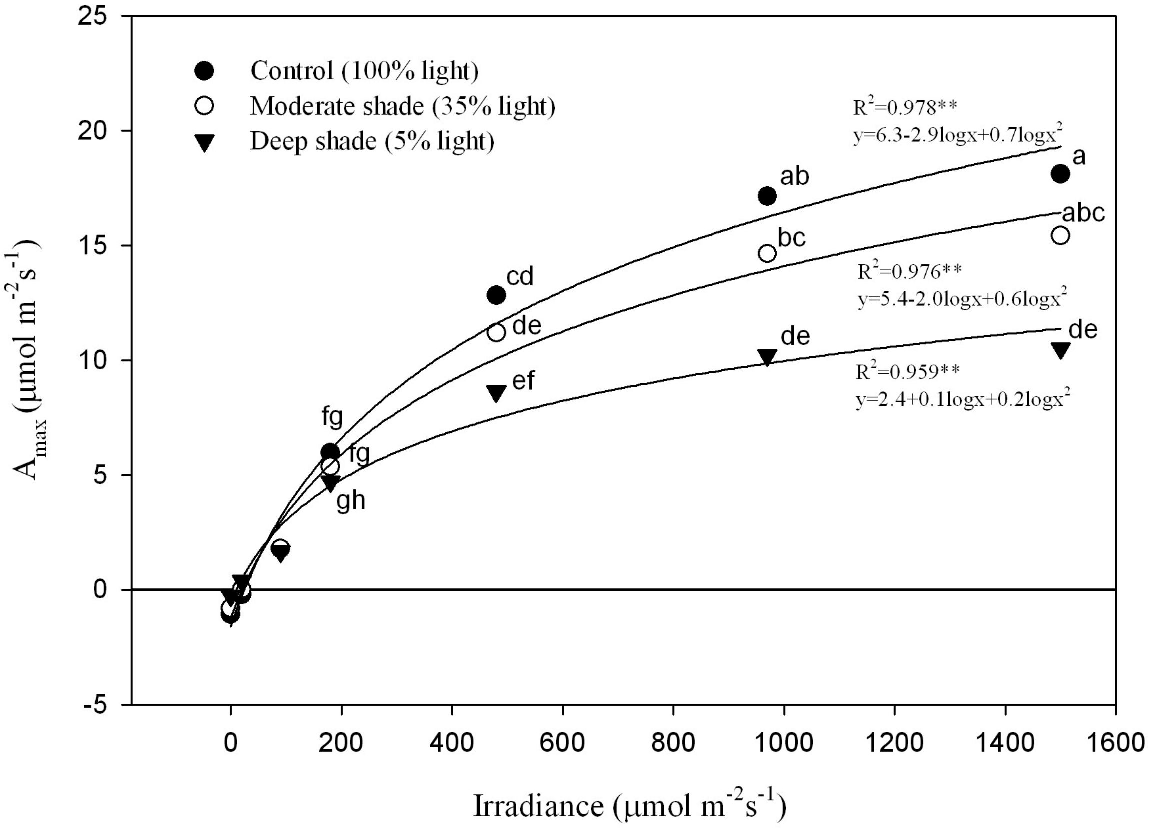

Figure 1.4. Experiment 1: Light-response curves measured on *A. donax* plants during summer 2010 under three shading treatments. Two parameter logarithmic regression models best explained the relationships among treatments; control (F=66.15), moderate shade (F=61.99) and deep shade (F=35.07). Between treatment differences were compared using ANOVA, where all treatments were analyzed together. Letters represent significant differences between treatment groups and irradiances (Tukey HSD post-hoc tests, $\alpha = 0.05$). An enlarged view of the low irradiance measurements can be found in Figure 1.5.

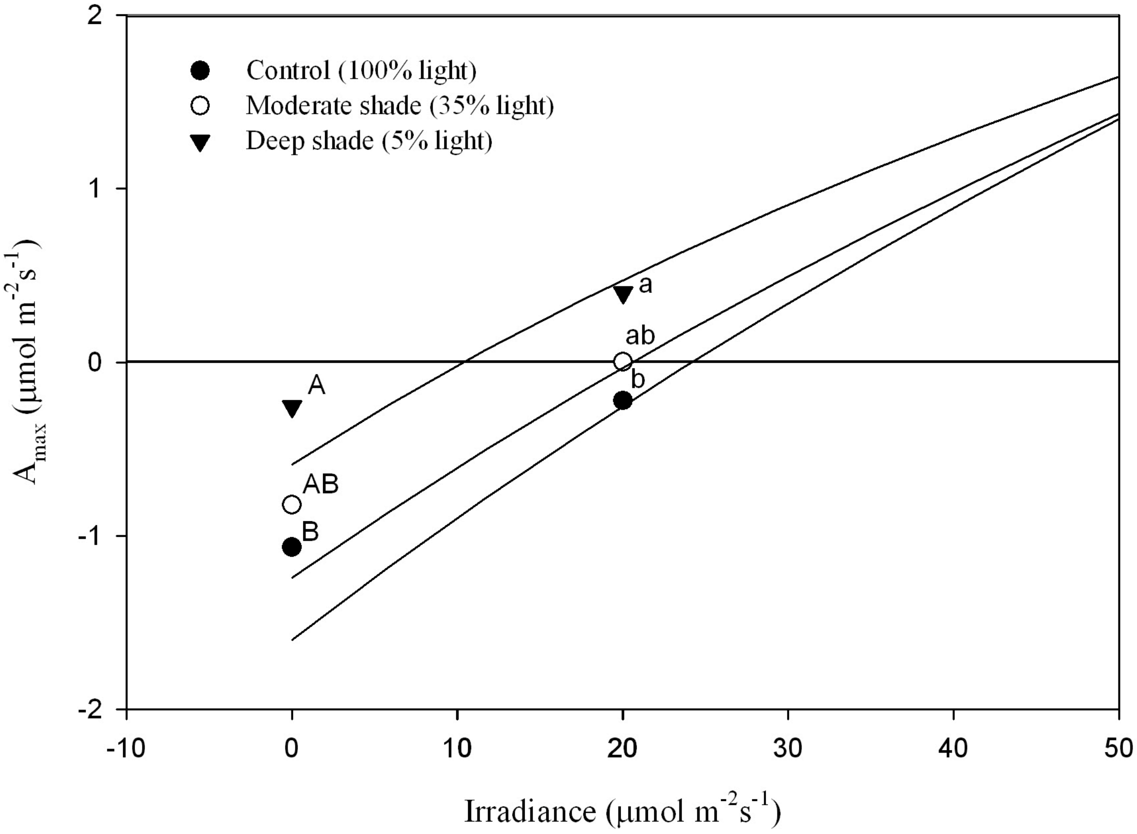

Figure 1.5. Experiment 1, harvest 2: Detail of *A. donax* light-response curves for low irradiance conditions during summer 2010. The complete set of light-response curves can be found in Figure 1.4. Letters represent significant differences between treatment groups analyzed separately at a given irradiance; A, B, C at 0 µmol m^{-2}s^{-1} and a, b, c, at 20 µmol m^{-2}s^{-1} (Tukey HSD post-hoc test, $\alpha = 0.05$).

Competitive effects of native woody species on the establishment of giant reed (*Arundo donax* L.*)*

ABSTRACT

Giant reed (*Arundo donax* L.) is an invasive hydrophytic grass found widely in southern California riparian ecosystems and throughout Mediterranean climates worldwide. Managing this species is a challenging, multi-year process, which usually requires application of herbicides. We tested whether cultural control using competitive native shrub species was sufficient to inhibit *A. donax* establishment into both a controlled competition experiment, which simulated active restoration, as well as within various mature riparian communities in the wildland. In controlled field experiments we found that mulefat (*Baccharis salicifolia*) delayed or inhibited *A. donax* establishment in all treatments, whereas sandbar willow (*Salix exigua*) facilitated invasion of *A. donax* during periods of winter dormancy. In the wildland, both soil moisture and irradiance were important in explaining *A. donax* plant growth and survival. Mature riparian communities were found to be resistant to invasion by small rhizome propagules of *A. donax*, while control treatments of the same experiment (no native canopy) were the only instances where *A. donax* plants established (1.7% of total planted). These results clearly demonstrate differences between the competitive effects of native species, potentially influencing decisions by land managers in how they restore areas prone to *A. donax* invasion. We recommend planting *B. salicifolia* at high density in the fall to achieve maximum inhibition of *A. donax* growth and establishment where *A. donax* management has occurred or where invasion is likely.

INTRODUCTION

Many wildland weeds are ruderal herbaceous species (Grime 1974, 1977), which require a temporary suspension of competitive interactions (e.g., disturbance) in order to allow successful establishment and invasion (Sakai *et al.* 2001). Clonal species can have both ruderal and competitive life stages, where vegetative reproduction facilitates competitive exclusion of neighbor plants (Wang *et al.* 2008; Quinn & Holt 2008). Active management of exotic clonal species is usually required in wildlands to reintroduce ecosystem functions lost to invasion, especially within the riparian ecosystem (Cushman & Gaffney 2010).

Frequent flooding defines the historical disturbance regime of the riparian plant community, whereby many ruderal species have evolved. Many woody riparian species can be defined as ruderal due to their small seed size, need for cross-pollination, high fecundity, rapid growth, and relatively short lifespan (Radosevich, Holt, & Ghersa 2007). Southern California riparian communities are typically not limited in either soil nutrients or soil moisture but are limited in radiation since ruderal species quickly form a closed canopy, minimizing the amount of transmitted light to the soil surface (Keddy, Fraser, & Wisheu 1998).

Arundo donax L. (giant reed, Poaceae) is a wildland exotic species that has invaded riparian plant communities in Mediterranean climates throughout the world. It is a tall, clonal plant with massive stores of carbohydrate belowground in storage stems (rhizomes) and has a growth form that is novel to southern California riparian ecosystems (Bell 1997; Quinn 2006). This growth form has recently been given a unique classification, large-statured invasive grass, a label which captures both the form and ecological hardiness of the characterized species (Lambert, Dudley, & Saltonstall 2010). *A. donax* is also fire-adapted, an adaptation that most native riparian species do not possess, allowing it to rapidly reestablish dense cover and minimize competitive interactions (Coffman 2007). These adaptations have contributed to the monotypic dominance of *A. donax* in many riparian ecosystems of the United States, creating a novel climax community in southern California (Rieger & Kreager 1989).

Typical management of *A. donax* includes aboveground (or whole plant) biomass removal followed by several applications of herbicide to control plant regrowth (Bell 1997). This type of disturbance may allow recruitment and establishment of ruderal weed species within treatment areas. Invasive species management combined with various forms of ecosystem reclamation can lead to a variety of community trajectories and altered states, including a return to the pre-invasion state (Harms & Hiebert, 2006; Suding, Gross, & Houseman, 2004; see also Chapter 3).

A goal of many researchers and land managers is to restore habitats so they are resistant to invasion (Pokorny *et al.* 2005; Funk *et al.* 2008). Many mechanisms are important in explaining the invasion process, including biotic factors such as plant diversity (Case 1990; Stohlgren *et al.* 1999; Naeem *et al.* 2000; Kennedy *et al.* 2002; Stohlgren, Barnett, & Kartesz 2003; Levine *et al.* 2003; Pokorny *et al.* 2005; Fridley *et al.* 2007), abiotic factors such as resource heterogeneity (Suding, LeJeune, & Seastedt 2004) and environmental stress (Burke & Grime 1996; Alpert, Bone, & Holzapfel 2000), or spatial-temporal combinations of factors (Pysek & Hulme 2005). Restoring for resistance requires knowledge of the dominant mechanism that facilitate invasion in a system. For example, within competitive communities exotic species that exhibit traits such as phenotypic plasticity (Sakai *et al.* 2001) or delayed senescence (Zotz, Franke, & Woitke 2000) are often successful invaders. Even in relatively resistant systems fluctuating abundance of resources and both the severity and frequency of disturbances can create abiotic derived windows for invasion to occur (Davis, Grime, & Thompson 2000; Davis & Pelsor 2001). In areas where abiotic environmental conditions are generally benign during the growing season, such as the riparian plant community, the ability to form a closed canopy may confer invasion resistance (Pywell *et al.* 2003; Galatowitsch & Richardson 2005), although the riparian community is known to be especially poor at resisting exotic invasion (Stohlgren, Barnett, & Kartesz 2003). In riparian communities found to be resistant to invasion, competition for solar radiation may be the dominant mechanism inhibiting exotic species (Quinn & Holt 2009).

If invasion occurs within an established native community competitive success may be controlled by the seasonality of the native community. Dormancy enables plants to survive unfavorable environmental conditions, but may provide a window of opportunity for invaders. Phreatophytic deciduous riparian species display winter dormancy, a process that allows understory species an opportunity for increased radiation capture and growth (Gasith & Resh 1999). Shade avoiding species may gain a competitive advantage during these periods of increased radiation.

During secondary succession, as after a catastrophic flood disturbance, *A. donax* has a competitive advantage over sexually reproducing native species. Rhizome size is positively correlated with *A. donax* shoot growth enabling rapid stem elongation (Quinn, Rauterkus, & Holt 2007), which is maximized in shaded conditions (Else 1996). *A. donax* is a shade avoiding species (Keddy, Fraser, & Wisheu 1998). Sandbar willow (*Salix exigua* Nutt.) and mulefat (*Baccharis salicifolia* (Ruiz & Pav.) Pers.) are native riparian shrubs (Baldwin *et al.* 2012) that form closed canopies and have been indicated as good competitors with *A. donax* (Rauterkus 2004; Quinn 2006). *S. exigua* represents a native winter deciduous competitor whereas mulefat represents a native evergreen competitor. These are both important species for locally occurring sensitive wildlife (Kus 2001; Sharp & Kus 2006) and can also be collected and propagated on site using the branch (pole or whip) cutting method, which allows rapid canopy development while conserving local plant genetics (Hoag 1991, 2007).

Once established, *A. donax* becomes an invasive “transformer” species (Richardson *et al.* 2000) which is defined by a species which alters the character, condition, form or nature of an ecosystem over a broad area; therefore, managing specifically for invasion resistance would be valuable for long term control of this species (Quinn & Holt 2009). Although *A. donax* is widespread in riparian communities in the southwest US, it is unknown whether it will establish and invade whenever it enters the riparian plant community. We performed three separate field experiments to test the competitive ability of *A. donax* with varying biotic (competitor species identity), spatial (competitor planting density), and temporal (competitor winter dormancy) conditions. Invasive success was measured in three field experiments including 1) a simulated restoration planting with varying degrees of competitive interaction, 2) wildland conditions to determine what community factors were important to plant survival and success, and 3) a simulated restoration planting to determine if temporal invasion windows occurred during winter dormancy of native shrubs.

Hypotheses

H1. Native shrub competitors will inhibit the growth and establishment of *A. donax* in a simulated restoration, and inhibition will increase with native planting density.

H2. *A. donax* success will be affected by competitor growth form in riparian wildland conditions of southern California.

H3. *A. donax* grown in competition for solar radiation with a native deciduous species will display increased A_{max} during periods of winter dormancy relative to non-dormancy periods, increasing the likelihood of invasive establishment.

MATERIALS AND METHODS

Study System

All experiments were conducted in Riverside County, California, with controlled experiments planted at the University of California, Riverside (UCR) and a wildland experiment planted along the Santa Ana River (city of Riverside) in the riparian plant community. Mature riparian communities were composed of phreatophytic trees (*Platanus racemosa*, *Populus fremontii*, *Salix goodingii* and *S. lasiolepis*) with an herbaceous understory and a perimeter comprised of phreatophytic and xeric shrub species (*B. salicifolia* and *S. exigua*).

Field Experiment 1: Responses to season and timing of competition

This experiment was conducted under controlled conditions within one field in the agricultural experiment station at UCR. The field was fallow for at least one year prior to planting and prepared by deep tilling the soil (60 cm) to remove compaction from prior agriculture use. Soils were part of the Arlington Series and consisted of very fine sandy loam to loam (Nelson *et al.* 1917). The field was divided in half so that seasonally replicated plantings could be made adjacent to one another.

The experimental design was a randomized complete block with five blocks, oriented in the direction of irrigation flow and three subreplicate plants per plot. Plots were 1 m^2 in size centered in contiguous 2 m^2 shallow basins to facilitate flood irrigation. *S. exigua* and *B. salicifolia* branch cuttings were soaked for seven days and planted at five monotypic densities (0, 3, 6, 9, or 12 m^{-2}) to create an additive competition design. Each block received one control (0 m^{-2}) and each of the four remaining planting densities for both native competitors, equaling nine total treatments. Seasonal plantings were split to include two temporal treatments, concurrent planting where the native shrubs were allowed to establish for 0 days and delayed planting where the native shrubs were allowed to establish for 90 days prior to the planting of *A. donax*. Thus each seasonal planting contained 90 plots (9 treatments x 5 blocks x 2 temporal treatments), where the planting season was defined by the planting of the native competitors. Seasonal plantings included spring (March 2009) and fall (September 2009). In total four planted experimental areas were created and identified by the *A. donax* planting season, including spring (concurrent planting, 2009), summer (delayed planting, 2009), fall (concurrent planting, 2009), and winter (delayed planting, 2010).

Branches of native shrubs 1 m in length were collected locally and trimmed of lateral branches and new growth before planting. Native shrub seedling recruitment into plots was minimized by choosing only male parent plants for branch propagation. Planting holes were formed with a 2.6 cm diameter drill bit to reach the desired planting depth (60 cm). Buffers 0.5 m wide surrounding the 1 m^2 plots were planted with the same species found in the plot at a density of 6 m^{-2}. A gridded 1 m^2 quadrat was used to plant either *S. exigua* or *B. salicifolia* in each plot. Between plots the quadrat was turned 90 degrees to stagger planting layouts. Due to the clonal habit of *S. exigua* each block was planted with cuttings from a single and different genet. To ensure inclusion of multiple genotypes of *S. exigua* collections were made at various locations across southern California.

All *A. donax* plants were collected as rhizome fragments from a local source, trimmed to a standard size (245+/-5g), and held at 4 C until planting. Rhizomes were planted equidistant, three per plot to a depth of 1 cm, and served as subsamples. Fertilizer (Scott's slow-release Osmocote, 14-14-14) was applied to the soil surface at the time of native planting at a rate of 71 g m^{-2} and at three month intervals. This is the labeled rate for planting bedding plants. Irrigation was initially by drip for four hours, twice a week (T-tape: T808HR, 38 L $hr^{-1}plot^{-1}$). The drip system was replaced by PVC piping with adjustable irrigation bubblers in July 2009 due to repeat animal damage. Both methods flooded the shallow 2 m^2 basins that held the individual plots.

Measurements

A. donax emergence was recorded daily until all plants had emerged. Leaf area index (LAI) for native shrub canopies and growth parameters for *A. donax* were taken biweekly. LAI was determined using a 1 m long leaf area sampler (SunScan Canopy Analysis System, SS1-UM-1.05, Delta-T Devices Ltd, www.delta-t.co.uk) and measured between 10 am and 2 pm prior to *A. donax* harvest. The mean of three measurements per plot was used for treatment comparisons. Transmitted light (photosynthetically active radiation, PAR) was sampled and converted by this device to LAI ($\tau_{diff}^{(x,L)} = 1/\pi * \int_0^{\pi/2} 2\pi*\sin(\theta)*\cos(\theta)^{(-K(x,\theta)*L)} *d\theta$; where τ = transmission fraction of diffuse light, L = canopy leaf area index, d= direct beam of light, θ = zenith angle of a direct beam of light) (Lambert, Peeters, & Toussaint 1999). The number of growing days varied by planting date so destructive *A. donax* harvests were conducted when *A. donax* plants from the control treatments (no native canopy) surpassed the mean native shrub height in planted treatments: spring (91 days), summer (99 days), fall (229 days) and winter (155 days). Fresh and dry weights were recorded separately for shoots and rhizomes. Roots were not collected due to the inherent difficulty and inaccuracy in field collecting methods. Dependent variables that were measured included stem height (height of tallest stem), number of stems, shoot mass, rhizome mass, total mass, relative growth rate (RGR) and native canopy LAI. *A. donax* establishment was determined by the difference between maximum *A. donax* stem height and mean height of the competing native species per *A. donax* plant. Plants taller than the native competitor were classified as “established”. *A. donax* establishment is defined here as the stage when solar radiation becomes non-limiting, specifically when the shoot apex breaches the native canopy. After this point, long-term survival is assumed with *A. donax* suppressing native competitors over time.

When the fall field was planted all *A. donax* plants were individually caged with poultry fencing (25 cm diameter by 40 cm tall cylinder) to prevent grazing from rabbits. This method provided effective protection from grazing. Analyses of the fall or winter plantings do not include *S. exigua* treatments due to destructive rabbit grazing of the native shrubs.

Field Experiment 2: Competition in native riparian communities

Field experiment 2 was conducted in a wildland area along the Santa Ana River in spring to summer 2010. Sites were chosen based upon proximity to the active river channel and presence of desired native species, which were used as native canopy treatments. Three sites were chosen as study locations. Site 1 was located at Hidden Valley Wildlife Area (Norco, CA; 33.97 N, 117.49 W) while Sites 2 and 3 were located adjacent to Martha McLean – Anza Narrows Park (Riverside, CA; 33.97 N, 117.42 W). All sites were located within the floodplain but outside of the active channel. This minimized the risk of flood disturbance and loss of invasive propagules downstream (request by land manager). Soils at all three sites were similar having high porosity with texture consisting mostly of coarse sand and low abundance of silt and clay, typical of riparian floodplains. The climate was mild during the course of the experiment with a monthly? Weekly? Daily? mean high of 40.7 C of and a mean low of 5.2 C air temperature measured at the nearest weather station, U. C. Riverside #44 (33.965 lat; -

117.337 long; elevation, 313 m). Treatments were defined by the species composition of the native canopy and included native mature riparian woodland (mixed riparian trees), sandbar willow (*S. exigua*), mulefat (*B. salicifolia*), or control (no native canopy). *A. donax* rhizome fragments were collected and processed as in field experiment 1 but standardized to 30 +/-2 g, each with one obvious bud.

The experiment was established as a completely randomized split plot design with four native canopy treatments, each split by grazing treatment (*A. donax* caged or not), and ten replicates, for a total of 40 split plots for each of three sites and 240 rhizomes total. *A. donax* rhizomes were planted to 1 cm in depth (Apr. 2, 2010). Soils were moist during planting and plants were left to establish under natural conditions for five months. Caged plants were protected from aboveground grazing with mesh cages fixed in a cylinder to a 60 cm wooden stake, leaving a 25 cm diameter by 45 cm tall fixed cage (Vexar plastic netting, 6.4 mm mesh, OV 7822, www.industrialnetting.com). This cage was designed to inhibit rabbit grazing, the most common grazer observed at these sites.

Measurements

Plant height, soil temperature and moisture, and LAI below the native canopy were sampled April 2, June 2, July 28, and September 10, 2010. All plants were destructively harvested on the final sampling day to assess biomass.

Field Experiment 3: Physiological responses to mature riparian canopies

Native plantings from field experiment 1 (spring and summer) were reused for field experiment 3. Eight months elapsed between the final *A. donax* harvest in field experiment 1 and the planting of new rhizomes in field experiment 3 (May 2010). Shrubs were 1.25 yr old, mature and 2 m tall at the time of planting. This experiment was established as a randomized complete block design with 10 blocks. Rhizomes were collected, processed, planted and fertilized as in field experiment 1 but standardized to 50 +/-2g. Three rhizomes were planted in each of 90 plots and plants were allowed to establish for four months prior to initial physiological measurements.

One month after planting, rabbit grazing was observed, prompting individual caging of all ungrazed plants. Since most plants had been grazed prior to caging the experimental design could no longer be analyzed as blocks, degrading it to a completely randomized design. At least 3 replicate plants were caged per planting treatment.

Measurements

During experimental planning instantaneous maximum photosynthetic CO_2 assimilation (A_{max}) was measured on mature *A. donax* sun leaves (spring 2009) in order to calibrate which leaves had maximum rates per shoot. These plants were located on the UCR campus. Fully expanded leaves numbered five to eight, counting fully open leaves from the shoot apex and moving down the stem, were found to have similar, high A_{max}. A_{max} was measured at three time points including pre-dormancy (fall 2010), dormancy (winter 2011) and post dormancy of native deciduous species (spring 2011) using either a CIRAS-1 (www.ppsystems.com) or LI-6400 (www.licor.com) portable photosynthesis system. Both devices provided comparable data. For each experimental plant, leaf number 6 (± 1 leaf), was measured unless that blade was damaged. If the total number of leaves was less than six, the broadest, healthiest leaf was chosen for measurement. All measurements were made between 10 am and 2 pm under natural, incident light conditions (direct and diffuse light) where the cuvette was oriented toward the direction of the sun. LAI of the native canopy was measured as in field experiment 1. During spring 2011 light-response curves (0-1500 μmol $m^{-2}s^{-1}$) were measured on fully induced *A. donax* leaves per experimental treatment. It was determined that A_{max} did not significantly vary between planting density treatments (data not shown), so values were averaged over native competitor treatments in the experimental analysis. Due to grazing, replicates varied per treatment including no canopy control (3 plants), *S. exigua* (12 plants) and *B. salicifolia* (11 plants). A second round of growth measurements were taken during spring 2012 (May 2012) on both native competitor height and maximum *A. donax* stem height. No destructive harvests were made on *A. donax* plants.

Data Analysis

For field experiment 1, growth parameters were analyzed using a two-way ANOVA assuming a split-plot design to encompass variability from seasonal plantings. Comparisons between treatments were made with Tukey HSD post-hoc tests. All statistical tests for field experiment 1 used the statistical program Statistix 9 (http://www.statistix.com/). Slope analysis was performed for regressions using large-sample *Z* test for parallelism (Kleinbaum & Kupper 1978). For field experiment 2 a survival analysis (Gehan-Wilcoxon Test) was conducted to compare treatments for size and biomass of *A. donax*. High variability and plant mortality allowed only nonparametric statistical testing. For field experiment 3 a one-way ANOVA was used when comparing photosynthetic rates. Comparisons between treatments were made with

Tukey's HSD post-hoc tests. All statistical testing for field experiments 2 and 3 used the statistical program JMP version 9 (SAS Institute, Cary, North Carolina, USA).

RESULTS

In the controlled competition experiment (field experiment 1), a total of 92 of 360 *A. donax* plants were classified as established in all four seasonal plantings (Table 2.1). Of these, 32 plants established in competition with native shrubs (*S. exigua*, 23; *B. salicifolia*, 9) and 60 were control plants, grown with no competition. A vast majority of the establishing plants were observed in the spring planting (*S. exigua,* 21; *B. salicifolia*, 5) with all other plants establishing in summer (*S. exigua*, 2) and winter (*B. salicifolia*, 4) (Table 2.1).

In order to further evaluate reasons for differences in *A. donax* success, growth parameters were evaluated by planting season, native competitor identity, and native planting density in field experiment 1 (Tables 2.2 and 2.3). Stem height was reduced in *B. salicifolia* treatments in the fall and winter plantings, which was not observed in the spring and summer plantings. This inhibition of shoot elongation was also observed in the plants studied for their physiological responses to mature riparian canopies (field experiment 3) (Fig. 2.1).

The spring planting of the season and timing of competition experiment (field experiment 1) had limited competitive effects on *A. donax* growth overall; only plants grown with *B. salicifolia* (12 m^{-2}) displayed a significant ($p<0.05$) decrease in all growth parameters, including stem number, and shoot, rhizome and total plant mass relative to control plants (Tables 2.2). All other seasonal plantings of this field experiment had significant reductions in growth parameters associated with *B. salicifolia* treatments relative to control plants (Tables 2.2 and 2.3). Competitive effects increased with native planting density, except for the fall rhizome mass of *B. salicifolia* (6 m^{-2}). *S. exigua* had limited competitive effects on *A. donax* growth (mass), with spring and summer plantings each having one treatment displaying either above or belowground competitive effects (spring, 6 m^{-2}; summer 9 m^{-2}), but never both. In terms of height, *S. exigua* had no effect or increased mean *A. donax* height relative to the control (summer 3 m^{-2}). Variables which explained the greatest variation between treatments included total mass (spring, 38.6 percent) and native canopy LAI (summer, fall and winter; 80.4, 89.3 and 87.0 percent, respectively, data not shown). When LAI was found to explain the greatest variation in the dataset it was always due to the dense shading from *B. salicifolia* treatments.

Figure 2.2 compares transmitted light, total plant biomass and RGR between all seasons and treatments in field experiment 1. The summer planting showed increased light attenuation in both native species with increasing planting density relative to the control plants (Fig. 2.2 a, $F=22.56$, $p<0.001$), where *B. salicifolia* had an equal or greater ability to attenuate light over all seasonal plantings than *S. exigua*. For all experimental seasons *A. donax* RGR (based upon total mass) was only reduced relative to the control plants when there was also a significant reduction in radiation related to native canopy shading (Fig. 2.2 b). *B. salicifolia* reduced *A. donax* RGR in all seasons but spring, except for the summer 3 m^{-2} treatment. *S. exigua* never affected *A. donax* RGR, except for the summer 9 m^{-2} treatment where it was reduced. Linear regression analysis of the delayed plantings, including all planting treatments, showed significant relationships between *A. donax* plant biomass and transmitted PAR (summer, $R^2=0.62$, $p<0.001$, df=44; winter, $R^2=0.51$, $p<0.001$, df=44), with PAR positively correlated with plant growth (Fig. 2.3). Slope analysis found no difference between summer and winter plantings ($Z=1.10$, $p=0.125$).

Wildland-planted *A. donax* rhizomes in native riparian communities (field experiment 2) had very low rates of survival, with 21 of 240 plants surviving for five months (data not shown). Of these, only four plants were healthy, growing vigorously, and classified as established. These were from the no native canopy control treatment at site 1. Relative to these control plants, all competitive treatments inhibited *A. donax* growth when comparing total biomass (Fig. 2.4 a) and height (Fig. 2.4 b). Only living *A. donax* plants were compared in these analyses including no native canopy (4 plants, site 1), *S. exigua* (5 plants, site 3), *B. salicifolia* (1 plant, site 2) and mixed riparian tree (5 plants, site 1; 6 plants, site 2). Native plant composition was an important factor in explaining the variation in *A. donax* survival at two of the three sites using survival analyses, including site 2 ($X^2=22.76$, df=3, $p<0.001$) and site 3 ($X^2=27.75$, df=3, $p<0.001$), where *B. salicifolia* treatments always had short *A. donax* survival times (data not shown). Soil moisture and available PAR were correlated with *A. donax* survival (Fig. 2.5 and 2.6). A linear relationship was found between soil moisture and *A. donax* survival ($F=38.3$, $p=0.009$, $r^2=0.93$; Fig. 2.5), and a quadratic relationship was found between transmitted PAR and *A. donax* total biomass ($F=118.8$, $p<0.001$, $r^2=0.95$; Fig. 2.6). *B.*

salicifolia had the greatest impact on *A. donax* establishment, inhibiting both growth and survival relative to the control.

In response to riparian canopy treatments (field experiment 3), A_{max} of *A. donax* remained low in fall and winter months under *S. exigua* (<10μmol $m^{-2}s^{-1}$) and *B. salicifolia* (<5μmol $m^{-2}s^{-1}$) treatments (Fig. 2.7). A_{max} increased several fold from the winter to the spring season *S. exigua* (<30μmol $m^{-2}s^{-1}$) and *B. salicifolia* (<15μmol $m^{-2}s^{-1}$) treatments. *A. donax* control plants always had higher A_{max} than under *B. salicifolia* treatment plants. Plants under *S. exigua* treatments had A_{max} values that were equal to control plants in fall and spring seasons, displaying significantly diminished A_{max} only in the winter season. Plants in competitive treatments with *B. salicifolia* had diminished A_{max} relative to those with *S. exigua* in all seasons but fall. The winter sampling period displayed the only season where all three treatments had significantly different A_{max}, where *S. exigua* plants remained unchanged and *B. salicifolia* plants decreased A_{max} relative to fall measurements.

To explain the mechanism allowing this competitive advantage found in *A. donax* plants under *S. exigua* canopies, light-response curves were measured on *A. donax* leaves during spring 2011 sampling (field experiment 3). No differences were found in *A. donax* light-response curves between the no-native canopy control treatment plants and the *S. exigua* treatment plants, and neither group was found to light-saturate at high irradiance (1,500 μmol $m^{-2}s^{-1}$) (Fig. 2.8). *A. donax* plants under *B. salicifolia* became light-saturated at ~500 μmol $m^{-2}s^{-1}$. Values of A_{max} differed between *S. exigua* and *B. salicifolia* treatments, where irradiance greater than 120 µmol $m^{-2}s^{-1}$ always produced greater A_{max} in *S. exigua* treatments.

In all seasons, transmitted light was higher in the *S. exigua* treatment than the *B. salicifolia* treatment. Mean seasonal values of transmitted light under native shrub species were 110 (fall), 261 (winter) and 222 µmol $m^{-2}s^{-1}$ (spring) for *S. exigua* and 50 (fall), 90 (winter) and 134 µmol $m^{-2}s^{-1}$ (spring) in *B. salicifolia* (data not shown). Photosynthetic acclimation of *A. donax* was found in both *S. exigua* and *B. salicifolia* treatments relative to the control treatment plants, and *A. donax* under *B. salicifolia* was significantly more acclimated at very low light conditions than both the *S. exigua* and control treatments (Fig. 2.9).

DISCUSSION

Competitive effects from native shrub species

In this research, the growth of the riparian invader, *A. donax*, was reduced to the point of competitive exclusion by the native riparian shrub, *Baccharis salicifolia*, in both environmentally controlled (field experiments 1 and 3) and wildland experiments (field experiment 2). Competitor identity has been correlated with competitive reductions in *A. donax* growth in previous studies (Coffman 2007; Quinn & Holt 2009). In a common garden competition experiment, Quinn and Holt (2009) found that whenever *B. salicifolia* was in competition with *A. donax* there was an inhibitory effect on *A. donax* growth, which was not observed when *A. donax* was in competition with either a riparian tree (*Salix goodingii*) or wetland rush species (*Schoenoplectus pungens*) (Quinn & Holt

2009). In a wildland experiment, Coffman (2007) found that both *B. salicifolia* and a riparian tree species (*Salix laevigata*) had negative competitive effects on *A. donax* mass under high soil moisture, light, and nutrients. In those studies a focus was placed on aboveground interactions and not belowground carbon storage and rhizome growth of *A. donax*. Our results of the environmentally controlled competition experiments (field experiments 1 and 3) indicated that older, denser plantings of *B. salicifolia* had the greatest inhibitory effect on both above and belowground carbon pools; however, even at the sparsest planting density (3 m^{-2}) strong competitive effects were also evident.

Conducting our research in the controlled setting of an agricultural field (field experiments 1 and 3) minimized the confounding factor of soil heterogeneity, texture, and moisture, while the comparably short establishment period gave insights into the competitive effects of native species identity and planting density of a simulated restoration. Our results support H1in that native competitor identity and planting density had additive negative effects on *A. donax* growth and were most effective at inhibiting establishment when *B. salicifolia* was older (delayed planting). Similarly, when *A. donax* invasion was simulated in fall, establishment and growth were inhibited by the perennial native *B. salicifolia*, likely due to the slower growth and approaching dormancy of *A. donax*. Our results agree with both the Quinn and Holt (2009) and Coffman (2007) studies in that all three studies identified *B. salicifolia* as an important competitor with *A. donax*.

We have shown that competitive exclusion of *A. donax*, or failure to establish, was found in both environmentally controlled (field experiments 1 and 3) and wildland experiments (field experiment 2). Our definition of *A. donax* establishment, being the point when the shoot apical meristem of *A. donax* surpasses the mean native competitor in height, may lead to difficulty resolving differences between our results and other related *A. donax* competition studies (Coffman 2007; Quinn & Holt 2009). It should be mentioned that a lack of establishment in field experiment 1 may not be equivalent to competitive exclusion, due to the protracted 3 to 6 month growing period. If these experiments were conducted for a longer period there would undoubtedly be more *A. donax* plants classified as "established". That being said, results from our longer-term study (field experiment 3) found that under non-limiting soil moisture and nutrients, 1.25 yr old restoration plantings of *B. salicifolia* competitively excluded *A. donax* establishment, no matter the original planting density, for a period of at least two years. Shading from the native canopy was found to drive this competitive inhibition during early growth (see chapter 1) with root competition assumed to play a reduced role (see Chapter 1; Lamb et al. 2009). These results differ from the Quinn and Holt (2009) and Coffman (2007) studies, both of which found that *A. donax* was consistently able to establish under native riparian species. The discrepancy in these results is likely due to differences in native plant age upon *A. donax* rhizome planting, experimental conditions, and how establishment was quantified. Both the Quinn and Holt (2009) and Coffman (2007) studies simulated competition using immature native plants, similar to our field experiment 1, and the Coffman study was conducted in a wildland setting where other biotic and abiotic factors might influence competitive outcomes. Overall, both this research and the work of Quinn and Holt (2009) and Coffman (2007) showed that competition can be an important factor in riparian invasion. A similar study conducted in a wildland setting in Europe found that biotic interactions were directly related to invasion resistance to *Acer negundo* into the upper Rhone River by a native intermediate successional species with a greater growth rate, *Alnus incana* (Saccone *et al.* 2012).

Under wildland conditions (field experiment 2), the *B. salicifolia* canopy was again found to create the most competitive environment, with native canopy, available radiant energy, and soil moisture having strong inhibitory effects on *A. donax* growth and survival. Soil moisture has been linked to decreased performance in young *A. donax* plants (Perdue 1958) and more generally with success of establishing species of riparian plant communities in Mediterranean climates due to the high soil porosity and fluctuating pools of soil water (Else 1996; Pettit, Neil & Naiman 2006). A riparian study conducted in the water-limited southwestern United States found that competitive shading from a native riparian tree (*Populus deltoides*) was linked to reductions in cover of an established exotic invasive shrub species (*Tamarix ramossisima*) (Taylor, Smith, & Haukos 2006). Similar results were found in a meta analysis conducted by Levine et al. (2004), which found that both biotic and abiotic factors were important in resisting invasion or slowing the rate of invasion in wildlands. In the wildland experiment reported here, a total of four plants all found in one control treatment were classified as established. This represented one extreme of the survival spectrum, as most plants emerged and soon failed. Here, in contrast to the controlled field experiments, soil moisture, radiation, and other environmental variables could have been limiting, leading to plant failure in all competitive environments. These results supported H2 in that the competitor's growth form affected *A. donax* success, with shrub species having the greatest effect, similar to controlled experiment results. In addition, results suggest that if small rhizome fragments of *A. donax* invade a mature riparian plant community, no matter the species makeup, it will most likely fail to establish if soil moisture is limited.

Seasonal effects

A. donax plants were observed to be semi-dormant in the fall and winter months of 2009, a period when very little shoot growth occurred (field experiment 3). Perennial species often have a seasonal shift from above to belowground allocation of photosynthates in advance of dormancy; this shift in *A. donax* results in production of new rhizome and root tissues (Dudley 2000; Decruyenaere & Holt 2001). This pattern has also been observed in common reed (*Phagmites australis*), a relative of *A. donax*, prior to dormancy (Soetaert *et al.* 2004). The semi-dormant period of *A. donax* overlapped the leafless winter dormancy period of *S. exigua*. Although *A. donax* plants displayed depressed photosynthetic rates in both the *S. exigua* and *B. salicifolia* treatments relative to control plants in the winter, *A. donax* in the *S. exigua* treatment was more photosynthetically active than in the *B. salicifolia* treatment. The dormant period of *S. exigua* created an environment with a higher likelihood of future invasion, allowing *A. donax* to potentially capture more radiant energy, increasing rhizome mass at a more rapid rate than when growing with *B. salicifolia*.

In the same experiment, in the spring of 2012 when the *A. donax* plants were nearly two years old, successful establishment was observed in all *S. exigua* treatment plots. This result was not observed in any *B. salicifolia* plots, where *A. donax* plants survived but were unhealthy and stunted. These results support H3 but conflict with our findings from the wildland experiment (field experiment 2) where very few *A. donax* rhizomes established. The differences in these studies are likely due to the non-limiting soil resources (water and nutrients) supplied to the experimental plants in field experiment 3. These plants remained photosynthetically active throughout the experiment, whereas plants from the wildland experiment encountered extended periods of drought under shrub canopies, likely reducing *A. donax* stomatal conductance, total carbon gain and therefore, potential for successful invasion (Butterfield, Rogers, & Siemann 2004; Quinn & Holt 2008).

Effects of competition on *A. donax* photosynthesis

All *A. donax* plants grown in competition had higher photosynthetic rates at very low PAR relative to control-grown plants (field experiment 3). These low light conditions were similar to the measured PAR of the native shrub competitive environments, indicating that *A. donax* had the ability to acclimate to shade, as do many woody perennial species (Bjorkman 1981). Photosynthetic acclimation to shade develops in juvenile leaves in response to the quantity and quality of radiation in their growth environment. As with shade tolerant species, the photosynthetic systems of shade acclimated leaves are optimized to maximize carbon gain while minimizing cellular respiration which effectively lowers the intensity of irradiance needed to achieve the light compensation point relative to sun leaves (Boardman 1977; Givnish 1988; Walters 2005). This is one explanation why, under the deep shade canopy of *B. salicifolia*, *A. donax* plants survived for multiple years without succumbing to carbon starvation (field experiment 3).

Factors important to invasion success

From the whole of our field research, three factors appeared to be important in explaining the successful invasion of *A. donax* into *S. exigua* treatments. These included photosynthetic acclimation to low intensity irradiance by *A. donax*, elevated PAR under *S. exigua* in both immature and mature shrub canopies relative to *B. salicifolia* canopies, and winter dormancy of the native competitor. As in the *B. salicifolia* treatment, photosynthetic acclimation to shade facilitated *A. donax* survival in the *S. exigua* treatment when soil moisture and nutrients were non-limiting, which was not observed in the wildland field experiment 2. Increased PAR under *S. exigua* canopies relative to *B. salicifolia* canopies gave a competitive advantage to *A. donax* in these treatments, resulting in more massive plants (field experiment 1). The winter dormant period of *S. exigua* provided a window of time where elevated PAR increased the rate of carbon storage and rhizome growth of *A. donax* (field experiment 3), facilitating future invasion of the shrub canopy.

A possible factor that might explain the shade growth response and success of *A. donax* is a process known as dynamic photosynthetic acclimation (Athanasiou *et al.* 2010). Analysis of light-response curves indicated that *A. donax* plants grown under *S. exigua* canopies displayed both photosynthetic acclimation under low irradiance conditions and did not light-saturate at high irradiance, as was found in the *B. salicifolia* treatments. Until recently, photosynthetic acclimation was only thought to occur in juvenile leaves. In the Athanasiou et al. (2010) study, Arabidopsis (*Arabidopsis thaliana*) plants that were capable of dynamic acclimation were found to attain elevated A_{max} at both low and high irradiance by altering the ratio of chlorophyll a/b, without altering the total chlorophyll content (Murchie *et al.* 2002). This process of dynamic acclimation required a minimum of one week of high light conditions, suggesting that within our study winter deciduousness in the *S. exigua* treatment may be sufficient to allow dynamic acclimation to occur in *A. donax* (Athanasiou *et al.* 2010). If correct, this would allow *A. donax* an increased ability to take a greater advantage of sunflecks (short periods of full light filtering through the native canopy) when in competition with *S. exigua*, due to the increased transmitted PAR found under the *S. exigua* canopy, than when in competition with *B. salicifolia*. Sunfleck size and quantity are both important in understanding carbon gain and should be quantified in future experiments (Chazdon & Pearcy 1986a; b). If supported in future work, it may provide an explanation for why this species has been such a successful invader in Mediterranean and other winter deciduous riparian ecosystems worldwide.

Conclusions

Results of this research suggest that the probability of invasion by a small rhizome fragment of *A. donax* into an established riparian plant community is low in wildlands. We found several factors which affected the odds of successful invasion of *A. donax* including biotic factors (native competitor growth form, canopy LAI, and planting density) and abiotic factors (soil moisture and establishing season). Past studies have indicated that total soil nitrogen (Quinn, Rauterkus, & Holt 2007), as well as disturbances like flood (Bell 1997) and fire (Coffman, Ambrose, & Rundel 2010) are correlated with *A. donax* invasion. These environmental factors (soil and disturbance), which have been found to increase the probability of *A. donax* invasion, are frequently met in low elevation urban riparian systems. Flood disturbance removes biotic competitors, disperses *A. donax* stem fragments, wets soils, and deposits nitrogenous compounds from urban runoff. We found that in these disturbed systems competitor identity had the strongest inhibitory effect on invasion by *A. donax*. Specifically, the xeric shrub *B. salicifolia* was the strongest competitor in both simulated restoration plantings and in the wildland, leading to greater invasion resistance overall.

IMPLICATIONS FOR MANAGEMENT

The use of a native species to impose cultural control of an exotic invasive species has many benefits including the immediate creation of habitat for sensitive wildlife, monetary savings on long term weed management and total applied herbicides, and a reduction of the total applied herbicide. Our recommendations agree with those of Quinn (2006) who suggested that restoration designs should focus on species identity when considering invasion resistance of *A. donax* as a restoration goal. To optimize habitat value, we recommend planting *B. salicifolia* at a high density in order to produce cover quickly, with other native herbs, shrubs, and trees planted at a lower density to provide variable structure, habitat and forage for wildlife. When *B. salicifolia* is planted for invasion resistance, it should be planted at a minimum of one meter spacing between plants and with a sex ratio equal to that of the local ratio, or 1:1 if not known. The recommended time to plant is in the fall as this planting season has been shown to be most effective in inhibiting *A. donax* establishment, with *A. donax* winter semi-dormancy providing a window of opportunity for native shrubs to establish robust canopies prior to active *A. donax* shoot growth.

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Table 2.1. Values indicate the number of established[1] *A. donax* plants at the time of harvest per experimental season, by native competitor and by native planting density.[2]

Treatment	Planting season				Total
	Spring 2009	Summer 2009	Fall 2009	Winter 2010	
No native competitor	15	15	15	15	60
S. exigua (3 m^{-2})	5	2	NA	NA	7
S. exigua (6 m^{-2})	7	0	NA	NA	7
S. exigua (9 m^{-2})	2	0	NA	NA	2
S. exigua (12 m^{-2})	7	0	NA	NA	7
B. salicifolia (3 m^{-2})	1	0	0	3	4
B. salicifolia (6 m^{-2})	3	0	0	0	3
B. salicifolia (9 m^{-2})	0	0	0	1	1
B. salicifolia (12 m^{-2})	1	0	0	0	1
Total	41	17	15	19	92

[1] See text for definition of establishment.

[2] Fifteen rhizomes were planted per experimental treatment for a total of 540. Due to rabbit herbivory of *S. exigua* shrubs in the fall and winter seasons, 420 *A. donax* plants were used in the analysis.

Table 2.2. Field experiment 1: Concurrent plantings of *A. donax* (spring and fall).
Values indicate mean (+/-95% CI) *A. donax* growth parameters when in competition with differing densities of native shrub species. Bold text indicates values significantly different from that of the control (Tukey's HSD post-hoc tests p<0.05).

Treatment	Stem ht. (cm)	Stem num. (count)	Shoot wt. (g DW)	Rhizome wt. (g DW)	Total wt. (g DW)
		Spring concurrent planting			
Control (0 m^{-2})	105.8 (8.9)	10.4 (2.1)	217.6 (28.7)	115.9 (14.8)	333.5 (41.6)
S. exigua (3 m^{-2})	101.9 (12.8)	10.5 (1.8)	221.0 (45.1)	121.7 (16.2)	342.7 (58.4)
S. exigua (6 m^{-2})	101.9 (13.6)	7.9 (1.1)	**168.3 (26.2)**	101.0 (13.2)	**269.3 (28.2)**
S. exigua (9 m^{-2})	106.2 (11.8)	11.0 (2.9)	227.1 (47.2)	114.8 (15.7)	341.8 (61.0)
S. exigua (12 m^{-2})	124. 1(14.0)	8.7 (2.1)	224.9 (41.2)	113.9 (16.5)	338.8 (54.9)
B. salicifolia (3 m^{-2})	105.8 (10.2)	10.5 (1.8)	221.1 (37.4)	113.2 (12.0)	334.2 (45.8)
B. salicifolia (6 m^{-2})	106.8 (14.5)	8.0 (1.9)	190.7 (26.3)	107.5 (9.6)	298.2 (32.7)
B. salicifolia (9 m^{-2})	101.0 (9.6)	8.5 (2.6)	177.9 (28.5)	100.1 (9.2)	278.0 (35.6)
B. salicifolia (12 m^{-2})	100.4 (11.5)	**7.6 (1.6)**	**158.8 (21.9)**	**97.0 (9.0)**	**255.8 (29.2)**
Treatment effect (%)	13.5	35.1	37.6	24.3	38.6
$F_{(8, 134)}$	0.64	2.30*	2.70*	1.53	2.89*
		Fall concurrent planting			
Control (0 m^{-2})	72.8 (8.9)	11.8 (2.3)	120.0 (34.1)	97.3 (14.9)	217.4 (48.1)
B. salicifolia (3 m^{-2})	62.9 (12.8)	**6.6 (1.8)**	**45.4 (16.1)**	**75.5 (7.3)**	**120.9 (21.6)**
B. salicifolia (6 m^{-2})	72.5 (7.6)	**7.1 (1.3)**	**46.2 (14.9)**	78.8 (6.4)	**125.0 (20.3)**
B. salicifolia (9 m^{-2})	64.7 (14.0)	**4.8 (1.6)**	**27.5 (9.4)**	**72.0 (5.5)**	**99.5 (13.8)**
B. salicifolia (12 m^{-2})	**52.1 (8.9)**	**6.7 (3.6)**	**20.2 (9.4)**	**71.1 (7.7)**	**91.4 (16.1)**
Treatment effect (%)	16.7	43.3	59.3	41.5	55.2
$F_{(8, 134)}$	0.90	3.39**	6.15***	2.97*	5.19***

* Level of significance: *p<0.05, **p<0.01, and ***p<0.001

Table 2.3. Field experiment 1: Delayed plantings of *A. donax* (summer and winter).
Values indicate mean (+/-95% CI) *A. donax* growth parameters when in competition with differing densities of native shrub species. Bold text indicates values significantly different from that of the control (Tukey's HSD post-hoc tests p<0.05).

Treatment	Stem ht. (cm)	Stem num. (count)	Shoot wt. (g DW)	Rhizome wt. (g DW)	Total wt. (g DW)
Summer delayed planting					
Control (0 m^{-2})	84.9 (22.9)	10.1 (1.5)	124.7 (58.1)	83.3 (15.4)	208.1 (72.9)
S. exigua (3 m^{-2})	**116.2 (24.1)**	8.2 (1.8)	133.9 (30.3)	91.8 (16.4)	225.7 (45.0)
S. exigua (6 m^{-2})	87.8 (17.4)	**6.7 (1.9)**	101.4 (17.0)	78.0 (8.2)	179.4 (22.9)
S. exigua (9 m^{-2})	94.2 (20.4)	**5.1 (1.5)**	81.2 (8.1)	**61.8 (11.2)**	**143.0 (15.4)**
S. exigua (12 m^{-2})	101.0 (13.5)	**7.1 (2.2)**	94.0 (17.1)	77.2 (10.6)	171.2 (26.4)
B. salicifolia (3 m^{-2})	81.7 (15.7)	**5.9 (1.6)**	**69.8 (5.3)**	**65.6 (6.4)**	**135.4 (11.0)**
B. salicifolia (6 m^{-2})	83.4 (12.8)	**4.4 (1.0)**	**66.9 (4.7)**	**58.9 (6.8)**	**125.9 (10.6)**
B. salicifolia (9 m^{-2})	67.2 (17.5)	**4.3 (1.2)**	**65.3 (5.4)**	**52.9 (8.6)**	**118.3 (12.9)**
B. salicifolia (12 m^{-2})	70.2 (13.6)	**4.7 (1.3)**	**61.7 (3.4)**	**57.7 (7.4)**	**119.5 (9.3)**
Treatment effect (%)	51.4	59.4	37.3	56.3	43.9
$F_{(8, 134)}$	2.81*	5.94***	2.92*	6.24***	3.84**
Winter delayed planting					
Control (0 m^{-2})	99.9 (12.7)	7.5 (1.3)	114.3 (30.3)	123.1 (12.4)	237.4 (42.0)
B. salicifolia (3 m^{-2})	94.4 (8.9)	**4.3 (1.2)**	**56.4 (16.7)**	**97.8 (10.6)**	**154.3 (25.9)**
B. salicifolia (6 m^{-2})	**75.2 (9.2)**	**3.7 (0.8)**	**31.4 (4.8)**	**84.3 (5.5)**	**115.7 (9.2)**
B. salicifolia (9 m^{-2})	**78.9 (15.2)**	**2.9 (0.6)**	**28.9 (6.4)**	**77. 7 (5.0)**	**106.6 (11.1)**
B. salicifolia (12 m^{-2})	**74.8 (9.8)**	**2.7 (0.5)**	**22.7 (4.3)**	**72.8 (3.8)**	**95.5 (6.5)**
Treatment effect (%)	47.1	70.1	77.1	73.8	77.5
$F_{(8, 134)}$	4.11**	14.09***	14.65***	13.31***	15.4***

* Level of significance: *p<0.05, **p<0.01, and ***p<0.001

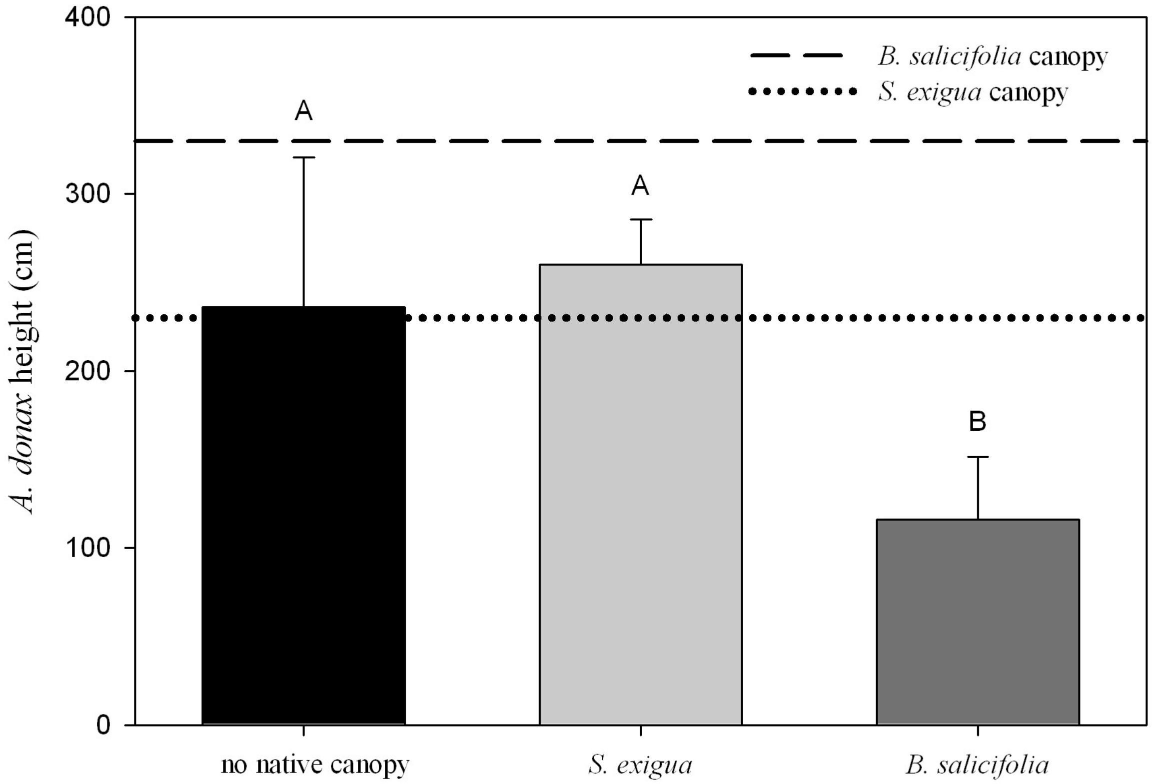

Figure 2.1. Field experiment 3: Mean height (+/- 95% CI) of *A. donax* plants grown for two years with or without native shrub competition. Mature (3 yr old) native shrub canopy heights represent treatment means for *B. salicifolia* (---) and *S. exigua* (....). Letters represent significant differences between groups (Tukey HSD post-hoc tests, α = 0.05).

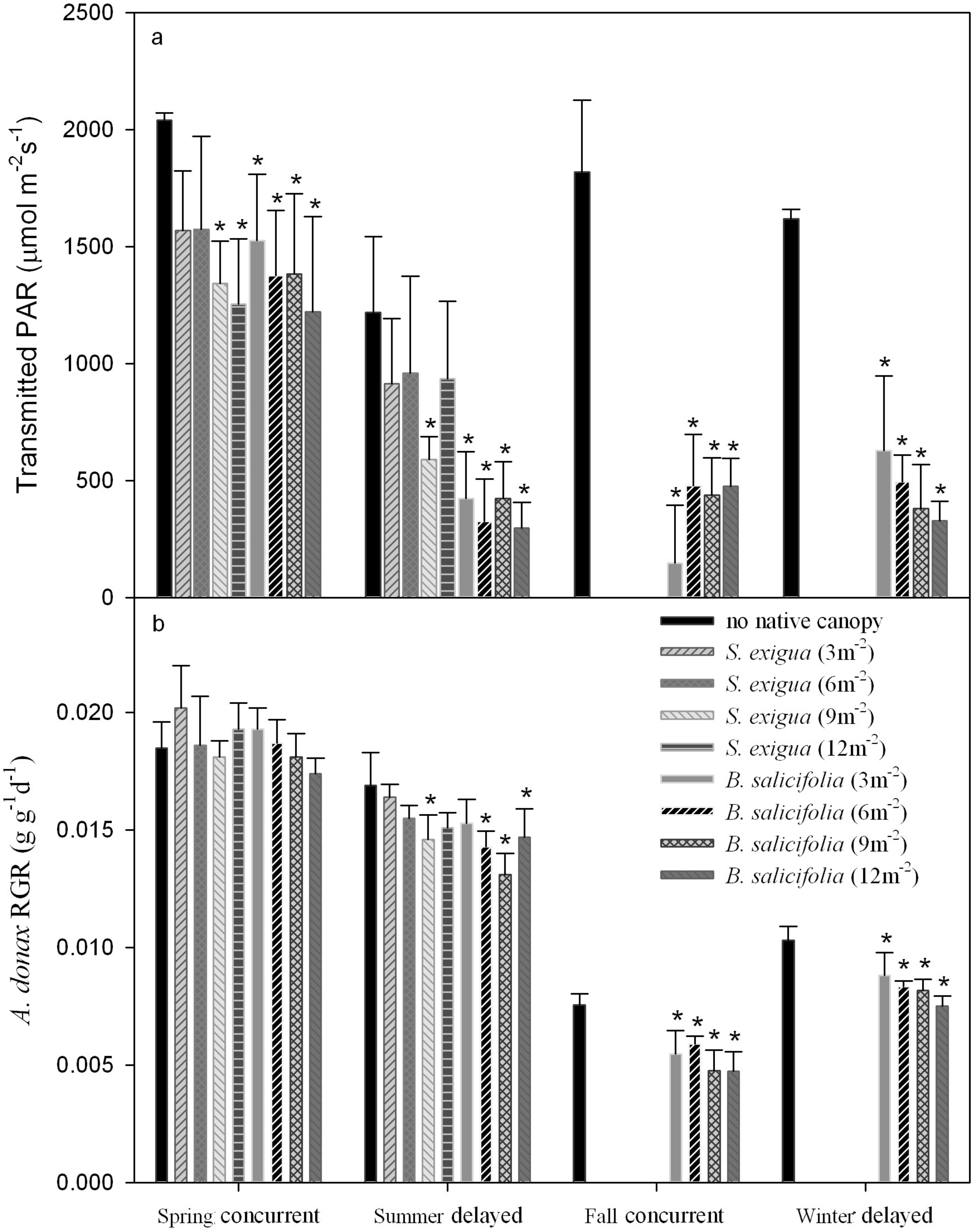

Figure 2.2. Field experiment 1: Mean native canopy transmitted PAR (+/- 95% CI) measured during *A. donax* harvest (a) and RGR (b) of the four seasonal competition trials. A star (*) represents a significant difference from the control (no native canopy) (Tukey HSD post-hoc tests, $\alpha = 0.05$).

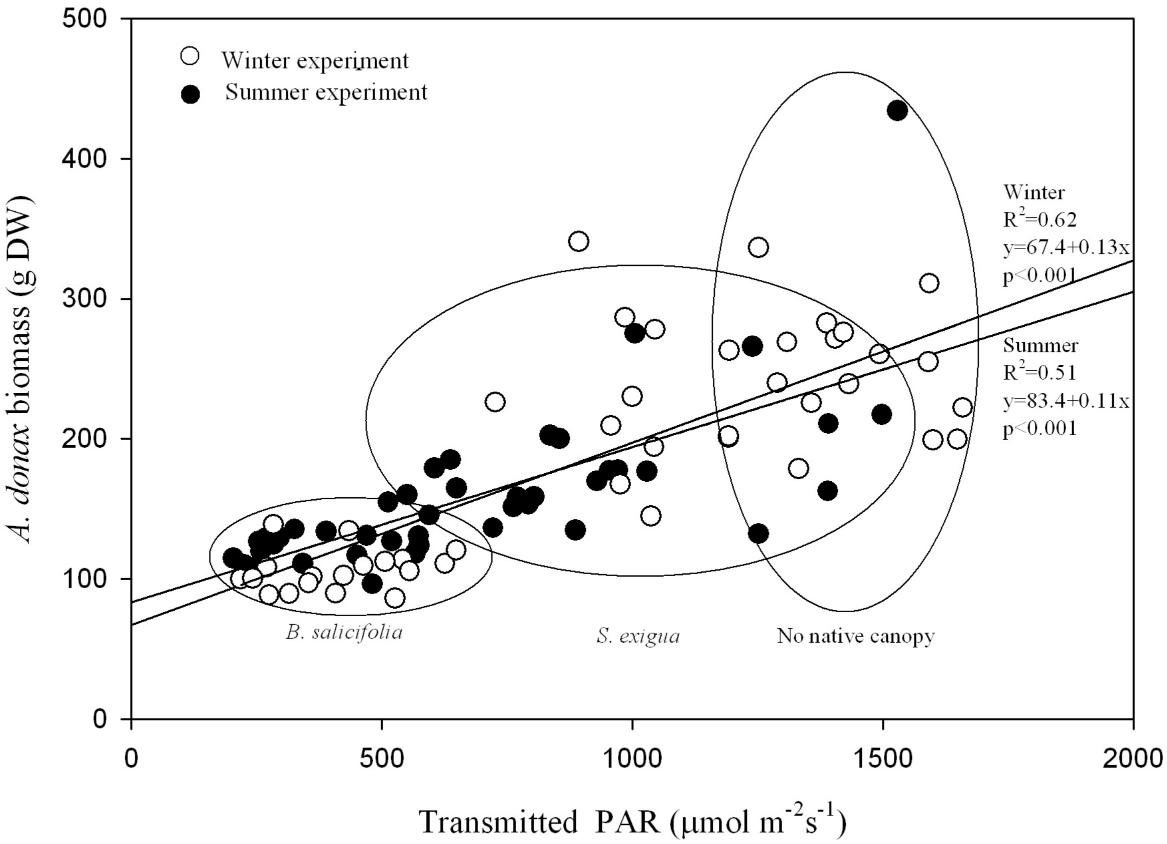

Figure 2.3. Field experiment 1: Linear regression model showing the effect of radiation intensity on *A. donax* growth for the two delayed planting trials (summer and winter). All nine planting treatments were included. The large ovals represent the location of all *A. donax* plants grown in competition with the individual treatments. Slopes of regression lines were not different when compared using a large-sample *Z* test for parallelism (*Z*=1.10, p=0.125).

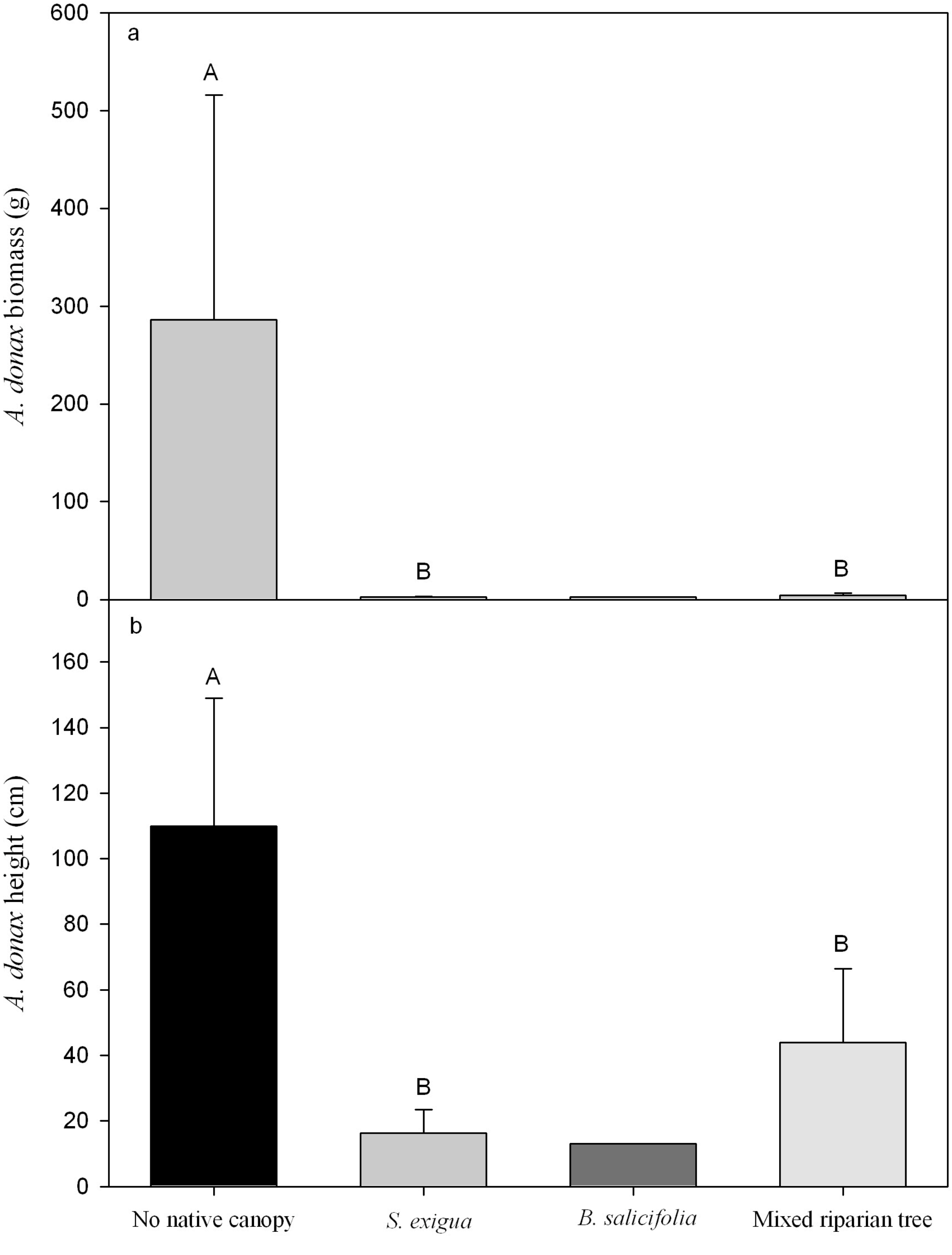

Figure 2.4. Field experiment 2: Harvest mean (+/- 95% CI) *A. donax* biomass (a) and height (b) of wildland-grown plants, planted under several competitive native plant canopy compositions. Data presented are for surviving plants. *B. salicifolia* had one surviving plant. Letters represent significant differences between groups (Tukey HSD post-hoc tests, $\alpha = 0.05$).

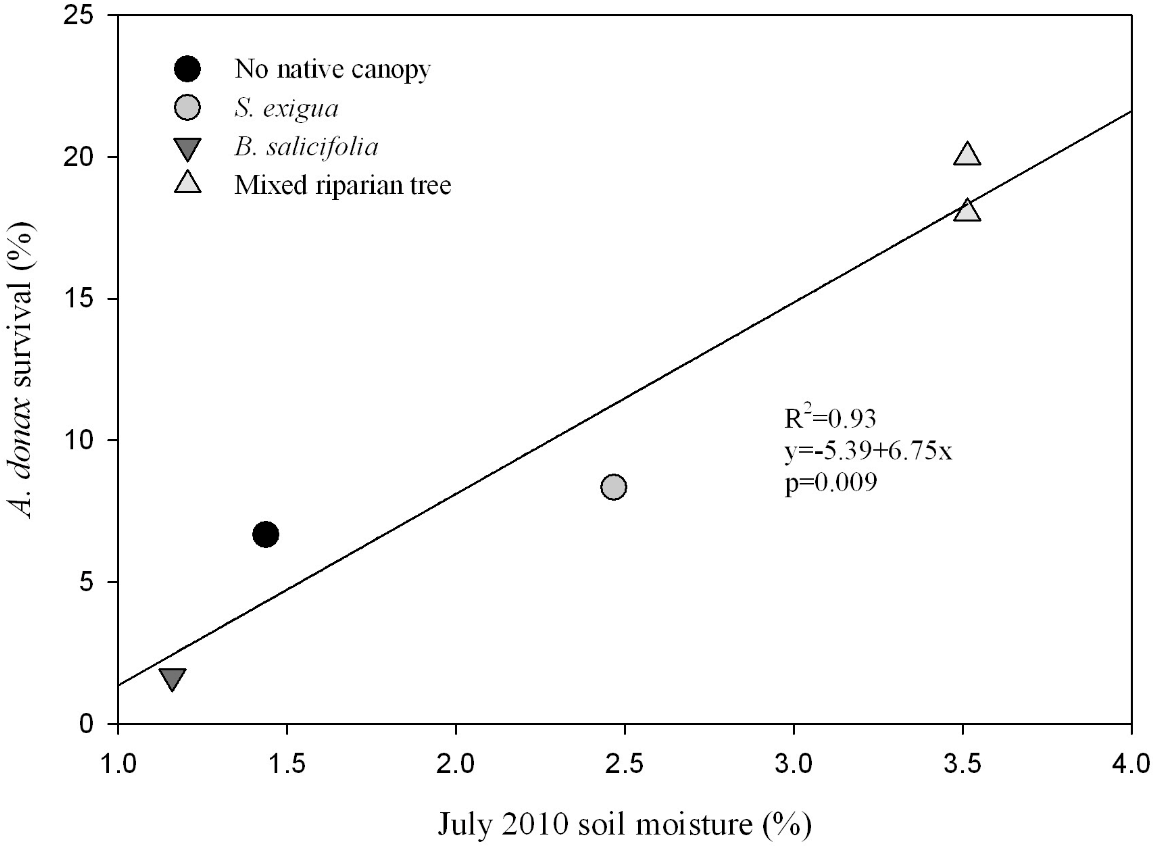

Figure 2.5. Field experiment 2: Linear regression of *A. donax* survival by summer soil moisture (F=38.3, p=0.009, df=4). Points represent mean survival of wildland-planted rhizomes per native canopy planting treatment.

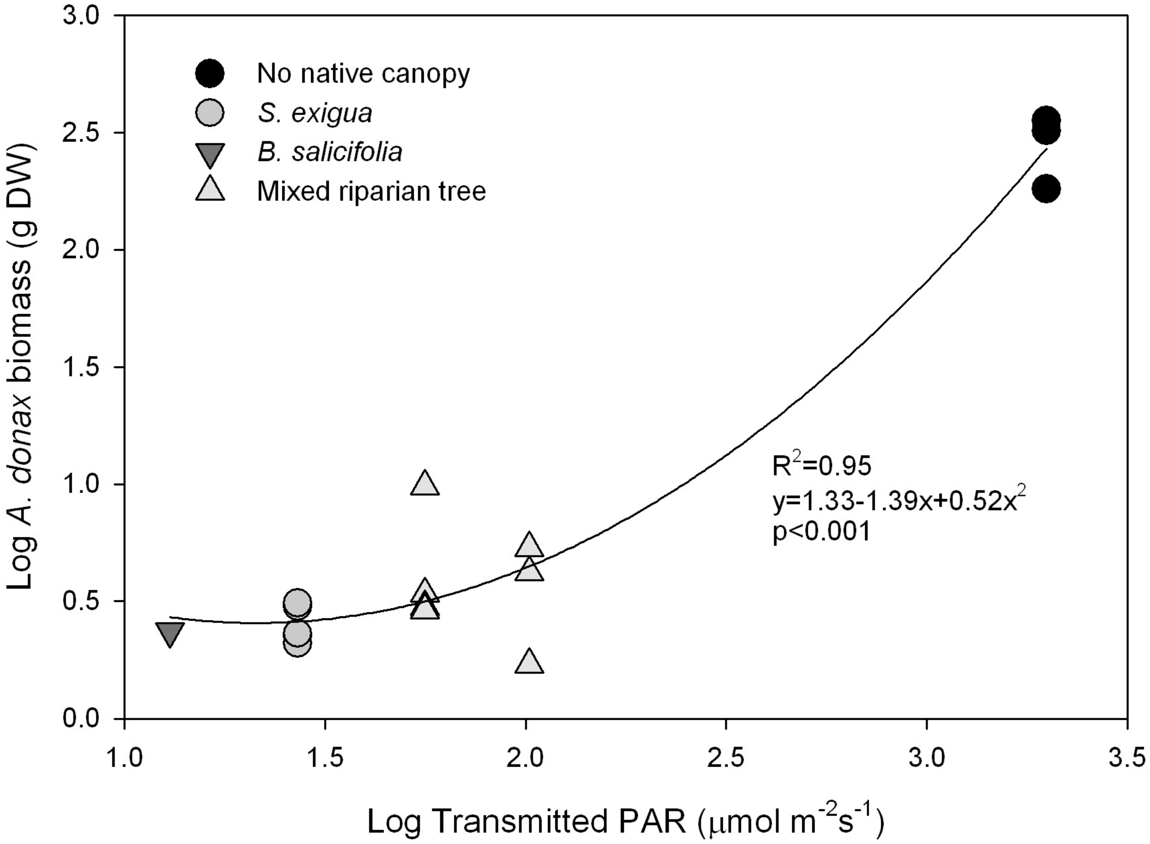

Figure 2.6. Field experiment 2: Quadratic regression model of the effect of radiation intensity on *A. donax* growth in the wildland (F=118.8, p<0.001, df=16). Points represent indiviual *A. donax* whole plant biomass of surviving plants by native canopy planting treatment.

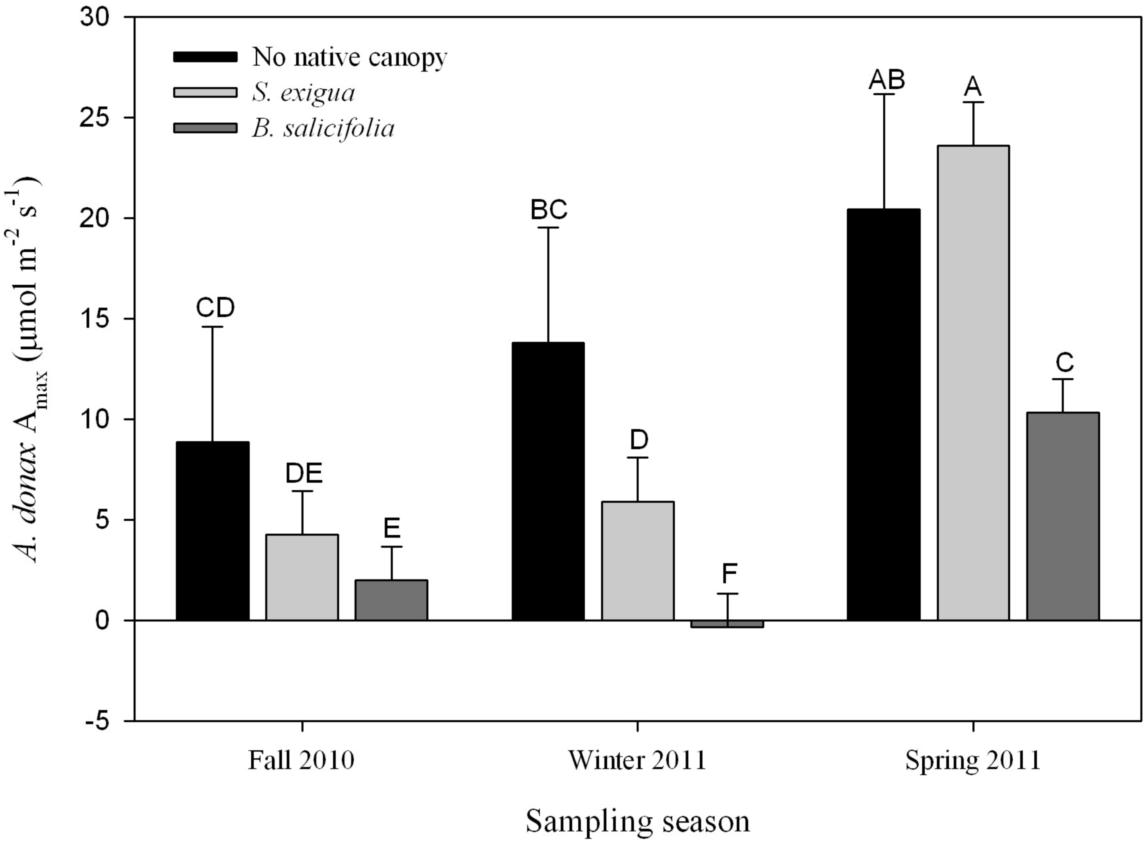

Figure 2.7. Field experiment 3: Seasonality of *A. donax* instantaneous mean photosynthesis (A_{max} +/- 95% CI) for plants grown under three native competitive environments. Winter 2011 represents measurements taken during *S. exigua* winter dormancy when shrubs were lacking leaves. Letters represent significant differences between groups (Tukey HSD post-hoc tests, $\alpha = 0.05$).

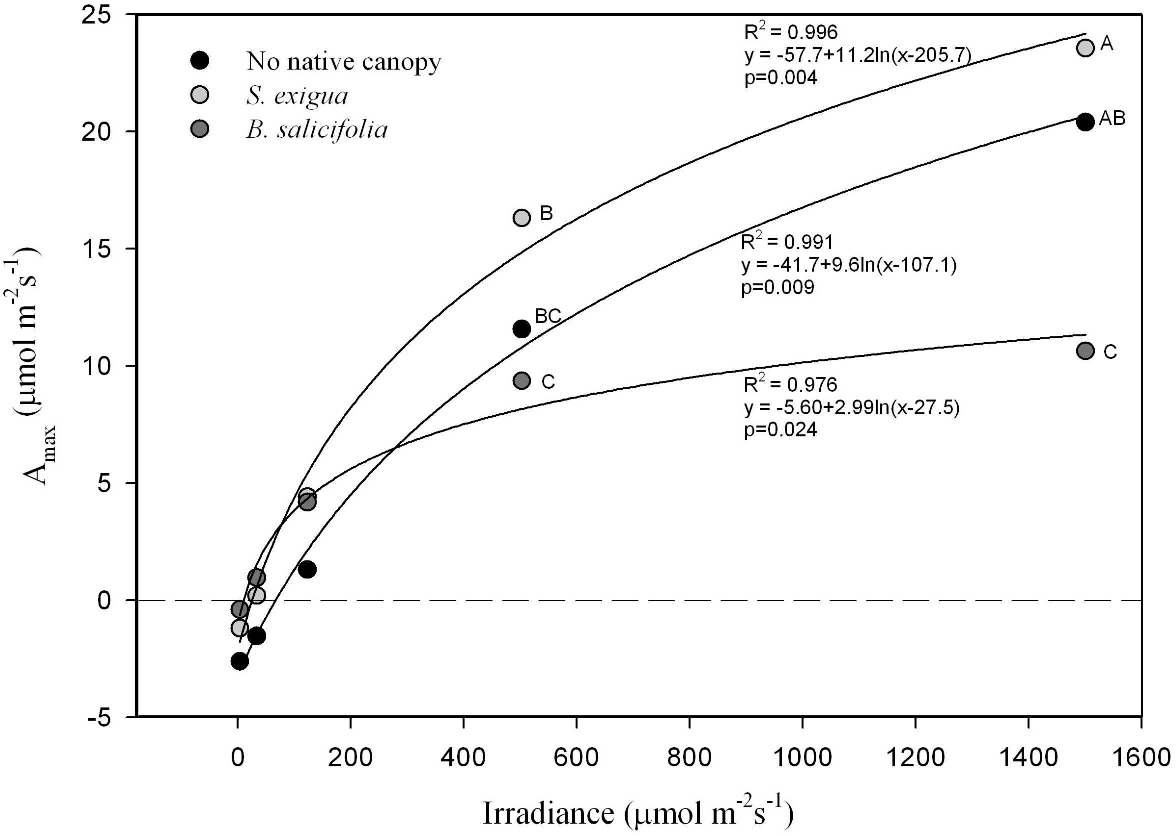

Figure 2.8. Field experiment 3: *A. donax* light-response curves of actively growing plants during spring 2011 under three native competitive environments; no native canopy (F=253.4, p=0.004, df=4), *S. exigua* (F=114.5, p=0.009, df=4) and *B. salicifolia* (F=40.4, p=0.024, df=4). Letters represent significant differences between groups (Tukey HSD post-hoc tests, $\alpha = 0.05$). An enlarged view of the low irradiance measurements can be found in Figure 2.9. Statistical comparisons between low irradiance measurements can be found in Figure 2.9.

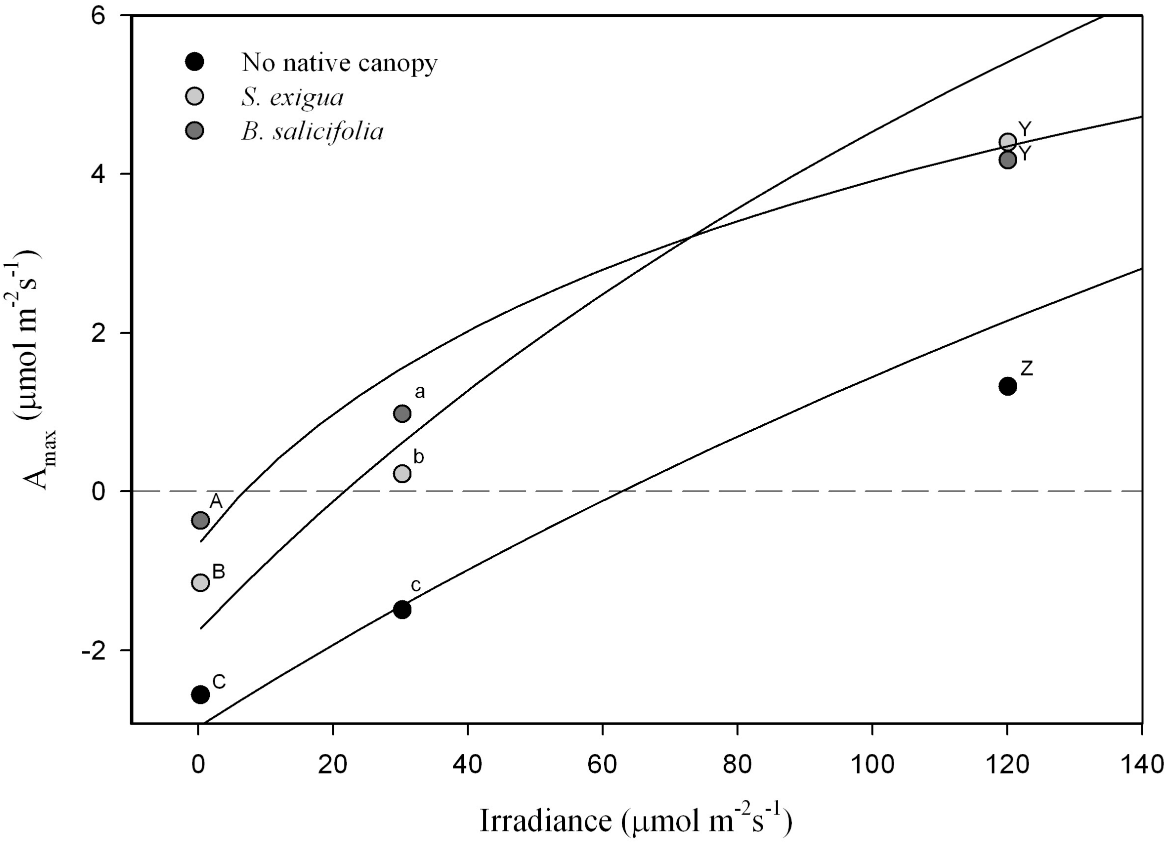

Figure 2.9. Field experiment 3: Detail of *A. donax* light-response curves for low irradiance conditions during spring 2011 field conditions. The complete set of light-response curves can be found in Figure 2.8. Letters represent significant differences between treatment groups analyzed separately at a given irradiance; A, B, C at 0 µmol m^{-2}s^{-1}; a, b, c, at 30 µmol m^{-2}s^{-1} and Y, Z at 120 µmol m^{-2}s^{-1} (Tukey HSD post-hoc test, $\alpha = 0.05$).

Native species recruitment following giant reed (*Arundo donax* L.) removal in relation to site factors and management techniques

ABSTRACT

Mechanized, multi-acre, wildland invasive weed management is a recent endeavor and few studies have been conducted to measure the long-term effects of such anthropogenic disturbance. Community composition, scale-dependent, and abiotic factors were analyzed across 59 riparian restoration sites across southern California in a retrospective survey of up to 20 years to test what factors are related to native species recovery after exotic removal. Principal components analysis found strong spatial-temporal dependent relationships between site location and native recovery, where distance to the active water channel, site width, a proxy for minimum native recruitment distance, and time since removal measured as years since *A. donax* removal was initiated, were all important in explaining native recruitment to passively restored sites. Whether actively managed for native recovery or not, sites recruited equivalent species richness and displayed increasing native cover with time on a regional scale. When considering a management chronosequence, native recruitment in passive sites was delayed by at least 5 years relative to active sites with similar histories. If passive sites were wide and large in area (>1ha), native recruitment generally progressed very slowly and dominant exotic species may be inhibiting native recovery. Recommendations are to plant islands of native shrubs in these large *A. donax* removal sites, decreasing recruitment distance and potentially increasing native recruitment rates.

INTRODUCTION

Wildland invasive weed management is vital to resource conservation but few studies have measured the long-term impacts of these projects (Galatowitsch & Richardson 2005; Allen *et al.* 2005; Middleton, Bever, & Schultz 2010; Lennox *et al.* 2011; McLane *et al.* 2012). Recruitment of native species into these management areas may be delayed, especially where environmental conditions favor exotic establishment, as in the high-resource environments present in riparian plant communities (Planty-Tabacchi *et al.* 1996). Mature riparian forests of southern California are composed of phreatophytic trees (to 15 m) with primarily an herbaceous understory and perimeter of xeric shrub species. The flora is adapted to flood disturbance (Sher, Marshall, & Gilbert 2000) but other perturbations to the system, including invasive species management, may delay native species revegetation. Recruitment of native species is stochastic and associated with post high water or flooding events, which wet soils prior to propagule dispersal during late winter and spring (Hughes 1997; Levine & Stromberg 2000). Factors that increase the length of time soils remain moist have been indicated as important for plant establishment in riparian plant communities of arid regions, such as southern California, and include soil texture (Pettit, Neil & Naiman 2006), as well as amount of organic matter (Francis & Gurnell 2006) and woody debris (Bhattacharjee *et al.* 2008).

Control of invasive plants creates an open niche that can be filled by other plant species, including native or undesirable exotic species. The trajectory of recruiting vegetation associated with management has been shown to be dependent on the scale of the removal project (Ogden & Rejmánek 2005) or in some cases the severity of the soil disturbance (Stylinski & Allen 1999). Soil impacts vary by control method, which also may influence restoration success. Mechanical methods that attempt whole plant removal create a highly disturbed landscape and extract a large fraction of potential soil organic matter, while the magnitude of soil disturbance is greatly reduced for chemical application methods which leave belowground plant organs for in situ decomposition. Biologically active nitrogen compounds have been found to act as barriers to restoration because in some situations, it can increase the likelihood of exotic invasion (Prober, Thiele, & Lunt 2002). Benefits from increasing soil organic matter include increased soil water holding capacity and decreased biologically active nitrogen compounds (Morghan & Seastedt 1999).

The goal of restoration is to return to the disturbed landscape the native plant species, community composition, processes and pre-invasion ecosystem that existed pre-disturbance, or in this case, pre-invasion (Harris 1999). As in Shafroth et al. (2008), we use the term “restoration” broadly to include projects with the goal of converting stands of exotic species to a replacement vegetation type and returning part or all of the pre-invasion ecosystem dynamics. This can be accomplished through active restoration (directional management) or passive restoration (non-directional management).

Active restoration falls on a spectrum of management intensity that may include planting and/or seeding of native species, supplemental irrigation, protection from herbivory (caging), and multiple applications of weed control measures. This process is meant to facilitate native species establishment and reduce exotic cover during the active management period (3 to 5 years) with the objective of the expedient conversion of degraded habitat to a representative, self-sustaining climax community (Parker 1997; Harris 1999). Passive restoration removes select exotic species or a group of species from an area, allowing natural successional processes to provide native recruitment over a longer time scale than active restoration. The passive restoration method assumes successional processes are intact and that they favor native species success over exotic. Under natural conditions, the trajectory of native recruitment and percent cover can be positive, negative or non-directional (Suding, Gross, & Houseman 2004; Harms & Hiebert 2006), and can be influenced by the exotic species being removed (Corbin, Antonio, & D’Antonio 2004; Corbin & D’Antonio 2012).

Arundo donax L. (giant reed) is an exotic, invasive plant to North America and found throughout subtropical and Mediterranean climates worldwide. It is adapted to flood disturbance with large, buoyant, water-dispersed stem and rhizome propagules that can emerge and grow rapidly even within a competitive environment (Bell 1997; Boose & Holt 1999; Decruyenaere & Holt 2001; Rauterkus 2004; Wijte *et al.* 2005; Quinn 2006). It is a tall (to 10 m. in southern California) clonal plant that typically creates large monotypic patches of poor quality riparian habitat (Herrera & Dudley 2003) and is found throughout coastal California and inland below 500 m (Bell 1997). Once established, this species creates a dense canopy excluding native plant competitors and degrading habitat quality for wildlife (Rieger & Kreager 1989; Quinn 2006; Guthrie 2007; Going & Dudley 2008; Quinn & Holt 2008). The belowground plant organs of *A. donax* produce a large biomass input to systems they invade. Within the past 30 years many restoration projects have been completed in California with the goal of removing *A. donax* and returning lands to functioning native riparian systems.

Factors increasing native establishment are important in passive management of the riparian system. One study assessing the removal of tamarisk (*Tamarix* spp.), an invasive riparian exotic tree, observed re-establishment of an exotic dominated system in some passive restoration sites (Harms & Hiebert 2006). Removal of *A. donax* is similar to tamarisk in that removal of dense monocultures can leave large-scale impacts, including large areas of bare ground, over a heterogeneous landscape. For *A. donax,* removal typically occurs during late summer or fall when surface soils are dry, allowing invaders an opportunity to colonize and dominate these disturbed areas during suboptimal precipitation years (Stromberg *et al.* 2007; McLane *et al.* 2012).

The response of riparian vegetation to various forms of revegetation methods has provided valuable insights into successional processes (Tompkins & Kondolf 2007; Lennox *et al.* 2011; McLane *et al.* 2012), and the resulting community structure provides insights into the formative processes creating the riparian community (Parker 1997). Long-term research has been limited to case studies, however, often with conflicting findings, making it difficult to translate results to a regional scale (Stylinski & Allen 1999; Zedler & Callaway 1999; Taylor, Smith, & Haukos 2006). The use of a chronosequence to compare similar sites across a region with variable treatment histories has been used to follow general successional trends related to the removal of an invasive exotic species (Bay & Sher 2008; McLane *et al.* 2012). The benefit of this type of study is that it allows elucidation of regional trends not found in site-specific long-term studies.

Generalizing lessons from restoration studies is important to policy formation designed to compensate for damage to habitats (e.g. National Environmental Policy Act, 1969; the Clean Water Act, 1972; and the Endangered Species Act, 1973).

Mechanized, multi-acre, wildland invasive weed management is a recent endeavor and few studies have been conducted measuring the long-term effects of such anthropogenic disturbance (Zedler & Callaway 1999; Ruiz-Jaen & Aide 2005; Kondolf *et al.* 2007; Lennox *et al.* 2011). It is only now that long-term effects from these projects can be compared with rigor over large spatiotemporal scales. The management of *A. donax* provides an opportunity for this type of comparison. In this research I asked whether methods, scale of *A. donax* removal and type of restoration affect the subsequent trajectory of establishing vegetation and long-term habitat composition. Invasive species removal methods have been found to influence native seedling survivorship in other systems (Hartman & McCarthy 2004), but this has not been investigated in the context of large-scale *A. donax* removal projects. We sampled 22 revegetation areas and 6 *A. donax* removal areas in a retrospective survey across southern California (0 to 20 years since *A. donax* removal was initiated) to test whether what factors are related to native species recovery after exotic removal. It was hypothesized that:

H1. Active restoration of *A. donax* removal sites results in more native woody cover than passive restoration of similar age sites.

H2. Spatial factors impact native recruitment into *A. donax* removal sites.

H3. Methods incorporating chemical applications during the initial phase of *A. donax* control promote more native establishment than mechanical removal in passive restoration sites.

H4. *A. donax* removal sites where passive restoration is performed are more species-rich than active restoration sites.

MATERIALS AND METHODS

Study System

The study area for this research is coastal southern California, encompassing Ventura County to the north, San Diego County to the south, Riverside County to the east, and the Pacific Ocean to the west. *A. donax* occurs within all major watersheds in this region including the Santa Clara River, Los Angeles River, San Gabriel River, Santa Ana River, Santa Margarita River, San Luis Rey River, San Diego River, Sweetwater River, and Tijuana River. Across this range, large-scale *A. donax* management projects, ranging in age from 5 to 20 years since project initiation, were located and measured for current habitat composition.

Research Site Selection

Sites were selected from a state funded weed control database provided by UC Davis (Roelle & Gladwin 1999; Taylor, Smith, & Haukos 2006). "*Arundo donax*" was queried with counties including "Ventura, Los Angeles, San Bernardino, Riverside, Orange, and San Diego" to find projects focused on the removal of *A. donax* within southern California (March 16, 2011). This provided a list of 50 projects. Information concerning precise project boundaries and management histories were collected during site visits (when possible) with project-related personnel. If either the removal method or year of removal were unknown, projects were excluded from the study. In addition, projects were also excluded with elevation greater than 305 m (1000 ft), pre-removal cover of *A. donax* less than 75 percent, or where intense wildfire or flooding had recently altered plant composition. These criteria resulted in the inclusion of 22 areas (Table 3.1).

Using the Historical Imagery option on Google Earth (version 6.0.3.2197), which provided aerial images, project land areas were assessed for *A. donax* presence (pre-removal) and removal areas (post-removal). To generate study sites, polygons were delineated on project maps representing treatment areas. When possible, three polygons were created, and each was subsampled three times per site.

Data Collection

The line-intercept method was employed to measure vegetative cover of woody species (Dudley *et al.* 1998; Elzinga, Salzer, & Willoughby 1998). Transects (15 m) were randomized by time by placing start points on historic imagery in areas with known high *A. donax* cover prior to removal. This ensured that the pre-removal state of the sampled area was nearly 100 percent *A. donax* cover, minimizing erroneous sampling of pre-existing native vegetation as well as bias related to field randomization. Transect direction was predetermined so that each line started from a random point and was placed perpendicular to the active river channel. This method captures the greatest perennial plant diversity (mesic and xeric species).

Transects were sampled for both point and line intercept of all vegetation (thin belt transect, 5 cm wide). Point data were sampled per meter for species presence. Line intercept data were sampled by cover class. Classes were defined by plant growth form and nativity, including native woody (tree + shrub), native herbaceous (forb + grass), or total exotic cover (nonnative tree + shrub + vine + herbaceous), and then by species when woody perennial. Rare species observed but missed during transect sampling were recorded separately. All species observed were compiled per site and represented site richness. Soil moisture and temperature were measured at the start and end of each transect.

Six reference sites (dense stands of *A. donax*) were selected to represent an estimate of the pre-restoration state (no *A. donax* removal). Though preferable, it was not possible to sample these areas in the same manner as the restoration sites due to the extremely high *A. donax* shoot density. The sites were observed from a proximate vantage point and estimates of species richness and percent cover were made. Soil samples and abiotic data were collected as in the restoration sites, but from the reference site perimeter.

Historical or environmental variables collected from project contacts or via Google Earth included the following: *A. donax* infestation size (removal area), shortest infestation width (site width), method of *A. donax* removal (removal method), restoration type (active or passive), pesticide applied (herbicide), year of removal (time since removal), distance to surface water (distance to water), and distance to nearest native propagule source at time of *A. donax* removal (recruitment distance). Google Earth was used to estimate distances between data sampling locations, and both nearest source of surface water and nearest native vegetation present in historic photos immediately following *A. donax* removal. These measures, though crude, represent the best historical estimates of proximity to water and shortest native recruitment distance, respectively.

It was not possible to discriminate between types of active management techniques, which include various combinations of native planting method, diversity, density and presence of supplemental irrigation, due to low site replication. Thus, the variable ‘restoration type’ was classified into active or passive restoration. The planting of native woody vegetation via pots or whip cuttings (Hoag & Fripp 2003) was the unifying factor for all nine active restoration sites.

Removal method was defined as the technique used to remove *A. donax* biomass in combination with the type of herbicide used in subsequent chemical applications. Removal methods were categorized into 6 groups, including (1) stems removed and AquaMaster applied to cut surface (Glyphosate, N-(phosphonomethyl) glycine, in the form of its isopropylamine salt, Monsanto Company, 800 North Lindbergh Boulevard, St. Luis, Missouri 63167, USA), (2) no stem removal and Habitat (Isopropylamine salt of Imazapyr (2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1H-imidazol-2-yl]-3-pyridinecarboxylic acid) applied to whole plant, BASF Corporation, 100 Park Avenue, Florham Park, New Jersey 07932, USA) , (3) no stem removal and AquaMaster applied to whole plant, (4) whole plant mechanical removal, (5) stems mulched with AquaMaster applied to resprouts and (6) stems mulched with Habitat applied to resprouts. Records confirmed that all pesticide use complied with legal labeled rates. Specific application rates were not available. Method 2 was removed from analyses due to a lack of replicates.

Data Analysis

Principal component analysis (PCA) was conducted to compare correlations between all environmental variables (n = 13) and all samples (n = 37) at passive restoration sites. Variables included native tree cover (tree), native shrub cover (shrub), native vine cover (vine), native herbaceous cover (herbaceous), total exotic species cover (total exotic), *A. donax* removal area, site width, distance to active channel, time since removal, percent soil litter (soil litter), percent bare soil (bare soil), soil moisture (soil moisture), and soil temperature. Site width is a proxy for minimum recruitment distance, as other methods of estimating this variable were less reliable or not possible due to the passage of time, including measuring distance to current native propagule sources or estimating this distance at the time of *A. donax* removal with historic aerial images. Seven important variables within principal components (PC) 1 to 3 were included within a final PCA; these include tree, shrub, total exotic, time since removal, site width, distance to active channel, and soil litter.

PCA was also conducted to compare the linear correlations between all environmental variables (n = 14) and all samples (n = 22) at active restoration sites. Environmental variables were equivalent between both passive and active analyses. Eight important variables within PC 1 to 3 were included within a final PCA, including tree, shrub, herbaceous, time since removal, site width, distance to active channel, soil moisture, and soil litter. A factor loading rotation using Varimax was performed and later rejected as it did little to increase the explainability of PC axes 1 and 2. Removal method was compared using regression analysis of native woody cover (tree + shrub + vine) in a chronosequence.

Species richness was compared by rarefaction across southern California by time since removal classes and restoration type using EstimateS (Version, 7.5.2, http://purl.oclc.org/estimates). Rarefaction is either individual or sample-based and is a method for estimating species richness in relation to sampling intensity using interpolation (Tipper 1979). As data represented the number of species intercepts per transect, comparisons constituted a sample-based rarefaction. Three age classes were compared (years since *A. donax* removal) including 5–10, 11–15, and 16–20 years. In order to compare species richness across sites receiving different sampling intensity bootstrapped estimates were compared at nine samples (transects), which was equivalent to the least sampled group (Gotelli & Colwell 2001). This relationship between sampling intensity and species richness or frequency allowed for direct comparison between sampling units.

Data on native woody and total exotic cover were analyzed with the Wilcoxon non-parametric test. Due to the preponderance of high variance and occasional bimodal distribution, data transformations were ineffective at meeting statistical assumptions of normality and homogeneity of variance. Unless otherwise stated analyses were performed with the statistical program JMP version 9 (SAS Institute, Cary, North Carolina, USA).

RESULTS

Differences in recruitment between active and passive *A. donax* restoration sites (H1)

It was hypothesized that native woody cover would be greater in active restoration sites than passive restoration sites or no *A. donax* removal sites (H1). When the three treatments were compared, sites receiving active restoration had more native woody cover (X^2=14.63, p<0.001) and less exotic cover (X^2=21.47, p<0.001) than both passive and no *A. donax* removal sites (Fig. 3.1). Neither native tree (X^2=3.00, p=0.083) nor native shrub cover (X^2=2.55, p=0.110) were significantly different between active and passive sites when analyzed separately. These data support H1 but they do not test the temporal aspect of the question, how restoration time since removal interacts with native recruitment between restoration types.

When sites from all three restoration treatments, which vary by restoration age, were compared using a chronosequence with initiation of *A. donax* management as time point 0, a temporal difference between treatments was found. Relative to no *A. donax* removal, native woody cover was greater (X^2=23.94, p<0.001) and exotic species cover was less (X^2=26.42, p<0.001) when invasive management was performed, passive or active (Fig. 3.2). When comparing age classes active restoration sites were higher in native woody cover than the youngest passive restoration sites (5-10 yr) in all but one age class, 11-15 yr (Fig. 3.2a). Total exotic cover of active restoration sites was always less than the youngest passive restoration age class (5-10 yr) (Fig. 3.2b). A separate analysis of this chronosequence using regression analysis found significant (α=0.05) positive and negative relationships with time since removal for native woody cover and total exotic cover, respectively (Fig. 3.3). Both active and passive restoration sites had similar successional trajectories, but active sites increased more rapidly as a logarithmic regression model rather than the linear regression models observed in passive sites. These data support the temporal aspect of H1, that active restoration establishes native riparian vegetation more rapidly than passive restoration of *A. donax* sites.

Spatial factors impact native recruitment into *A. donax* removal sites (H2)

Passive restoration sites

Spatial variables, including project size and distance to water, were hypothesized to be important to native recruitment into *A. donax* removal sites (H2). Seven total environmental variables were included in a PCA for passive restoration sites, which found three significant PCs (α=0.05), accounting for 78.4 percent of total variation (Table 3.2). Native tree cover was strongly associated with PC 1 (-0.742 loading) and negatively correlated with total exotic species cover, site width, distance to water and soil litter. Native shrub cover was strongly associated with PC 2 (0.814 loading) and positively correlated with time since removal and soil litter. Native tree cover was strongly associated with PC 3 (0.540 loading) and positively correlated with time since removal. A factor loading rotation using Varimax was performed and later rejected as it did little to increase the explainability of PC axes 1 and 2.

Active restoration sites

Eight total environmental variables were included in a PCA for active restoration sites, which found three significant PCs (α=0.05), accounting for 78.2 percent of total variation (Table 3.2). Native shrub cover was strongly associated with PC 1 (0.730 loading) and positively correlated with site width, time since removal and distance to water. Native herbaceous cover was strongly associated with PC 1 (-0.600 loading) and negatively correlated with site width, time since removal and distance to water. Native tree and herbaceous cover were strongly associated with PC 2 (0.655 and 0.530 loading, respectively) and positively correlated with soil moisture and soil litter. Native tree and herbaceous cover were strongly associated with PC 3 (-0.630 loading) and negatively correlated with each other. A factor loading rotation using Varimax was performed and later rejected as it did little to increase the explainability of PC axes 1 and 2.

In addition to those relationships indicated by PCA, Pearson's product moment correlations indicated several other important relationships within passive and active restoration sites (Table 3.3). For passive restoration sites, native shrub cover was negatively correlated with total exotic cover ($r=-0.505$, $p=0.002$), site width ($r=-0.485$, $p=0.002$) and distance to active channel ($r=-0.351$, $p=0.033$). Total exotic cover was positively correlated with site width ($r=0.580$, $p<0.001$). Time since removal was positively correlated with soil litter ($r=0.337$, $p=0.041$). For active restoration sites, native shrub cover was negatively correlated with total exotic cover ($r=-0.451$, $p=0.035$). Total exotic cover was negatively correlated with site width ($r=-0.461$, $p=0.031$). Time since removal was positively correlated with soil litter ($r=0.522$, $p=0.013$). Soil litter was positively correlated with soil moisture ($r=0.521$, $p=0.013$).

A. donax removal method impacts native recruitment (H3)

It was hypothesized that methods incorporating chemical applications during the initial phase of *A. donax* control would promote the establishment of more native cover than the mechanical removal of the whole plant (H3). When native woody cover was compared among all removal methods of passive restoration sites, method 5a was correlated with the most rapid increase in native woody cover (r^2=0.91, p=0.04), followed by methods 1, 6, 5b and 4 was highly variable (Fig. 3.4). Methods 1 and 6 were composed of small-scale removal areas (<1 ha) as in method 5a. Excluding method 5b and comparing methods 5a, 1, and 6 allows for the direct comparison between chemical methods while minimizing the confounding factor of spatial scale. When considering time since removal, native woody cover was most dense where Aquamaster was applied (methods 1 and 5a) than where Habitat was applied (method 6). All methods led to increases in native woody cover when compared to no *A. donax* removal treatment, except for one site in method 4 where no native species were present (Fig. 3.4). The data presented do not support H3, but do support the findings for H2 that spatial scale is important in the recruitment of native riparian woody species into *A. donax* removal areas.

Passive restoration sites are more species-rich than active restoration sites (H4)

It was hypothesized that species diversity would be highest in passive restoration sites (H4). Table 3.4 includes a list of all species encountered by sampling location. Vegetation groups did not differ between passive and active restoration sites for species richness (Fig. 3.5). These data do not support H4 when time since removal classes were pooled and analyzed. When analyzed separately native woody richness decreased with age in active sites and increased with age in passive sites (Fig. 3.6). This was most pronounced between the oldest age classes where passive sites had the greatest species richness (12 spp) and active sites had the lowest (2 spp; Fig. 3.6a). Native herbaceous species richness did not change with age when comparing within a treatment, but when comparing between treatments active sites were always more diverse than passive restoration sites (Fig. 3.6b). Exotic species richness decreased with age in active restoration sites but only in the oldest passive restoration sites (16-20 yr) was a decrease observed (Fig. 3.6c). When considering time since removal, native woody and total exotic species richness supported H4 but native herbaceous species richness did not.

Site specific passive restoration

Figure 3.7 compares all passively restored sites based upon native woody cover and PC 1 as a linear regression. Both axes are dependent on native tree cover but vary in relative importance of native shrub cover. This figure represents an ordination of sites and is useful for land managers associated with this research to compare their site to other sites based upon spatial and biological factors. Sites found on the extremes of the PC 1 axis display strong spatial correlations with native woody cover. Sites with negative values are smaller, closer to the active channel and are on a trajectory toward native recovery. Sites with positive values are larger and farther from the active channel, and generally support high exotic species cover.

DISCUSSION

As with all disturbance events that remove vegetation, impacts associated with *A. donax* removal and the subsequent reestablishment of native species have been shown to be scale-dependent. Factors such as time since removal, proximity to the active channel, site width, and restoration type all influenced the rate of native plant recruitment and success. Whether replanted, as in active restoration which directs plant community trajectories, or in passive restoration which does not, sites disturbed during *A. donax* removal recruited equivalent species richness and displayed increasing native cover with time on a regional scale. When considering native recruitment time between passive and active restoration, there is at least a five year lag period for passive sites to catch up with the expedited recruitment observed in active sites. If passive sites were wide and large in area (>1ha), native recruitment generally progressed very slowly and dominant exotic species may be inhibiting native recovery. For optimal restoration, therefore, recommendations are to plant islands of native shrubs in these large *A. donax* removal sites, decreasing recruitment distance and possibly increasing native recruitment rates (Robinson & Handel 2000).

Long-term effects of passive restoration

Two spatially dependent variables [proximity to the active channel (distance to active channel) and recruitment distance (site width)], and one temporal variable (time since removal) were found to be important to the success of natural recruitment of native woody vegetation into riverine passively restored *A. donax* removal sites of southern

California. Dramatic differences were observed between restoration sites, ranging from mature, native dominated riparian woodland in small restoration sites located near water, to complete infestation of invasive exotic wildland weeds in large restoration sites far from water. Abiotic factors, such as soil moisture and soil litter were less predictive of native species presence, likely due to the sampling period (summer) when surface soils are dry and both annual and deciduous species have not yet deposited biomass to the soil surface.

Soil moisture and recruitment distance are important factors when considering site selection for the prioritization of active riparian restoration (Russell, Hawkins, & O'Neil 1997). Russell et. al. (1997) recommends that sites with moist soil near existing vegetation should be left to passively recover while dry sites at distance from existing vegetation should be actively restored. A retrospective study assessing 28 *Tamarix* spp. removal projects (1-18 yr) in the southwest United States found similar results where proximity to perennial water was the most important factor favoring native establishment (Bay & Sher 2008). Our results support the findings of these studies and suggest that spatial and abiotic factors are the most predictive measures of native riparian success in passively restored *A. donax* removal sites.

Native tree species were reliably found closer to the active water channel and native shrub species were found interspersed with trees and at distance from the active channel. This suggests that the more xeric shrubs, comprising the alluvial scrub vegetation type, are recruiting into the entire width of the riparian ecosystem and are being outcompeted by the trees in the more favorable soil environments near the active channel. For both growth forms establishment is a slow but steady process. Exotic species were found away from tree species and at distance from the active channel. They were not associated with shrubs but found in the intershrub gaps, indicating biological factors (plant competition) may best predict exotic species success (Levine, Adler, & Yelenik 2004). Native vegetation was often observed in discrete patches or foci, surrounded by a canopy of exotic herbaceous vegetation. When viewed over the chronosequence these foci of native species appeared to have expanded. Once a native focus has established competitive exclusion is likely the mechanism favoring native woody species to the disadvantage of exotic species. Exotic species presence appeared to slow the native recruitment process but it did not eliminate it.

Long-term recruitment limitation caused by exotic species is problematic in riparian ecosystems (Farnsworth & Meyerson 1999; Galatowitsch & Richardson 2005; Harms & Hiebert 2006), as well as in shrubland ecosystems after large-scale invasive removal projects (Ogden & Rejmánek 2005) or with severe soil disturbance (Stylinski & Allen 1999). The dominance of exotic species and lack of native recruitment, even in older restoration sites (>10 yr), may provide evidence of an ecosystem in a fixed degraded state (Suding, Gross, & Houseman 2004). Native herbaceous cover was found to be low in all sites. Exotic cover decreased with time since removal but it was always the dominant herbaceous canopy in passively restored sites (30 to 75 percent cover). Exotic herbaceous species may have competitively excluded local recruitment of existing native herbaceous species as they are functionally similar groups (Pokorny *et al.* 2005).

Species richness was not different between passively and actively restored sites, with one interesting exception. Mexican elderberry (*Sambucus mexicana*) was consistently a dominant species within passively restored landscapes and missing within most actively managed sites. This species is a bird dispersed, disturbance following, xeric shrub or tree species typically associated with the coastal sage scrub plant community. It is not uncommon to find it present as a waif within the riparian ecosystem of southern California, but in several large-scale passive sites it was found in abundance. This is likely reflective of the site's disturbance history (Didham & Watts 2005), lack of safe sites for native riparian species establishment (Polzin, Rood, & Alberta 2006), and more evidence of an ecosystem in a continuously degraded state (Suding, Gross, & Houseman 2004). Active restoration may be necessary to bring these large sites onto a positive native successional trajectory.

Long-term effects of active restoration

Effects from active restoration were strongly visible throughout the chronosequence as these sites were commonly found to have high native woody cover, indicating a direct relationship between restoration type and native success. The overall regional trend of actively managed sites was a reliably positive trajectory of native cover and negative trajectory of exotic cover, both desired long-term restoration goals. Restoration success is often determined by the presence of a self-sustaining native-dominated riparian plant community (Sweeney, Czapka, & Yerkes 2002). All active restoration sites in this study achieved this goal. One biotic component, the native herbaceous canopy, was conspicuously absent or highly reduced in most of these sites. Lennox et al. (2011) found similar results when conducting a retrospective study of 89 riparian revegetation sites in California rangelands. Native woody trees and shrubs consistently dominated these landscapes, while the native understory, dominated by native herbaceous species, was found to decrease with native woody success.

The native herbaceous canopy (forbs and grasses) was limited at most of these sites. Woody cover may be the causative factor of herbaceous cover decline with time (data not shown) although a lack of inclusion of herbaceous species into the restoration planting may be the cause of this observed pattern. Restoration of the native herbaceous canopy is a common problem indicated by Lennox et al. (2011). They recommend that land managers plant shade-tolerant native species to increase species richness. Native woody vegetation success, especially shrub success, is the most likely biotic factor contributing to low overall herbaceous cover (native and exotic) through resource competition (Brown & Archer 1999; Sher, Marshall, & Gilbert 2000; Quinn 2006; Lennox *et al.* 2011).

Total vegetation was found to have a mean value of approximately 150 percent cover across the entire management chronosequence (data not shown), indicating maximum cover for available niche space. This was achieved by year 5 after *A. donax* removal. As the oldest actively managed site had native woody cover approaching this value it appears that this age class represents the maximum achievable native cover for the region of southern California. The composition of this habitat was high in shrub cover, including *B. salicifolia*, a species shown to inhibit *A. donax* growth (Quinn 2006), but poor in species richness. The presence of *A. donax* proximally to most sites indicates the potential for reinvasion, although it was not observed. Further research would be needed to determine why reinvasion did not occur, as factors limiting *A. donax* dispersal and establishment were not measured in the current study.

Facilitation of native establishment through the planting and tending of native species and management of exotic species creates a semi-artificial ecosystem where species assemblages can vary more due to site management than natural successional processes. We found certain environmental factors important to native species success in these managed systems, including moist soils with litter for tree species and older and wider project sites further from the active channel for shrub species. Herbaceous species were found negatively correlated with shrubs but dispersed between and below the tree canopy. It is a bit perplexing why distance from the active river channel was not important in explaining the presence of tree species as this relationship is typically correlated with soil moisture and phreatophyte success under natural conditions (Hughes 1997). The unnatural conditions found in active restoration sites give advantage to native species, with some species persisting in areas where they might not otherwise establish naturally. Nonetheless, soil moisture was found to be an important factor with native success, indicating shallow soil water is important to plant survival (also see Racelis et al. 2012). The more xeric shrub species were found where expected, in drier soils outside of the tree canopy, and the herbaceous species were also found where expected, associated with moist soil under or near the tree canopy. The process of active restoration including selection of where to restore, alteration of site topography, depth of planting, odd species assemblages and use of irrigation to establish plants has created artificial or semi-artificial ecosystems, but with the passage of time these systems are trending toward the natural successional state observed in older passively restored sites.

Another conundrum is the decrease of native woody species richness with time since removal. This indicates either local extinction of rare species as climax species become dominant (Planty-Tabacchi *et al.* 1996; Lennox *et al.* 2011) or that methods of active management have changed with time where species-poor plantings of climax species remain unchanged in older sites and younger sites have been planted with higher species diversity. This could not be resolved due to an incomplete dataset of site-specific planting records. The diversity of native herbaceous species remained stable with time indicating that this niche remained intact even as native woody cover increased. This was not the case with total exotic species diversity, which decreased with time since removal. This could be an example of restoration acting as a filter to invasion through resource competition, selecting shade tolerant native herbaceous species (Bakker & Wilson 2004).

Long-term effects of *A. donax* removal methods

High variation was found between the two mechanical removal sites indicating that this method had less of an important role in determining native recruitment into passive restoration sites than environmental factors. For chemical methods native recruitment always increased over the chronosequence. Additional sampling of younger removal projects (time since removal 0 to 5 yr.) would add important data and possibly reveal differences between *A. donax* removal methods. These data do not suggest one method allowed for higher native recruitment over another, but it suggests that chemical treatments support steady native recruitment with less dependence on environmental factors to be successful.

Differences were found when comparing treatment methods using the herbicides Aquamaster (glyphosate) or Habitat (imazapyr). Glyphosate always had higher rates of native recruitment into passive restoration sites than imazapyr sites when excluding the large removal sites of method 5b. Imazapyr has soil residual activity not found in glyphosate (McDowell *et al.* 1997; Borggaard & Gimsing 2008). Imazapyr soil residues increase after foliar treatment. One study found soil residues reached maximum concentrations at day 231 post application (Lee *et al.* 1991), likely from the combined effects of residues washing from plant surfaces with rain and the re-release of residues by root exudation and plant decomposition. The half-life of imazapyr soil residues varies greatly with temperature, 6.4 days at 30 degrees C to 155 days at 15 degrees C (McDowell *et al.* 1997) but temperature combined with other abiotic factors like soil texture and high organic matter can increase the half life of imazapyr to 510 days (Mangels & Ritter 2000). Soil uptake by neighbor plants has been shown to display herbicide effects (Da Silva *et al.* 2005) for up to 434 days in field conditions (Lewis & McCarthy 2008). An important consideration in the use of this herbicide to manage *A. donax* is the re-release of imazapyr residues into the soil with rhizome decomposition. We hypothesize that the large storage rhizomes of *A. donax*, once treated with this herbicide, may absorb and then release the herbicide into soil and extend injurious effects in excess of 62 weeks, and multiple chemical applications would extend effects even longer. If this hypothesis is correct imazapyr may delay native species establishment and habitat recovery, which would explain differences observed between removal methods utilizing different herbicides. These results should be interpreted cautiously as project size and sample size could be confounding factors in this current study.

IMPLICATIONS FOR MANAGEMENT

Results presented here offer estimates of the potential success of passive restoration projects if spatial factors related to removal site location and *A. donax* patch dimensions are known. No recommendations can be made from this research regarding choice of *A. donax* removal method or herbicide, although herbicide residues from imazapyr found in the soil may pose significant risks to native seedling recruitment and other establishing plants sensitive to this herbicide (e.g. restoration plantings) (Lee *et al.* 1991), and therefore the long-term success of restoration.

An interesting difference in species richness was found when comparing the oldest active and oldest passive restoration sites (16-20 yr), with active sites having depauperate flora relative to passive sites. It was noticed that in the oldest active restoration site natural recruitment of native plants was limited, as evidenced by a still-uniform planting array of shrubs and trees. The desire of managers to create a uniform planting array at high planting densities appears to limit long-term recruitment of native species and may reduce total species richness with time (Weiher, Clarke, & Keddy 1998).

For current or future large-scale passive restoration projects we recommend planting discrete patches of native woody vegetation, which will have the immediate effect of creating local native seed sources and the potential long term effect of increased native establishment (Parsons, Ehrenfeld, & Handel 1998; Quinn 2006). Whenever possible the whip cutting method should be used to preserve local genetics and minimize project costs, using shrub species able to impart invasion resistance to the plant community (Lawson, Giessow, & Giessow 2005). This planting method uses locally collected branch cuttings which can be planted directly into the soil (Hoag & Fripp 2003). Plantings should be from many different individual genets to increase genetic diversity and planted at either 1:1 or the site-specific sex ratio if plants are dioecious (Bowler, unpublished). Areas least likely to recruit native species should be prioritized for patch planting, which include those areas far from an active channel (Russell, Hawkins, & O'Neil 1997). All other plantings should be randomized throughout the site. Active restoration projects with the *a priori* goal of creating native habitat resistant to exotic invasion should plant large, dense, shrub-rich patches to promote high competition for both radiation and soil resources, while leaving canopy gaps. These gaps allow for the recruitment of new species, increasing site richness.

Restoring for invasion resistance is a recent topic that holds promise for species specific management (Funk *et al.* 2008). It has been shown to be effective in managing grassland (Bakker & Wilson 2004; Blumenthal, Jordan, & Svenson 2005) and Mediterranean annual community invasions (Prieur-Richard et al. 2002), but to have limited success in resource poor, arid systems (Mangla *et al.* 2011). Under optimal conditions woody native species are favored in riparian ecosystems, creating tall, dense thickets that appear to be resistant to invasion by shade sensitive exotic species (Mangla *et al.* 2011). Active restoration sites represent an expedited trajectory toward a closed native canopy resistant to invasion. The novel growth form of *A. donax* has allowed its dominance in this highly competitive ecosystem (Quinn & Holt 2008) but no restored community has been found resistant to this species (Quinn 2006; Coffman 2007), except for specific instances discussed within Chapter 2.

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Table 3.1. Southern California *A. donax* removal research sites.

Site No.	Site Name	Site Abbrev.	County	Watershed	Site lat. Site long.	Site Age[1]	Control Method[2]	Resto. Type[3]	No. of Reps.
1	Carbon Canyon	CC	Orange	Santa Ana River	33.9501 -117.7318	7	1	AR	3
2	Forester Creek	FC	San Diego	San Diego River	32.8404 -116.9962	6	4	AR	1
3	Hidden Valley Wildlife Area	HV	Riverside	Santa Ana River	33.9669 -117.4540	11	5	PR	5
4	Lakeside	LK	San Diego	San Diego River	32.8595 -116.9292	5	4	AR	3
5	Moor Park	MP	Ventura	Calleguas Creek	34.3071 -118.8010	20	4	AR	3
6	Pendleton	PE1[4]	San Diego	Santa Margarita River	33.2833 -117.3654	16	5	PR	1
7	Pendleton	PE2	San Diego	Santa Margarita River	33.2833 -117.3654	10	4	PR	2
8	Prado Basin	PB	Orange	Santa Ana River	33.9300 -117.5391	5	5	PR	3
9	San Diego River	SD	San Diego	San Diego River	32.8496 -116.9494	9	4	AR	3
10	San Luis Rey River	SLR	San Diego	San Luis Rey River	33.3458 -117.0892	7	3	AR	3
11	Sandia Creek	SM	San Diego	Santa Margarita River	33.4167 -117.2211	16	1	PR	3
12	Santa Ana River	SA	San Bernardino	Santa Ana River	34.0415 -117.3445	8	5	PR	1
13	Santiago Creek	SC	Orange	Santa Ana River	33.7936 -117.6019	7	5	PR	5
14	Sepulveda Basin	SE	Los Angeles	Los Angeles River	34.2088 -118.3936	11	4	PR	3
15	Sweetwater River	SW1	San Diego	Sweetwater River	32.6585 -117.0409	15	1	PR	4
16	Sweetwater River	SW2	San Diego	Sweetwater River	32.6585 -117.0409	15	1	AR	2
17	Whittier Narrows	WN1	Los Angeles	San Gabriel River	34.0664 -117.9481	11	4	PR	3

18	Whittier Narrows	WN2	Los Angeles	San Gabriel River	34.0729 -117.9922	11	2	PR	1
19	Whittier Narrows	WN3	Los Angeles	San Gabriel River	34.0553 -117.9859	7	6	PR	3
20	Whittier Narrows	WN4	Los Angeles	San Gabriel River	34.0553 -117.9859	7	6	PR	3
21	Yorba Linda	YL1	Orange	Santa Ana River	33.8814 -117.7348	13	4	AR	3
22	Yorba Linda	YL2	Orange	Santa Ana River	33.8817 -117.7335	8	4	AR	1

[1] Site age is years since *A. donax* removal was initiated.

[2] Control method is coded for both *A. donax* removal and the pesticide applied: (1) stems removed and AquaMaster (glyphosate) applied to cut surface, (2) no stem removal and Habitat (imazapyr) applied to whole plant, (3) no stem removal and glyphosate applied to whole plant, (4) whole plant mechanical removal with glyphosate applied to resprouts, (5) stems mulched with glyphosate applied to resprouts and (6) stems mulched with imazapyr applied to resprouts.

[3] Restoration type is active (AR) or passive restoration (PR).

[4] Numbers associated with site abbreviations indicate multiple sampling locations within one named site.

Table 3.2. PCA loadings matrix of environmental variables from all study sites (active restoration, n=22; passive restoration, n=37), including all three significant PCs (eigenvalue, $p<0.05$). Data in bold represent significant variables (loading ≥0.5).

	Component 1	Component 2	Component 3
Passive Restoration	loading-	loading-	loading-
Environmental variable (unit)	spatial-exotic (41.9)*	temporal (23.8)	temporal (12.7)
Native tree cover (%)	**-0.742**	-0.207	**0.540**
Native shrub cover (%)	-0.332	**0.814**	-0.252
Exotic species cover (%)	**0.798**	-0.291	-0.246
Site width (m.)	**0.815**	-0.182	0.283
Site age (yr.)	0.132	**0.682**	**0.500**
Dist. to active channel (m.)	**0.763**	0.045	0.362
Soil litter (%)	**0.609**	**0.613**	-0.098
Active Restoration	loading-	loading-	loading-
Environmental variable (unit)	spatial-temporal (41.4)	soil variables (24.9)	native comp. (12.1)
Native tree cover (%)	0.170	**0.655**	**-0.630**
Native shrub cover (%)	**0.730**	-0.253	-0.053
Native herb. cover (%)	**-0.600**	**0.530**	**0.525**
Soil moisture (%)	0.032	**0.853**	0.266
Site width (m.)	**0.826**	-0.056	0.328
Site age (yr.)	**0.951**	0.103	0.030
Dist. to active channel (m.)	**0.795**	0.036	0.267
Soil litter (%)	0.415	**0.687**	-0.144

*Percentage of variation explained by the principal component.

Table 3.3. Spearman's rank correlation for environmental variables (n=13) on all study sites at 95 percent confidence (active restoration, n = 22, and passive restoration, n = 37). Only significant relationships are presented.

Environmental variables		compared to:	r	Prob.
Passive restoration sites				
	Native tree cover	Total exotic cover	-0.669	<0.001
		Site width	-0.446	0.001
		Distance to active channel	-0.425	0.001
		Soil litter	-0.530	<0.001
	Native shrub cover	Total exotic cover	-0.505	0.002
		Site width	-0.485	0.002
		Site age	0.368	0.025
		Distance to active channel	-0.351	0.033
	Total exotic cover	Site width	0.580	<0.001
	Site age	Soil litter	0.337	0.041
Active restoration sites				
	Native tree cover	Soil moisture	0.465	0.029
		Soil litter	0.423	0.050
	Native shrub cover	Native herbaceous cover	-0.476	0.025
		Total exotic cover	-0.451	0.035
		Site width	0.558	0.007
		Site age	0.711	<0.001
		Distance to active channel	0.625	0.002
	Native herbaceous cover	Site age	-0.632	0.002
	Total exotic cover	Site width	-0.461	0.031
	Site age	Soil litter	0.522	0.013
	Soil litter	Soil moisture	0.521	0.013

Table 3.4. Species list - combined over all study sites[1].

				Site[2]															
Species	Common name	Family	Growth form	CC	FC	HV	LK	MP	PE	PB	SD	SLR	SM	SA	SC	SE	SW	WN	YL
Exotic species																			
Ailanthus altissima (Mill.) Swingle	tree of heaven	Simaroubaceae	t													x		x	
Amaranthus sp.		Amaranthaceae	h							x				x		x			
Anagallis arvensis L. [*A. caerulea, A. foemina*]	scarlet pimpernel	Myrsinaceae	h	x	x				x						x				
Arundo donax L.	giant reed	Poaceae	g	x		x	x	x	x	x	x	x		x	x	x	x	x	x
Asparagus asparagoides (L.) Druce [*A. densiflorus*]	African asparagus fern	Asparagaceae	v														x		
Avena fatua L.	wild oat	Poaceae	g								x							x	
Bidens laevis (L.) Britton et al.	bur-marigold	Asteraceae	h							x									
Brassica nigra (L.) W.D.J. Koch	black mustard	Brassicaceae	h														x		x
Brassica tournifortii Gouan	Sahara mustard	Brassicaceae	h			x													
Bromus diandrus Roth	ripgut grass	Poaceae	g	x		x									x		x		
Bromus madritensis subsp. *rubens* (L.) Husn.	red brome	Poaceae	g			x	x				x				x				
Carduus pycnocephalus L. subsp. *pycnocephalus*	Italian thistle	Asteraceae	h	x		x	x	x	x	x	x		x		x	x	x	x	x
Carpobrotus edulis (L.) N.E. Br.	freeway iceplant	Aizoaceae	h									x							
Catalpa sp.		Bignoniaceae	t													x			
Centaurea [*Cnicus*] *benedictus* (L.) L.	blessed thistle	Asteraceae	h			x													
Centaurea melitensis L.	Maltese star thistle	Asteraceae	h	x		x	x	x					x	x	x	x	x	x	x
Centaurea solstitialis L.	yellow star-thistle	Asteraceae	h															x	
Chenopodium album L.	lamb's quarters	Chenopodiaceae	h	x		x				x				x	x			x	
Chrysanthemum coronaria (L.) Spach	crown daisy	Asteraceae	h				x										x	x	
Cirsium vulgare (Savi) Ten.	bull thistle	Asteraceae	h			x		x										x	
Conium maculatum L.	poison hemlock	Apiaceae	h	x		x			x	x		x	x		x	x		x	x

	Common		Growth	Site[2]															
Species	name	Family	form	CC	FC	HV	LK	MP	PE	PB	SD	SLR	SM	SA	SC	SE	SW	WN	YL
Cortaderia selloana (Schult. & Schult. f.) Asch. & Graebn.	Pampas grass	Poaceae	g										x						
Cotula australis (Spreng.) Hook. f.	Australian cotula	Asteraceae	h		x	x													
Cynodon dactylon (L.) Pers.	Bermuda grass	Poaceae	g											x	x		x		
Cyperus sp.		Cyperaceae	h		x		x			x	x		x	x	x		x	x	
Dysphania [*Chenopodium*] *ambrosioides* (L.) Mosyakin & Clements	Mexican tea	Chenopodiaceae	h	x					x	x		x				x			
Erodium sp.		Geraniaceae	h														x		
Eucalyptus sp.		Myrtaceae	t										x	x			x	x	x
Festuca [*Vulpia*] *myuros* L.	rattail six-weeks grass	Poaceae	g									x						x	
Festuca perennis (L.) Columbus & J.P. Sm. [*Lolium multiflorum*]	rye grass	Poaceae	g							x									
Ficus carica L.	edible fig	Moraceae	t								x								
Foeniculum vulgare Mill.	fennel	Apiaceae	h		x				x		x		x		x	x	x	x	x
Fraxinus sp.		Oleaceae	t								x				x	x		x	
Galium sp.		Rubiaceae	h										x		x			x	
Helminthotheca [*Picris*] *echioides* (L.) Holub	bristly ox-tongue	Asteraceae	h	x	x				x		x	x			x	x	x	x	
Hirschfeldia incana (L.) Lagr.-Fossat	shortpod mustard	Brassicaceae	h	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Hypochaeris glabra L.	smooth cat's-ear	Asteraceae	h														x		
Iris sp.		Iridaceae	h												x				
Kochia [*Bassia*] *scoparia* (L.) Schrad. subsp. *scoparia*	red sage	Chenopodiaceae	h						x	x									
Lactuca serriola L.	prickly lettuce	Asteraceae	h	x		x	x			x	x		x		x	x	x	x	
Lepidium latifolium L.	perennial pepperweed	Brassicaceae	h			x		x	x	x	x	x			x			x	x
Marrubium vulgare L.	horehound	Lamiaceae	h					x								x			
Melilotus albus Medik.	white sweetclover	Fabaceae	h	x		x	x			x	x		x	x	x		x	x	
Myoporum laetum G. Forst.	ngaio tree	Scrophulariaceae	t														x		

Species	Common name	Family	Growth form	Site[2]															
				CC	FC	HV	LK	MP	PE	PB	SD	SLR	SM	SA	SC	SE	SW	WN	YL
Nasturtium officinale W.T. Aiton [*Rorippa nasturtium-aquaticum*]	water cress	Brassicaceae	h				x						x		x				
Nicotiana glauca Graham	tree tobacco	Solanaceae	s	x		x		x		x			x		x	x			
Parthenocissus inserta (A. Kern.) Fritch [*P. vitacea*]	woodvine	Vitaceae	v											x				x	
Passiflora caerulea L.	blue passion flower	Passifloraceae	v															x	
Pennisetum clandestinum Chiov.	kikuyu grass	Poaceae	g		x									x				x	
Persicaria maculosa Gray [*Polygonum persicaria*]	lady's thumb	Polygonaceae	h							x		x	x	x	x			x	
Phoenix canariensis Chabaud	Canary Island palm	Arecaceae	t														x		
Phytolacca americana L. var. *americana*	pokeweed	Phytolaccaceae	h															x	
Plantago arenaria Waldst. & Kit. [*P. indica*]	Indian plantain	Plantaginaceae	h															x	
Plantago lanceolata L.	English plantain	Plantaginaceae	h								x							x	
Plantago major L.	common plantain	Plantaginaceae	h								x							x	
Polypogon monspeliensis (L.) Desf.	rabbitfoot grass	Poaceae	h	x	x	x	x			x					x				
Portulaca oleracea L.	purslane	Portulacaceae	h											x					
Prunus persica (L.) Batsch	peach	Rosaceae	t								x								
Pulicaria paludosa Link	false-fleabane	Asteraceae	h	x					x						x			x	x
Raphanus sativus L.	wild radish	Brassicaceae	h				x		x		x	x					x	x	
Ricinus communis L.	castor bean	Euphorbiaceae	s	x			x		x	x	x	x		x	x	x	x	x	x
Robinia pseudoacacia L.	black locust	Fabaceae	t					x											
Rubus armeniacus Focke [*R. discolor*]	Himalayan blackberry	Rosaceae	s								x								
Rumex crispus L.	curly dock	Polygonaceae	h	x	x	x	x				x	x	x	x	x	x	x	x	
Salsola australis R. Br. [*S. tragus*]	Russian thistle	Chenopodiaceae	h			x							x			x			
Schinus molle L.	Peruvian pepper tree	Anacardiaceae	t														x		
Silybum marianum (L.) Gaertn.	milk thistle	Asteraceae	h	x				x	x				x			x		x	
Sisymbrium sp.		Brassicaceae	h			x													

	Common		Growth	Site[2]															
Species	name	Family	form	CC	FC	HV	LK	MP	PE	PB	SD	SLR	SM	SA	SC	SE	SW	WN	YL
Sonchus asper (L.) Hill subsp. *asper*	prickly sow thistle	Asteraceae	h				x												
Sonchus oleraceus L.	common sow thistle	Asteraceae	h						x		x				x	x			x
Sorghum halepense (L.) Pers.	Johnson grass	Poaceae	g			x												x	
Stipa miliacea (L.) Hoover var. *miliacea* [*Piptatherum miliaceum*]	smilo grass	Poaceae	g	x	x		x				x		x		x	x		x	
Tamarix ramosissima Ledeb.	saltcedar	Tamaricaceae	t			x			x	x		x							x
Tanacetum [*Chrysanthemum*] *parthenium* (L.) Sch. Bip.[3]	feverfew	Asteraceae	h								x								
Ulmus parvifolia Jacq.	Chinese elm	Ulmaceae	t								x						x	x	
Verbesina encelioides (Cav.) A. Gray subsp. *exauriculata* (B.L. Rob. & Greenm.) J.R. Coleman	golden crownbeard	Asteraceae	h			x				x									
Wachingtonia robusta H. Wendl.	Mexican fan palm	Arecaceae	t		x	x				x							x	x	
Native species																			
Acer negundo L.	box elder	Sapindaceae	t		x						x	x							
Acmispon [*Lotus*] sp.		Fabaceae	h										x		x				
Acmispon americanus (Nutt.) Rydb. var. [*Lotus purshianus var. purshianus*]	Spanish clover	Fabaceae	h				x										x		
Acmispon flaber (Vogel) Brouillet [*Lotus scoparius*]	deerweed	Fabaceae	s												x				x
Alnus rhombifolia Nutt.	white alder	Betulaceae	t												x				
Ambrosia acanthacarpa Hook.	annual bur-sage	Asteraceae	h			x	x		x	x				x		x		x	x
Ambrosia confertiflora DC.	ragweed	Asteraceae	h													x		x	
Ambrosia psilostachia DC.	western ragweed	Asteraceae	h	x	x	x		x	x		x	x	x		x	x	x		
Amorpha fruticans L.	false indigo	Fabaceae	s				x												
Amsinckia menziesii (Lehm.) A. Nelson & J.F. Macbr.	common fiddleneck	Boraginaceae	h			x													
Anemopsis californica (Nutt.) Hook. & Arn.	yerba mansa	Saururaceae	h						x										
Apium graveolens L. Celery	wild celery	Apiaceae	h		x		x				x		x				x	x	

	Common		Growth	Site[2]															
Species	name	Family	form	CC	FC	HV	LK	MP	PE	PB	SD	SLR	SM	SA	SC	SE	SW	WN	YL
Artemisia californica Less.	California sagebrush	Asteraceae	s	x				x					x		x	x	x	x	x
Artemisia douglasiana Besser	mugwort	Asteraceae	h	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x
Artemisia dracunculus L.	tarragon	Asteraceae	s					x											x
Artemisia palmeri A. Gray	San Diego sagewort	Asteraceae	s								x								
Aster sp.		Asteraceae	h		x	x		x	x	x			x					x	
Atriplex prostrata DC. [*A. triangularis*]	fat-hen	Chenopodiaceae	h				x		x	x		x					x		
Baccharis pilularis DC.	coyote bush	Asteraceae	s	x		x		x	x						x	x	x		x
Baccharis salicifolia (Ruis & Pav.) Pers. subsp. *salicifolia*	mule fat	Asteraceae	s	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Baccharis sarathroides A. Gray	broom baccharis	Asteraceae	s		x												x		
Bebbia juncea (Benth.) Greene var. *aspera* Greene		Asteraceae	s												x				
Bidens frondosa L.	sticktight	Asteraceae	h							x									
Brickellia californica (Torr. & A. Gray) A. Gray	California brickellbush	Asteraceae	s												x				
Calystegia macrostegia (Greene) Brummitt	morning-glory	Convolvulaceae	v										x		x				
Camissoniopsis [*Camissonia*] *bistorta* (Torr. & A. Gray) W.L. Wagnrer & Hoch		Onagraceae	h	x															
Castilleja sp.		Orobanchaceae	h												x				
Clematis pauciflora Nutt.	southern California clematis	Ranunculaceae	v									x				x			
Croton californicus Mull. Arg.	California croton	Euphorbiaceae	h					x										x	x
Cucurbita foetidissima Kunth	calabazilla	Cucurbitaceae	h	x								x	x			x		x	
Cuscuta californica Hook. & Arn.	chaparral dodder	Convolvulaceae	h	x		x						x	x		x				
Cuscuta indecora Choisy var. *indecora*	large-seeded dodder	Convolvulaceae	h											x				x	x
Datura wrightii Regel	Jimson weed	Solanaceae	h	x			x	x				x	x			x		x	

	Common		Growth	Site[2]															
Species	name	Family	form	CC	FC	HV	LK	MP	PE	PB	SD	SLR	SM	SA	SC	SE	SW	WN	YL
Deinandra [*Hemizonia*] *fasciculata* (DC.) Greene	fascicled tarweed	Asteraceae	h												x				
Elymus [*Leymus*] *triticoides* Buckley	beardless wild rye	Poaceae	g			x	x		x										
Encelia californica Nutt.	coast sunflower	Asteraceae	s								x								x
Epilobium brachycarpum C. Presl	annual willowherb	Onagraceae	h				x												
Epilobium sp.		Onagraceae	h	x					x			x			x		x	x	
Erigeron [*Conyza*] *canadensis* L.	horseweed	Asteraceae	h	x		x			x	x			x	x	x	x	x	x	x
Eriodictyon crassifolium Benth.	yerba santa	Boraginaceae	s																x
Eriogonum fasciculatum Benth.	California buckwheat	Polygonaceae	s	x			x				x		x		x				
Helianthus annuus L.	sunflower	Asteraceae	h	x		x	x			x				x		x		x	x
Heliotropium curvisavicum L. var. *oculatum* (A. Heller) Tidestr.	seaside heliotrope	Boraginaceae	h	x		x							x	x			x		x
Heteromeles arbutifolia (Lindl.) M. Roem.	toyon	Rosaceae	s														x		
Heterotheca grandiflora Nutt.	telegraph weed	Asteraceae	h	x					x				x	x			x		x
Isocoma menziesii (Hook. & Arn.) G.L. Nesom	coastal goldenbush	Asteraceae	s					x	x										x
Iva hayesiana A. Gray	San Diego marsh-elder	Asteraceae	s		x		x				x						x		
Juglans californica S. Watson	southern California black walnut	Juglandaceae	t	x		x			x		x		x			x		x	
Juncus acutus L. subsp. *leopoldii* (Parl.) Snogerup	southwestern spiny rush	Juncaceae	h								x								
Laennicia [*Conyza*] *coulteri* (A. Gray) G.L. Nesom	Coulter's horseweed	Asteraceae	h							x									
Lepidospartum squamatum (A. Gray) A. Gray	scale-broom	Asteraceae	s											x	x				
Lonicera subspicata Hook. & Arn.	honeysuckle	Caprifoliaceae	s										x						
Malacothamnus fasciculatus (Torr. & A. Gray) Greene	chaparral mallow	Malvaceae	s	x				x					x						

Species	Common name	Family	Growth form	Site[2]															
				CC	FC	HV	LK	MP	PE	PB	SD	SLR	SM	SA	SC	SE	SW	WN	YL
Malacothrix saxatilis (Nutt.) Torr. & A. Gray	cliff dandelion	Asteraceae	s	x		x										x			
Malosma laurina (Nutt.) Abrams	laurel sumac	Anacardiaceae	s	x									x		x				x
Mimulus cardinalis Benth.	scarlet monkeyflower	Phrymaceae	h												x				
Mimulus guttatus DC.	seep monkeyflower	Phrymaceae	h											x					
Oenothera elata subsp. *hookeri* (Torr. & A. Gray) W. Dietr. & W.L. Wagner	Hooker's evening primrose	Onagraceae	h		x				x		x	x			x		x	x	
Opuntia littoralis (Engelm.) Cockerell	prickly-pear	Cactaceae	s									x		x					x
Phacelia minor (Harv.) F. Zimm.	wild canterbury bells	Boraginaceae	h												x				
Phacelia ramosissima Lehm.	caterpillar phacelia	Boraginaceae	h	x				x	x	x		x	x		x				x
Phacelia sp.		Boraginaceae	h			x									x				
Platanus racemosa Nutt.	western sycamore	Platanaceae	t		x		x	x				x	x		x			x	x
Pluchea sericea (Nutt.) Coville	arrow-weed	Asteraceae	h							x	x								x
Populus fremontii S. Watson subsp. *fremontii*	Fremont cottonwood	Salicaceae	t		x	x	x	x			x	x	x	x			x		x
Populus trichocarpa Hook. [*P. balsamifera subsp. Trichocarpa*]	Black cottonwood	Salicaceae	t										x						
Pseudognaphalium [*Gnaphalium*] *californicum* (DC.) Anderb.	everlasting	Asteraceae	h	x															
Pseudognaphalium [*Gnaphalium*] *sp.*		Asteraceae	h										x		x				
Quercus agrifolia Nee	coast life oak	Fagaceae	t				x	x					x		x		x		
Rosa californica Cham. & Schltdl.	California rose	Rosaceae	s			x		x					x				x		
Rubus ursanus Cham. & Schltdl.	California blackberry	Rosaceae	v		x		x		x	x	x		x		x				
Salix exigua Nutt.	sandbar willow	Salicaceae	s		x	x		x	x	x	x	x	x		x	x	x	x	x

	Common		Growth	Site[2]															
Species	name	Family	form	CC	FC	HV	LK	MP	PE	PB	SD	SLR	SM	SA	SC	SE	SW	WN	YL
Salix gooddingii C.R. Ball	Goodding's black willow	Salicaceae	t	x	x	x	x		x	x	x	x		x		x	x	x	x
Salix laevigata Bebb	red willow	Salicaceae	t	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Salix lasiolepis Benth.	arroyo willow	Salicaceae	t	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Salvia apiana Jeps.	white sage	Lamiaceae	s																x
Salvia clevelandii (A. Gray) Greene	Cleveland sage	Lamiaceae	s				x												
Salvia mellifera Greene	black sage	Lamiaceae	s													x			x
Sambucus nigra L. subsp. *caerulea* (Raf.) Bolli [*S. mexicana*]	blue elderberry	Adoxaceae	t	x		x	x	x	x				x			x		x	
Schoenoplectus [*Scirpus*] *americanus* (Pers.) Schinz & R. Keller	Olney's three-square bulrush	Cyperaceae	h				x								x				
Solanum douglasii Dunal	nightshade	Solanaceae	h	x					x	x		x		x	x	x		x	
Spartium junceum L.	Spanish broom	Fabaceae	s												x				
Stachys sp.		Lamiaceae	h						x				x		x				
Stephanomeria exigua subsp. *deanei* (J.F. Macbr.) Gottlieb	wirelettuce	Asteraceae	h										x						
Toxicodendron diversilobum (Torr. & A. Gray) Greene	western poison oak	Anacardiaceae	s	x					x	x		x	x		x				x
Typha sp.		Typhaceae	h				x						x		x			x	x
Urtica dioica L.	bull nettle	Urticaceae	h	x		x		x	x	x		x	x	x		x		x	x
Verbena lasiostachys Link	vervain	Verbenaceae	h					x							x				
Vitis girdiana Munson	desert wild grape	Vitaceae	v			x			x	x	x	x	x					x	
Xanthium strumarium L.	cocklebur	Asteraceae	h	x	x	x	x		x	x	x		x	x	x	x	x	x	x

[1] Plant nomenclature from Baldwin et. al. 2012. Synonymized names in brackets from Hickman 1993. Note e = exotic, n = native, g = grass, h = herbaceous, v = vine, s = shrub, and t = tree.

[2] Refer to Table 3.1 for site name abbreviations.

[3] Species not found in Baldwin et. al. 2012. Integrated Taxonomic Information System (http://www.itis.gov/) used to find species information.

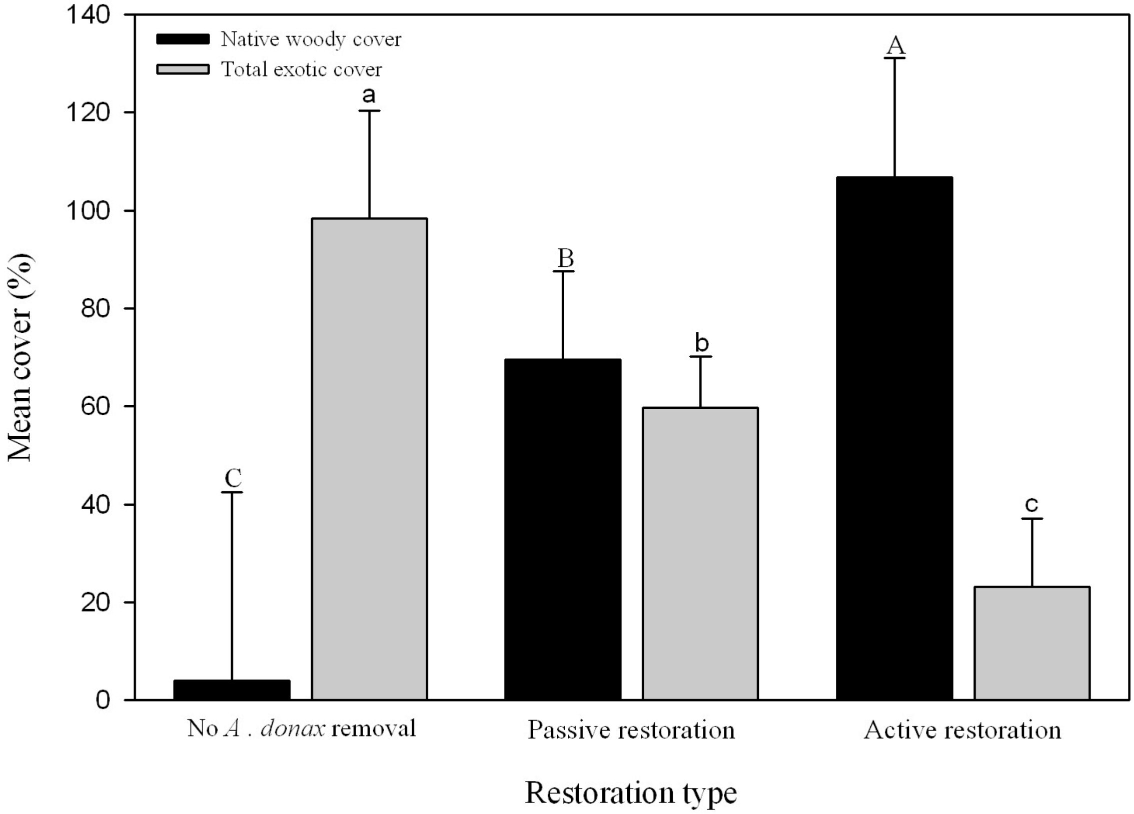

Figure 3.1. Mean percent cover (+/- 95% CI) of restoration methods including no *A. donax* removal, active restoration or passive restoration sites. Letters represent significant differences between groups analyzed separately; A, B, C native woody cover; a, b, c, exotic cover (Tukey HSD post-hoc test, $\alpha = 0.05$).

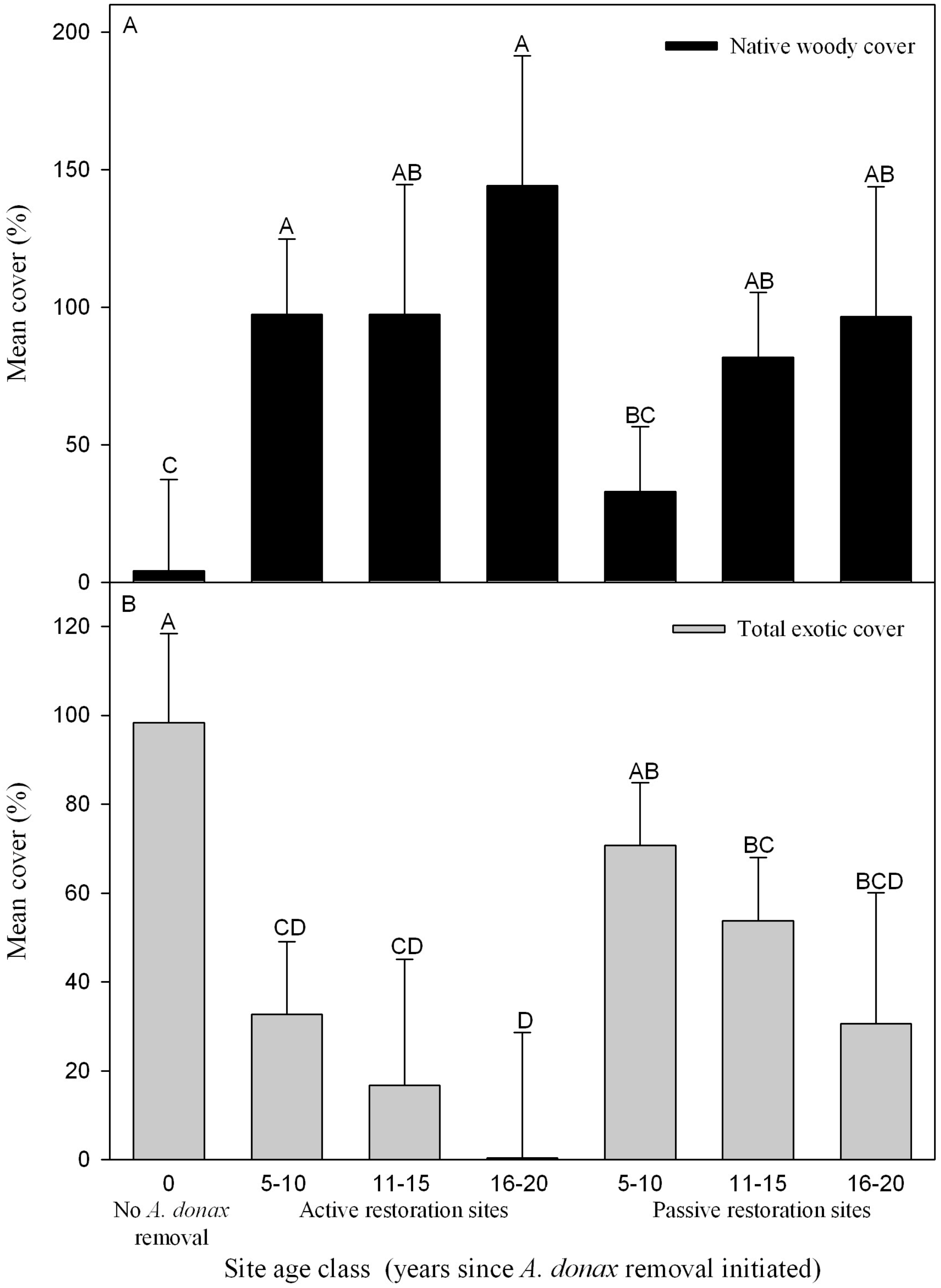

Figure 3.2. Mean percent cover (+/- 95% CI) of pooled vegetation age classes of either native woody (A) or total exotic cover (B). Letters represent significant differences between groups (Tukey HSD post-hoc tests, $\alpha = 0.05$).

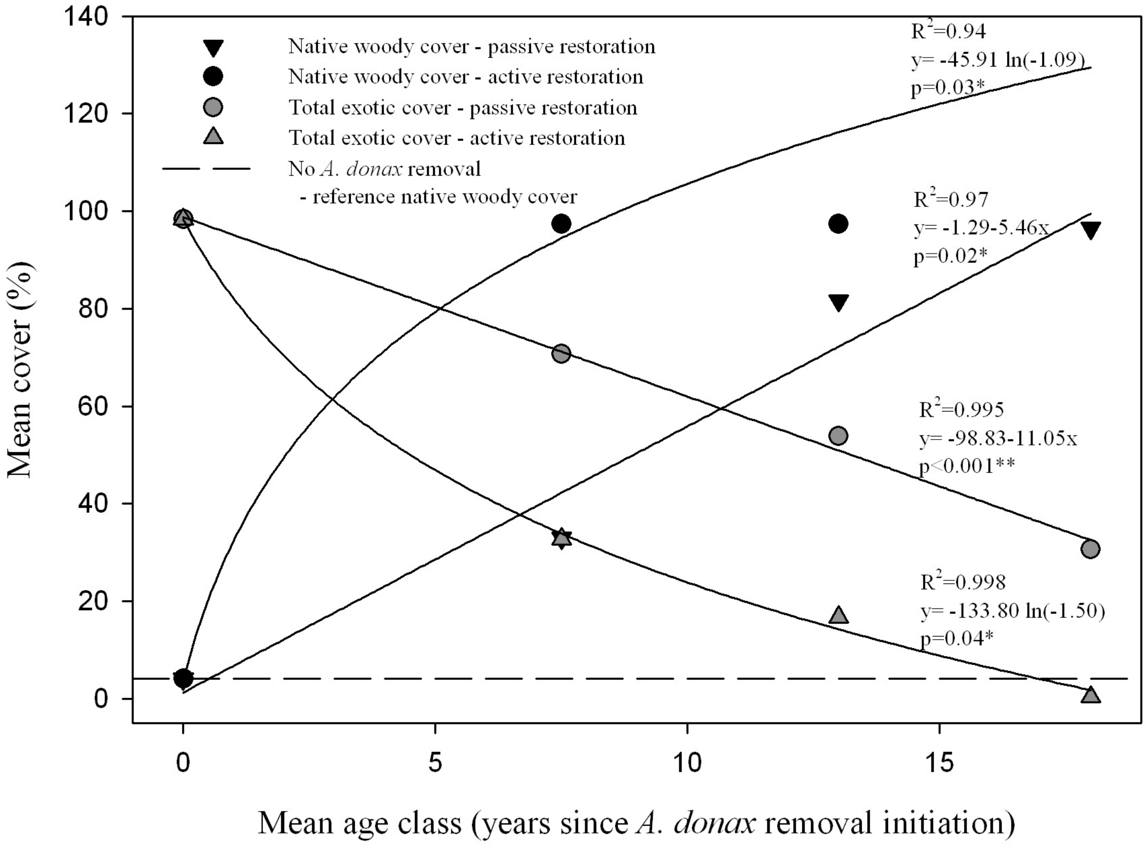

Figure 3.3. Regressed chronosequence of the change in native woody and total exotic cover between site age classes. Age classes 0, 5-10, 11-15 and 16-20 years since *A. donax* removal initiated are presented as mean years: 0, 7.5, 12.5 and 17.5 yr. Timepoint 0 represents an estimate of native woody (4.04 percent) and total exotic cover (98.3 percent) prior to *A. donax* removal, which was measured in 'no *A. donax* removal' sites.

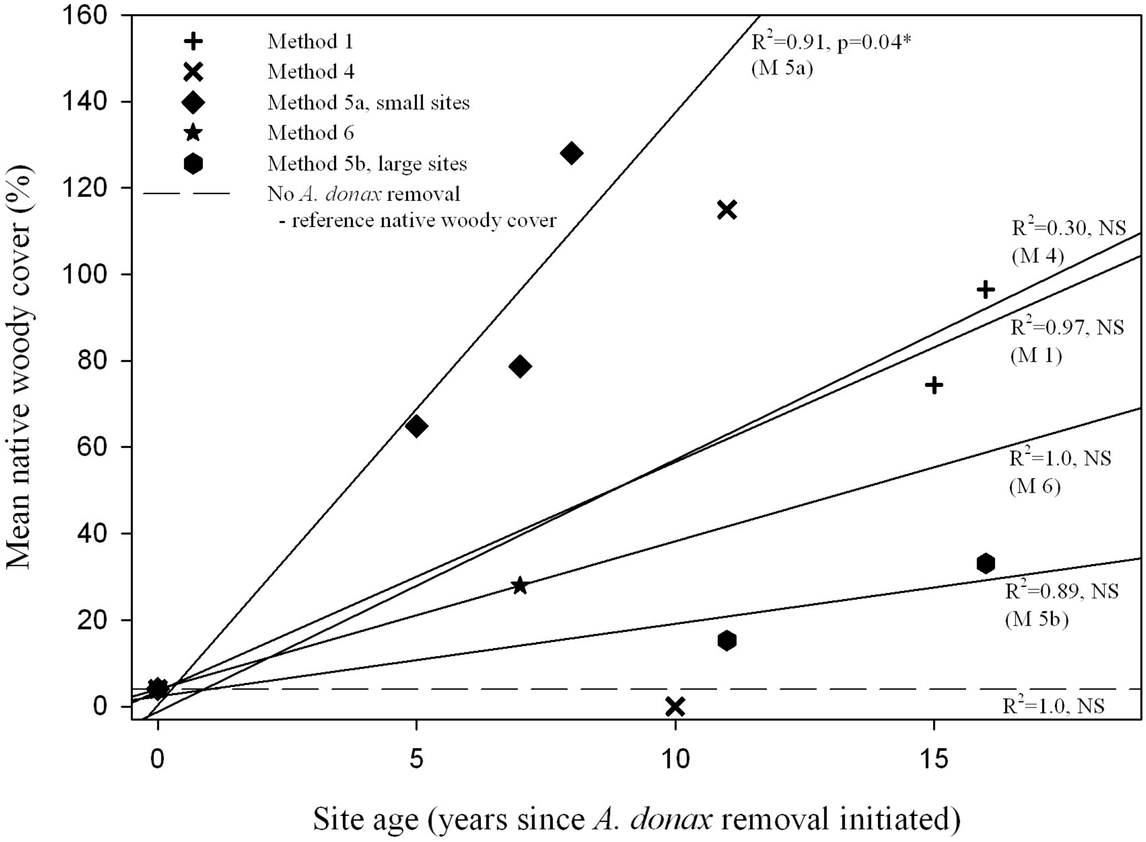

Figure 3.4. Points indicate native woody cover of passive restoration sites. Timepoint 0 represents native woody cover prior to *A. donax* removal (4.04 percent), which was measured in ‘no *A. donax* removal’ sites. Each point represents one sampling location. Methods include: (1) stems removed and AquaMaster applied to cut surface, (4) whole plant mechanical removal with AquaMaster applied to resprouts, (5) stems mulched with AquaMaster applied to resprouts and (6) stems mulched with Habitat applied to resprouts. Method 5 was divided into small (5a) and large (5b) sites.

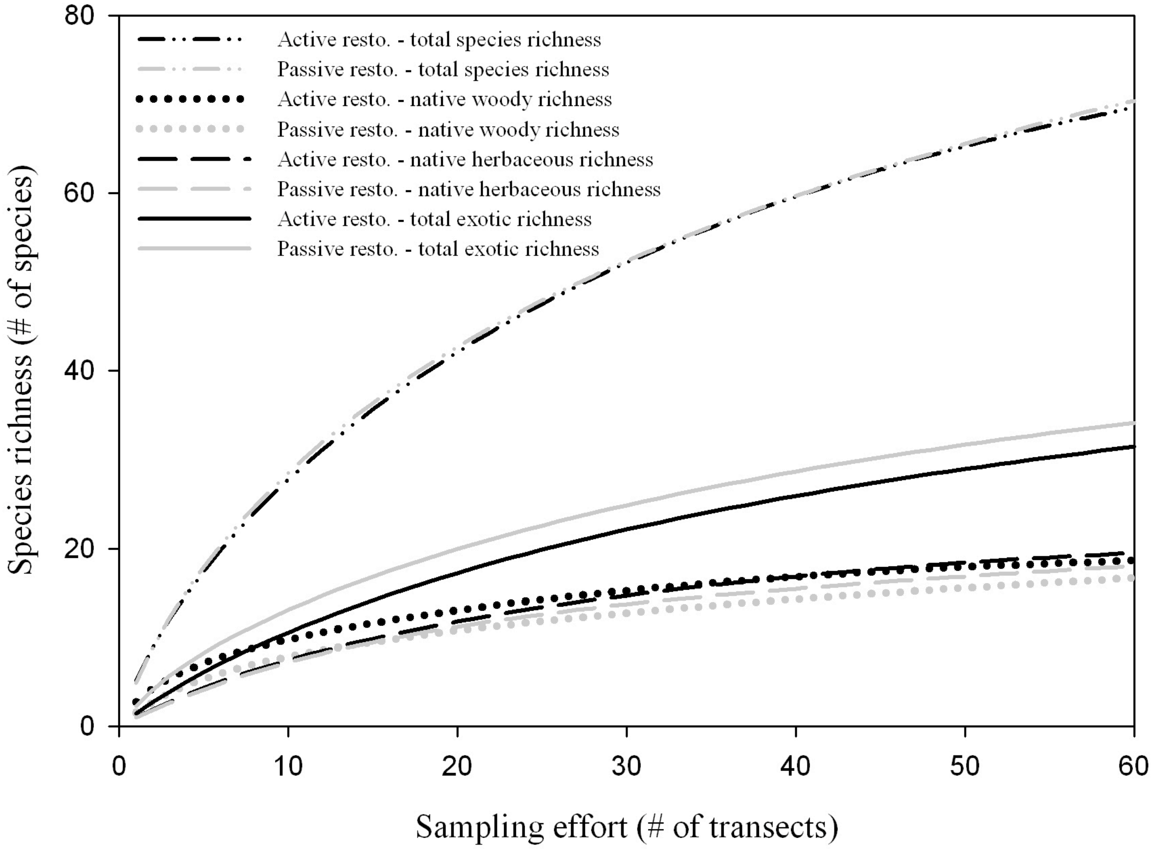

Figure 3.5. Sample-based rarefaction of species presence between sites receiving either active or passive restoration and by vegetation cover class (total species, native woody, native herbaceous, and total exotic richness). All *A. donax* removal sites were included in these analyses. No species richness differences were found when comparing same vegetation cover classes between restoration method, nor between rates of increasing richness ($\alpha = 0.05$).

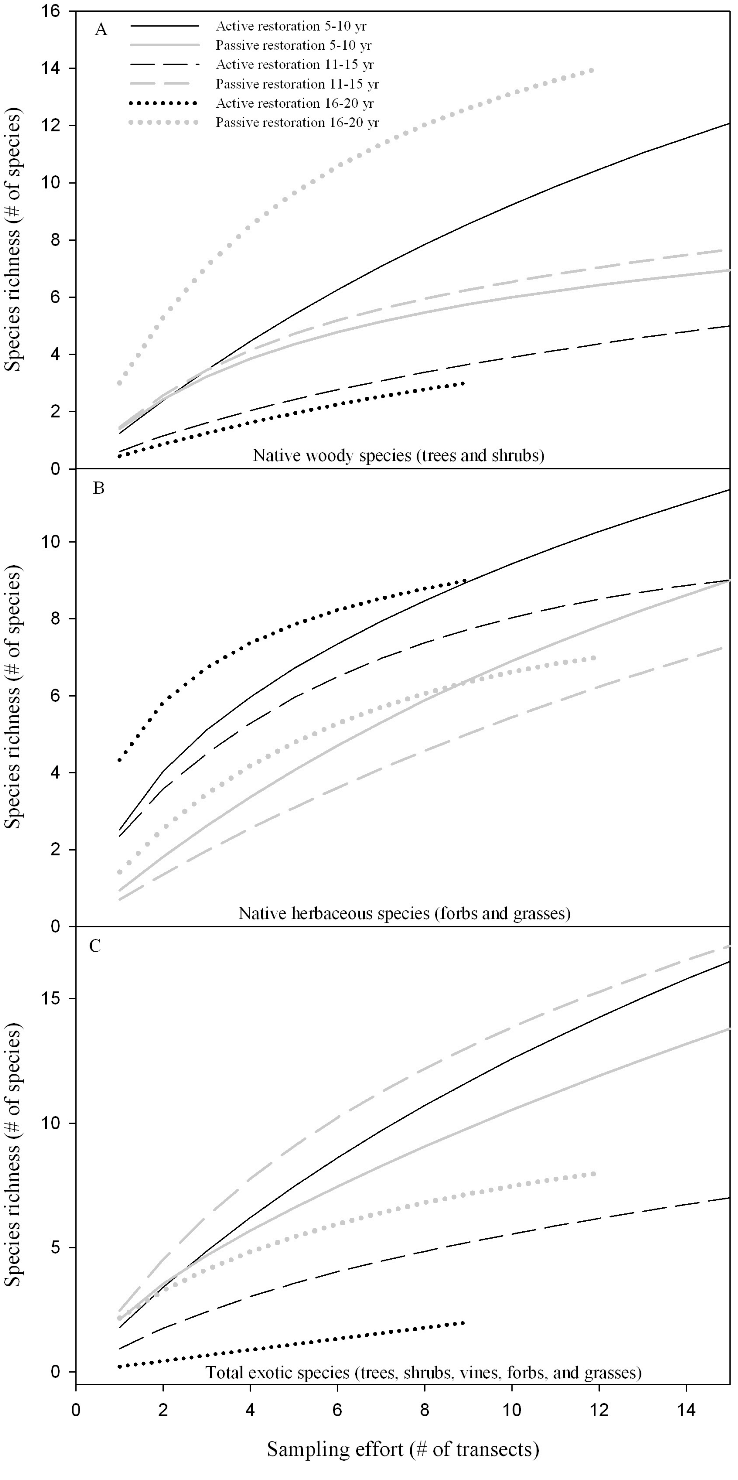

Figure 3.6. Sample-based rarefaction of species presence between all sites receiving either active or passive restoration and by *A. donax* removal site age classes. Graphs A (native woody species), B (native herbaceous species) and C (total exotic species) represent different vegetation classes plotted separately.

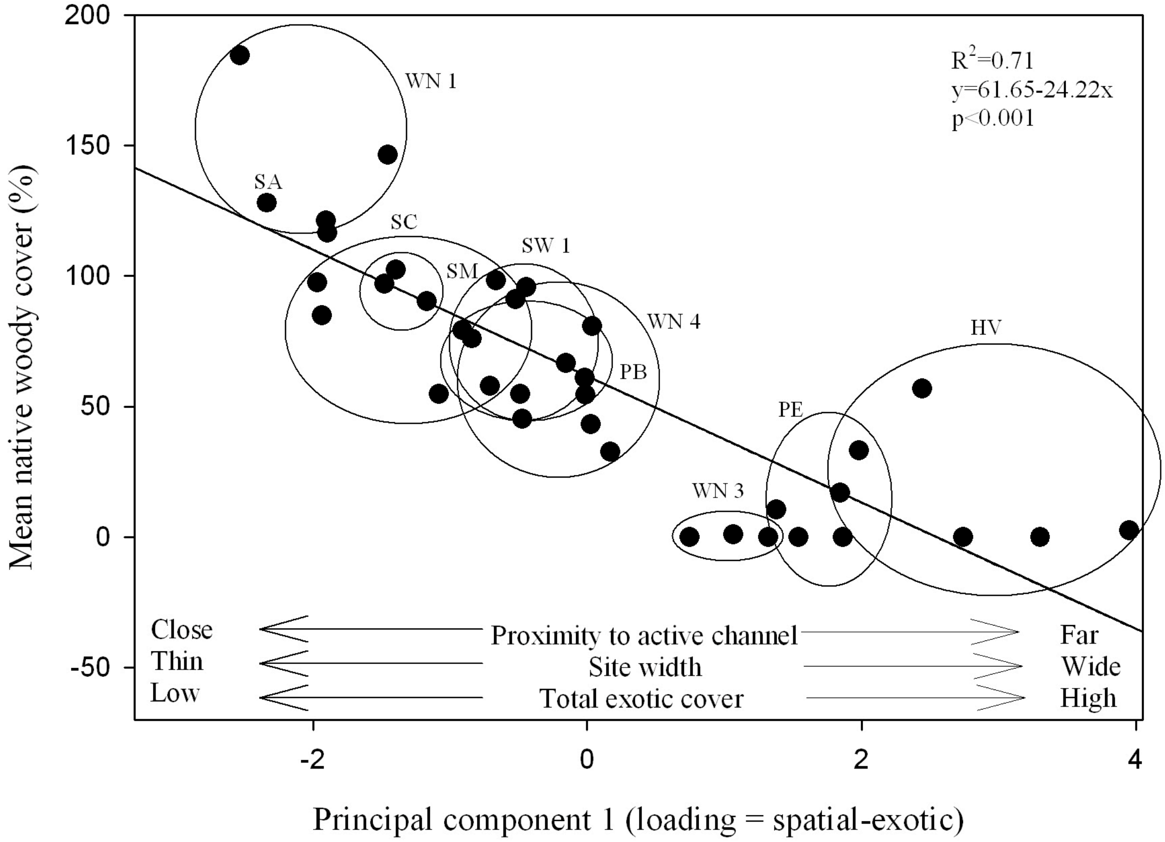

Figure 3.7. Native woody cover of passive restoration sites plotted against principal component 1 (PC 1). Each dot represents a replicate and is the mean of three samples (transects). Circles include all of the replicates found at a site and labeled with the abbreviated site name (Table 3.1). Sites near to each other along the linear regression represent site similarities with respect to important scale-dependent variables (width of *A. donax* removal site and proximity to active channel) and one biological variable (total exotic cover) of PC 1.

CONCLUSIONS

As in other studies testing the competitive ability of native species and their effects on *A. donax* establishment, we found distinct competitive differences between native species (Coffman 2007; Quinn & Holt 2009). More so than growth form, species identity was an important factor determining the success of the invader and to a lesser extent, planting density (Coffman 2007; Quinn & Holt 2009). Including multiple functional groups, increasing community richness and utilizing the complimentary hypothesis have not been shown to decrease the likelihood of *A. donax* establishment in past research (Quinn & Holt 2009), but in my research the annual maximal utilization of one resource, light, through competitive shading by certain native species was shown to effectively inhibit establishment and decrease the likelihood of successful invasion.

My research supports the sampling effect hypothesis, in that a single dominant species with extreme traits can maximally decrease certain resources (Loreau 2000; Loreau & Hector 2001), negatively affecting the success of an invader. This was also supported in research by Quinn and Holt (2009), but only when *A. donax* was grown under one-year-old competitive canopies which included mulefat (*Baccharis salicifolia*). Competitive effects were not found when *A. donax* was grown under two-year-old competitive canopies. Our research indicates that native evergreen shrub canopies older than one year inhibit establishment of small rhizome fragments of *A. donax* under optimal soil resource conditions (e.g. non-limiting water and nitrogen). Four major differences between this study and the Quinn and Holt (2009) study were apparent.

1. The current research grew *A. donax* for multiple growing seasons, where only single season measurements were made in their study.
2. The current research standardized rhizome mass prior to planting, where rhizome fragments varied in mass between year one and two plantings in their study.
3. The current research used small rhizome fragments, smaller than fragments used in their study.
4. The current research did not experience recruitment of undesired woody species into the experimental plots as only male individuals were chosen for use, whereas recruitment was common in year two of their study.

Incongruent results between these studies indicate that the methodological differences highlighted above may have played an important role. Standardizing *A. donax* rhizome mass and the sexual identity of the competitor species to only include males limits the influence variability derived from these factors has on the resulting data. I found that rhizome mass positively influenced the competitive ability of *A. donax* in stressful environments, supporting results by Quinn and Holt (2009). As stem elongation is facilitated by stored carbohydrates in the rhizome (also see Decruyenaere 1999; Decruyenaere & Holt 2001), there is potentially a limit to the inhibitory effect biotic competition can have on *A. donax* establishment based upon rhizome size. It is likely that that this rhizome mass limit, or threshold, was surpassed by Quinn and Holt (2009), leading to competitive avoidance by *A. donax*. This threshold exists in rhizome fragments weighing between 120 and 240 g, or roughly the size of a hand made into a loose fist. Based on my results it is apparent that native competition by evergreen shrub species can create effective invasion resistance against smaller rhizome fragments of *A. donax*. This was supported over the course of more than two growing seasons.

Potential confounding factors not measured in my research include root competitive interactions, soil chemistry and changes in the microbial community by the invader, which have been indicated as significant in previous invasion research (Hierro & Callaway 2003; Ehrenfeld 2003; Callaway & Ridenour 2004; Sigüenza, Corkidi, & Allen 2006; Corbin & D'Antonio 2012). Although these factors were not specifically tested, both glasshouse and field experiments indicated that belowground interactions were less important than aboveground interactions (shading) in explaining *A. donax* growth. As glasshouse shading treatments were created to simulate the shaded environments of both of the native competitor species, light-response curves confirmed that shading intensity was the dominant factor influencing the photosynthetic machinery in both sets of studies, as well as determined that the photosynthetic output of *A. donax* was most limited when in competition with *B. salicifolia*.

Facilitation of *A. donax* growth and establishment in both the moderate shading and sandbar willow (*Salix exigua*) treatments indicated that this light intensity provides adequate energy for aboveground plant growth but limits the plant's belowground storage capacity; making plants vulnerable to secondary stressors like drought or herbivory. Even though establishment is facilitated by the winter deciduous species this diminished belowground storage capacity creates a potential opportunity for management.

IMPLICATIONS FOR MANAGEMENT

Management of *A. donax*, in the form of pruning or herbicide application, should have increased efficacy and minimize the total pesticides applied to a given area if competition exists for radiant energy. Older, established evergreen shrub canopies provide the best resistance to riparian invasion, while winter deciduous shrub and tree species will likely provide windows of opportunity to control *A. donax* when belowground storage is diminished. Furthermore, in competitive riparian habitats natural shoot herbivory (see Quinn & Holt 2004) or biocontrol agents (Moran & Goolsby 2009; Goolsby *et al.* 2009) should also have increased negative effects on *A. donax* growth, increasing the efficacy of management measures.

In areas where *A. donax* had been removed and natural succession allowed to repopulate sites (passive restoration), recruitment of native woody species was found to be successful when sites were both small in area and close to the active water channel. If removal sites were large (>1 ha) and far from the active channel, these sites were most likely to have few native recruits and abundant exotic species. In these low recruitment areas it is recommended that discrete islands of native shrubs and trees be planted in order to decrease native recruitment distance into the rest of the site, potentially increasing native recruitment rates, native cover and restoration success. Of these passively restored areas site age was correlated with native cover, indicating a continuous recruitment of native species with time. It was also found that no matter the type of restoration, equivalent species richness returned to sites on a regional scale (southern California) given enough time, potentially up to 20 years.

Replanting native woody species, or active restoration, was found to facilitate early establishment of native woody cover. This provides both short and long-term benefits to a site, which are both increased if a dominant portion of the selected native species are evergreen shrub species. Short-term benefits include decreased *A. donax* growth potential if invasion reoccurs in that location, rapid creation of wildlife habitat for sensitive species that may have been displaced, and the ability to create habitat in large or distant *A. donax* removal sites that might otherwise be dominated by exotic species. Long-term benefits include invasion resistance to *A. donax*, with habitat that becomes increasingly more dense and potentially more useful for sensitive wildlife (Sharp & Kus 2006).

Potential risks to active management when using a high degree of evergreen shrub species is the inability of the site to recruit novel native species due to the dense canopy created to reduced *A. donax* success (see Quinn & Holt 2009). Based upon the regional sampling of active restoration sites of southern California, where *B. salicifolia* is locally abundant and commonly planted as a dominant restoration species, there did not appear to be a large-scale, regional effect indicating a lack of native recruitment. If present, there would have been a decrease in species richness in active restoration sites relative to passive restoration sites. A explanation for this finding is that the frequently flood-disturbed riparian system creates canopy openings and disperses propagules via hydrochory, increasing the likelihood of native recruitment into these otherwise recruitment limiting sites (Else 1996; Shafroth *et al.* 1998).

Using native evergreen shrub species as cultural control, specifically *B. salicifolia*, has the potential to minimize long-term management costs of *A. donax* by providing effective long-term invasion resistance. Areas especially appropriate for this type of management include those that are infrequently managed and hard to access or that contain sensitive species which would benefit from expedited canopy establishment and habitat creation. As in any management program where eradication is the goal, monitoring for *A. donax* reinvasion will be necessary to ensure restoration success, especially when large rhizome fragments are common. These fragments can potentially invade most, if not all competitive environments when the abiotic environment is non-limiting. Areas at high risk to invasion have canopies composed primarily of winter deciduous species and where the abiotic environment is favorable, or where flood disturbance has removed competing species. This research highlights the finding that when used as part of an integrated weed management plan, restoring for invasion resistance should be considered a viable tool in the long-term management of *A. donax*.

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