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Environmental and Community Factors Influencing the Distribution of Pennisetum setaceum in California

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RIVERSIDE

Environmental and Community Factors Influencing the Distribution of
Pennisetum setaceum in California

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

Doctor of Philosophy

in

Plant Biology

by

Lynn Catherine Sweet

December 2011

Dissertation Committee:
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DEDICATION

"The tree which moves some to tears of joy is in the eyes of the others only a green thing that stands in the way. Some see nature all ridicule and deformity... and some scarce see nature at all. But to the eyes of the man of imagination, nature is imagination itself."

-William Blake, <u>Letter to Reverend Dr. Trusler,</u> 1799

To my mother, Karen, who is an inspiration.

ABSTRACT OF THE DISSERTATION

Environmental and Community Factors Influencing the Distribution of
Pennisetum setaceum in California

by

Lynn Catherine Sweet

Doctor of Philosophy, Graduate Program in Plant Biology
University of California, Riverside, December 2011
Dr. Jodie S. Holt, Chairperson

Non-native African fountain grass (*Pennisetum setaceum*) has been increasing in

California over the last century; however, its potential distribution and impacts have not

been determined. Coarse-scale species distribution models trained using data from the

native range of *P. setaceum* indicated broad areas of suitability for *P. setaceum* in

southern and coastal California. MaxEnt models produced using native range

information showed a broader potentially suitable area than models based on the invaded

range data. At a finer scale, suitable area in the Colorado Desert occurs where there are

factors associated with increased soil moisture. This study demonstrates that these

methods can be used to provide regional risk-planning information as well as to inform

local early-detection efforts. Within this broader area, biotic factors also influence invasion. Where *P. setaceum* occurs adjacent to native C_3 *Stipa pulchra* grasslands, it is unknown whether differences in physiology between the two species will be conducive to or prevent invasion by *P. setaceum* into *S. pulchra*-dominated areas. A competition experiment was carried out to determine the competitive interactions of the two species from the cool winter season into the warm summer season. Results of this study showed that *P. setaceum* may experience intense competition by *S. pulchra* in the cool season but a release from this competition and an opportunity to thrive later in the season. As little is known about potential impacts of *P. setaceum* on coastal sage scrub communities in southern California, several sites were analyzed during two growing seasons for cover of native and exotic species and soil nutrients in areas containing *P. setaceum*. With increased cover of *P. setaceum*, reductions in native species cover were found in both years in Santa Monica Mountains (SAMO) sites and in one year in San Diego sites; reductions in native species richness were found in both years in SAMO; and higher nitrate, soil water content and potassium were found in both regions in the second year. Rarefaction analysis of beta-diversity showed smaller differences between invasion levels than expected. These potential impacts of *P. setaceum* call into question the use of this ornamental grass in landscaping.

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GENERAL INTRODUCTION

Exotic plants in a local region are species that evolved in a different ecosystem (island, continent, etc.) relative to where they currently occur, and are therefore non-native to the area. Many species introduced for use as ornamental plants have escaped cultivation and invaded native habitats, resulting in habitat degradation and a loss of biodiversity. The impact of these invasive exotic plants on natural areas around the world is one of the most important issues in biodiversity conservation (Vitousek 1986). Evaluating the potential distribution and impacts of exotic plants is critical to minimize costs and prevent further damage to native wildlands (Hulme 2003).

As the fields of invasion biology and ecology have matured, so has our theoretical understanding of invasion and invasibility, as well as knowledge of ways to use this information for management of invasive species (Sakai et al. 2001, Richardson 2004). Several lines of research have focused on using applied ecology and physiology to help solve invasive plant problems, and these tools and approaches are continually being reassessed and redirected (Hulme 2006).

Weed risk assessment schemes have focused on identifying and predicting which species will become invasive (e.g., Pheloung et al. 1999). Another area of research in invasive species science and management has focused on mapping and modeling the potential distribution of invasive plants. This research uses modern mapping (Geographic Information Systems) tools and many modeling techniques (mechanistic, climate envelope, and correlative) to investigate and predict distributions of invasive

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plant species (Hulme 2003, Peterson 2003, 2005). A third challenge to researchers studying invasive plants is focused on documenting impacts of invasive plants on communities and ecosystems, looking at effects on threatened and endangered species (Wilcove et al. 1998, Gurevitch and Padilla 2004), community structure and composition (Gordon 1998, Funk and Vitousek 2007) and impacts on ecosystem processes, such as nutrient cycling, hydrologic cycles and fire cycles (D'Antonio and Vitousek 1992, Mack et al. 2001, Brooks et al. 2004).

This dissertation is an investigation of the potential distribution of and problems associated with an exotic invasive plant, African fountain grass (*Pennisetum setaceum* (Forssk.) Chiov.) in Southern California ecosystems. This research addressed the following questions: What areas are suitable for growth of *P. setaceum* in California? Are interactions with other species influencing the success of this species? What types of vegetation are correlated with *P. setaceum* occurrence and can we detect any impacts from this invasion? These studies detail several physical and community factors in addition to climate that are affecting the distribution of *P. setaceum* in the region.

P. setaceum is an invasive perennial grass that has spread aggressively in Hawaii (Goergen and Daehler 2002) and in the southwestern U.S., where it was introduced as a drought-tolerant ornamental plant (Williams et al. 1995). Early herbarium records in California show introduction of *P. setaceum* to the Los Angeles area sometime before 1917. By 1970 it was documented in at least 10 counties (Consortium of California Herbaria, *ucjeps.berkeley.edu/consortium/* accessed February, 2008). As a common landscape ornamental, it is now widely planted in southwestern states. *P. setaceum* seeds

may disperse readily from existing populations via wind, animals, and automobiles (Tunison et al. 1994, Goergen and Daehler 2002). Repeated introductions through landscape plantings, which increase propagule pressure, are important in the spread of pampas grass (*Cortaderia selloana*) in California (Okada et al. 2007), and are likely important in range expansion of *P. setaceum*, as well.

P. setaceum is a warm-season grass that has C_4 biology (Winter et al. 1976); thus, while this plant may be ideal for growth in water-conscious landscaping in a warm climate (due to its decreased transpiration rates), its ability to become invasive within winter-rainfall areas has been questioned (Poulin et al. 2007). However, *P. setaceum* has demonstrated broad ecological tolerance and plasticity in other invasive ranges (Rundel 1980, Williams and Black 1993, Williams et al. 1995). In California it has been documented invading areas within the coastal sage scrub habitat (L. Sweet, personal observation), a vegetation type that has already been impacted extensively by the combined effects of changes in fire cycle as well as invasion by exotic grasses (O'Leary and Westman 1988).

In Hawaii, extensive study of the effects of *P. setaceum* on native habitats in terms of carbon pools (Litton et al. 2006), fire frequency (Cuddihy 1990, Blackmore and Vitousek 2000), recruitment of native species (Carino and Daehler 2002, Goergen and Daehler 2002) and native species restoration (Cabin et al. 2002) has provided extensive documentation of impacts that are useful to management. Thus, *P. setaceum* is a Hawaii State Listed Noxious Weed (Division of Plant Industry 2003). While *P. setaceum* is increasing in California, its ability to spread and potential impacts on local communities

there are unknown, though it has been listed as a plant of moderate concern by the California Invasive Plant Council (Cal-IPC 2006).

This dissertation work focuses on the invasion of *P. setaceum* in California in terms of three specific objectives: 1) discover the factors that influence the distribution of *P. setaceum* (a) on a coarse-scale and (b) on a fine-scale; 2) determine the impact of *P. setaceum* on native species diversity in coastal sage scrub; and 3) examine competitive interactions of *P. setaceum* with a native species.

Chapter 1: "Modeling Factors Affecting Distribution of *Pennisetum setaceum* in California."

(a) Coarse-scale: To explore factors affecting the distribution of *P. setaceum* in California, two modeling methods were used. A physiology-based climate envelope model was developed based on moisture and temperature tolerances of *P. setaceum*. A maximum entropy model, MaxEnt (Phillips et al. 2004), was also used in order to further investigate other factors correlated with *P. setaceum* occurrence in California and the native range of the species at a coarse scale, including seasonality of precipitation, and elevation. Both models produced predictive maps of *P. setaceum* occurrence statewide.

(b) Fine-scale: Within southern California, *P. setaceum* occurrences have been documented in many locations in the Coachella Valley (Colorado Desert) (A.C. Sanders, pers. comm.). However, it appears to be distributed non-randomly within this landscape, and I hypothesized that other physical factors such as aspect (direction of the slope) and soil type explain distribution on a fine scale. In order to explore fine-scale patterns of *P.*

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setaceum distribution, and predict future distribution in the Coachella Valley, populations in a smaller area, Philip L. Boyd Deep Canyon U.C. Reserve were mapped and a MaxEnt model was produced for habitat suitability for *P. setaceum*. The prediction produced by the model for Deep Canyon was also used to produce a prediction of distribution within the broader Coachella Valley. The outcome of this study showing suitable habitat adjacent to landscaped urban areas, combined with documented impacts of *P. setaceum* elsewhere, call into question the use of this common ornamental plant as a desirable landscaping choice in the Palm Springs area.

Chapter 2: "Seasonality of competition between bunchgrasses C$_4$ *Pennisetum setaceum* and C$_3$ *Stipa pulchra*: implications for post-disturbance invasion."

Competition and interspecific interactions have been shown to affect species distributions (Goldberg and Barton 1992). As a result, interactions with other species may prevent a species from establishing at a particular location, despite climatic suitability. Competition experiments allow evaluation of the relative impacts of species on one another. Such experiments are being used here to evaluate the relative performance of *P. setaceum* compared to a perennial native grass when grown in monoculture and mixtures.

P. setaceum co-occurs with native *Stipa pulchra* (Hitchc.) (syn. *Nassella pulchra* Hitchc. Barkworth) (purple needlegrass) in some areas, and although *P. setaceum* has a high relative growth rate (Litton et al. 2006), it is unknown whether *P. setaceum* can out-compete *S. pulchra*. An experiment was carried out to study growth and competition of

these grasses during winter and spring. I predicted that any physiological advantage of *S. pulchra* during the cool season can be overcome by *P. setaceum*'s drought- and heat-tolerance in the late spring and summer. The outcome of this experiment may be used to inform management decisions in areas supporting the native bunchgrass community.

Chapter 3: "Impacts and Vegetative Correlates of *Pennisetum setaceum* in Coastal Sage Scrub."

Many studies have quantified impact of invasive plants on native community composition, structure, and processes (Parker et al. 1999). Since impacts of *P. setaceum* on native California habitats was unknown, this study was designed to investigate which species are present where *P. setaceum* is invading and what impacts, if any, *P. setaceum* has on this community. I hypothesized that *P. setaceum* decreases resource availability for native species in similar habitats, resulting in a decrease in native species diversity in invaded areas. Replicated plots within invaded areas of *P. setaceum* were inventoried for species present, and physical variables were recorded over two seasons in two regions of Southern California. Several analyses were used to investigate the relationship between *P. setaceum* invasion and native cover, richness, soil nutrients and plant functional composition by region.

Significance

The ultimate goal of this research is to understand the factors regulating the distribution of a potentially highly invasive grass in California. This research will

provide the first scientific study of *P. setaceum* invasion in this state, revealing physical and plant community correlates of *P. setaceum* distribution as well as its effects on native species. *P. setaceum* is a known threat to native landscapes elsewhere and it has the potential to impact several sensitive ecosystems in California. Given the documented impacts of this grass in other ecosystems, it is a critical time to assess this species before it spreads more widely. In addition to gathering basic ecological information about the species, these studies will test the viability of several novel methods, including using species distribution modeling to predict the spread of an invasive species and using rarefaction to look at invasion impacts at multiple scales.

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Chapter 1: "Modeling Factors Affecting Distribution of *Pennisetum setaceum* in California"

Abstract

Non-native African fountain grass (*Pennisetum setaceum*) has been increasing in California over the last century; however, its potential distribution has not been determined. To predict areas of suitable growth of *P. setaceum* in California at fine and coarse scales, several predictive models were used. Coarse-scale models were trained using distribution data from the native range of *P. setaceum* in North Africa and the Middle East. A climate-matching model (CLIMEX) indicated a broad area of climatic suitability for *P. setaceum* in southern and coastal California. A MaxEnt model was also developed at a coarse scale and showed similar areas of suitability; however, MaxEnt models produced using the native range environmental information showed a broader potentially suitable area than the model based solely on the invaded range distribution data. In order to investigate distribution at a finer scale, locations within a smaller area, Deep Canyon, near Palm Desert, CA were mapped and modeled using geospatial data describing physical variables such as slope, soil, aspect, and vegetation type. Model results indicated that habitat suitability for *P. setaceum* increased with slope, was higher on northwest-facing slopes, and was highest from 200 to 600m in elevation. Also, several soil types were important predictive variables. Using this model, a prediction was produced for the Coachella Valley showing high accuracy for test locations outside Deep Canyon. The outcome of this study demonstrates that species distribution modeling can

be used to locate potentially suitable areas for invasive species, especially where information from a native range is included. The coarse-scale models show broad areas of suitable habitat in coastal California, while at the finer scale in the Colorado Desert, suitable habitat occurs where there are factors associated with increased soil moisture. These at-risk areas generally bound the landscaped urban area of Palm Desert and Palm Springs in the west, providing ample opportunity for this horticultural plant to escape along this interface. Combined with documented impacts of *P. setaceum* elsewhere, these findings call into question the use of this plant as a desirable landscaping choice.

Introduction

Distributions of species are dictated by many complex factors, and modeling the potential distribution of invasive species poses many challenges (Hulme 2003, Peterson 2003). Temperature and moisture availability are factors that limit plants physiologically; thus, on a broad scale geographic distributions of plants are dictated by climate (Grinnell 1917). However, other environmental factors may cause species to deviate from occupying a habitat that is predicted to be climatically suitable. These include biotic factors such as dispersal limitation and abiotic factors such as substrate and nutrient availability that differ from those suitable for the species (Tyre et al. 2001). On a small scale, other biotic factors such as relationships with other species may influence species distributions (Elton 1927, Connell 1961, Austin 1999).

Recent discussion has focused on how to define the niche that is evoked in models of species distribution (Soberon 2007, Hirzel and Le Lay 2008). Although a model based on physiological tolerances should reflect the fundamental niche of a species (Hutchinson 1957), this model may not project a realistic picture of actual species distribution. Invasive species modeling may be especially problematic in this respect, as adequate information about physiology may be lacking and inferred tolerances based on climate may be biased by biotic and local processes, such as disturbance regimes (Araujo et al. 2005, Hierro et al. 2005) , especially at range edges, where these interactions may be relatively more important (Brown et al. 1996). Additionally, efforts using solely data from the novel invaded range will be biased against any circumstances that have not been encountered, as the absence of the species may be due to problems with sampling, limited dispersal, or other temporal processes (Hirzel and Le Lay 2008). Similarly, defining the modeled space as the realized niche may also be problematic, as both fine-scale and coarse-scale interactions may influence the deviation of the distribution from what is expected based on the fundamental physiological tolerances of the species (Soberon 2007). Some authors argue that the niche that is modeled is usually closer to the realized niche (Guisan and Zimmermann 2000), or that these might not be as different as initially thought, as biotic interactions acting at short distances should still allow competitor-free space due to spatial heterogeneity (Hirzel and Le Lay 2008).

Thus, it has become apparent that it is more productive to think about goals of species distribution modeling in terms of Grinnellian and Eltonian niches (as summarized in Soberon, 2007). That is, there are factors for which quantitative data are relatively

easier to find with which to model distribution at the coarse-scale, such as climate,

elevation, macrotopography, latitude, and light availability. It follows that biotic and

resource-dynamic processes are easier to study at the fine-scale (Gause 1934, Tilman

1994). Other factors, including land-use patterns, disturbance, microtopography, grazing,

and land-cover may best be studied at the fine scale. As these models are meant to

correlate environmental variables with species distribution, if quality quantitative data are

available there should be no reason why hypotheses regarding the relationship of those

factors to species distribution may not be tested. Efforts are underway to make datasets

of increasingly fine spatial grain (Araújo et al. 2005) .

New methods in species distribution modeling are allowing scientists and land

managers to use the increasingly available datasets to inform risk-management and

planning decisions regarding habitat conservation (Thuiller et al. 2005, and for example,

Embert et al. 2011) as well as concerning invasive species (Holt and Boose 2000,

Peterson et al. 2003, Brusati 2008). Many more time-intensive (and skill-intensive)

methods have long been available to model species distributions, including climate-

envelope methods, generalized linear model (GLM) and generalized additive (GAM)

models, and abundance models (reviewed in Potts and Elith 2006, and in Elith et al.

2006). Not only have some of these models shown incredible power and accuracy, but

many have increasingly user-friendly interfaces that have been developed by modelers

for use by applied scientists (Sutherst and Maywald 1985, Phillips et al. 2006).

MaxEnt, a machine-learning approach to species distribution modeling, has been

shown to be among the most robust species distribution modeling tools, due to its ability

to fit complex variable responses and applicability to situations where only presence data exists; in fact, it was developed specifically for modeling using presence-only data (Phillips et al. 2004, Phillips et al. 2006). When comparing presence-only methods, including climate envelope models, models such as these that can weigh variables differentially consistently outperform those that can only fit simple variable responses. Maxent also has an adjustable regularization setting that can help reduce overfitting (or a model that fits too tightly to the training data when the user has a small sample size), one noted limitation of this model (Elith et al. 2006). This model has been used to evaluate potentially suitable habitat of invasive species in many cases (Ficetola et al. 2007, Ward 2007, Rodder et al. 2008, Kadoya et al. 2009, Simon et al. 2010, Jarnevich and Reynolds 2011), although some questions have been raised about the quality of the predictions when used with specific types of data (Veloz 2009) and transferability (Peterson et al. 2007 but see response by Phillips 2008).

Modeling the potential distributions of species has been accomplished successfully, despite the limitations described above. Climate-matching or climate-envelope models use physiological responses (with caveats listed above) to predict species distributions in new ranges, and have been used to model suitable habitat for biocontrol agents as well as plant species (Holt and Boose 2000, Goolsby 2004, Pattison and Mack 2008). Some limitations of these types of models have also been expressed (see Hampe, 2004 and response by Pearson and Dawson 2004), mostly concerned with the necessity of being explicit about the questions being addressed, and the spatial scale

of applicability of the resultant model (Pearson and Dawson 2003, Araujo et al. 2005, Zalucki and van Klinken 2006).

Pennisetum setaceum is an invasive perennial bunchgrass, native to Africa, that is present and invasive in many areas worldwide (Le Roux et al. 2007). This species has been shown to have a broad altitudinal range in Hawaii (Rundel 1980), demonstrating plasticity in physiology and broad physiological tolerances in general (Williams et al. 1995). In the southwestern US, *P. setaceum* has been increasing in Arizona, Nevada and California (Brooks and Esque 1999). *P. setaceum* has been increasing in southern coastal and interior California, as well as in the interior Colorado Desert (A.C. Sanders, pers. comm.), and there is increasing concern about this species due to its documented ability to alter fire cycles (Blackmore and Vitousek 2000). The potential range of this species in North America has not yet been determined. This study system provides an opportunity to evaluate the applicability of these modeling methods to determine potential distribution of a species using information from its known native range and from an invaded range. Additionally, results of this approach would be useful in risk management planning for this invasive species.

P. setaceum has been present in California for less than 100 years. As such, this species most likely has not realized its potential invasive range. Information based on physiological tolerances inferred from the native range of the species, as well as climactic factors correlated with species presence in the native range may be helpful in predicting further spread in California. Coarse-scale models based on climate and a macrotopography factor (elevation) were developed using both CLIMEX, a mechanistic

model (Sutherst and Maywald 1985) and MaxEnt, a machine-learning tool (Phillips et al. 2004). In order to investigate finer-scale distribution within the broader framework of climate, a more intensive study was performed by mapping *P. setaceum* occurrences in an invaded desert canyon and the surrounding region. Due to the limitations inherent in climate-matching and machine-learning approaches, as well as in finding suitable data from both fine and coarse scales, an integrated approach was used here to examine the factors that may influence *P. setaceum* distribution in the future.

Materials and Methods

For the coarse-scale CLIMEX and MaxEnt models, 291 species datapoints, comprising geographic localities of *P. setaceum*, were obtained from the Consortium of California Herbaria (*ucjeps.berkeley.edu/consortium/* accessed October, 2010), including localities that could be georeferenced to within 1km of accuracy using locality information in the data record (Table 1.1). Thirty-three locations within the native range of *P. setaceum* were downloaded from the Global Biodiversity Information Facility (www.gbif.org, accessed October 2010), an online source for international occurrence data. Several of these records that lacked geographic coordinates were georeferenced by the author using locality information in the data record in order to increase the size of the dataset.

For the fine-scale MaxEnt model, *P. setaceum* was mapped on foot in the study area, Boyd Deep Canyon U.C. Reserve (33.648/-116.377) using a Garmin GPS unit (Dakota™ 20, Garmin International, Inc., 1200 East 151st Street, Olathe, Kansas 66062)

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and ground-truthed using printed digital aerial ortho-quads gridded with UTM

coordinates (WGS 1983, Zone11N). All field data collection was accomplished over a

one-year period. One hundred ninety-seven individual locations of *P. setaceum* were

recorded within the study area. Additionally, a validation set of data was collected using

a different protocol; a set of 26 independent (outside of the study area) locations of *P.

setaceum* were found using local knowledge of invaded areas and mapped on foot by

GPS within a larger adjacent area, Coachella Valley (approximately 40 x 40km),

surrounding Palm Springs (33.8, -116.5). Locations of plants were entered into database

files (Table 1.1).

For the coarse-scale MaxEnt model, interpolated gridded climate data at 2.5 arc-

minute resolution, elevation, and calculated derived climate indices were downloaded

from the Worldclim dataset (Hijmans et al. 2005, online at http://www.worldclim.org/)

(Table 1.1). The acquired data were calculated from 1960-1990 averages using several

sources (see Hijmans et al. 2005). Elevation data from Worldclim was from the Shuttle

Radar Topography Mission (SRTM) dataset. All data were maintained in the WGS 1984

datum and not cartographically projected (henceforth "projected" refers only to the

MaxEnt capability of producing Habitat Suitability values for a novel set of

environmental data). Only raster data from within the boundaries of California or

bounded by the species native range in Africa and the Middle East were included. Data

were exported from ArcGIS 9.3 (ArcGIS 9.3 © ESRI) in ASCII grid format.

Physical and biophysical variable data (elevation, slope, aspect, vegetation cover

and type, and soil type) for the fine-scale model were obtained from LANDFIRE,

SSURGO, and EDNA (Table 1.1). No climate data were used for this study area, an approximately 40 x 40 km area of the Coachella Valley and an approximately 4 x 4 km area at Deep Canyon. Data were geoprocessed in ArcGIS 9.3 to convert polygon data (e.g., soil) to raster data, match all layers to the same projection (WGS 1983, UTM Zone 11N) and the same raster data resolution (maximum of the inputs, 30 meters), align grid cells, and match study area extents. The resultant datasets were exported from ArcGIS as ASCII grid files.

Habitat suitability models for the fine and coarse-scale studies were generated using a Maximum Entropy model, MaxEnt (Phillips et al. 2004, Maxent; v3.3.3e; available from http://www.cs.princeton.edu/~schapire/maxent/). For the coarse-scale study, models were generated for the native range and the range in California, using all data points except for a 20% random sample (the test data percentage is set and evaluated within the MaxEnt program) and using the derived climate variable layers, with 500 iterations of the algorithm. The program was set to exclude duplicate presences within the same cell; thus, the California dataset included 156 records (126 training/30 testing) and the native range model contained 28 records (24 for training/4 for testing). Models were also produced for projection onto the same environmental layers in the other respective range using only the bioclimatic variables, producing an output raster prediction of the logistic Habitat Suitability statistic (scale of 0-1) for each grid cell of the novel geographic range.

For the fine-scale study, 125 presence points were used within the study area, and 26 points were used in the adjacent area (Coachella Valley). A mask was produced in

ArcGIS that documented an index of "study intensity" to use as a bias file in MaxEnt; values assigned were 10 for the Deep Canyon study area and 1 for the surrounding valley. The model was run using several combinations of training and test data, as well as included environmental variables. First, it was run using the study area as the training set and the Coachella Valley samples as the test set using the (sampling bias) mask, next, it was run using the same test and training points, but without elevation as a variable and without the mask, and lastly, the model was run using both Deep Canyon and Coachella Valley data points, without the mask and with a random 20% test percentage.

The method for parameterizing the physiological CLIMEX model for *P. setaceum* followed those of Holt and Boose (2000). CLIMEX parameters, including temperature (DV0 (temperature below which no growth occurs), DV1 (minimum optimum temperature for growth), DV2 (maximum optimum temperature for growth, DV3 (temperature at which no growth occurs) and soil moisture (SM0, SM1, SM2, SM3 (defined similarly to temperature variables)) preferences and stresses (Sutherst et al. 2004), were adjusted to match the climate of the native range (Table 1.2 and key). Climate data (monthly average high and low, monthly rainfall) used was in an interpolated 0.5 degree grid included in CLIMEX 2.0, provided by Climatic Research Unit (CRU), Norwich (http://www.cru.uea.ac.uk/cru/data/hrg.htm). Parameters were adjusted until the prediction (ecoclimatic index, EI) matched areas where populations of the study species were known to persist (defined as EI scores >30), and stress parameters limited plant growth in areas that were too cold, hot, wet or dry (Table 1.2).

This climate-matching model, parameterized on the native range of the species, was used to evaluate suitable areas for growth of *P. setaceum* in California. The model was run for 321 locations in California corresponding to NOAA climatic data stations (monthly average high/low temperature, average rainfall, average 9am and 3pm relative humidity) (NOAA, Climatography of the United States No. 81). EI values of 30 or above greater are considered to be suitable habitat as this indicates that during the approximately 6-month growing season, the growth rate is adequate to sustain the population (Sutherst et al. 2004).

For all MaxEnt models, response curves were generated for each variable and jackknifing as well as calculation of permutation importance was performed in MaxEnt to assess variable importance. The area under the curve (AUC) of the receiver operating characteristic, a commonly-used statistic to describe the performance of presence-only habitat suitability models, was used to assess model performance (Fielding and Bell 1997). This statistic describes the probability that a randomly-drawn presence point will have a higher value than a randomly-drawn absence point. Pseudo-absence points are normally drawn from random background values in MaxEnt. The AUC scores for the training and testing data for each model (non-projected models) were calculated in MaxEnt.

To assess the predictions produced for the projections onto novel geographic range in the coarse-scale study, Habitat Suitability values were extracted from the projected MaxEnt raster file in ArcGIS using Spatial Analyst for both the actual locations of *P. setaceum* in the novel range and for 1000 random background (or pseudo-absence)

points. These files were imported into R Statistical package (R Development Core Team 2004), and AUC scores were produced using the RROC package by Sing et al. (2009).

Results

Coarse-scale CLIMEX Model

The CLIMEX model based on physiological tolerances of *P. setaceum*, inferred from its native range, predicted suitable conditions for growth of *P. setaceum* in California (Figure 1.1). Parameters inferred via range-fitting indicated temperatures for growth from 10-42°C, with cold stress accumulating below 10°C and heat stress accumulating above 45°C (Table 1.2). Dry stress was set to accumulate below 0.02 (unit-less value on a scale from 0 (dry) to 1 (saturated)), and wet stress to accumulate above 1.1 (meaning over-saturated soil). However, this model overpredicted occurrences in the Central Coast and Central Valley areas (Figure 1.1).

Coarse-Scale MaxEnt Model

The MaxEnt model produced using all Worldclim variables in the native range (Figure 1.2) showed a strong ability to correctly predict suitable habitat based on the training data (Table 1.3). The variables that were most important to the model algorithm were elevation, annual range of temperature, and October and November precipitation. However, the variables that were most strongly predictive on their own (permutation importance) were June, March, and February precipitation, as well as temperature seasonality. Fitted response plots show that *P. setaceum* suitable habitat is strongly correlated with a narrow range of average precipitation values in June and correlated with

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a larger range of precipitation values (less strongly) in February and March (Figure 1.3), and also correlated with less-extreme temperature seasonality compared to background values within Africa and the Middle East.

When only the bioclimatic variables were used from the Worldclim dataset, the habitat suitability map trained in the native range decreased somewhat in the specificity of the model (the proportion of pseudo-absences correctly identified as being unsuitable), showing a larger area of suitable habitat (AUC of the training data=0.955) (Figure 1.4a, Table 1.4). The variables with the highest contribution to this model were temperature seasonality, precipitation of the driest month and mean temperature of the driest quarter (Table 1.4). The variables that were most explanatory on their own were temperature seasonality (highest suitability where lower compared to background values), annual precipitation (peak between 250-1000mm), and precipitation of the driest quarter (peak between 20-100mm) (Table 1.4, variable response data not shown).

When projected onto California, the model trained using bioclimatic variables in Africa performed well in California (AUC 0.85) (Table 1.4, Figure 1.5b). Clamping was overall low throughout the projected range, meaning that the environmental values given were within the bounds of the data used to train the model (Appendix 1). In addition to predicting suitable habitat where *P. setaceum* currently occurs, a large area of potentially suitable habitat was predicted in the Eastern Sierra Nevada, running east toward the Owens Valley as well as in a band along the coast north to Mendocino County, and picking up again in Humboldt County.

In comparison, the MaxEnt model trained using the bioclimatic variables in California predicted a smaller area of suitable habitat within the state (Figure 1.5a). The variables of importance for the model were isothermality and mean temperature of the coldest quarter (Table 1.4). The variables that were most predictive on their own were mean temperature of the coldest quarter (higher suitability where >12°C), precipitation of the driest quarter (highest below 10mm), and annual precipitation (slight increase in suitability above 50% probability between 250-500mm; otherwise, low probability) (variable response data not shown).

When this model (trained using distribution and environmental data in California) was projected onto the native range of the species, there was an increase in the area of predicted suitable habitat over the model based on native range training data (Figure 1.4b). The map of clamping showed a large amount of geographic area with 1 or more variables outside the range of training data given (Figure 1.6a). In large areas of southern Africa, precipitation of the warmest quarter was the most different from the test training data (Figure 1.6b). The AUC score for this model, however, was still high at 0.854 (Table 1.4), though suitability was not predicted at several presence points in Algeria, in North Africa, and there was a large area in southern Africa of predicted suitable habitat (Figure 1.4b).

The MaxEnt results for the coarse-scale model of California using all climate variables performed well within this respective area (Figure 1.7, Table 1.4). The particular algorithm used by the model to enact a successful fit placed weight particularly on maximum December temperature and isothermality. The variables that were most

explanatory (regardless of the algorithm path used to make the successful model) were October precipitation (mainly low suitability except between 10-15mm), July precipitation (mainly indicating low suitability above 10mm), June precipitation (mainly low above 3mm), and Maximum December Temperature (strong increase between 17-20°C) (Table 1.4).

For reference, an enlarged picture was made to show how the coarse-scale MaxEnt model (with all Worldclim data, trained on California) performed in the fine-scale study area (Figure 1.8). As shown, a broad area of the Coachella Valley was predicted to be suitable using the coarse-scale model.

Fine-Scale MaxEnt Model

For the fine-scale study, the model trained on Deep Canyon data points and the data layers in Table 1.5 showed good performance (AUC 0.984) for the training area and data, but only fair performance over random in predicting the test dataset in the wider valley (AUC 0.81) (Figure 1.9a and Table 1.5). The lower accuracy was mostly due to omission errors in that this model failed to predict the higher-elevation data points in the test sample set. Thus, the restricted area of study may have affected model performance. The model was also run excluding elevation as a variable (Figure 1.9b and Table 1.5). This model predicted a much wider area of potential distribution, elevated the importance of the values of soil type and aspect in the training data, and also vegetation cover as explanatory variables (Table 1.5). The last model run, with all data as training data and all environmental variables, had the highest AUC score and had similar variable weighting to the model trained using just the study area data (Figure 1.9c and Table 1.5).

The output from the MaxEnt model trained using all of the data in the study area as well as the Coachella Valley shows variables that may be important on a fine scale, within the larger scenopoetic variable of climate (*sensu* Hutchinson 1978) (Table 1.6). Rock outcroppings, rubble land, and river washes showed higher suitability than other soil types such as fine sands. Additionally, the north-northwest-facing aspect showed higher suitability values than the southerly aspects. Slope was positively correlated with *P. setaceum* occurrence, including values up to the maximum slope. Vegetation cover was correlated with 20% values.

Discussion

The methods used in this study were all able to model the distribution of *P. setaceum*, based on either physiological parameters, inferred responses to bioclimatic variables in new ranges, or fine-scale microhabitat preferences. At a broad-scale, climate was explanatory of current distribution, and indications of further suitable habitat may indicate areas in which early-detection efforts should be focused.

A C_4 (warm-season) grass, *P. setaceum* has a broad bioclimatic range within California, stretching from coastal areas with a Mediterranean climate into very dry inland Colorado Desert areas and into the Sonoran Desert to the east (Poulin et al. 2007). It is known as a tolerant and plastic species, able to persist in a variety of habitats (Williams et al. 1995). In spite of the broad range spanning very dry habitats, none of the models of species distribution showed a strong correlation with precipitation in the warmest quarter. Mean temperature of the coldest quarter was important in California,

however, as well as maximum December temperature, indicating that this species may grow best in the cool, wetter season in this invasive range. The negative relationship of July precipitation in California to distribution may be more predictive of areas where *P. setaceum* is not present, rather than explaining suitable areas. That is, there are many areas that receive summer rainfall in California, but most have temperate climates and very few are monsoonal (summer rainfall) areas; thus, most areas with high summer rainfall would likely be unsuitable because they are temperate (too cold).

There is no direct explanation for the dissimilarity in area between the predictions for California based on native (Africa) vs. invasive range (California) data. However, these results are likely because *P. setaceum* has not reached its full biogeographic potential in this invasive range due to dispersal processes. Referencing the Hutchinson (1957) concept of the niche, the observed California distribution may also be the realized invasive niche (a subset of the predicted fundamental niche), a distribution that is limited by biotic and other factors; thus, the range predicted based on the native range is larger in area than the one predicted using the invaded range. The prediction of potential suitable habitat in the Eastern Sierra Nevada and Owens Valley, however, is suspect due to the very cold winter temperatures. This prediction may have been influenced by inaccuracies in the native range data used to train the model as well as the small sample size of the training data set. Along similar lines, it is unclear why the California-trained model predicted such a large area of suitable habitat in Africa. This may be due to incomplete native range location data, or differences in biotic factors or other factors not modeled (as above). The envelope model, CLIMEX, may better represent the potential fundamental

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niche in California; however, when it is trained using the native range of the species, this model may also be biased towards modeling a realized niche.

An important finding by the coarse-scale models is that many coastal Southern California areas are predicted to be suitable habitat for *P. setaceum;* these are already some of the most at-risk areas due to type conversion and human development (Talluto and Suding 2008, Freudenberger et al. 1987). These areas include coastal sage scrub, grassland, and chaparral communities, as well as many areas of special conservation status. While it cannot be definitively determined whether local variables and processes are conducive to *P. setaceum* or what the time-scale of this invasion might be, it is important to know that these areas are at-risk.

The match of models to the distribution of the species is influenced by the dynamic process of invasion as well as the complexity of factors that may be interacting in novel ways in the invasive range of the species. Environmental stochasticity may be important in plant abundance and persistence, especially in desert systems (Levine and Rees 2004), and the use of interpolated climate normals for both types of coarse-scale models may limit the predictive power of these techniques. The CLIMEX model, in particular, is subject to human error during parameter fitting. Both models based on the native range are subject to the constraints of extrapolation. As well, concerning the use of herbarium data, though much of it is produced by experts, the "methods and intent" of the collectors is unknown (Elith et al. 2006) and the geographic accuracy, especially of older records, may be suspect and introduce error into the model-fitting process. Model transferability was increased by using biologically-relevant bioclimatic variables;

however, the dissimilarity in importance values between native-range models and introduced-range models demonstrates that extrapolation is risky, and therefore, these correlations and predictions must be interpreted with caution.

The fine-scale modeling effort was hampered somewhat by the availability of relevant data at such a fine scale. As well, a large area of potential occurrence was inaccessible during the survey period in the Coachella Valley. Although there is an increasing amount of this data available, as of this date much of it (including soil surveys) is incomplete for many areas. Additionally, the training and test dataset, when used independently, did not perform as well as when used together. Thus, when the datasets were combined, they became part of the same, auto-correlated dataset, and the results presented here may therefore reflect more about the dataset than the true preferences of the species (Hijmans et al. 2000, Soberon et al. 2000).

However, even based on the few variables given, the fine-scale model was able to successfully predict occurrences in a broader area. The correlations with rock outcrops, washes and rubble, as well as slope, elevation and aspect are useful as a guide for management by predicting potential micro-sites that can be targets of survey and eradication efforts. As well, these predictions fit what would be expected for this grass: rock outcrops and washes may hold additional moisture that would be available for growth into the warm season. North-facing slopes offer a slight respite from heat, and thus, evapotranspiration, also possibly increasing moisture availability. This is in contrast to distribution in coastal sage scrub, where *P. setaceum* is found almost exclusively on southwest-facing slopes (L. Sweet, Chapter 3). These predictions may be

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more indicative of biotic factors such as competition than they are explanatory on their own, but it is impossible to distinguish between confounding (and auto-correlated) factors in this study.

Modelers are generally cautioned against using methods that use static data to represent dynamic processes such as invasion. As mentioned, several factors influence species distributions, including dispersal and local extinction dynamics and biotic limitations, as well as dynamic temporal and spatial processes (Mustin et al. 2009). Additionally, extrapolation of models onto new ranges is "hazardous and should be avoided" (Hirzel and Le Lay 2008).

Elith et al. 2006, however, contend that while the niches of species may not be described well by a method such as that used here, these models are accurate enough for conservation planning. As demonstrated here, valuable information about species characteristics and preferences can be gained from studies such as these, especially where limitations of the predictions are explicitly addressed. As expected, distribution predictions varied based on the training and environmental data used. However, the coarse-scale models generally showed similar areas of potential suitability in California, which may guide statewide risk assessment. The fine-scale predictions may be useful in guiding local early detection efforts in the desert, but these fine-scale factors may not be generalizable to other areas of the state. These predictions of potential spread on a fine and coarse scale should be useful guidelines for management of this species, as well as for directing further investigation into factors that affect these predictions and informing concepts of invasion and species distribution.

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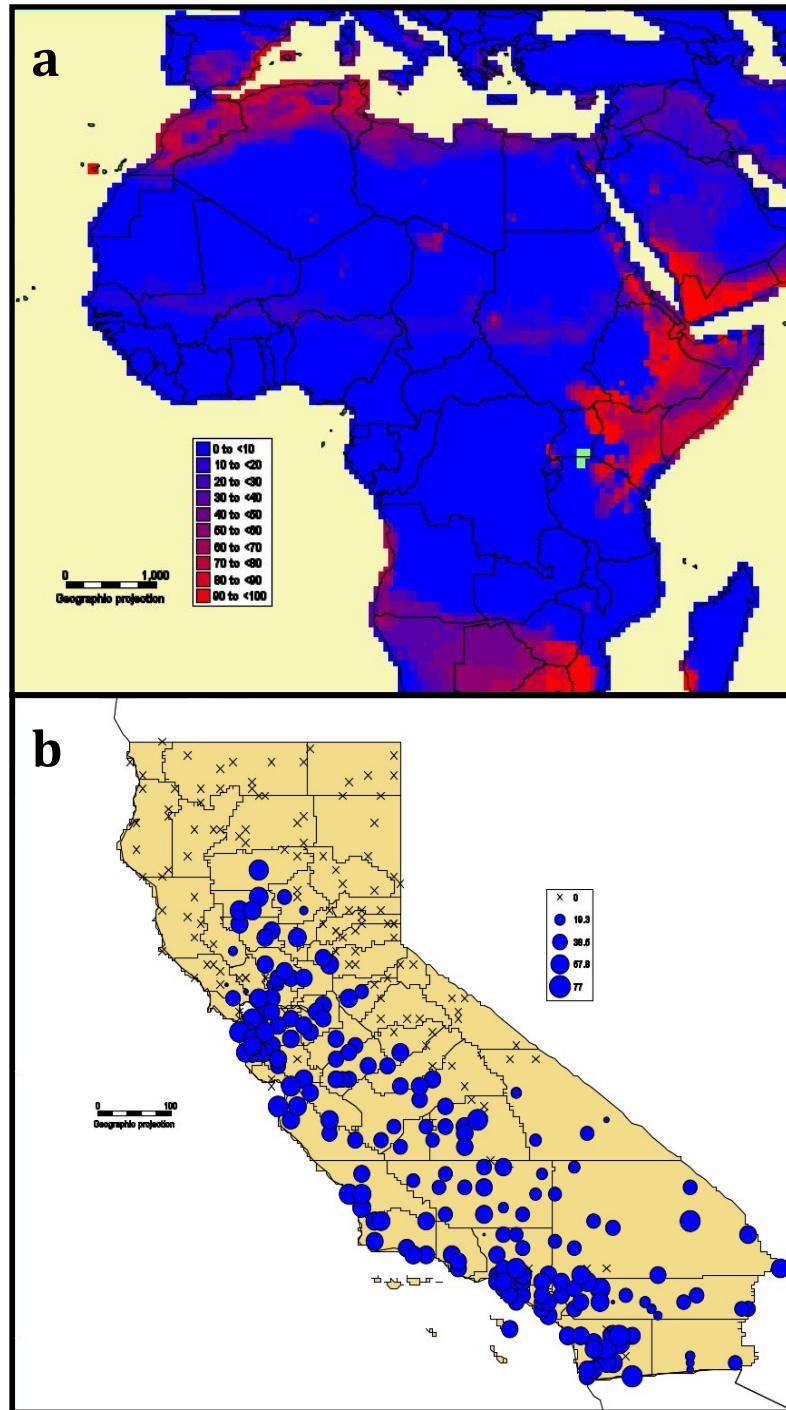
Figure 1.1. Maps generated using CLIMEX describing Ecoclimatic Index (EI) for *P. setaceum* in **(a)** its native range in Africa and **(b)** predicted range in California based on physiological parameters set using the species range in Africa. Locations shown in California are values for discrete climate station data locations. EI values are based on interpolated, gridded climate data. EI>30 is considered suitable habitat.
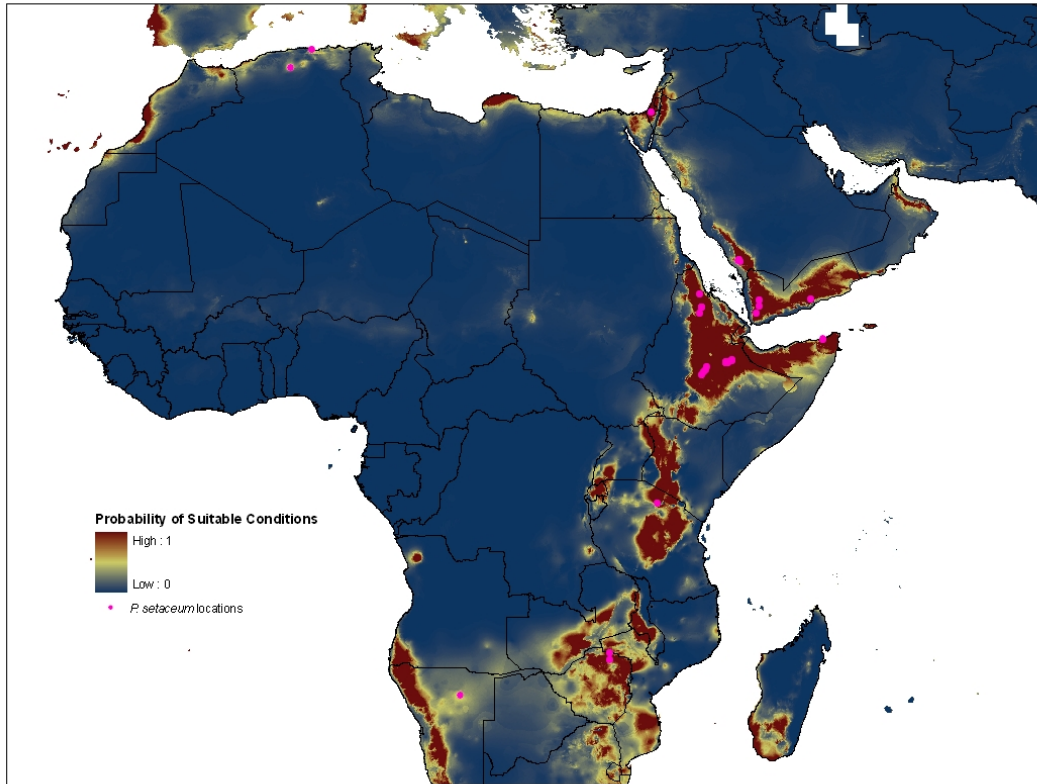
Figure 1.2. MaxEnt Habitat Suitability values for the native range of *P. setaceum* in Africa and the Middle East created using point-locations of *P. setaceum* and all Worldclim climate variables, as described in the text (Hijmans et al. 2005). Color-ranges represent the probability of suitable conditions, the logistic output from MaxEnt.
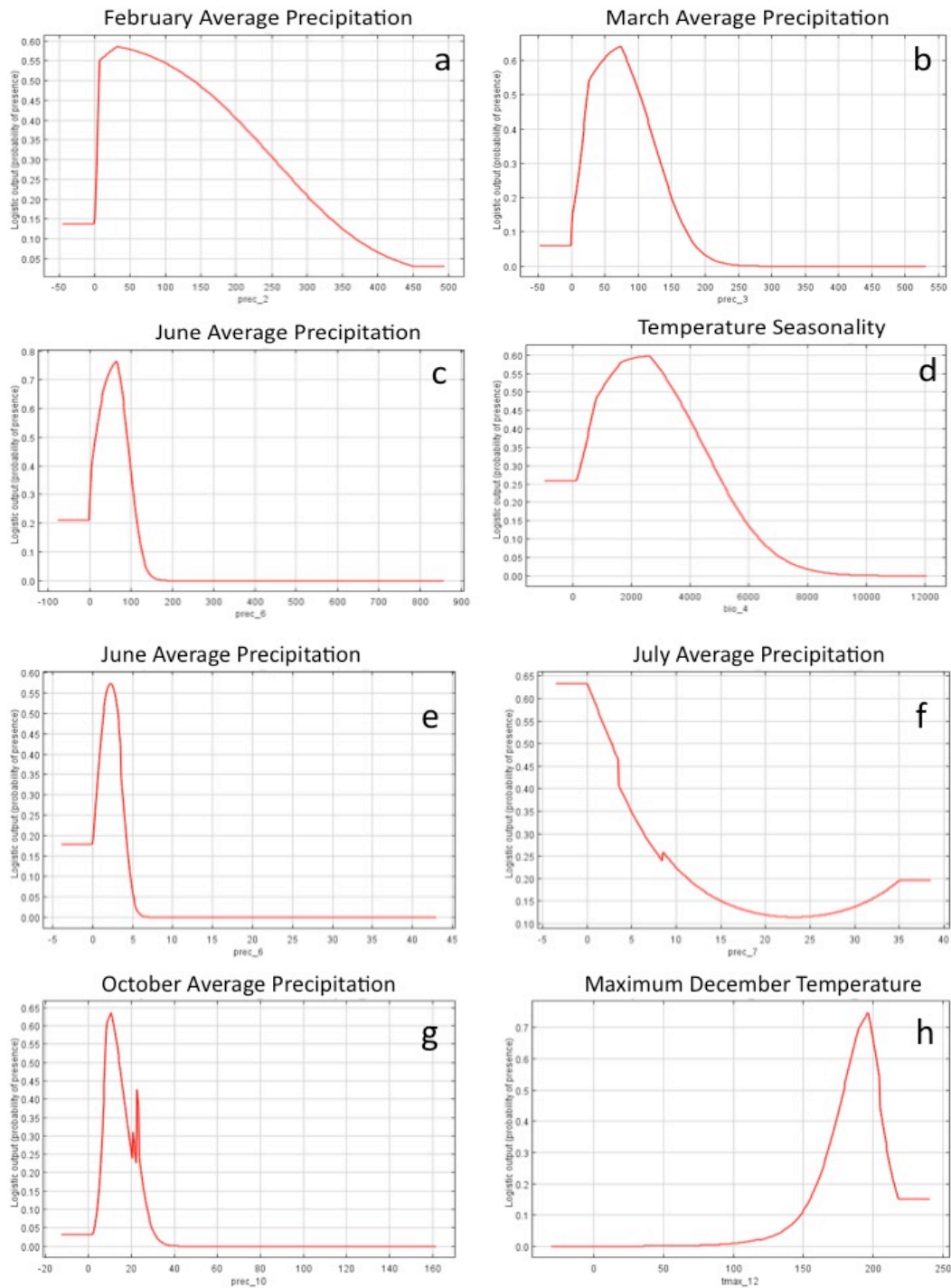
Figure 1.3. Output from the MaxEnt program showing fitted variable responses for the top 4 permutation importance variables for the MaxEnt models trained using all WorldClim data (Hijmans et al. 2005). **(a-d)** Native range model. **(e-h)** California range model. Temperature data is in °C*10.

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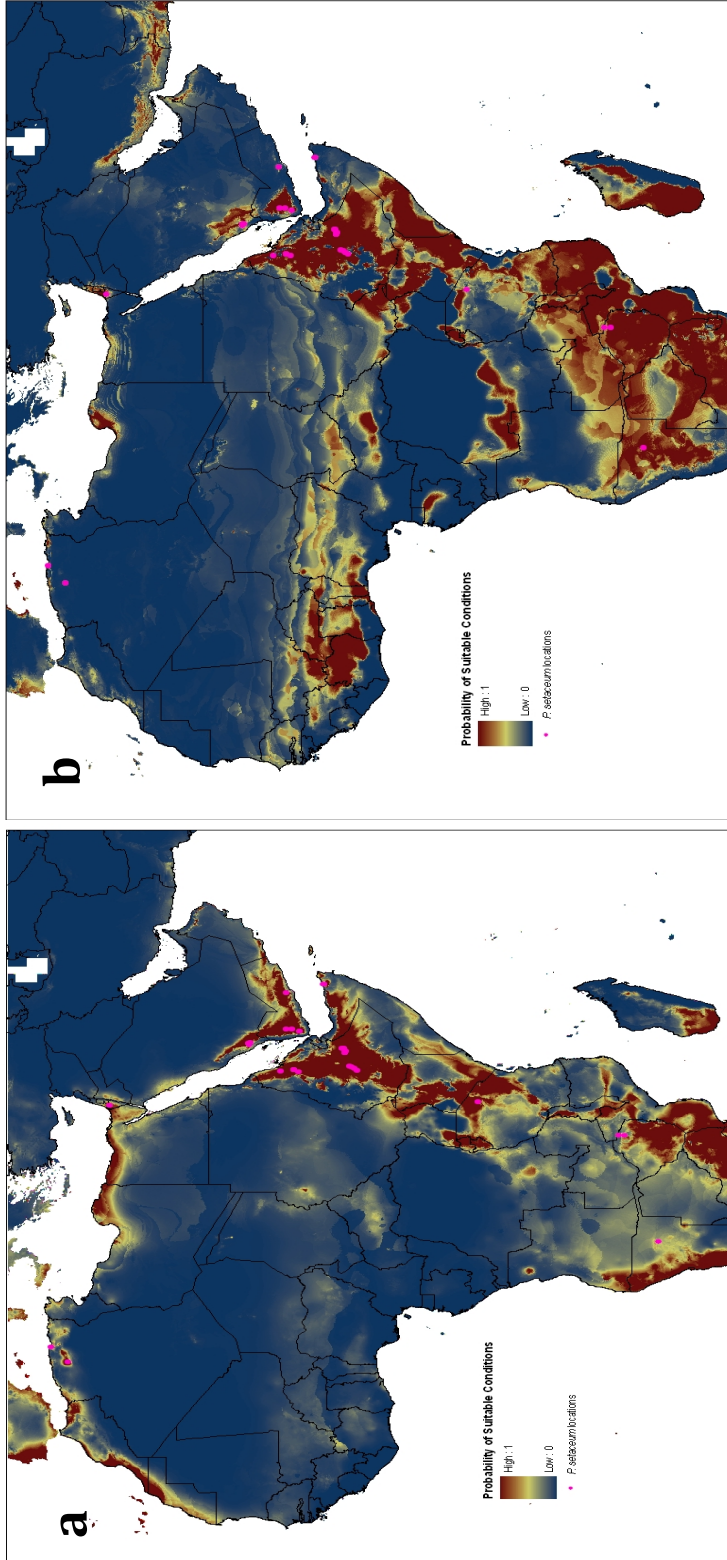
Figure 1.4. MaxEnt Habitat Suitability values for the native range of *P. setaceum* using derived climate variables (**a**) showing values when the model is trained on the native range and (**b**) when the model is trained on data from California.
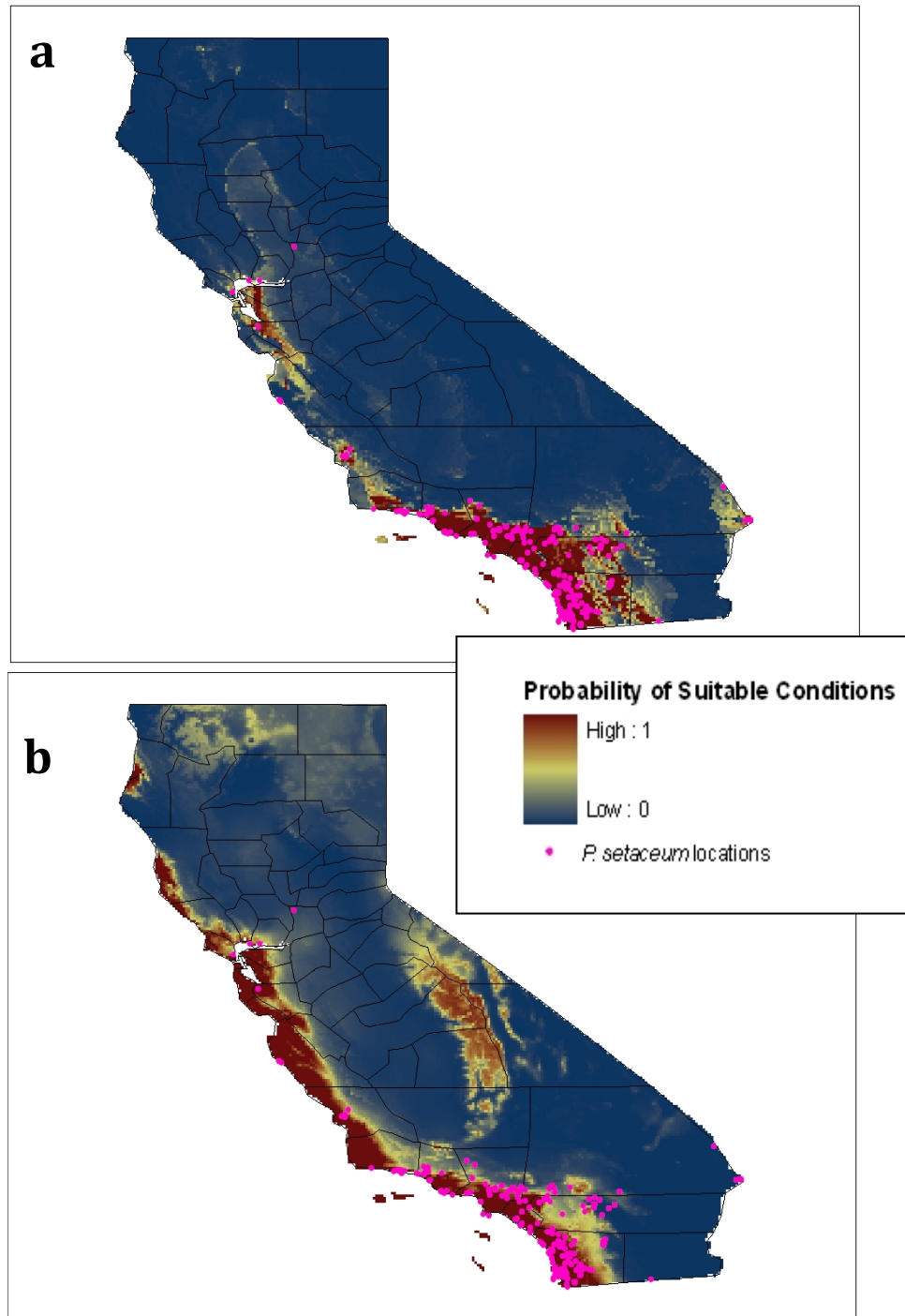
Figure 1.5. MaxEnt Habitat Suitability values for the invaded range of *P. setaceum* in California using derived climate variables. Maps show suitability output **(a)** when the model is trained on California data and **(b)** when the model is trained on data from the native range in Africa.
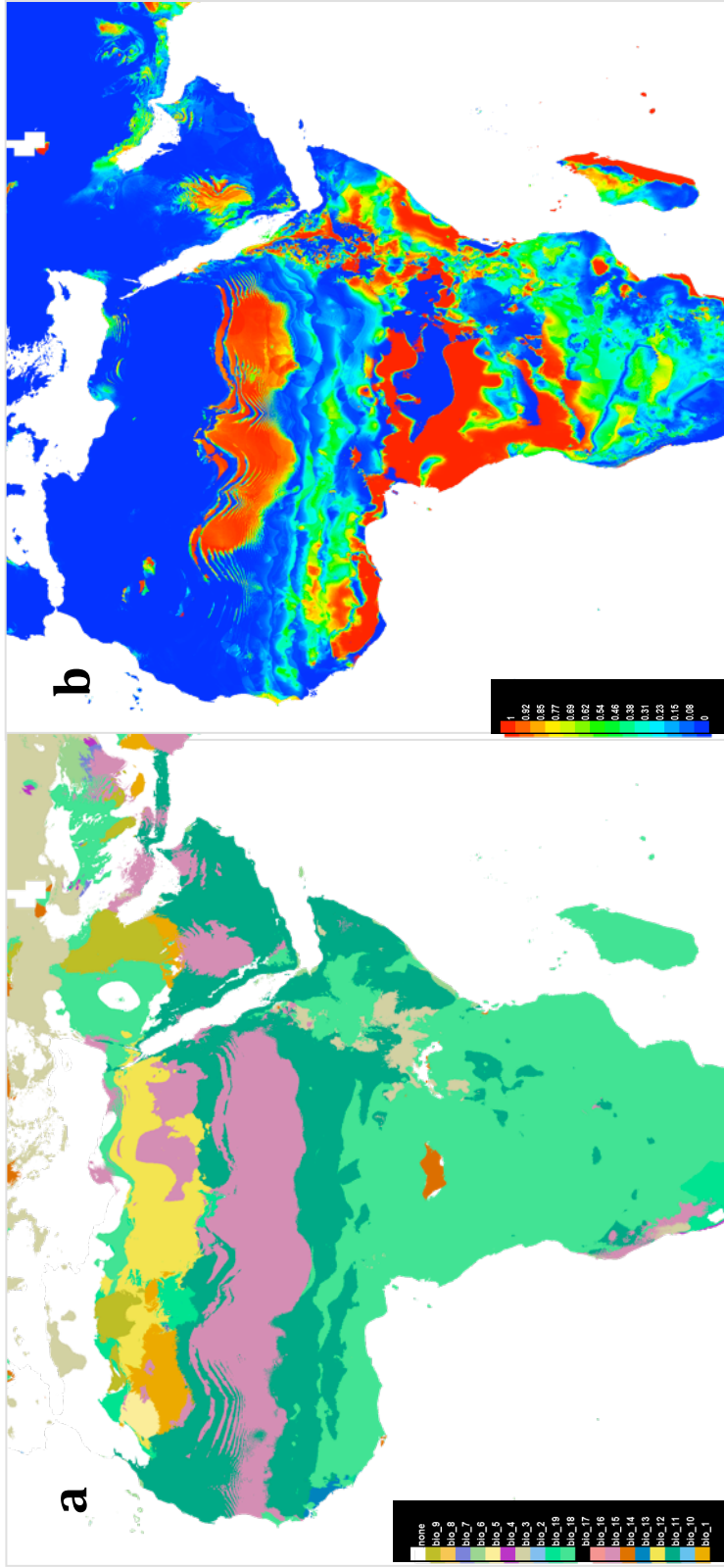
Figure 1.6. **(a)** MaxEnt output showing areas where the variables used are far enough outside the range of training values given that they may affect predictions of suitability. **(b)** Variables that are the farthest outside the range of training values geographically. See Table 1.4 for descriptions of variables.

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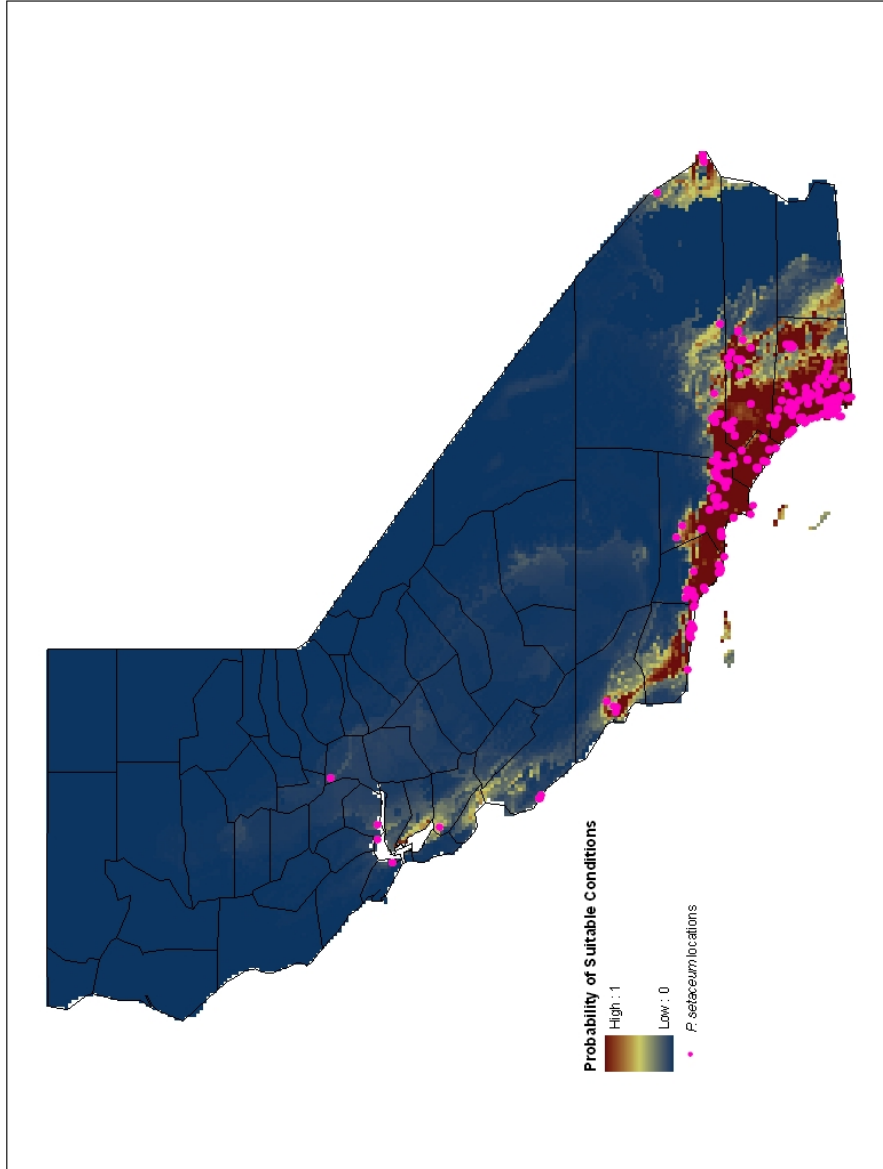
Figure 1.7. MaxEnt Habitat Suitability values for the invaded range of *P. setaceum* in California using California point locations as training data, and all of the Worldclim climate variables (Hijmans et al. 2005).
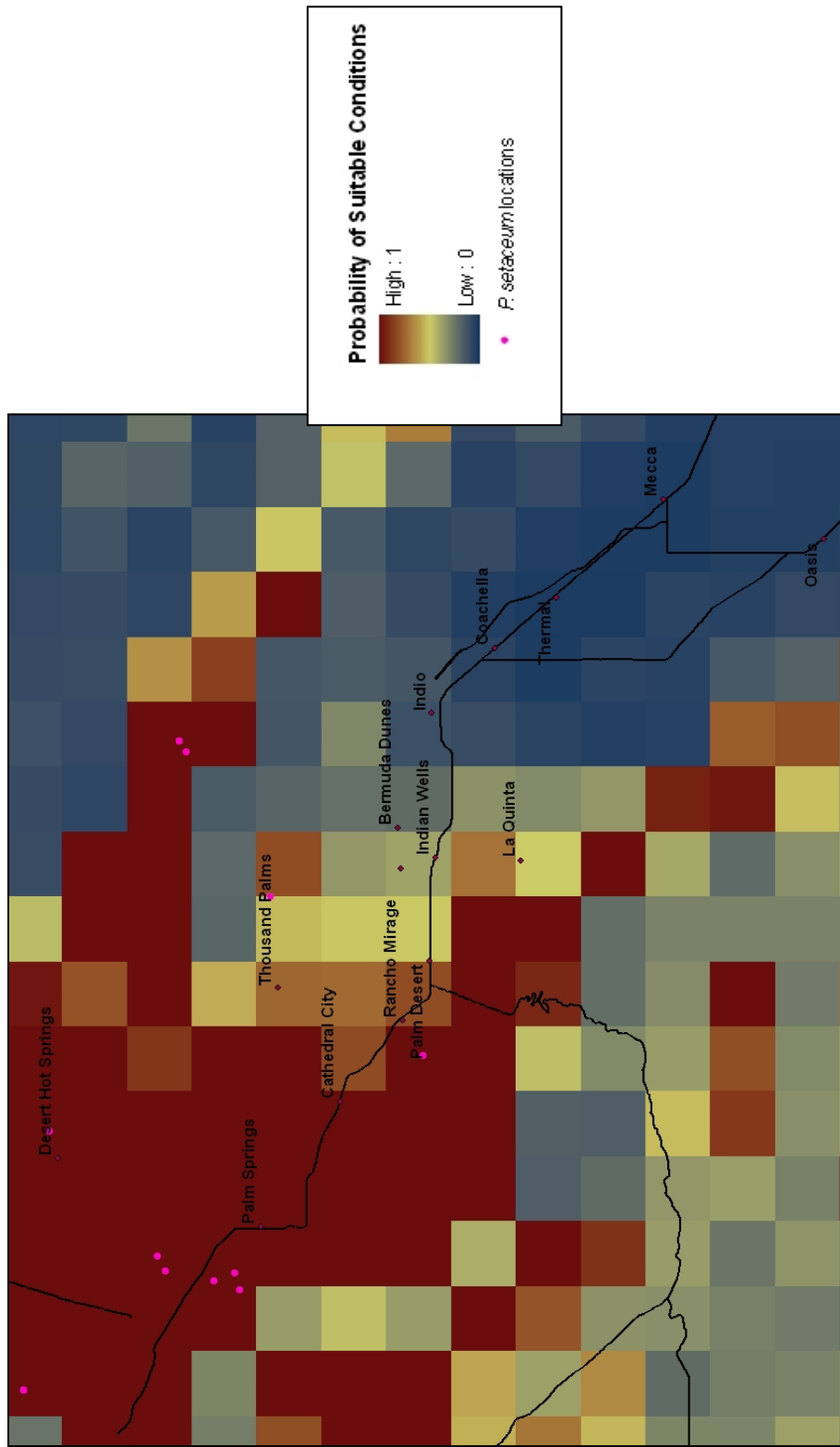
Figure 1.8. Zoomed-in view of the California MaxEnt model (from Figure 1.7, all variables used), showing the study area used in fine scale mapping. Pixels are 2.5 arc-minutes.
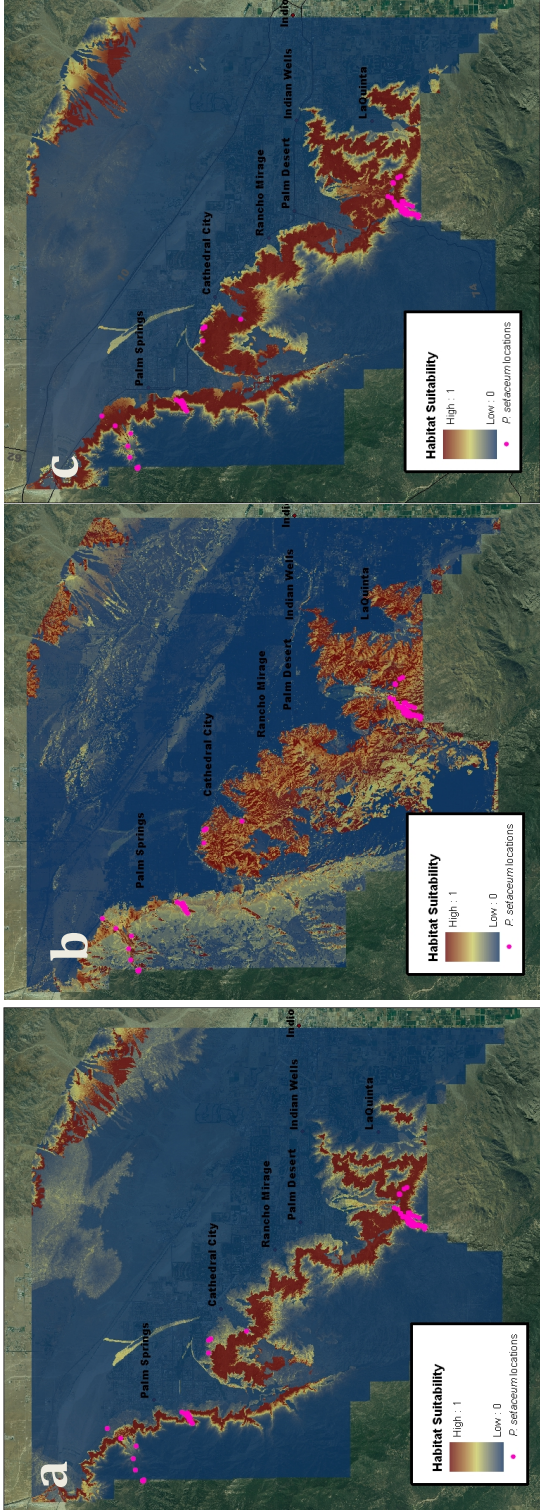
Figure 1.9. MaxEnt Habitat Suitability values for *P. setaceum* in the Coachella Valley, California. **(a)** Model trained using test data from the study area only. **(b)** Model trained on the test data, but excluding elevation as a variable. **(c)** Model trained using all data (study area and region-wide).

Model	Plant Locality Information	Sample Size	Dataset/Data Publisher	Environmental Predictor Variable	Grain size	Dataset/Data Publisher
Fine	Boyd Deep Canyon, CA	197	field collected by author	Aspect	1 meter	EDNA/USGS [1]
				Slope		EDNA/USGS [1]
	Coachella Valley, CA	26	field collected by author	Elevation		EDNA/USGS [1]
				Vegetation Type		LANDFIRE [2]
				Vegetation Cover		LANDFIRE [2]
				Soil Type		NRCS SSURGO/NRCS [3]
Coarse	California	291	Consortium of California Herbaria [4]	Derived Climate Variables	2.5-arcminute	WorldClim [5]
	Native Range	33	Botany (UPS)/GBIF–Sweden [6]	Elevation		WorldClim [5]
			Herbario de la Universidad de Salamanca: SALA/GBIF-Spain [6]			
			Herbarium Senckenbergianum (FR)/Senckenberg [6]			
			Missouri Botanical Garden [6]			
			National Herbarium Nederland/ Netherlands Centre for Biodiversity Naturalis [6]			
			Real Jardin Botanico (Madrid), Vascular Plant Herbarium (MA)/GBIF-Spain [6]			
			Royal Botanic Gardens, Kew [6]			
			The AAU Herbarium Database/Herbarium of the University of Aarhus [6]			
			The System–wide Information Network for Genetic Resources (SINGER)/Bioversity International [6]			
			United States National Plant Germplasm System Collection [6]			

1: Raster Digital Data, 2006, Elevation Derivatives for National Applications (EDNA), U.S. Geological Survey, EROS, Sioux Falls, SD, http://www.edna.usgs.gov
2: LANDFIRE Existing Vegetation Cover, United States Forest Service, 2008, USDA Forest Service, Missoula, MT, http://www.landfire.gov
3: SSURGO, 2008, USDA Natural Resources Conservation Service, Fort Worth, Texas http://soildatamart.nrcs.usda.gov
4: from the participants in the Consortium of California Herbaria, available at http://ucjeps.berkeley.edu/consortium/ (retrieved October, 2010)
5: Hijmans et al. 2005, available at www.worldclim.org
6: from the participants in the Global Biodiversity Information Facility, available at www.gbif.org (retrieved October, 2010)

Table 1.1. Dataset sources for the localities of *P. setaceum* and environmental data information.

Parameter Type	Parameter	Value
Soil moisture (capacity in mm)		100
Diapause Index (not used)		
Evapotranspiration co-efficient		0.8
Light Index (not used)		
Temperature indices	DV0[1]	9
	DV1	10
	DV2	42
	DV3	44
	PDD	600
Moisture indices	SM0	0.02
	SM1	0.03
	SM2	0.8
	SM3	1.1
Cold stress indices	TTCS	0
	THCS	-0.001
	DTCS	10
	DHCS	-0.0005
	TTCSA	0
	THCSA	0
Heat stress indices	TTHS	45
	THHS	0.001
	DTHS	0
	DHHS	0
Dry stress indices	SMDS	0.02
	HDS	-0.1
Wet stress indices	SMWS	1.1
	HWS	0.1

[1] DV0 (°C), lower temperature threshold for growth; DV1 (°C), lower limit of optimal temperature for growth; DV2 (°C), upper limit of optimal temperature for growth; DV3 (°C), upper temperature threshold for growth; PDD (d °C), annual thermal accumulation, or degree-days above DV0, necessary to complete a generation; SM0*, lower limit of soil moisture capacity necessary for growth; SM1*, lower limit of optimal soil moisture capacity for growth; SM2*, upper limit of optimal soil moisture capacity for growth; SM3*, upper limit of soil moisture capacity necessary for growth; TTCS (°C), average weekly minimum temperature below which 'cold stress' accumulates; THCS (wk^{-1}), rate at which 'cold stress' accumulates below TTCS; DTCS (d °C), 'cold stress' degree-day threshold; DHCS (wk^{-1}), 'cold stress' accumulation rate below DTCS; TTCSA (°C), mean weekly average 'cold stress' temperature threshold; THCSA (wk^{-1}), 'cold stress' accumulation rate once average temperatures drop below TTCS; TTHS (°C), average weekly maximum temperature above which 'heat stress' accumulates; THHS (wk^{-1}), rate at which 'heat stress' accumulates above TTHS; DTHS (d °C), 'heat stress' degree-day threshold; DHHS (wk^{-1}), 'heat stress' accumulation rate above DTHS; SMDS*, average weekly soil moisture level below which 'dry stress' accumulates; HDS (wk^{-1}), rate at which 'dry stress' accumulates below SMDS; SMWS*, average weekly soil moisture level above which 'wet stress' accumulates; HWS (wk^{-1}), rate at which 'wet stress' accumulates above SMWS; *Values are unitless. (Adapted from Pattison and Mack 2008; Sutherst et al. 2004). For explanation, please see Sutherst and Maywald, 1985.

Table 1.2. Parameters set in the CLIMEX program for the model of *P. setaceum*.

Region	AUC Training/Test	Variable (from Hijmans et al. 2005)	% Contribution	Permutation Importance	Average Value
California	0.978/0.958	Maximum December Temperature °C	**33.5**	**5.3**	18
		Isothermality (BIO2/BIO7[1]) (* 100)	**26.8**	2.8	52
		August Minimum Temperature °C	**5.6**	0	12
		Mean Temperature of the Coldest Quarter °C	**4.7**	1.6	12
		July Precipitation (mm)	1	**13.9**	3
		October Precipitation (mm)	0.9	**21.7**	12
		June Precipitation (mm)	0.3	**6.7**	2
Africa	0.986/0.98	Elevation (m)	**25.3**	0.1	1490
		Temperature Annual Range °C (BIO5-BIO6[1])	**11.5**	7.3	21
		October Precipitation (mm)	**9.1**	7.5	24
		November Precipitation (mm)	**8.4**	3.4	28
		June Precipitation (mm)	6.1	**13.1**	91
		March Precipitation (mm)	5.2	**19.2**	53
		Temperature Seasonality (standard deviation *100)	3.2	**29.2**	2381
		February Precipitation (mm)	2.8	**8.3**	52

[1] See Table 1.4 for variable descriptions

Table 1.3. Assessment of variable importance for MaxEnt models using all Worldclim layers fit to the distribution of *P. setaceum* for California and the African native range of the species. Average values for the training data area listed for qualitative interpretation. The top four contributing variables are in **bold**.

Training Data:

Variable Name	Variable Description (from Hijmans et al. 2005)	California		Native	
		% Contribution	Permutation Importance	% Contribution	Permutation Importance
BIO1	Annual Mean Temperature °C	0.2	0.3	9.3	0
BIO2	Mean Diurnal Range °C (Mean of monthly (max temp - min temp))	1.1	0.5	0.5	0.2
BIO3	Isothermality (BIO2/BIO7) (* 100)	**29.2**	1.2	0.4	0
BIO4	Temperature Seasonality (standard deviation *100)	1.1	0	**13.4**	**52.6**
BIO5	Max Temperature of Warmest Month °C	1.2	0.9	0.7	0
BIO6	Min Temperature of Coldest Month °C	1.1	0.2	3.8	1.2
BIO7	Temperature Annual Range °C (BIO5-BIO6)	0	0	12	0
BIO8	Mean Temperature of Wettest Quarter °C	2.2	0.7	2.3	11.4
BIO9	Mean Temperature of Driest Quarter °C	0.4	2.9	**11.4**	0
BIO10	Mean Temperature of Warmest Quarter °C	3.7	6.6	0	0
BIO11	Mean Temperature of Coldest Quarter °C	**48.2**	**45.5**	0	0
BIO12	Annual Precipitation (mm)	0.3	**10.8**	10.1	**17.4**
BIO13	Precipitation of Wettest Month (mm)	0.7	0.3	0	0
BIO14	Precipitation of Driest Month (mm)	1.8	3.9	6.1	2.5
BIO15	Precipitation Seasonality (Coefficient of Variation)	1.2	7	0.7	0
BIO16	Precipitation of Wettest Quarter (mm)	0.4	1.2	0.5	0
BIO17	Precipitation of Driest Quarter (mm)	0.5	**16.7**	**18.5**	**11.8**
BIO18	Precipitation of Warmest Quarter (mm)	0.6	0.6	5.6	1.2
BIO19	Precipitation of Coldest Quarter (mm)	**6.1**	0.8	4.8	1.7
	Training AUC	0.974		0.955	
	Test AUC	0.934		0.99	
	AUC When Projected onto Novel Range	*0.847*		*0.854*	

Table 1.4. Assessment of variable importance using derived climate variables only for MaxEnt models fit to the distribution of *P. setaceum* for California and the African native range of the species. The top three contributing variables are in **bold**.

Training Data: Test Data:	Deep Canyon Coachella Valley		Deep Canyon Coachella Valley		All 20% Random	
Variable	% Contribution	Permutation Importance	% Contribution	Permutation Importance	% Contribution	Permutation Importance
Soil Type	**37.8**	**23.9**	**49.8**	**64.4**	**39.9**	**43**
Elevation	**54.3**	**70.3**	--	--	**39**	**49.7**
Aspect	3.4	1.6	15.9	7.2	8.3	2.8
Vegetation Type	2.4	1	**19.4**	8	9.3	0.7
Slope	1.5	2.7	5.4	8.8	2.7	2.9
Vegetation Cover	0.6	0.5	9.6	**11.6**	0.8	0.9
Training AUC	0.984		0.935		0.973	
Test AUC	0.805		0.91		0.962	

Table 1.5. Assessment of variable importance for MaxEnt models fit to the distribution of *P. setaceum* in Deep Canyon, Palm Desert, CA and the Coachella Valley, CA. The top two contribution variables are in **bold.**

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Variable	Average Value or Top Catagorical Variables
Soil Type	Rock Outcropping
	Rubble Land
	River Wash
Elevation	362 meters
Aspect	North-Northwest
Vegetation Type	Sonoran-Mojave-Creosotebush Bursage Desert Scrub
	Mojave Mid-Elevation Mixed Desert Scrub
	North American Warm Desert Riparian Systems
	Barren
Slope	22 degrees
Vegetation Cover	20% cover (category)

Table 1.6. Specific variable values for the MaxEnt model fit to the distribution of *P. setaceum* in the Coachella Valley, CA using all datapoints and environmental variables.

Chapter 2: "Seasonality of competition between bunchgrasses C$_4$ *Pennisetum setaceum* and C$_3$ *Stipa pulchra*: implications for post-disturbance invasion"

Abstract

Pennisetum setaceum, African fountain grass, a C$_4$ exotic species, occurs in some southern California areas that are adjacent to native C$_3$ *Stipa pulchra* grasslands. Although these areas are predicted to be climatically suitable for growth of *P. setaceum*, biotic factors such as competition also influence invasive success. It is unknown whether the difference in physiology between the two species will be conducive to or prevent invasion by *P. setaceum* into *S. pulchra*-dominated areas. A competition experiment was carried out under controlled conditions to determine the competitive interactions of the two species from the cool winter season into the warm summer season. Above-ground vegetative and reproductive biomass were harvested and weighed separately for each species in May and August. As expected, *S. pulchra* had higher gains in biomass in the cooler season and showed strong intraspecific competition as well as suppression of *P. setaceum* growth. *P. setaceum* showed no suppression of *S. pulchra* growth in the early season; by contrast the biomass of *S. pulchra* was higher as the proportion of *P. setaceum* in the plot increased, indicating strong intraspecific competition by *S. pulchra*. In the second (warm-season) harvest, *S. pulchra* showed relatively less suppression of *P. setaceum*, and *P. setaceum* showed increased growth in the warm season. Leaf-level photosynthetic measurements showed that both species increased their photosynthetic rates from late winter to late spring, and *P. setaceum* had a higher photosynthetic rate in

the late season. Plot-based gross primary productivity (GPP) measurements in July

showed higher GPP in *P. setaceum* plots. Phenological difference were noted between

the two species, as *S. pulchra* reproductive culms were past mature in August, and much

of the vegetative biomass was nearing dormancy, while *P. setaceum* was actively

growing and producing reproductive culms. Results of this study, meant to quantify

differences in post-emergence growth of two perennial grasses in California, show that

the C_3 *S. pulchra* can slow initial growth of C_4 *P. setaceum*, but that late-season growth

by *P. setaceum* can overcome initial suppression to survive and reproduce at both low

and high densities. Thus, after a disturbance event arriving propagules of *P. setaceum*

may experience intense competition by *S. pulchra* in the cool season, but a release from

this competition and an opportunity to thrive later in the season.

Introduction

Interactions between invasive species and the invaded community, including

competitive interactions (Cadotte and Lovett-Doust 2002) may be important processes in

determining invasion success (Sakai et al. 2001, Levine et al. 2004, MacDougall et al.

2009). At a various scales, biotic factors, including competition, are important in

determining abundance of any species (Elton 1927, Hutchinson 1957, Goldberg and

Barton 1992, Brown et al. 1996).   Therefore, an understanding of competitive

interactions between an invasive plant and a recipient community are key to the study of

an invasion (Levine et al. 2004).

Competition experiments have been used to evaluate competitive hierarchies that exist between species (Roush and Radosevich 1985, Puliafico et al. 2011) and are arguably strong determinants of community composition (Keddy and Shipley 1989, Shipley and Keddy 1994, Tilman 1994). In wildlands, experiments are often aimed at establishing the importance of these competitive relationships, that is, the ecologically-relevant outcomes, such as changes in reproductive output or survival (Welden and Slauson 1986; but for recent discussion, see Freckleton et al. 2009).

Competitive relationships may be relatively more important in early stages of establishment (Radosevich and Roush 1990), and may be very important in high-disturbance environments (Grime 1977, Davis et al. 2000). These relationships may also change along gradients such as CO_2 (Johnson et al. 1993, Ziska 2000), soil fertility and disturbance (Fynn et al. 2005), and temperature (Tilman et al. 1981).

In areas in southern California that are climactically suitable for *Pennisetum setaceum* (see Chapter 1), biotic interactions may lead to differential invasion of suitable habitats by either the facilitation or the suppression of invasion by native species. *Stipa pulchra* (Hitchc.) (syn. *Nassella pulchra* Hitchc. Barkworth) grassland communities occur in proximity to populations of invasive *Pennisetum setaceum* in several areas, including the Santa Rosa Plateau in Murrieta, California, and Malibu Creek in Malibu, California (L. Sweet, personal observation) in addition to being an occasional community component within *P. setaceum*-invaded areas (data from Chapter 3, not shown).

S. pulchra is a native C_3 perennial bunchgrass, historically occurring in many areas of California. In southern California, it occurs specifically in grassland and coastal

sage scrub areas in the Peninsular and Western Transverse Ranges and the South Coast (Hickman 1993). This grass is most actively growing from early winter into spring in southern California, depending on rainfall (Bartolome and Gemmill 1981). *S. pulchra* grasslands have probably been decreasing in California since European settlement (Huenneke 1989), and much attention has been paid to the conservation of this species, including interactions with exotic annual grasses (Dyer and Rice 1997, 1999, Hamilton et al. 1999, Abraham et al. 2009, Bartolome and Gemmill 1981), the differential impact of grazing (White 1967), impacts of disturbance (Dyer et al. 1996, Bartolome et al. 2004), and how genetic variation of this grass (commonly used for restoration plantings) is influenced by its competitive environment (Knapp and Rice 2011). However, there is some evidence that the decline of this species is not due to a lack of competitive ability. Corbin and D'Antonio (2004) found that, over time, *S. pulchra* could competitively dominate plots over exotic grasses, and cited other factors such as climate change or land use change for the type-conversion of many areas from *S. pulchra*-dominated into annual exotic grasslands. Biomass of *Centaurea solstitialis L.*, yellow star-thistle, was reduced when planted in competition with *S. pulchra* (Callaway et al. 2006). Indeed, there is evidence that the *S. pulchra* grassland system may be quite resistant to invasion (Seabloom 2007); however, other studies have suggested that exotic annual grasses will outcompete *S. pulchra* (Nelson and Allen 1993, Dyer and Rice 1997, Hamilton et al. 1999, Abraham et al. 2009).

P. setaceum is a warm-season grass (C_4 $NADP^+$ -ME) (Winter et al. 1976) that is able to respond plastically to moisture with opportunistic growth year-round (Goergen

and Daehler 2001), and occurs at altitudes of up to 2800 meters in Hawaii (Wagner et al. 1990). In its native range in Egypt, *P. setaceum* occurs in Sinai and the Nile Delta, where the mean minimum temperature of the coolest month is 5-15°C and mean maximum temperatures of the hottest month can be up to 35°C (Batanouny et al. 1988).

In California areas where exotic *P. setaceum* co-occurs with *S. pulchra,* rainfall occurs primarily during the winter months, when maximum temperatures range from 19°C in January up to 22°C (24°C in some locations) in May (Western Regional Climate Center historical monthly average temperatures for stations: Santa Monica, #047950; Getty Center, #043392; Ventura, #049285; and El Cajon, #042705). Interestingly, these locations are similar in average July and January mean air temperature and seasonal rainfall pattern to a subalpine dry forest study site in Hawaii where *P. setaceum* occurs (see Table 1, Williams et al. 1995). It should be noted, however, that in the 1995 study, growth parameters measured indicated superior growth of *P. setaceum* at warmer, more coastal sites. Thus, *P. setaceum* may grow in cooler conditions, but shows optimum growth in the warm season.

Phenological differences that lead to a temporal release from competition may be responsible for facilitating invasions (Wolkovich and Cleland 2010), and these differences have also been exploited for management of invasives (Marushia et al. 2010). Phenology has also been used to explain seasonality of dominance and niche differentiation between C_3 and C_4 grasses co-occurring in other systems (Kemp and Williams 1980, Maragni et al. 2000). While there is no doubt that optimum conditions differ for C_3 and C_4 species (Ehleringer 1978), research is ongoing to determine whether

competitive dominance or abundance of these species are most influenced by temperature (Tieszen 1970, Williams 1974, Monson et al. 1983) or timing of precipitation (Winslow et al. 2003), or both (reviewed in Niu et al. 2005). In fact, Niu et al. (2005) found that the C_4 species they studied in competition plots responded best to water during the warm season, while the C_3 species responded to water during the cooler periods.

Although *P. setaceum* has not yet been documented invading an *S. pulchra* grassland, where these two species co-occur early-season growth and flowering of *S. pulchra* may leave a late-season niche available for *P. setaceum*, assuming there is sufficient moisture for growth available at that time. Thus, this study was initiated in order to investigate whether *P. setaceum* may overcome competitive suppression during the cooler early season to survive and reproduce in the warm season, which is the importance of competition in this case. This question was addressed through competition experiments and comparison of carbon capture.

Materials and Methods

Plant Material

Seeds of *Stipa pulchra* were collected the late spring of 2009 from the field in Murrieta, California (33.5453°N, -117.2691°W), at the Santa Rosa Plateau Ecological Reserve in a grassland community. Seeds of *Pennisetum setaceum* were collected during the summer of 2009 from plants grown in a greenhouse at U.C. Riverside. Seeds were stored in paper envelopes at room temperature until use. Seedlings of both species were grown in black 2", 200-cell Speedling flats (Speedling, Inc., P. O. Box 7220, Sun City,

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FL 33586-7220) in an unheated greenhouse prior to the start of the field portion of the

experiment, from mid-November, 2009 until planting in February, 2010. Soil in the trays

consisted of UC Mix #3 (peat + sand, 40:60 by volume, with micronutrients), as well as

one gram per cell of field soil (for mycorrhizae inoculum), collected from Murrieta, CA,

where *Stipa pulchra* occurs in abundance (Gillespie and Allen 2006). Monospecific trays

of the two species were placed, alternating, on two greenhouse benches and these trays

were rotated once per month. The flats were watered from below approximately to field

capacity using large stainless steel trays and allowed to dry out between watering. Dilute

fertilizer solution (21-5-20 N-P-K fertilizer solution, Peters® Excel at 100 ppm nitrogen,

Grace-Sierra Horticultural Products Company 1001 Yosemite Drive, Milpitas, CA

95035) was applied once per month. Above-ground biomass of five randomly-selected

plants of each species was determined prior to planting, and there was no difference in

fresh shoot weight between the two species (two-sample *t*-test: *S. pulchra*

mean=0.442g/plant; *P. setaceum* mean=0.62g/plant p=0.167). Flats were cold-hardened

for five days prior to planting in the field by placing the trays outside the greenhouse on

wooden benches.

Competition

A field of 64 plots was established January of 2010 at the U.C. Riverside

Experiment Station, California (33.97°N, -117.34°W), in a randomized complete block

design that included 4 blocks of 16 plots (4 by 4) each. The eight treatments consisted of

two densities and four proportions of planting mixtures of the two species; two sets of

treatments were planted per block to permit two separate harvests. Proportions of *P.*

setaceum and *S. pulchra*, including monospecific plots, were planted in a substitutive design, including 100%/0%, 66.7%/33.3%, 33.3%/66.7% and 0%/100%, respectively, of the two species in mixture. Hereafter, proportions are referred to using the percentages of *P. setaceum* present in the plot (0, 33, 66, 100). The two densities used were nine per square meter (Low) and 25 per square meter (High). Each plot was surrounded on all sides by a single row of plants in the same density and proportion as the treatment inside the plot. For all plots, nine plants were used for biomass measurements and harvest, which included all non-buffer row plants in the lower density plots and the central nine in the higher density plots.

Plots were irrigated twice a week for the first two weeks for establishment using overhead sprinklers on risers set at 1m height. Subsequently, they were watered to approximate average weekly rainfall for the areas where these two species co-occur in Eastern San Diego County and Malibu (Western Regional Climate Center, monthly climate summary for El Cajon Station and Topanga Ranger Station, http://www.wrcc.dri.edu/). Irrigation dates and amounts, natural precipitation and daily minimum and maximum temperature during the growth portion of the experiment are shown in Figure 2.1. A wire fence was installed surrounding the field to curtail some early herbivory by local rabbits. Plants that died during the first month of the experiment were replaced, and there were only 2 plants that died subsequently during the experiment. Plots were weeded as necessary using a hula-hoe.

Plots were measured biweekly for plant height (longest central leaf) and two widths. Above-ground biomass was harvested from plots at two different times, 3

months (May) and 6 months (August) after planting. At harvest, plants were cut off at the soil surface. Tillers containing inflorescences (where spikelet tips were visible) were bagged and weighed separately as reproductive biomass. The August harvest included all biomass, including early growth, some of which had senesced. To determine fresh and dry weight, all aboveground biomass was weighed fresh, dried in a drying oven in paper bags at 60°C for 2 weeks and then removed and re-weighed. Only dry weights were used for analysis. Samples of soil in the field were taken at the beginning of the experiment, dried and ground, and analyzed to determine fertility in the field by University of California Davis Analytical Lab (http://anlab.ucdavis.edu/). Soil nutrients in the experimental field (average values: extractable NO_3-N=2.33 ppm, bicarbonate extractable P=7.95ppm, extractable K 108.5ppm, KCl-extractable NH_4-N=0.74ppm) were within the normal limits for areas where these grasses co-occur, with the exception of NH_4, which was slightly lower than wildland values (L. Sweet, unpublished data). No additional fertilizer was added during the experimental period.

Photosynthetic performance

Photosynthetic measurements at both the plot- and single leaf-level were taken in order to examine carbon capture and conductance differences between the two species by season. The first set of measurements was recorded using an area-based (plot-level) method due to incipient dormancy of plants resulting in difficulty in locating leaves of acceptable quality for leaf-based measurements. Area-based methods can be used to document basic differences in carbon capture per species. Measurements were recorded just prior to harvest in August 2010 at the plot-level by placing a 1-m^2 tent over plants

and measuring photosynthesis with a portable infrared gas analyzer (LI-840, LI-COR Inc., Lincoln, NE, USA), using the method of Chen et al. 2009 (Chen et al. 2009). This method estimates Net Ecosystem Exchange (NEE) and ecosystem respiration (R_e) by measuring decreases in CO_2 levels from carbon capture immediately after the plant is tented and then increases in CO_2 from respiration when the plant is tented and covered with light inhibiting cloth. Gross Ecosystem Productivity (GEP) (μmol m^{-2} s^{-1}) is calculated from NEE and R_e (for calculations, see Chen et al. 2009). Monospecific plots in each block were used for measurements, with 4 replications.

Subsequent measurements were taken using a LI-6400 portable photosynthetic system (Li-Cor, Lincoln, Nebraska, 68504), using un-harvested border plants in February and May of the following year. In February, leaf-level measurements were made using the LI-6400 in late morning under ambient radiation (1490-1670 μmol m^{-2} s^{-1}) with leaf temperature, humidity, and CO_2 levels held constant (typically 22-23°C, 15-18% relative humidity, 399-401 μmol CO_2 mol^{-1}). Due to an error in the flow rate setting, only 2 usable measurements were produced for *P. setaceum*. In May, leaf-level measurements were made in late-morning under saturating PPFD conditions (1500 μmol m^{-2} s^{-1}) with leaf temperature, humidity, and CO_2 levels held constant (typically 25-27°C, 28-30% relative humidity, 399-401 μmol CO_2/mol^{-1}). Because leaves of both species did not fill the cuvette, measured variables for each plant were corrected using actual leaf area values obtained from a Li-Cor leaf area meter (model Li-3000, using the Transparent Belt Conveyer Accessory, LI-3050A; Li-Cor).

Statistical Analysis:

Mean plant dry weight biomass per treatment for vegetative and reproductive biomass was compared using JMP statistical software (Copyright © 2011 SAS Institute Inc., SAS Campus Drive, Building S, Cary, NC, 27513). Plant weights were averaged to obtain one average value per species per plot. ANOVA was used for normal variables and Kruskall-Wallis for non-parametric data. Post-hoc testing was performed using Tukey's Honestly Significant Difference (HSD) for all possible combinations. Plants that died after one month were excluded from the per-plant analyses, but accepted as error for the relative yield portion of the analysis.

Relative yield was calculated (using dry weight per plot) separately for each species, vegetative and reproductive biomass, Low and High density plots, as well as for each of the two harvests as follows: RY=(plot yield per species)/(plot yield for species in monoculture) (Radosevich et al. 2007). 100% of each species (proportion of 1.0) is considered the monoculture standard value for each comparison, and the expected proportions of yield in other treatments are calculated proportional to the yield of this treatment. 95% confidence intervals for each value were produced from ANOVA, in order to compare relative yield values to the expected value for each treatment.

Leaf-level photosynthetic data, corrected for leaf area, was compared for species and month using T-tests, and mean standard error rates are reported for all comparisons. Calculated GEP values for the two species were compared using a *t*-test.

Results

Vegetative and Reproductive Biomass

For both species in both seasons, average plant vegetative and reproductive biomass was lower in High-density plots compared with Low-density plots (Figures 2.2 and 2.3, respectively; Table 2.1). In May, *S. pulchra* vegetative biomass was highest in Low-density mixture plots (Figure 2.2c). Biomass was lowest in the monoculture High-density plots, but did not differ between the 3 High-density proportions and the high density plot with the least *S. pulchra*. *S. pulchra* reproductive structures were further-developed phenologically than those of *P. setaceum* at the time of harvest (Figure 2.2f, l). Reproductive biomass of *S. pulchra* was lowest in the high-density monospecific plots, and higher but not different between the mixture plots (Figure 2.2f). The Low-density plots had higher average reproductive biomass than the High-density plots (Figure 2.2e), but did not differ between the proportions (Figure 2.2f).

For *P. setaceum* in May, average vegetative biomass was highest per plant in monospecific Low-density plots and lower in both mixture plots, which did not differ from each other (Figure 2.2i). Average vegetative biomass was lowest in High-density mixture plots. Reproductive biomass in *P. setaceum* in May was phenologically limited to unemerged inflorescences with immature spikelets. Reproductive biomass was overall very low, averaging 0.1 g/plant (dry weight) in the High-density plots (Figure 2.2k) with no differences between High-density treatments (Figure 2.2l). Reproductive biomass was highest in Low-density plots (Figure 2.2k), but again, treatments did not differ (Figure 2.2l).

Figures 2.4a-b show the May plot vegetative yields relative to a monoculture standard (0 for *S. pulchra* and 1.0 for *P. setaceum*) for each density. In the Low-density

plots (Figure 2.4a), *S. pulchra* over-yielded in mixture and *P. setaceum* under-yielded relative to monoculture plots of each respective species. In High-density plots (Figure 2.4b), *S. pulchra* did not significantly over-yield relative to expected values in the 66% *P. setaceum* mixture. *P. setaceum* under-yielded in 33% plots, but did not differ from expected values in 66% plots.

Relative reproductive yield patterns for the May harvest echoed the vegetative yield patterns for both species (Figures 2.4e-f). *S. pulchra* was not significantly different from expected values in the low-density treatments (Figure 2.4e), but highly over-yielded in the 33% high-density treatment (Figure 2.4f). *P. setaceum* did not differ from expected values for any treatment.

In the August harvest as in the May harvest, for both species, average plant vegetative and reproductive biomass was lower in High-density plots compared with Low-density plots (Figure 2.3). *S. pulchra* average vegetative biomass was highest per plant in Low-density plots, which did not differ from each other (Figure 2.3c). Average vegetative biomass was lowest in High-density plots and lower than all but the monoculture Low-density plots (Figure 2.3c). Average reproductive biomass was higher than all other treatments in the Low-density 66% plots, but not different between the Low-density 33% mixture and monoculture treatments (Figure 2.3f). The High-density monoculture and 33% mixture treatments had the lowest average reproductive biomass (Figure 2.3f).

P. setaceum average vegetative biomass in August was lower overall in the High-density mixture plots than in the Low-density monoculture plots (Figure 2.3h).

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Vegetative biomass differed only between the Low-density monoculture plots, which were higher, and the High-density 33% plot, which were lower, while all other treatments were not significantly different than any other (Figure 2.3i). Average reproductive biomass was highly variable and although it differed between densities overall (Figure 2.3k), it did not differ between any proportion treatments (Figure 2.3l). Higher variance for the Low-density 33% mean was influenced by inter-block variation (failure of several plants to thrive in one block).

Examining the relative yield patterns in the Low-density plots in the late harvest, (Figure 2.4c), only *S. pulchra* slightly overyielded in the 66% treatment, while all other *P. setaceum* vegetative yields were not significantly different than expected relative to monoculture plots of each respective species. In High-density plots (Figure 2.4d), *S. pulchra* and *P. setaceum* did not differ significantly from expected values.

Relative reproductive yield for *S. pulchra* in August showed an over-yield in all mixture plots (Figures 2.4g-h). It should be noted that, for this species, reproductive biomass sampled in August no longer contained seeds, and thus, dry reproductive biomass is actually lower in August than in May. In Low and High-density plots (Figure 2.4g-h), *P. setaceum* yield was not different from expected yields. Variance was much higher in *P. setaceum* than in *S. pulchra* in this late-harvest.

Physiological Measurements

Photosynthetic rates, intercellular CO_2 concentration, transpiration and conductance to H_2O showed some differences between species and season (Figure 2.5). Leaf temperatures during the February measurements averaged 23-24°C (data not

shown). There were no differences in photosynthetic rate or intercellular CO_2 between the species in February; however, conductance and transpiration were both higher in the C_3 *S. pulchra*. In May, leaf temperatures during measurements were between 25-28°C (data not shown). Photosynthetic rate was higher in the C_4 *P. setaceum*. Conductance and transpiration were similar between species during these measurements.

From February to May, *S. pulchra* increased in photosynthetic rate, decreased in intercellular CO_2, and decreased in conductance and transpiration rates. *P. setaceum* increased in photosynthetic rate, decreased in inter-cellular CO_2 concentration, and both conductance and transpiration remained similar between seasons.

Gross Ecosystem Productivity Measurements

Evaluation of Gross Ecosystem Productivity (GEP) (μmol CO_2 m^{-2} s^{-1}) in August between monospecific plots showed higher GEP values for *P. setaceum* August compared to *S. pulchra* (Figure 2.6). No differences in respiration were seen between the two types of monoculture plots (data not shown, p=0.130).

Discussion

Physiological differences in functional traits may affect the establishment and competition of an exotic species in a recipient community (Funk and Vitousek 2007, Funk et al. 2008). Competition experiments carried out under relatively controlled conditions allow insight into interactions between species, and results can establish the importance of these relationships in ecological systems (Shipley and Keddy 1994, Gibson et al. 1999, Radosevich et al. 2007). In California coastal sage scrub and grasslands,

generally low-resource systems, high growth rate and preemption of resources may theoretically confer an advantage (Clements 1929, Tilman 1988), especially early in the growing season (Hamilton et al. 1999). Results of the present study indicate that although *S. pulchra* is able to suppress growth of *P. setaceum* at high densities, *P. setaceum* may persist and thrive during the warm season.

Vegetative yields and gas exchange measurements in the cooler season agreed with expected results of seasonal differences in photosynthetic rates of C_3 *S. pulchra* and C_4 *P. setaceum* (Keeley and Rundel 2003). *S. pulchra* over-yielding in mixture plots indicates that this species is more strongly affected by intraspecific competition than by interspecific competition with *P. setaceum*. As the percentage of *P. setaceum* increased, mean relative *S. pulchra* vegetative and reproductive biomass increased, demonstrating release from intraspecific competition. Indeed, during the cooler season, comparisons indicate strong growth and competitive dominance by *S. pulchra*, especially at high densities, though these densities are higher than estimated pre-settlement densities of 4.2 plants/m^2 (Dyer and Rice 1997) and observed contemporary densities of 2.18 plants/m^2 (Bartolome and Gemmill 1981). Photosynthetic comparisons showing higher photosynthetic rates in the cooler early season corroborate the strong seasonality of carbon capture in this species.

P. setaceum demonstrated a similar response to *S. pulchra* presence in plots; mean relative vegetative and reproductive biomass decreased as a function of increasing *S. pulchra* proportion. This indicates that *P. setaceum* is more affected by interspecific competition with *S. pulchra* than by intraspecific competition. Low reproductive yield of

P. setaceum in all plots in the cooler early season was expected due to its later phenological development relative to *S. pulchra*, but mixture plots indicated a suppression and delay in onset of flowering that persisted into the warmer season.

   P. setaceum also had depressed rates of photosynthesis in February, likely as a result of a higher photosynthetic temperature optimum. It should be noted that the values measured for *P. setaceum* are lower than expected at a leaf temperature of 23 ºC based on the data of Williams and Black (1993). However, maximum air temperature on the measurement date in February was only 18.3ºC (which was reached after measurements were taken), with nighttime air temperatures of about 5ºC (CIMIS data). Although differences in quantum yield explain higher photosynthesis in C_4 species relative to C_3 species at high temperatures (Ehleringer et al. 1997), there is no de-facto explanation for poor performance at low temperatures based on quantum yield differences. Kubien and Sage 2004(a) reviewed several possibilities for lower photosynthetic rates at low temperatures by C_4 species, such as depressions in the carbon fixation reactions (Kubien et al. 2003), or greater susceptibility to low-temperature photoinhibition due to a lack of alternative sinks for light energy when light harvesting reactions are slowed. After examining a low-temperature tolerant C_4 species, their results showed that these species have a lower Rubisco (ribulose-1,5-bisphosphate carboxylase oxygenase) capacity, based on Rubisco content in the plant, which is primarily responsible for the reduction in carbon capture at low temperatures (Kubien and Sage 2004b). Regardless of the cause of this depression, the pattern seen here in photosynthetic rate helps explain reduced biomass production of *P. setaceum* in the cooler months. Due to the low number of

observations, however, additional early season measurements would be necessary to confirm the depression in photosynthetic rate of the C_4 species seen here.

In the summer harvest, responses of both species were influenced by the vegetative legacy of early growth responses to cooler temperatures and competition treatments, which would likely bias results in favor of *S. pulchra*. Specifically, the leaf area index (LAI) resulting from the first experimental period of growth influenced continuing carbon capture capacity during the second period, which affected biomass at the second harvest. Additionally, formerly live biomass that had senesced persisted on *S. pulchra* plants and was included in the second biomass measurement. Nevertheless, several observed differences between the species in allocation to vegetative or reproductive growth reflected differences in phenological responses under this temperature and moisture regime, as predicted (Kemp and Williams 1980, Monson et al. 1983). By the August harvest, C_3 *S. pulchra* had dropped its seeds from reproductive structures and much of the *S. pulchra* vegetative biomass had begun to senesce (estimated by visual rating, data not shown). *P. setaceum*, in contrast, had few senescent leaves, most biomass was non-dormant (Appendix 2), and inflorescences were just attaining maturity (L. Sweet, pers. obs.).

S. pulchra mean vegetative biomass per plant, most of which was established in the cooler early season, still showed evidence of strong interspecific suppression of *P. setaceum* at the later harvest. However, in the low-density treatment, strong over-yielding performance had diminished, suggesting that by August C_4 *P. setaceum* was beginning to compete more strongly with the native C_3 grass at this density, perhaps

making way phenologically for *P. setaceum*. Continued overyielding in reproductive biomass of *S. pulchra* may be due to the fact that much of this biomass was formed during the cooler early season, and there was little opportunity for the warmer season growth surge of *P. setaceum* to affect reproductive allocation of *S. pulchra*.

The warmer summer growing season showed a respite, if not quite a reversal in dominance favoring *P. setaceum*. Although vegetative biomass changed little in terms of relative yield proportions from the cooler early season, *P. setaceum* allocation to reproduction showed a late surge in the low-density plots, with probable over-yielding. However, high variance in plots may be due to magnification of differential responses from the early season (Ross and Harper 1972). That is, outcompeted plants did not thrive, but those that were able to gain some leaf area were able to maximize that advantage and continue to grow and reproduce (Samson and Werk 1986).

Unfortunately, high variance in plots makes it difficult to be certain about these warmer late season differences between species. Overall, the pattern of mean reproductive biomass production in the low-density plots appears to be reversed between May and August, and *P. setaceum* was less strongly suppressed by *S. pulchra*. Thus, in the August harvest reproductive success of *P. setaceum* increased with increasing *S. pulchra* proportion, suggesting a reduction in interspecific competition.

Photosynthetic and gas exchange measurements in May and August conformed to the expectation that C_4 *P. setaceum* would outperform C_3 *S. pulchra* during the warmer season compared to the cooler months. Similar stomatal conductance values between species may indicate that plants were in a drying condition, and while *P. setaceum*

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continued to fix carbon via the C_4 pathway, photorespiration had become limiting in *S. pulchra*. Summer measurements showing Gross Ecosystem Productivity differences in the C_3 and exotic C_4 grasses confirm this switch in dominance at the landscape level.

Conclusions

Fluctuation in resource availability due to disturbance is a common occurrence in Southern California (Keeley 2001). Since *P. setaceum* appears to be competitively inferior, frequent disturbance can allow a species that is a good colonizer to invade, despite being an inferior competitor (Davis et al. 2000, Chakraborty and Li 2010), for example, in a native grassland after fire. *P. setaceum* can be a prolific seeder, and has shown the ability to colonize a diversity of habitats; thus, the remaining barrier to establishment is competition with resident (native and exotic) species. In a wildland setting, other factors may certainly be more important in the invasion of *P. setaceum;* the additional component of competition with exotic annual C_3 grasses may be an important factor post-disturbance (Nelson and Allen 1993 and others, as above). A strict interpretation of the physiological differences of these species would not predict establishment of *P. setaceum* in a C_3 grass-dominated habitat, because areas where C_3 species dominate tend to have cooler growing seasons. However, this species has a demonstrated capacity for temperature tolerance (as shown in a congener by Wilen and Holt, 1996) and plastic growth responses (Williams and Black 1993, Williams et al. 1995). This study investigated whether the barrier of a qualitative difference in life history may prevent the establishment of an exotic grass.

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Interpretation of competition experiments and extension of results to predict plant responses in wildlands is subject to some limitations, and interpretation of such experiments have caused some debate (Cousens 1991, Cousens and Oneill 1993, Shipley and Keddy 1994). However, as the goal of this experiment was to investigate the importance of the interspecific competitive impacts of these species (Welden and Slauson 1986), a controlled experiment was necessary to isolate effects of physiological differences on ecologically-relevant processes. While density was manipulated to be higher than reported naturally-occurring densities of mature *S. pulchra* monocultures, several other studies dealing with early-stage competition have also employed higher densities (White 1967, Dyer and Rice 1997, 1999), especially where competition of *S. pulchra* at the seedling stage is being considered (Abraham et al. 2009). In addition, inoculum from native soil was included in this experiment, since there may be an effect of symbiotic mycorrhizae on competition between plant species (Allen and Allen 1990).

Results of this study, meant to quantify differences in post-emergence growth of two perennial grasses in California, show that the C_3 *S. pulchra* can slow initial growth of *P. setaceum*, but that late-season growth by *P. setaceum* can overcome initial suppression to survive and reproduce at both low and high densities. Thus, in recently burned grassland dominated by *S. pulchra*, one may expect arriving propagules of *P. setaceum* to experience intense competition in the cool season, but a release from this competition and an opportunity to thrive later in the season. Following up on these results, further investigation would reveal whether mature *S. pulchra* grassland would be able to suppress recruitment of an immature propagule of *P. setaceum*. With relevance to natural

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systems in Southern California, managers of *S. pulchra* grasslands should institute

effective control of *P. setaceum*-dominated areas in close proximity to *S. pulchra*,

especially post-disturbance, where maintenance of uninvaded grassland is a management

goal.

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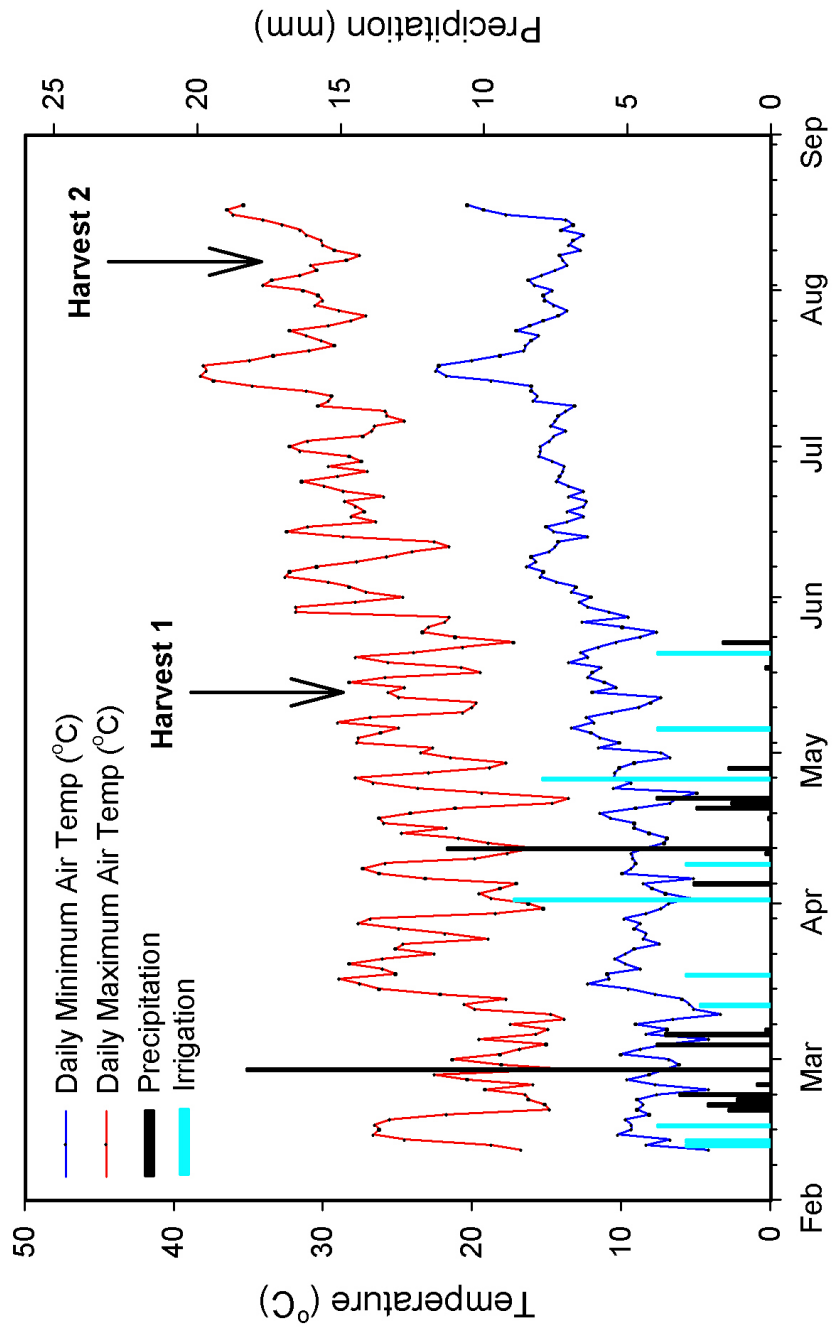
Figure 2.1. Weather during the competition experiment in 2010 at the Agricultural Experiment Station, U.C. Riverside, CA. Temperature and precipitation data from CIMIS weather observation data (California Irrigation Management Information System, California Department of Water Resources). Irrigation amounts are average amounts from in-field rain gauges.
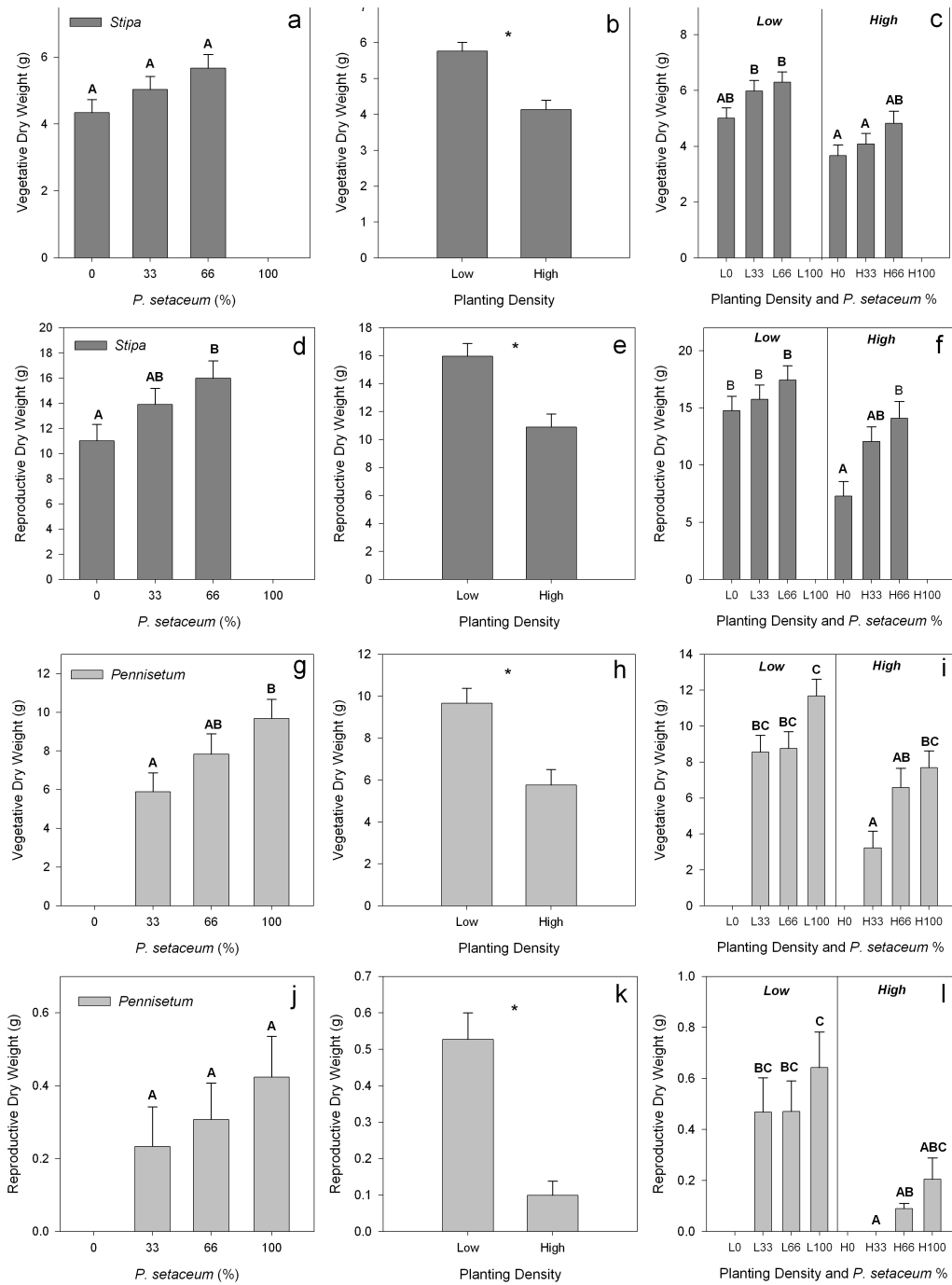
Figure 2.2. May mean dry weights per plant of vegetative **(a, b, c, g, h, i)** or reproductive **(d, e, f, j, k, l)** biomass in each treatment for *Pennisetum* and *Stipa* from ANOVA comparisons. *P. setaceum* densities are low, 9 plants m^2 and high, 25 plants m^2. Error bars are one Standard Error. Letters are from Tukey's HSD comparison of all possible combinations. Bars with different letters within a graph are significantly different at 0.05; *, P<0.05
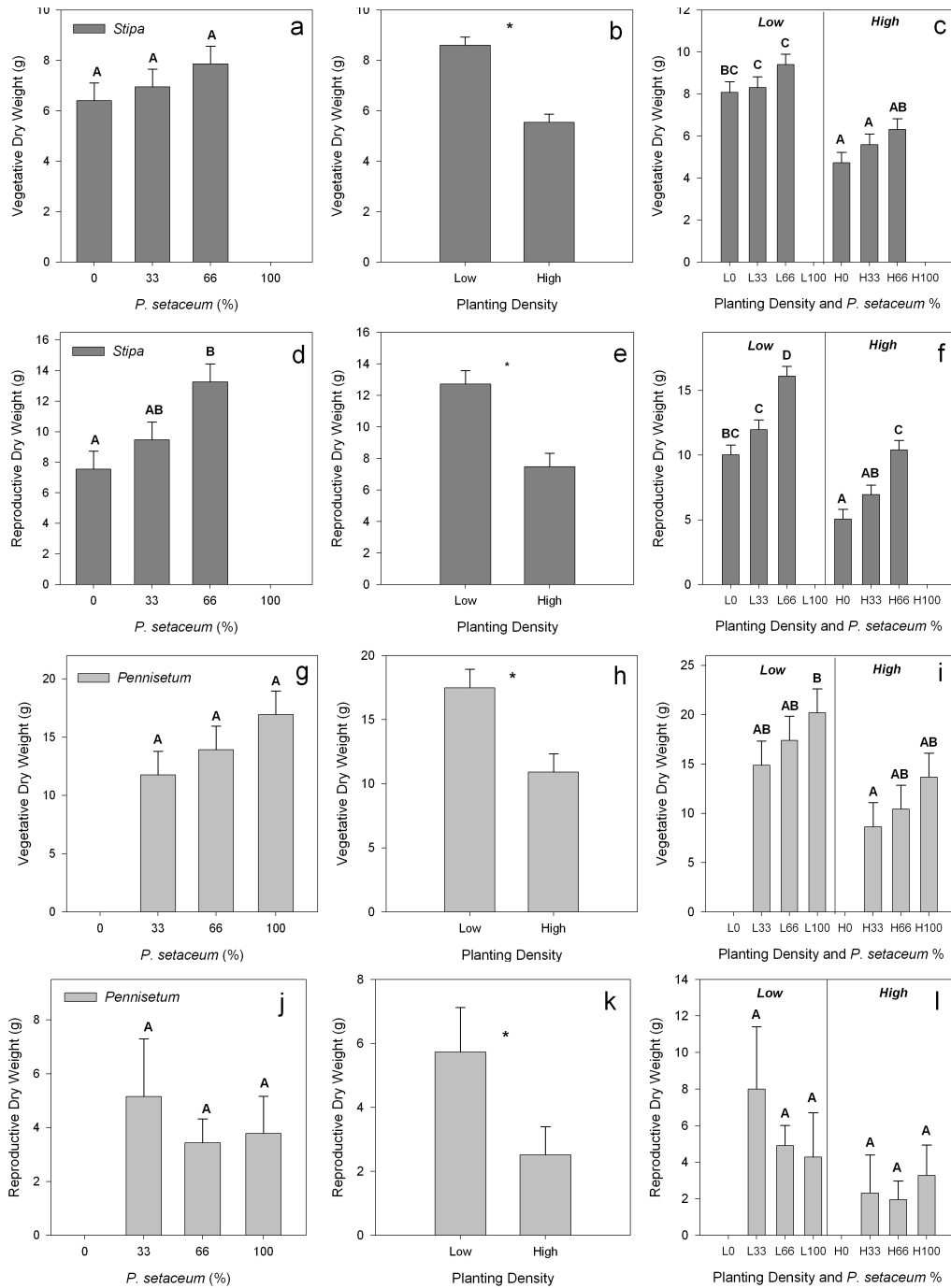
Figure 2.3. August mean dry weights per plant of vegetative **(a, b, c, g, h, i)** or reproductive **(d, e, f, j, k, l)** biomass in each treatment for *Pennisetum* and *Stipa* from ANOVA comparisons. *P. setaceum* densities are low, 9 plants m^2 and high, 25 plants m^2. Error bars are one Standard Error. Letters are from Tukey's HSD comparison of all possible combinations. Bars with different letters within a graph are significantly different at 0.05; *, P<0.05.

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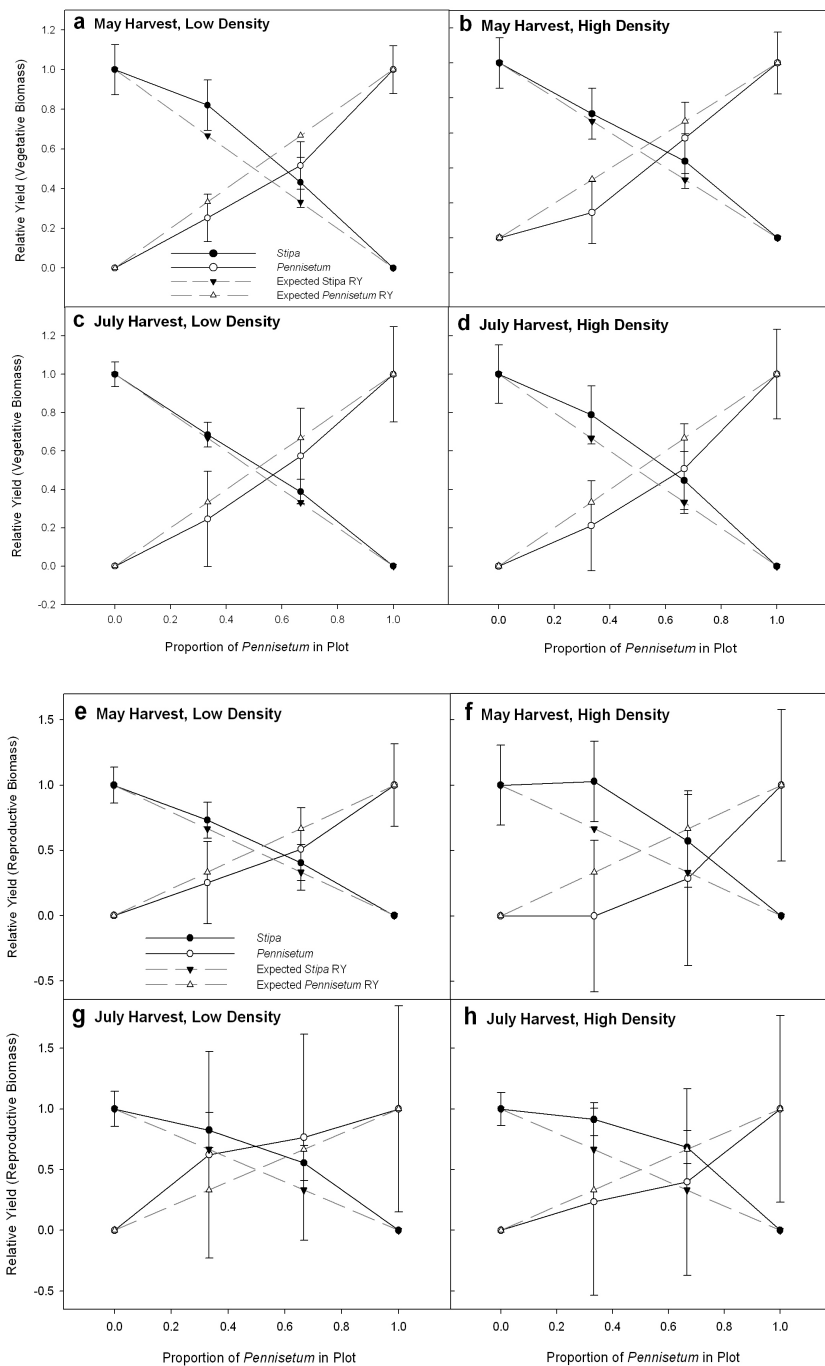
Figure 2.4. Relative above-ground vegetative (**a-d**) and reproductive (**e-h**) yield of *Pennisetum* and *Stipa* in competition in Low- ($9/m^2$) or High- ($25/m^2$) density plots, harvested in spring or summer (May or August). Relative Yield is dry biomass per species per plot relative to expected yields for that species grown in monoculture. Error bars are 95% confidence intervals from ANOVA.
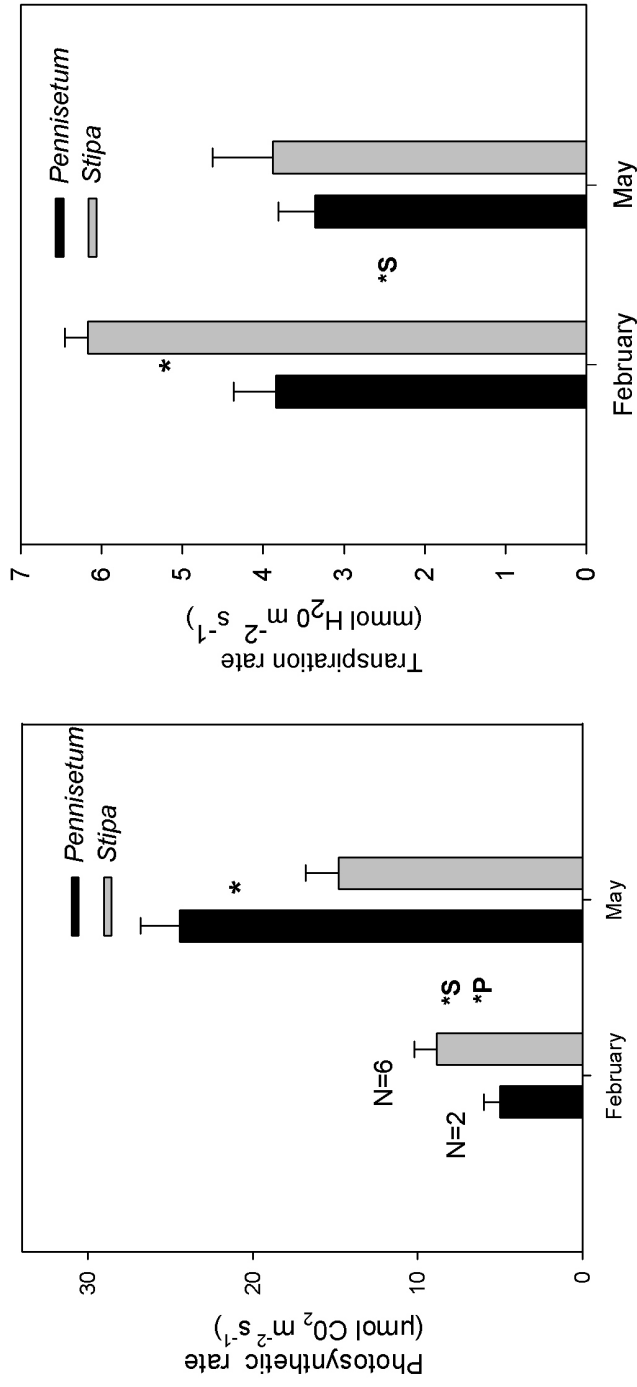
Figure 2.5. Photosynthetic variables measured in February and May on monospecific plots of *Pennisetum* and *Stipa*. * denotes significance (P<0.05) for the species comparison. *P and *S indicate a significant difference between monthly averages for *Pennisetum* and *Stipa*, respectively. Error rates reported are Mean Standard Error.
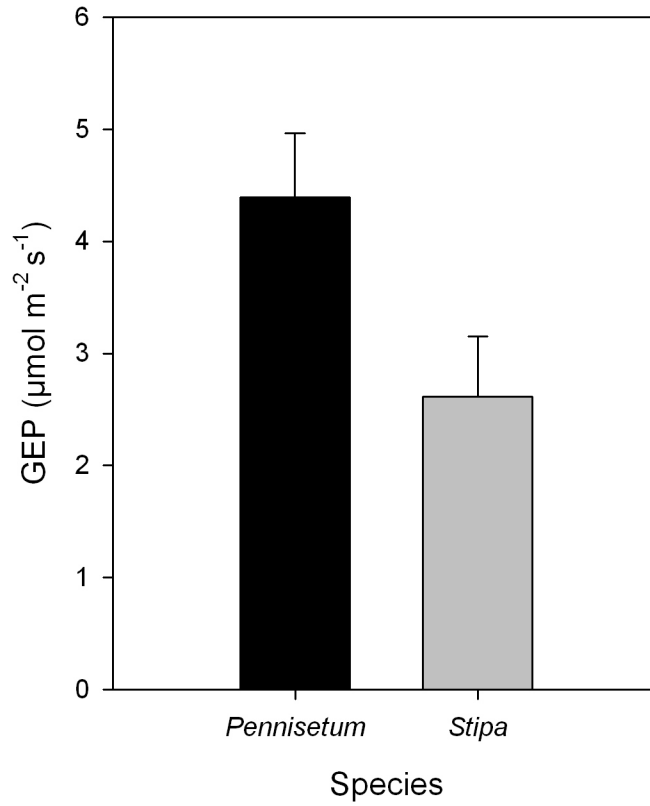
Figure 2.6. Gross Ecosystem Productivity (GEP) in July, measured over 1m^2, in *P. setaceum* and *S. pulchra* in monoculture plots.

Harvest Month	Species	Treatment	Variable	DF	ChiSquare	Sum of Squares	Mean Square	F Ratio	Prob>ChiSq	Prob > F
May	*Stipa*	Density	Vegetative Weight	1		20.6771	15.171853	15.171853		0.0002*
			Reproductive Weight	1		14.7361	148.55721	148.55721		0.0010*
		% *Pennisetum*	Vegetative Weight	2		2.7351	6.567726	3.28386		0.0891
			Reproductive Weight	2		3.5334	94.05926	47.0296		0.0485*
		Density and % *Pennisetum*	Vegetative Weight	5		7.5124	21.052593	4.21052		0.0007*
			Reproductive Weight	5		7.8404	251.28964	50.2579		0.0005*
	Pennisetum	Density	Vegetative Weight	1		87.42448	87.42448	14.55		0.0010*
			Reproductive Weight	1	13.099				0.0003*	
		% *Pennisetum*	Vegetative Weight	2		57.5787	28.7893	3.6903		0.0432*
			Reproductive Weight	2	2.0362					0.3613
		Density and % *Pennisetum*	Vegetative Weight	5		154.50354	30.9007	8.8884		0.0003*
			Reproductive Weight	5	15.819				0.0074*	
August	*Stipa*	Density	Vegetative Weight	1		43.7804	55.876017	55.876		<.0001*
			Reproductive Weight	1		18.5512	165.06015	165.0602		0.0004*
		% *Pennisetum*	Vegetative Weight	2		1.0879	8.6409	4.32045		0.3581
			Reproductive Weight	2		6.1012	134.98908	67.4945		0.0095*
		Density and % *Pennisetum*	Vegetative Weight	5		12.8113	64.92255	12.9845		<.0001*
			Reproductive Weight	5		27.0245	300.7297	60.1459		<.0001*
	Pennisetum	Density	Vegetative Weight	1		10.6197	259.91002	259.91		0.0036*
			Reproductive Weight	1	4.8154				0.0282*	
		% *Pennisetum*	Vegetative Weight	2		1.6497	108.39933	54.1997		0.2161
			Reproductive Weight	2	0.035					0.9826
		Density and % *Pennisetum*	Vegetative Weight	5		3.0919	368.8656	73.7731		0.0346*
			Reproductive Weight	5	6.2627				0.2815	

Table 2.1. Results of ANOVA and Kruskal-Wallis (non-parametric) tests on dry vegetative and reproductive biomass by harvest, species and treatment.

Chapter 3: "Impacts and Vegetative Correlates of *Pennisetum setaceum* in Coastal Sage Scrub"

Abstract

Establishment of invasive species in natural systems can lead to reductions in light and nutrients available to native species. Fountain grass (*Pennisetum setaceum*) is a perennial C_4 African bunchgrass that is invasive outside its native range and spreading in wildlands in Hawaii and the Southwestern U.S. This species is increasing in California, but little is known about potential impacts. A climate-matching model based on abiotic characteristics of the native range showed that several habitats in California are suitable for *P. setaceum* establishment, including coastal sage scrub, a Mediterranean system containing no functional analogue to this exotic bunchgrass. In order to determine the correlates and impact of *P. setaceum* invasion on native communities, coastal sage scrub sites in two regions in Southern California were analyzed during two growing seasons (2009 and 2010) for cover of native and exotic species, using replicated plots containing four cover classes of *P. setaceum*. Relationships between *P. setaceum* invasion and native species richness were investigated in a third region, Riverside County, where *P. setaceum* largely occurred on rock outcrops, and this data was analyzed separately from the other two regions. Soil samples from low- and high-cover areas of *P. setaceum* were analyzed for nutrients. Significant reductions in native species cover were found with increased *P. setaceum* cover in both years in Santa Monica Mountains (SAMO) sites and in 2010 in San Diego sites. Native species richness decreased with increasing *P.*

setaceum cover in both years in SAMO sites but not in San Diego sites. However, rarefaction-based analysis of beta-diversity by treatment showed smaller differences between invasion cover classes than expected. In Riverside County, trends were seen in the opposite direction; increases in diversity were measured on outcrops where *P. setaceum* was most prevalent. Soil samples from high *P. setaceum* cover areas showed higher nitrate, percent water content and potassium in both regions in 2010 as compared to low cover areas. Principal components analysis (PCA) of abiotic variables associated with San Diego and SAMO sites showed a significant separation by region; SAMO sites were characterized by less surface area covered by rock, but rockier and drier soil, older fires, lower soil phosphorous, and differences in geographic aspect. These site differences, particularly in water content, may indicate a limiting resource that could change or mitigate the impact of *P. setaceum* on native species, and should be investigated further. Continued monitoring, larger-scale assessments of beta diversity, and follow up studies of nitrogen cycling at these sites, as well as experimental removal, addition, or recruitment studies would shed further light on the degree to which *P. setaceum* is impacting these communities.

Introduction

Debates about the impacts of invasive species on threatened and endangered species (Wilcove et al. 1998) and methods of predicting, categorizing and measuring impacts of invasive species have been increasing in the literature in the past 20 years (D'Antonio and Vitousek 1992, Vitousek et al. 1996, Gordon 1998, Parker et al. 1999,

Levine et al. 2003, Cleland 2011). There has also been recent discussion focus on the

need to base conservation decisions on evidence of adverse impact of a species rather

than whether the species is native or exotic (Brown and Sax 2005, Davis et al. 2011,

Simberloff and Signatories 2011). At the same time, many assumptions about the

impacts of invasive species on native communities have been questioned or tested,

including assumptions about the relationship of "invasiveness" and impact (Ricciardi and

Cohen 2007) and the past and future impacts of invasive plants on threatened and

endangered species (Davis 2003, Gurevitch and Padilla 2004). The need for

prioritization in invasive species management has led to an increase in demand for

information about the specific impacts of invasive species, and much recent research has

focused on documenting these impacts. Weed risk assessment schemes such as the

Australian (Pheloung et al. 1999) and California Invasive Plant Council Plant Assessment

form (Warner 2003) and others (Daehler et al. 2004, Darin et al. 2011) require

documentation of impacts, among other factors, for evaluation of risk. Heretofore, some

of this information has been anecdotal and based on expert opinion (Gurevitch and

Padilla 2004). As the published record is arguably the most vetted source of information,

the documentation of impacts, or the lack thereof (Levine et al. 2004), should be a goal of

applied literature.

Invasive plants are known to impact native systems through several mechanisms.

Early establishment by invaders can lead to preemption of space, specifically reductions

in light and nutrients available to native species. Mechanisms of interference involving

disproportionate resource acquisition may also impact native species (Radosevich et al.

2007). These mechanisms may be evidenced by changes in species cover and richness (Gordon 1998, Ehrenfeld 2003, Heneghan et al. 2006). Invasive species may also cause ecosystem-level effects on whole-system properties such as nutrient cycling, disturbance regime, and temporal variations in each of these processes (*sensu* D'Antonio and Vitousek 1992).

Purple fountain grass (*Pennisetum setaceum* [Forssk] Chiov.) is a perennial C_4 African grass that has spread aggressively in Hawaii (Goergen and Daehler 2002) and it is also increasingly problematic in the Southwestern U.S., where it was introduced as a drought-tolerant ornamental (Williams et al. 1995). *P. setaceum* invades dry landscapes and has been shown in Hawaii to alter fire cycles and microhabitats, facilitating a conversion from dry forest to grassland (Blackmore and Vitousek 2000). While *P. setaceum* is increasing in California, its impacts on local communities have not been determined.

The coastal sage scrub ecosystem in California is increasingly threatened by invasive species and other anthropogenic impacts (Fenn et al. 2010), and contains no species of the same functional type as *P. setaceum* (Kirkpatrick and Hutchinson 1977). Native functional types comprising this Mediterranean habitat type are drought-tolerant or drought-deciduous perennial shrubs, annual forbs, and occasional C_3 bunchgrasses. One C_4 grass occurs more commonly- the small annual grass species, *Muhlenbergia microsperma*. CAM species present include *Hesperoyucca whipplei* and *Dudleya* spp. Exotic functional types now occurring there include exotic annual C_3 grasses, several

annual exotic mustards, and several species of exotic *Erodium* species. Growth of most species is highest during the cool, wet winter months into spring.

P. setaceum, a C_4 bunchgrass, has shown a broad range of temperature tolerance and plasticity in phenology and growth, but was shown to have higher relative growth rates and biomass production in warmer temperatures (33/25°C (day/night) versus 25/13°C (day/night), controlled temperature environments) (Williams and Black 1993). Dissimilarity to native species may be conducive to invasion (Abrams 1983, Funk et al. 2008, Cleland 2011) and certain functional differences have been thought to increase the possibility of ecosystem-level impacts (Chapin 1996, Ehrenfeld 2003). Noting the differences between *P. setaceum* and the recipient native community in terms of physical structure, phenology, and photosynthetic pathway, changes or impacts on the native community at high cover levels of *P. setaceum* would be expected.

Many studies have used observed differences between invaded and uninvaded areas to infer effects on soil or plant communities due to invasion (Heneghan et. al. 2006, Vila et. al 2006, Maltez-Mouro et. al 2010, and many older studies reviewed by Parker et al. 1999). Several studies have incorporated observational and experimental approaches (Pickart et al. 1998, Truscott et al. 2008), although disturbance caused by plant removal may be confounding in experimental methods using removal (D'Antonio et al. 1998). Where study sites are located in ecologically-sensitive and protected areas it may be difficult to obtain permission for experimental addition of invasive species to a native community, or even physical removal of invasive species (due to resultant disturbance).

Brewer (2008) and Scott et al. (2010) employed longer-term approaches measuring both vegetation and changes in abiotic factors over several years. This method allows the documentation of the invasion process as it occurs and therefore reveals a more direct relationship between factors than in a short-term correlative study. Vila et al. (2006) as well as Alvarez and Cushman (2002) replicated observational experiments in multiple communities or habitats. This study design provides an opportunity to determine whether invasion impacts were consistent across community types and what factors might be responsible for changes in this relationship.

Due to the paucity of information concerning the ecology of *P. setaceum* in California and history of impacts elsewhere, I sought to answer several questions: do significant levels of native species co-occur with *P. setaceum* in these areas and therefore place them at-risk, what physical and geographic factors are correlated with *P. setaceum* invasion, and finally, is *P. setaceum* causing impacts to coastal sage scrub communities either in terms of species richness or diversity or by altering availability of water or nutrients in the soil? Similar to Alvarez and Cushman (2002), the study was conducted in several regions in order to investigate whether results are consistent across communities. In the research reported here, planting or removal of *P. setaceum* were not feasible; instead, vegetation surveys were carried out for two seasons in three different regions, and data at each site were collected along a gradient of invasion using a space-for-time substitution.

Materials and Methods

Study Sites

Field sites in three regions of southern California containing significant *P. setaceum* populations were sampled in the spring of 2009 and 2010, to coincide with peak biomass of many species (see map, Appendix 3). Populations in wildlands were selected that comprised areas greater than 10m in diameter and not located within cleared/scraped or highly-disturbed land or cut-slopes immediately adjacent to roads. No further criteria were used to exclude sites. Populations were sampled in the regions of northwest Los Angeles County (Point Mugu State Park, Malibu Creek State Park, and Mulholland Canyon Drive, all within Santa Monica National Recreation Area, a region collectively referred to here as "SAMO"), eastern San Diego County (San Diego National Wildlife Refuge (SDNWR) and Rios Canyon and Flinn Springs areas within Crestridge Ecological Reserve, referred to as "San Diego"), and Riverside County (Mt. Rubidoux City Park, Sycamore Canyon Ecological Reserve and Lake Perris State Recreation Area (2010 only), referred to as "Riverside"). At each site in 2009, aspect and slope were measured as well as the condition of the slope (rocky slope or outcrop, eroding soil or rocks) and the shortest distance from the invaded area to a trail or road. Surveys were repeated at the same locations in 2010 with one exception; in 2010, a site at San Miguel Mountain was substituted for the Campo Road site within SDNWR.

San Diego and SAMO sites were similar in overall vegetation and the same protocol was used for measurements at these sites (Figure 3.1). Riverside County sites were primarily rock outcrops, and an alternate measurement protocol was used at these

sites, as described below. In both San Diego and SAMO, transects of variable lengths (a minimum of 10 meters) were established at each site, each perpendicular to the direction of the slope (level across and along the hillside). All sites had 3 transects except for San Miguel Mountain in San Diego in 2010, which had 2 transects due to the small size and patchy distribution of *P. setaceum* at that location. Obvious areas of difference (such as washes or variations in aspect/direction) were excluded from transect sampling. Along each transect, which was run from at least 2m beyond the visible invasion boundary, line-intercept information was recorded for *P. setaceum* only, allowing a baseline of cover to be established over the entire transect. Point-intercept data were also taken at 2-meter intervals for all species along the entire transect. Soil samples were collected using a 10cm auger in high- and low-cover areas of each transect (2 areas on each transect, minimum of 100g per sample).

Study Design and Measurements

In order to document cover and richness of native and exotic species present in different levels of *P. setaceum* cover, eight 0.5x1.0 meter plots were established along each transect. Plots were located using a stratified random sampling method along the transect to ensure that a full range of cover of *P. setaceum* was represented. The four cover classes of *P. setaceum* were 0, 1-33, 34-66 and 67-100 percent. Plots were located either above or below the transect line, arranged with the half-meter side touching the transect tape (Figure 3.1). Cover for all plant species was visually estimated for each plot, as well as bare ground, rock, and litter. Total cover summed to >100% in areas with overlapping canopies of vegetation.

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In Riverside County, rocky outcrops were the only areas invaded by *P. setaceum*. Therefore, a modified design was used since overall cover of all species was low and vegetation was limited to spotty microsites. In 2009, 5 outcrops were surveyed at two sites; in 2010, 7 outcrops were surveyed at 3 sites. At each site, one uninvaded outcrop was included for comparison. On each outcrop, line-intercept information was recorded for all species on two random-direction diagonal axes. For the entire outcrop, number of *P. setaceum* plants present and species richness data were recorded for the continuous area (outcrops of various sizes, transect lengths similar to SAMO and SD; see Table 3.1).

For each outcrop, an invasion index was calculated as follows: *P. setaceum*/m^2 (number of total *P. setaceum* plants on the outcrop divided by the area of an ellipse, calculated using the two diagonal outcrop measurements as the major and minor axes) divided by the fracture rate found on the two axes (number of fractures found on axes 1 and 2 divided by the sum of lengths of axes 1 and 2) (Table 3.1). Fractures are defined as gaps in the rock where vegetation occurs (potential safe sites).

Analysis of Soils

In 2009, soils were air-dried and weighed. Soil was homogenized using a coffee grinder and passed through a 2 mm sieve. Percentage of rock by weight was determined by weighing the remaining particles of rock greater than the size of the screen and dividing this by the weight of the whole sample. In 2010, soils were weighed fresh and dried to obtain percent content of water by weight; fraction of rock was also determined as above. In both years, dried and ground soils were sent to University of California Davis Analytical Lab (http://anlab.ucdavis.edu/) and analyzed for soil fertility (KCl-

extractable NO_3-and NH_4, Olsen-P, extractable-K). For measurement of pH, a 1:1 volume solution of deionized water and soil was prepared, inverted and allowed to settle. The clear solution from each sample was tested at room temperature in a random order using an Accumet© Research AR15 pH meter (Fisher Scientific) and an Accumet© Phast 13 electrode. Twenty percent of solutions were retested to ensure accuracy of the measurements (all were within +/-0.1).

Statistical Methods

Data from SAMO and San Diego sites were analyzed separately using the same method in the JMP statistical package (Copyright © 2011 SAS Institute Inc., SAS Campus Drive, Building S, Cary, NC, 27513). Data from Riverside County outcrops were analyzed separately as described below. For statistical significance, alpha ≤ 0.05 was used, except for the analysis of soils.

Analysis of cover data was performed two ways: cover classes were compared as categories using Analysis of Variance, and measured variables were regressed against continuous percent cover of *P. setaceum*. Data for each cover class (two 0.5x1.0m plots) on each transect were averaged to yield 3 averaged samples per treatment per site. In ANOVA, sites were used as blocks within each region, and transects were treated as replications. Normality was assessed using the Shapiro-Wilke Test for Normality. In Results, p-values reported for ANOVA results are probability overall >F and for non-normal data the non-parametric test results are reported as prob>ChiSquare for the one-way test. Means comparison were done using a post-hoc Tukey's HSD test.

In order to compare alpha diversity (within-site) richness, a sample-based rarefaction method was used to smooth the species accumulation curve, providing the Mau Tau interpolated value for observed species (Colwell et al. 2004). Using the plot data from each site, rarefaction curves for each separate cover class, site, and year, with variance and confidence intervals, were computed using EstimateS (Version 8.2, R. K. Colwell, http://purl.oclc.org/estimates). This method was also used to examine trends in beta diversity by combining same-year data for all three sites for each of the two regions.

Due to the heterogeneous and sparse nature of vegetation patterns and overall cover, respectively, on the outcrops containing *P. setaceum* in Riverside County, rarefaction was the only method used to examine differences in invaded and uninvaded outcrops. On each outcrop, each sample was comprised of the vegetation occurring in a single rock fracture. All species (native and exotic) were used for this comparison, as native species richness was very low and could not be compared among treatments or sites using this method.

Another comparison of richness was performed using total richness per site per treatment. A comparison of total native species richness summed for 4 plots (a single value for 2 m^2 area) for each treatment (because every site had at least 4 plots per treatment) and each site was performed using ANOVA. The analysis was performed separately for each region and year, with sites treated as blocks (n=3 sites/reps per treatment).

Soil analysis results in the high- and low-cover areas were compared. First the San Diego and SAMO sites were analyzed separately, and then all sites were grouped

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together for analysis (to increase the sample size). Results were tested for normality

using the Shapiro-Wilke test, and for homogeneity of variances using the two-sided F-

test. Soil analysis results were analyzed using a matched-pairs *t*-test for each variable,

matching the high- and low-cover samples on each transect for comparison. For non-

normal variables and/or unequal variance, the Wilcoxon signed-rank test was used to

assess significance using prob>|Z| and the direction of difference.

To investigate abiotic differences between sites in the two regions, a multivariate

analysis was run in JMP using an averaged value for variables for each high- and low-

cover class area in each site. For plot variables, 2010 plot data from cover classes 1 and 2

were averaged for the "low" value and data from cover classes 3 and 4 were averaged for

the "high" data values. Sites were thus represented by two data points for the following

soil, geographic and plot variables: monthly average precipitation (from

http://www.worldclim.com/current); years since fire (one value per site, California

Department of Forestry and Fire Protection, accessed 10/20/10, available at

http://frap.cdf.ca.gov/data/frapgisdata/download.asp?rec=fire); Northness (cos(aspect));

Eastness (sin(aspect)); percentage of water by weight in the soil samples; soil rockiness

(percentage of rock by weight in soil samples); ammonium; nitrate; phosphorous;

potassium; percent bare ground in plots; percent cover of rock in pots; and percent cover

of litter in plots. A Principal Components Analysis was run using all variables (using the

varimax rotation to maximize the variance of the loadings); however, the analysis

presented here excludes monthly average precipitation, because the dominance of these

variables interfered with the ability to discern relationships among the other variables.

After PCA, values for Factor 2 (y axis) for each site were checked for normality and equality of variances as described above and used to perform a two-tailed *t*-test to check for a significant difference between the regions. Additionally, discriminant analysis of single variables was performed using all variables (including monthly average precipitation) in order to determine which variables are best able to differentiate between the two groups.

Results

Overall, the vegetation and soil characteristics measured using plots and transects differed between San Diego and Santa Monica Mountains regions and two study years. Results for the sample-based study of invaded outcrops in Riverside County are presented separately under *Rarefaction*. In ANOVA comparisons of means, greater differences between vegetation cover classes were found in Santa Monica Mountains (SAMO) sites in comparison to San Diego sites (Figures 3.2 and 3.3). Greater differences between vegetation cover classes were found in 2010 than in 2009. The magnitude of differences in soil characteristics in high- and low-cover areas also varied by region and by year. Overall cover of exotic species (excluding *P. setaceum*) in uninvaded control plots was consistently higher in San Diego than in SAMO in both years (32% vs. 18% and 40% vs. 19% in 2009 and 2010, respectively) (Figure 3.2). Details of the ANOVA and non-parametric tests are in Table 3.2.

Cover

In both regions and both years, the cover of exotic species (excluding *P. setaceum*) was greater in the uninvaded control plot than the highest cover class but did not differ not among the three cover classes that contained *P. setaceum* (Figure 3.2). Native cover in San Diego sites was greater in the uninvaded than in the highest cover class (as above) in 2010 only. In SAMO, native cover declined in both years from the lowest *P. setaceum* cover category to the highest, with a larger decline in 2010 (Figure 3.2).

In regression results by functional group, San Diego and SAMO results also differed (Table 3.3). Exotic grass (excluding *P. setaceum*) was not correlated with *P. setaceum* cover in any year or in either region (data not shown). Exotic forb cover (all annual species) was negatively correlated with *P. setaceum* cover only in SAMO in 2010. Total exotic annual (grasses and forbs) species cover was negatively correlated with *P. setaceum* cover in San Diego in both years and in SAMO in 2010 (Table 3.3). Overall cover, including exotic and native plants, increased significantly with increasing *P. setaceum* cover.

Native grasses and forbs were negatively correlated with *P. setaceum* cover in 2009 in both regions, and similar trends were observed in SAMO in 2010 (p=0.052 and p=0.077 respectively) (Table 3.3). A decrease in native annual species was correlated with *P. setaceum* cover in both regions in 2009. In SAMO in 2009, decreases in annual forbs and annual grass were also measured. Native perennial functional groups were also impacted by *P. setaceum* cover; perennial grass in 2009 in SAMO and perennial forbs in San Diego in 2009 both declined in the presence of *P. setaceum* (Table 3.3).

Richness

In ANOVA comparisons for San Diego, the only differences in species richness were found in 2010, where exotic species richness decreased from an average of 3.92 species in uninvaded plots to an average of 2.33 species in high *P. setaceum* cover plots (Figure 3.3). No differences in native richness were detected between cover classes. In SAMO, exotic species richness also declined in 2010 only, where the high cover plots had lower species richness than the uninvaded and lowest cover categories (Figure 3.3). Total native richness declined from the lowest to the highest *P. setaceum* cover classes in 2009, but the uninvaded control did not differ from any of the cover classes. In 2010, the uninvaded control had higher native richness than the two highest cover classes. Total richness was lower in the highest cover class than in the lowest cover class in both years.

The richness of exotic and native functional groups was impacted by increasing *P. setaceum* cover in SAMO; however, no impacts were found in San Diego in either year when regression analysis was used (Table 3.3). Total exotic richness, exotic annual forb richness, and total exotic annual richness were negatively correlated with *P. setaceum* cover in 2010 in SAMO. Total native richness decreased in both years in SAMO sites as did total species richness, while in San Diego total species richness showed a decreasing trend (p=0.053) in 2009 with increasing *P. setaceum* cover. Native grass richness decreased in SAMO in both years; a decline in native forb richness was near-significant in 2009 (p=0.055) and highly significant in 2010 (p<0.01). Other lower values for native species and functional groups were correlated with *P. setaceum* cover in the SAMO sites,

including annual grass richness in 2010, total annual richness in 2009, and perennial grass richness in 2009 (Table 3.3).

Species Richness per Treatment

A representation of percentage of total species richness contributed by each functional group, excluding *P. setaceum,* shows a preponderance of native forbs in both regions and years (Figure 3.4). Analysis of native species richness per treatment, summed per site, where San Diego and SAMO data were analyzed separately and sites were treated as replicates for both study years, suggests a trend of decreasing richness with *P. setaceum* cover, but no significant differences were found between treatments, which may be due to low statistical power (Figure 3.5). Interestingly, the data suggests a slight increasing richness trend in San Diego sites, in both years, in the medium-cover treatment (34-66% *P. setaceum*) over the low-cover (1-33%) treatment (Figure 3.5).

Rarefaction Species Curves

Results of sample-based species rarefaction analysis of species richness, showing 95% confidence intervals for the curves, revealed few curves that differed statistically from one another between cover classes (Figures 3.6, 3.7). However, some general trends were revealed by this analysis. The species richness rarefaction curves for cover classes 1 and 2 (0 and 1-33% *P. setaceum* cover, respectively) were initially steeper than for cover classes 3 and 4 (34-66% and 67-100% *P. setaceum* cover, respectively) in most graphs. In the pooled regional graphs for SAMO, cover class 2 showed the steepest curve among the cover classes in both years, while in San Diego County sites, cover class 1 showed the steepest curve (Figure 3.6). In rarefaction analyses conducted by site

within a region, the observed species richness curve for plots in the highest cover class of *P. setaceum*, cover class 4, were the only curves that differed from the other cover classes. The curve for cover class 4 was statistically flatter and lower than the following curves: cover class 2 in Mugu (in SAMO) in 2009, cover classes 1 and 2 in Rios Canyon (in SD) in 2009, and cover class 1 in Mulholland Canyon (in SAMO) in 2010 (Figure 3.7). Similarly, in the pooled regional analysis the overall curve for cover class 4 in SAMO sites was lower than that for cover class 2 (Figure 3.6). The rarefaction results for Riverside County did not reveal any differences in sample-based richness for any of the outcrops, though it should be noted that outcrops with higher invasion indices tended to have higher species richness (Figure 3.8).

Soil Characteristics

Soil characteristics varied with *P. setaceum* cover in both years (Figure 3.9). Variance was high in several soil nutrients, likely due to spatial heterogeneity in their distribution, and a priori knowledge from a power analysis would have been informative in decisions regarding sample size (Table 3.4) (Klironomos et al. 1999). Therefore, differences may be considered probable where $p > 0.10$ for these exploratory tests, acknowledging the insufficient sample size for the variance present. Nitrate-nitrogen was higher in high-cover areas vs. low-cover areas in 2010 in San Diego sites in paired *t*-test analysis and with both regions combined in paired *t*-test comparisons (comparison not shown, $p = 0.031$) (Table 3.4). Potassium was higher in high-cover areas in 2010 in SAMO sites and also with both regions combined in (comparison not shown, p=0.047). Percent water content, assessed only in 2010, was higher in high-cover areas in San Diego sites

and in SAMO sites. In 2009, in San Diego, pH was lower in the high-cover areas and in paired tests with regions combined (comparison not shown, p=0.027). Phosphorous showed a possible increase in San Diego in 2009. High- and low-cover areas did not differ in any analysis group in percent rock by weight or ammonium-nitrogen (Figure 3.9, Table 3.4).

Analysis of Regional Differences and Correlates

A look at average values for the abiotic correlates measured shows some microhabitat and nutrient ranges for microsites occupied by *P. setaceum* (Table 3.5). All sites had burned in the last 50 years, averaging approximately 15-25 years for both regions. A south or southwest-facing aspect was associated with all populations. Sites were characterized by high rockiness of the soil and averaged 8-15% surface cover of rock (Table 3.5).

The principal components analysis of abiotic site variables revealed differences among two regions in this study, SAMO and San Diego, and the loading and score plots show a graphical representation of the characteristics of each site with respect to these variables (Figure 3.10). Percent water content ("%WC"), nitrate ("NO3-N"), phosphorous ("Olsen-P"), potassium ("X-K") and percent cover of rock ("Rock") were all correlated positively with Factor 2 (Table 3.6). Years since fire ("Yrs_since_fire"), northness, soil rockiness ("%_Rock_by_Wgt") and percent cover of bare ground were all negatively correlated with this axis.   Litter as a variable was minimized by the varimax rotation with either axis.

Values of Factor 2 differed between the San Diego and SAMO regions (p=0.014) (Table 3.6). As indicated by lower values on Factor 2, SAMO sites had experienced

older fires, were lower in nitrate and potassium, and had more rocky soil and lower soil water content, and surface rock. By contrast, San Diego sites had higher Factor 2 values and were more recently burned, and had less-rocky soil and higher water content, phosphorous, potassium and surface rock (Table 3.5, 3.6)..

Discriminant analysis performed on the same dataset (and, in addition, monthly precipitation data) showed that several variables were able to discriminate between groups, including percent water content and percent content of rock in the soil (by weight), and December, January and February precipitation values (Table 3.7). Near-significant discrimination was found for years-since-fire, potassium, and percent cover of rock in plots.

Discussion

This study investigated the invasion of *P. setaceum*, an exotic perennial C_4 grass, in California's coastal sage scrub (CSS) habitat. Several different impacts of *P. setaceum* on biotic and abiotic components of CSS were found. These impacts of *P. setaceum* presence were found at the species, community, and ecosystem levels. Although further study is required to attribute causation, ecophysiological and functional differences between *P. setaceum* and other species occurring at the study sites may help explain these impacts.

Invasive plants may alter native plant community composition and or ecosystem processes via several mechanisms (D'Antonio and Vitousek 1992). If the exotic plant outcompetes all native species, similar decreases in richness and cover of all species at

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the plot level would be expected (Parker et al. 1999). If the exotic plant alters vegetation structure, changes "safe sites" (sites amenable to recruitment) available to native species, or alters availability of resources such as light and nutrients, differential effects on different functional groups would be expected. Ecosystem-level impacts, such as alteration of erosion, water table level, nutrient cycling rates or disturbance regimes may also differentially impact certain functional groups (Gordon 1998).

Species Level Impacts

P. setaceum occurred at up to 100% cover at the study sites. Overall, decreases in cover of other species were common at high *P. setaceum* cover, although community cover values were highly variable. Total exotic cover was lower in higher *P. setaceum* cover classes, and native cover declined with increasing *P. setaceum* cover in all region-year analyses. Overall negative correlations of resident native and exotic species with *P. setaceum* cover suggest that competition is occurring. However, a large amount of between-year variation in cover and richness was observed, likely due to inter-year climatic variability influences on plant germination and growth, especially for the many annual species present. Thus, ecosystem level differences between invasion sites might mask species level competition impacts in this system.

One goal of this study was to document co-occurring species in order to discover which species may be at-risk due to invasion of *P. setaceum*. As many of the plants at these sites, especially the rare plants, were occasional species, it was not possible to document species-specific responses or correlations. However, two rare plants were seen growing within invaded areas (*Ceanothus cyaneus*, California Native Plant Society Rare

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plant rank 1B.2; *Viguiera laciniata* CNPS Rare plant rank 4.2) (CNPS 2011), and thus, special attention and monitoring should be carried out to ensure that these populations do not decline.

Other studies have shown that the competitive success of a C_4 grass in a Mediterranean ecosystem is not necessarily predicted by biology (Keeley and Rundel 2003). Results of correlates of *P. setaceum* occurrence indicated that this exotic grass tends to occur primarily on southwest-facing slopes in CSS (the 95% confidence interval includes 167.68-196.17° azimuth). Vegetation on this aspect is sparse and these habitats may offer a low-competition environment. These steep slopes may also provide a mechanism for open site generation through erosion. *P. setaceum* was also present in burned areas, though the correlation with burn frequency or age was not the focus of this study. Since tolerance or affinity for fire by *P. setaceum* has been documented elsewhere (Cuddihy 1990), it is likely that *P. setaceum* is also fire-tolerant in southern California. Further investigation, including competition experiments, would be necessary to explain the success of *P. setaceum* in these habitats and evaluate the role of competition in invasion by this species.

Community Level Impacts

In this study, differential responses to *P. setaceum* cover were demonstrated by different functional groups. For example, cover of exotic annual grasses did not decrease as a function of *P. setaceum* cover, while perennial native grass and native forbs decreased in SAMO. *P. setaceum* has several life-history traits that may cause impacts on native community structure, including C_4 metabolism, a bunchgrass habit, perennial

life history, and unusual (for a C_4 species) tolerance to cold temperatures as evidenced by a broad altitudinal range (Winter et al. 1976, Rundel 1980). Grassland invasion by a bunchgrass, where it is a novel functional type in that ecosystem, with different nutrient use efficiency (NUE) and tissue chemistry, has been shown to alter several factors including net primary productivity (NPP) and soil nutrient availability and heterogeneity (Reed 2005). *P. setaceum* may have different resource efficiency rates from co-occurring native species in the sites studied here due to its C_4 biology, which is typically associated with higher NUE and water use efficiency (WUE) (Baruch et al. 1985, Mantlana et al. 2008). Such changes in resource use may constitute a community-level effect of invasive plants (Gordon 1998). In fact, resource-use efficient functional types may have an advantage in low-resource systems (Funk and Vitousek 2007). In contrast with a competition model (*sensu* Tilman 1980), several measures of resources showed increased availability of nutrients in high-*P. setaceum* plots in this study.

Increased nitrogen availability found in some cases in the soil nutrient analysis in high-*P. setaceum* cover plots could be due to greater NUE, or carbon gain per unit nitrogen (Swift 1979), and this may differentially affect the functional groups present. Differences in nitrogen in the soil or nitrogen cycling have been seen in areas invaded by a C_4 grass in Hawaii (Asner and Beatty 1996, Mack et al. 2001), and between C_4 and C_3-dominated grassland plots on the mainland U.S. (Tilman et al. 1997). These results may also be caused by feedback from litter content (Facelli and Pickett 1991). Although not measured in *P. setaceum* here, a higher C:N ratio is typical of C_4 plants (Murphy et al. 2002), resulting in low-quality litter, perhaps resulting in nitrogen immobilization.

Increased availability of water in soil from invaded plots, as seen by increased percent water content in soil samples in 2010, could be due to higher WUE of the C_4 *P. setaceum*, at least as far as generally lower transpiration rates of C_4 species may be related to amount of water drawn from the soil. Higher water content in invaded areas could also be due to increased shading of the soil by *P. setaceum*. Although shading was not measured directly as part of the analysis, total vegetation cover (as a proxy for shading) increased as a function of percent cover of *P. setaceum*. In fact, shading has been invoked as a possible alternative explanation for changes in nitrogen cycling seen in other cases (Levine et al. 2003). Additional experiments are needed to understand the relationship of these potentially confounding factors.

Results of this study revealed some changes in species richness and beta diversity with increasing *P. setaceum* cover. However, the changes were possibly less than would be expected due to the difference in functional group, life history, and physiognomic form. This suggests that *P. setaceum* might alter safe site characteristics for native species, which could subsequently alter community composition. Although not measured, a change in community vertical structure by *P. setaceum* could alter light availability at the soil surface, air current patterns, and shading of the soil surface (lower evapotranspiration and temperature), thereby changing the microclimate for germinating annual species (D'Antonio and Vitousek 1992).

If the changes in resource availability (e.g. nitrogen, water, phosphorous), or factors affecting resource availability (such as pH) seen in high-cover areas are caused by *P. setaceum*, functional groups would be expected to be impacted differently (Mueller-

Dombois and Whiteaker 1990). In fact differential impacts on functional groups were observed in this study. For example, the cover of exotic grasses, including *Bromus madritensis* ssp. *rubens*, shown to be an N-responsive grass in a fertilization study (Rao and Allen 2010), was not correlated with *P. setaceum* increase at any site, whereas native annual grass cover was negatively correlated with increased *P. setaceum* cover. Correlation of changes in soil characteristics and cover and richness of functional groups with *P. setaceum* suggest that invasion by *P. setaceum* into native habitats may be having community-level effects.

Where changes in species richness at the plot level were seen, rarefaction-based estimates of site diversity investigated whether there were changes in beta diversity with *P. setaceum* cover rather than simply smaller numbers of native species per plot. Although graphs from individual SAMO and San Diego sites showed a change in beta diversity for the highest cover class, species turnover within the cover classes within region was only slightly different in the highest *P. setaceum* cover class. However, the size of the error bars paired with the consistency with which the high-cover plots showed flatter curves in each site and region suggests that an increase in sampling effort may help elucidate any changes in diversity.

In Riverside County, species and community-level impacts could not be easily determined, and thus, impacts had to be detected at the level of beta diversity using rarefaction analysis. Rocky outcrops are much different in physical structure and properties than other habitats (Steers 2010), and therefore, analysis of the impacts of fountain grass on these communities is limited by these constraints. The results of

rarefaction analysis, by contrast to the SAMO and San Diego results, surprisingly suggest an increase in diversity in highly-invaded outcrops. Since these invasions are of unknown age, observed impacts may differ by site (Vila et al. 2006).

Ecosystem Level Impacts

No other perennial C_4 bunchgrass was found to co-occur at any of these study sites. It has been proposed that invaders that are more dissimilar to native species may be more likely to alter ecosystem-level properties (Chapin 1996, Callaway and Aschehoug 2000), or have greater impacts (Brewer 2008). However, published reports disagree about whether qualitative traits (such as the C_4 photosynthetic pathway) are more likely to alter these properties than qualitative traits (e.g., photosynthetic pathway and N-fixing species) (Ehrenfeld 2003). Photosynthetic pathway differences were invoked by Vitousek (Vitousek 1990) as a possible mechanism of ecosystem-level impacts of invasive species. As described above, the C_4 pathway of *P. setaceum* may change nitrogen availability to other plants; however, there is no evidence that the nitrogen cycling or other system-level processes are altered by *P. setaceum* at these study sites. Ecosystem-level change due to invasion changes in nitrogen availability in a resource poor environment is one of the first and best-documented instances of ecosystem-level impacts (Vitousek et. al 1987 as reviewed by Ehrenfeld 2003). However, according to Levine et al. (2003), a major limitation of studies showing a change in nitrogen availability or cycling is that many fail to make the connection between this change and community-level changes in assemblages, recruitment or diversity. Furthermore,

differences in soil nutrients in invaded sites are not necessarily caused by the invader, but rather may be the result of site selection by the invader.

Fire is a frequent component of vegetation dynamics in southern California, and the present study found that all of these sites have burned in the last 60 years, including three that burned within the past five years. A major ecosystem-level consequence of *P. setaceum*, changes in fire cycle, has been documented in Hawaii (Cuddihy 1990, Hughes et al. 1991, D'Antonio and Vitousek 1992, Mack et al. 2001), and this process has been implicated in the conversion of dryland forest habitat to grassland (Litton et al. 2006). Fire was not investigated here as a mechanism of change; however, it should be investigated in the future to determine the degree to which *P. setaceum* may be promoting fire or altering the fire cycle.

Other Factors Influencing Impact

In this research, more impacts on plot-level native species richness were seen in the Santa Monica Mountains sites than the San Diego sites. Characterization of regional differences showed that several factors differed consistently between these regions. Abiotic factors may buffer or change impacts of invasive plants at different locations, as impacts are thought to result from the interaction of the invader and the recipient community and the physical properties of the site (Alvarez and Cushman 2002, Vila et al. 2006, Funk and Vitousek 2007, Maltez-Mouro et al. 2010). Since many impacts result from changes in availability of resources, sites with more abundant resources may be more resistant to impacts from an invasive plant (reviewed in Levine and D'Antonio 1999). SAMO sites had a lower water content, older fires, and less potassium. These

sites were also less invaded by exotic species overall. All of these factors may mitigate

the impact of *P. setaceum* and affect the changes in species and community seen here.

Conclusions

Documenting impacts of invasive plant is an important step in management

(Parker et al. 1999, Gurevitch and Padilla 2004). Prioritization and risk assessment make

up a significant part of the formal goals and activities of federal, state and non-profit

agencies (USDA 2002, California Department of Food and Agriculture 2005, California

Invasive Plant Council 2006), as well as the informal day-to-day decisions of land

managers. This is the first documentation of the impact of *P. setaceum* in the Southern

California Mediterranean ecosystem, which is quite different from systems such as the

Hawaiian dryland forest and the Sonoran Desert. As shown here, *P. setaceum* can be

implicated in community level changes such as resource availability and differential

changes in species richness, although as stated, these are smaller than expected.

Although correlative studies are limited by the inability to disentangle correlation

and causation, the majority of studies to date of invasive species impacts have used this

method to elucidate possible impacts and evidence of community change (e.g. Woods

1993, Heneghan et al. 2006, Vila et al. 2006 and reviewed in Parker et al. 1999). Some

have paired observational studies with experimental studies that support the findings of

the correlative method (Alvarez and Cushman 2002, Truscott et al. 2008, Brewer 2011).

Unfortunately, it is often difficult to determine whether measured effects are due to

habitat alteration (such as anthropogenic disturbance or atmospheric nitrogen deposition)

that simultaneously facilitates invasion and causes native species declines (Gurevitch and Padilla 2004) rather than to impacts of the invader itself.

These results document possible changes in native communities caused by *P. setaceum* invasion, and provide hypotheses to be examined via experimentation and further study. Practical considerations prevented the introduction of *P. setaceum* to the sensitive protected areas used in this study or removal of this large perennial grass, which would have constituted a major disturbance that could change short-term nutrient availability or release seeds in the seedbank from dormancy (see D'Antonio et al. 1998 for discussion). In such cases longer-term monitoring approaches might provide useful information as baseline data from uninvaded areas prior to invasion. Although an invasion continuum was used here to substitute space for time, and recruitment occurred in previously uninvaded plots in the second year, longer term studies would be needed to determine whether *P. setaceum* is able to spread and reach high cover in these areas. Continued monitoring, larger-scale assessments of beta diversity, and follow up studies of nitrogen cycling at these sites, as well as experimental removal, addition, or recruitment studies would shed further light on the degree to which *P. setaceum* is impacting these communities.

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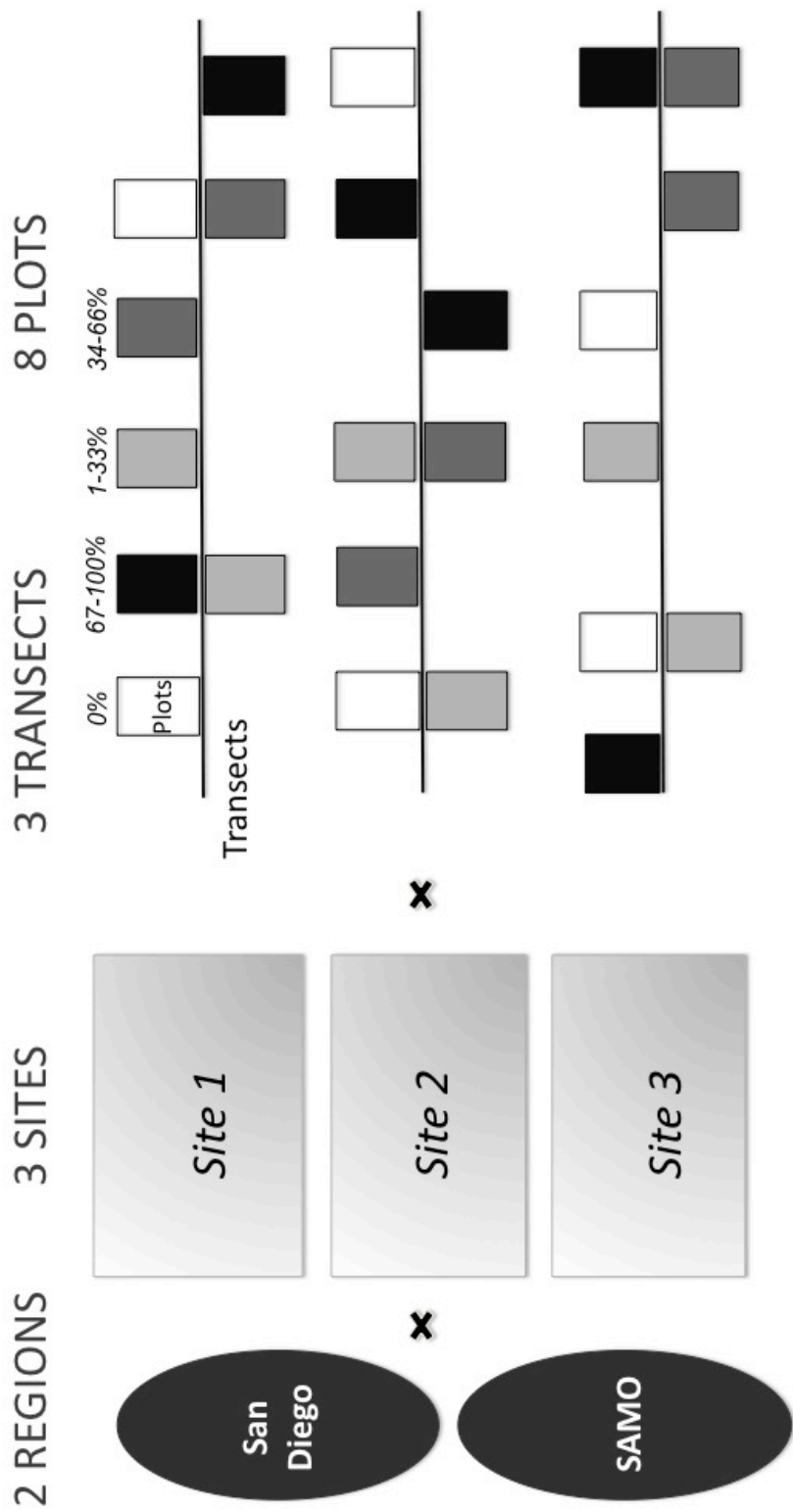
Figure 3.1. Study design template for cover and richness data in the Santa Monica Mountains (SAMO) and San Diego. sites.
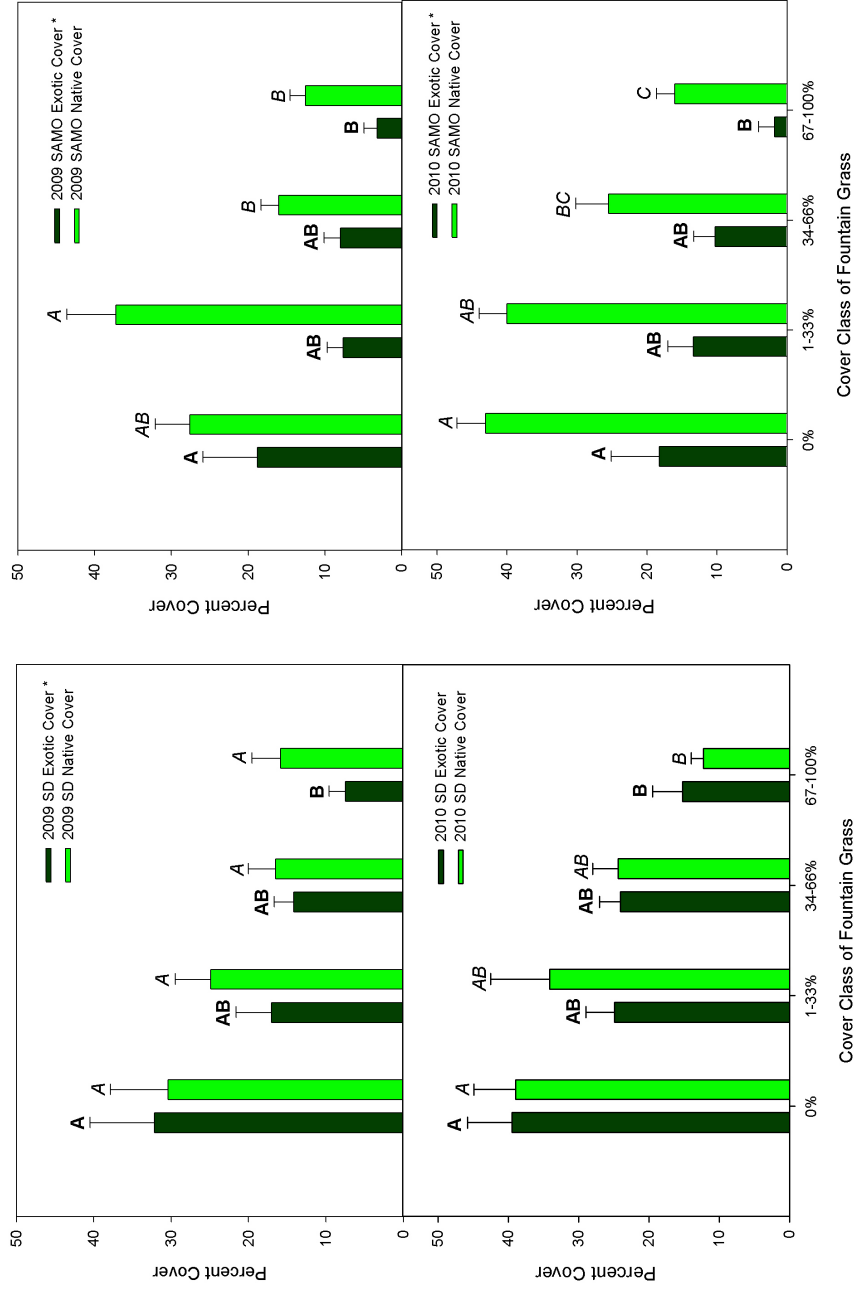
Figure 3.2. Mean cover of native and exotic species in 4 fountain grass cover classes for 2009 and 2010 in San Diego and the Santa Monica Mountains. * Distribution comparisons for these variables tested using Kruskal-Wallis (non-normal data). All other variables tested using ANOVA. Means reported from untransformed data. Different letters in the same font within a functional group indicate significant differences from post-hoc testing using Tukey's HSD.
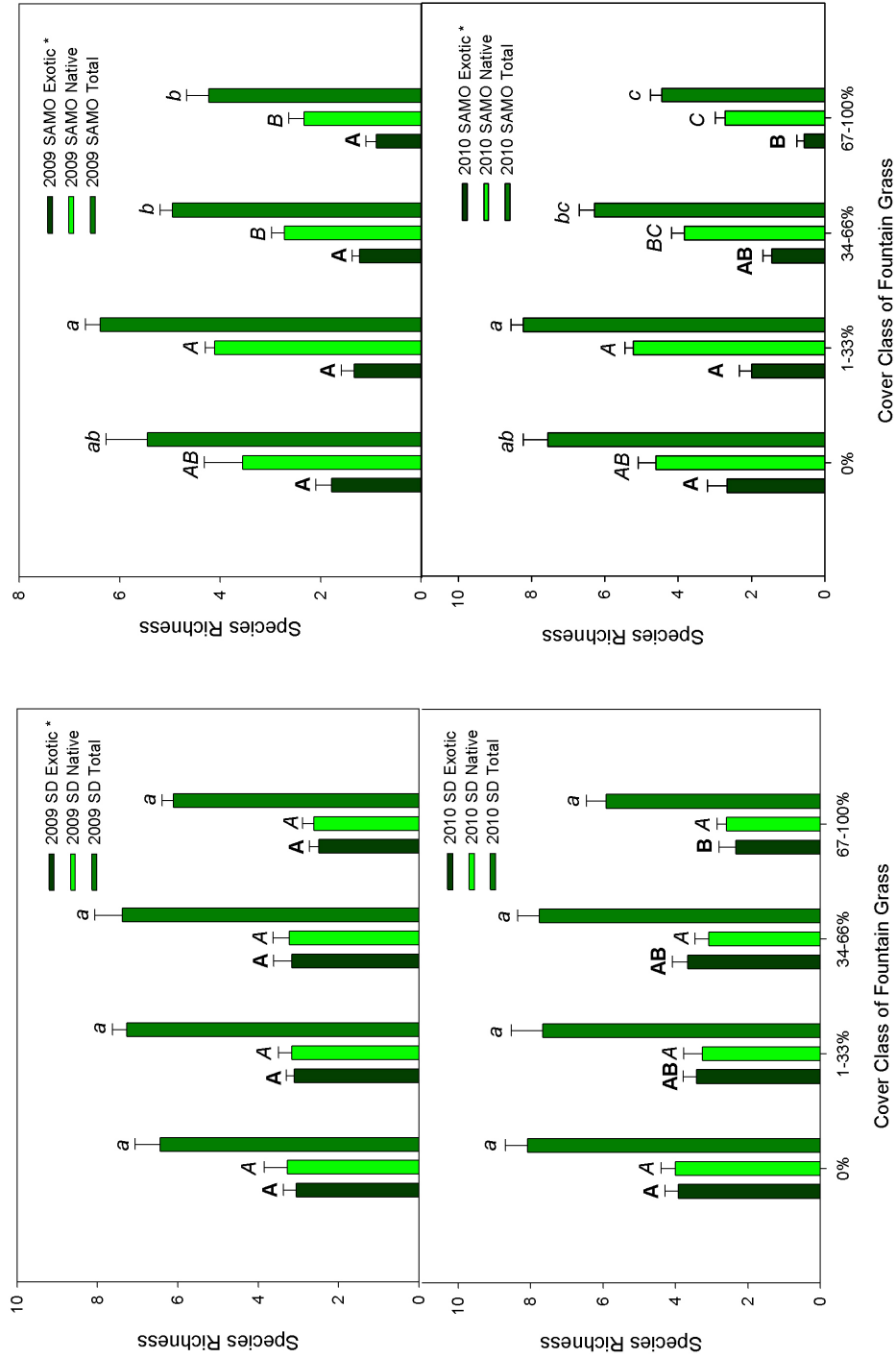
Figure 3.3. Mean richness of native and exotic species, as well as total richness in 4 fountain grass cover classes for 2009 and 2010 in San Diego and the Santa Monica Mountains. * Distribution comparisons for these variables tested using Kruskal-Wallis (non-normal data). All other variables tested using ANOVA. Means reported from untransformed data. Different letters in the same font within a functional group indicate significant differences from post-hoc testing using Tukey's HSD.

Functional Group Richness

2010 San Diego

Total Species: 55

2010 SAMO

Total Species: 55

2009 San Diego

Total Species: 64

2009 SAMO

Total Species: 52

EF (Exotic Forbs)
EG (Exotic Grasses)
NF (Native Forbs)
NG (Native Grasses)
NS (Native Shrub)
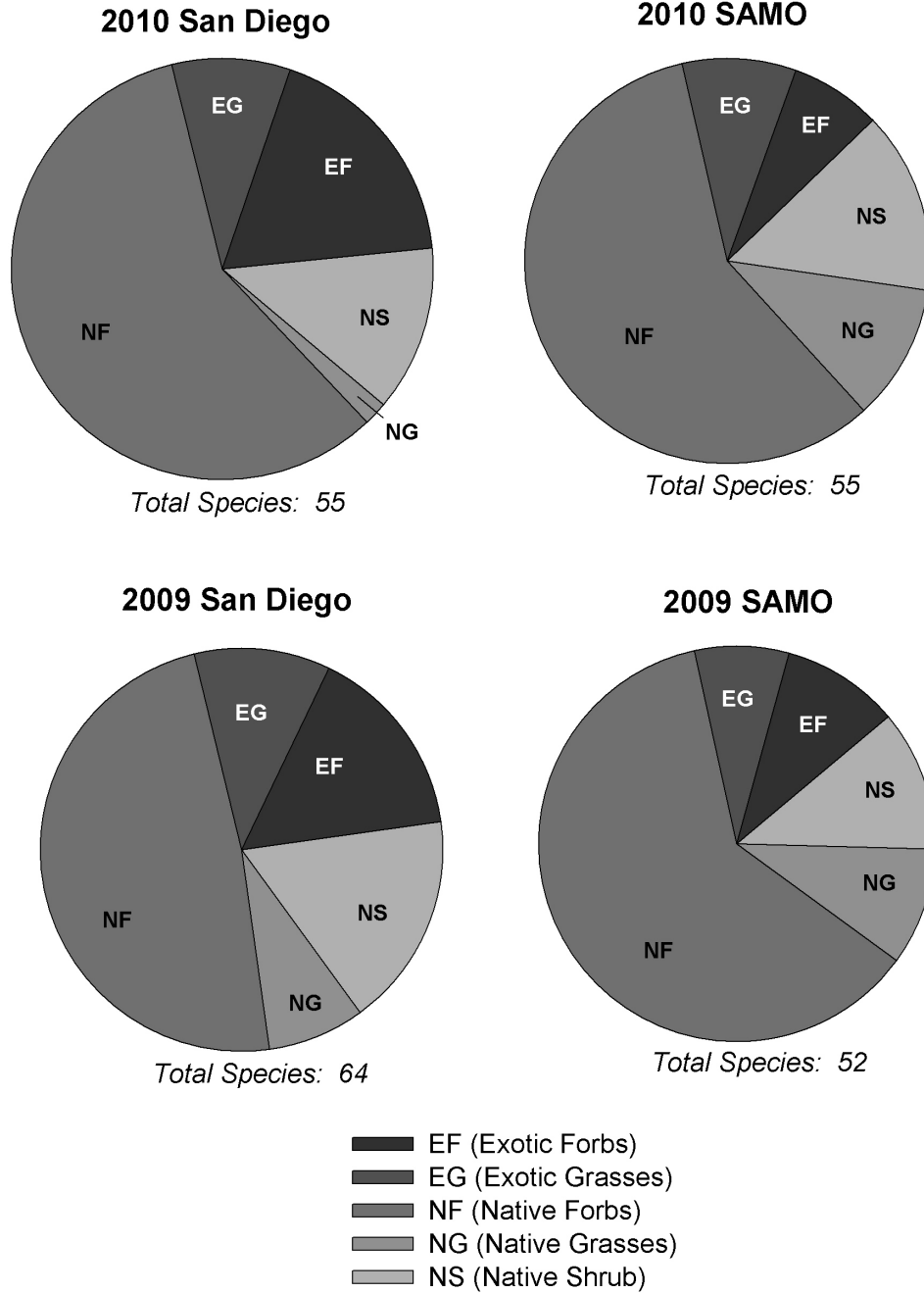
Figure 3.4. Percentage of species found in plots by functional group out of the total richness for each region and year.
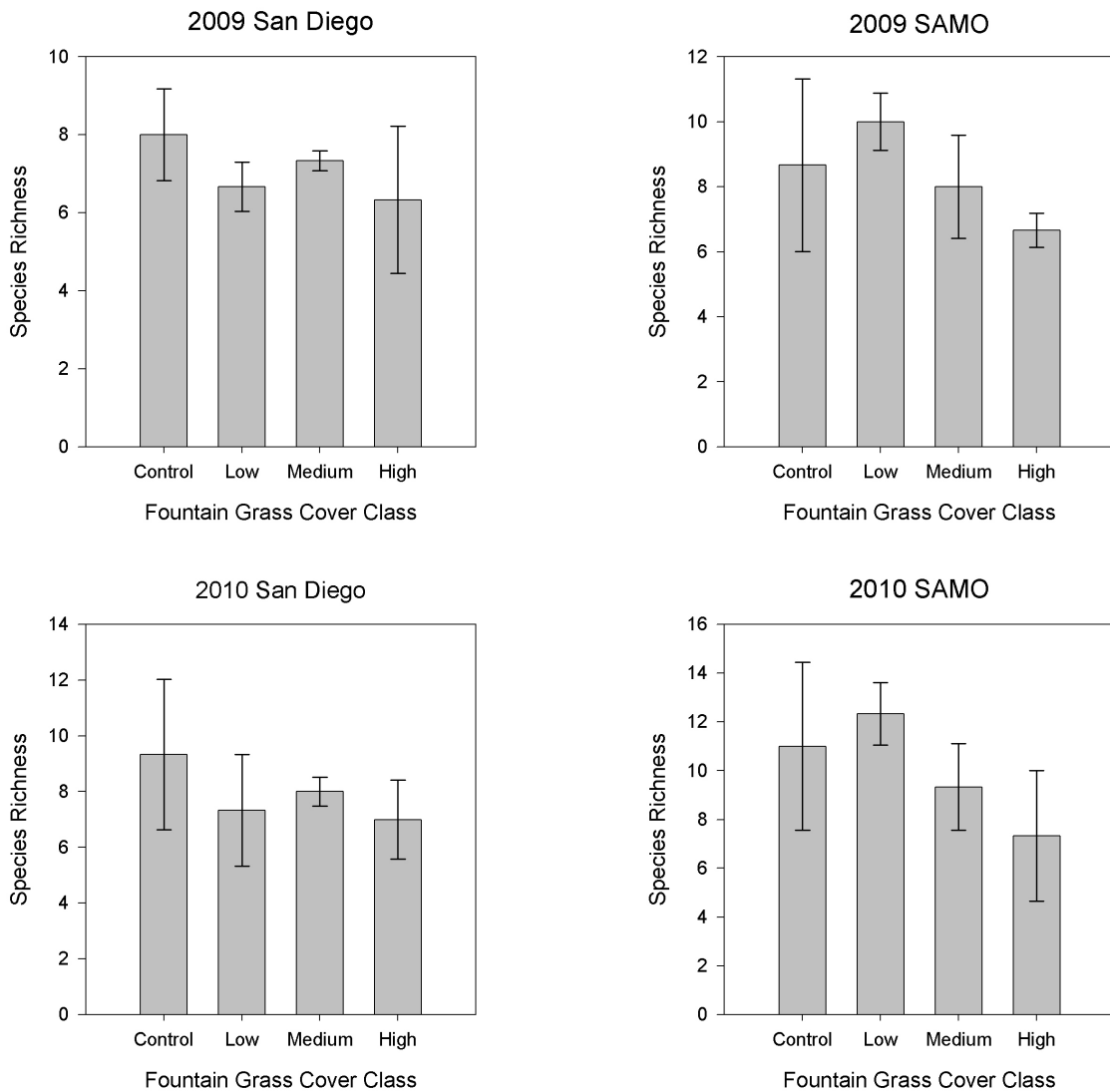
Figure 3.5. Average total native species richness for 4 plots on two transects (due to unequal plot numbers) of each cover class at each site. Cover classes are Control (0% *P. setaceum*), Low (1-33% *P. setaceum)*, Medium (34-66% *P. setaceum*), High (67-100% *P. setaceum*). Graphs are by year and region, with 3 sites per region represented. ANOVA results obtained by using sites as blocks.
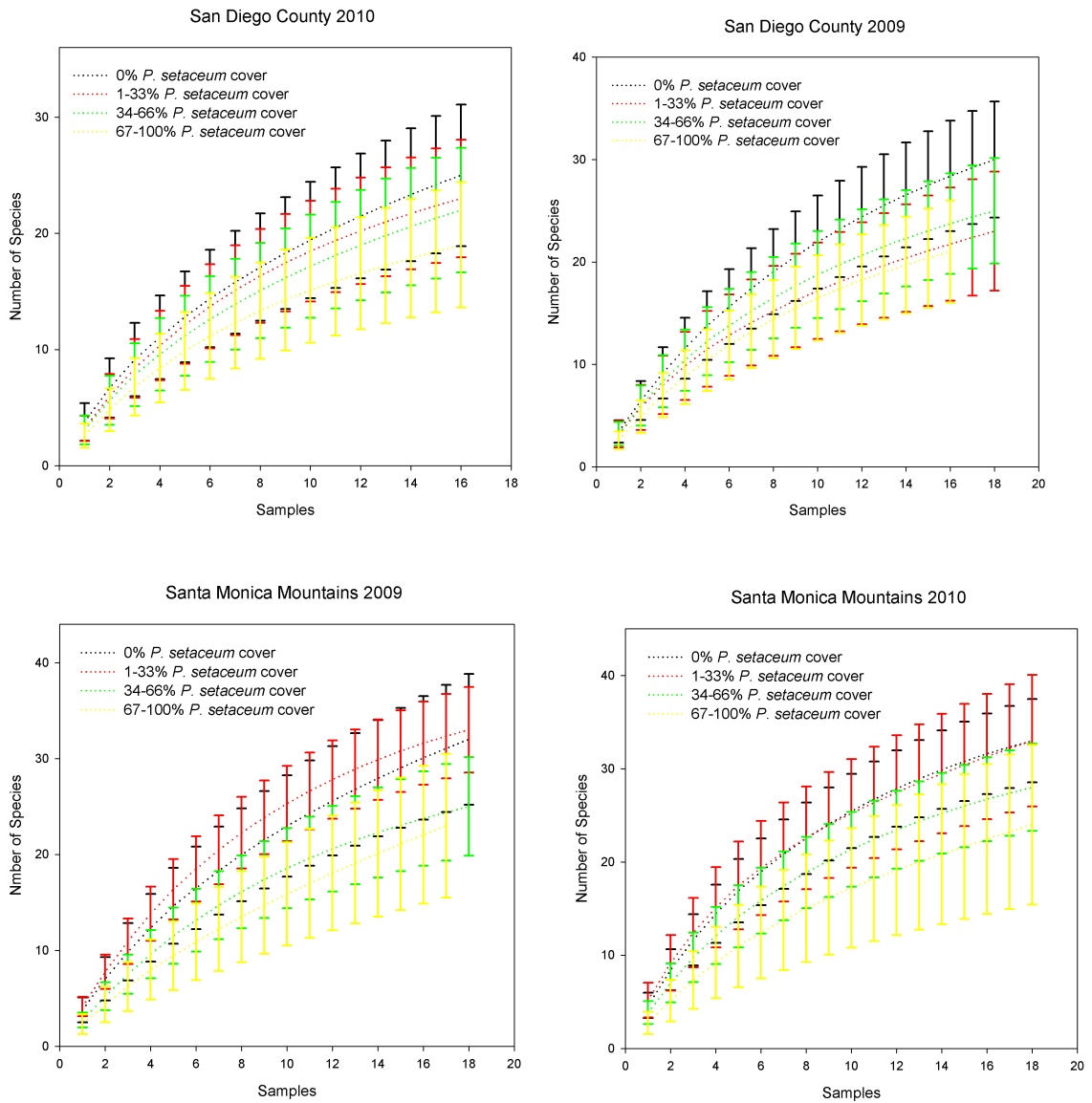
Figure 3.6. Rarefaction estimates of native species richness based on Mau Tau observed species calculations (Sobs) of interpolated points (Colwell et al. 2004). Three sites were pooled to comprise the data for each region and year. Data are shown with 95% confidence intervals.
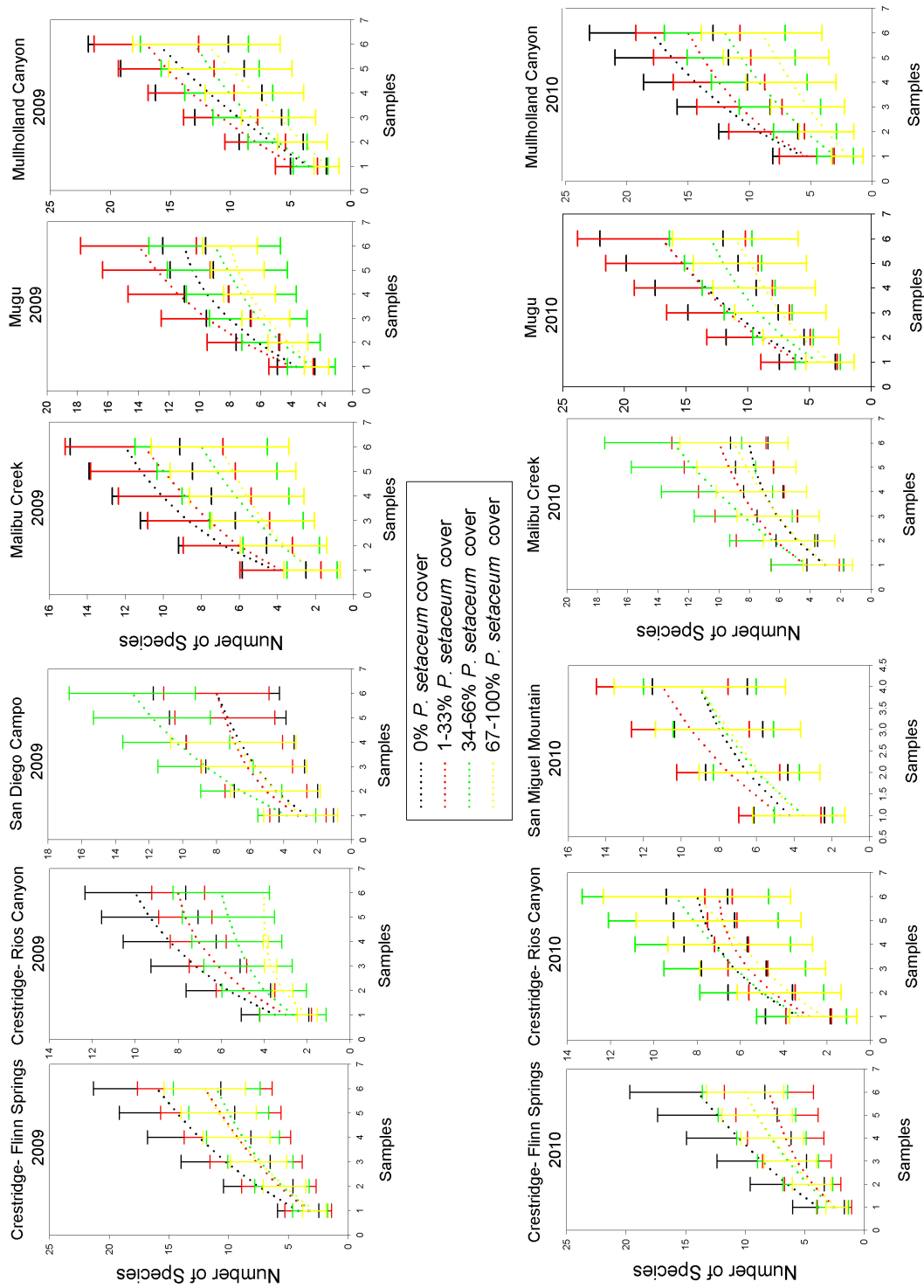
Figure 3.7. Rarefaction estimates of native species richness based on Mau Tau observed species calculations (Sobs) of interpolated points (Colwell et al. 2004). Sites and years shown separately, with 2009 above, and 2010 results below. Data are shown with 95% confidence intervals.
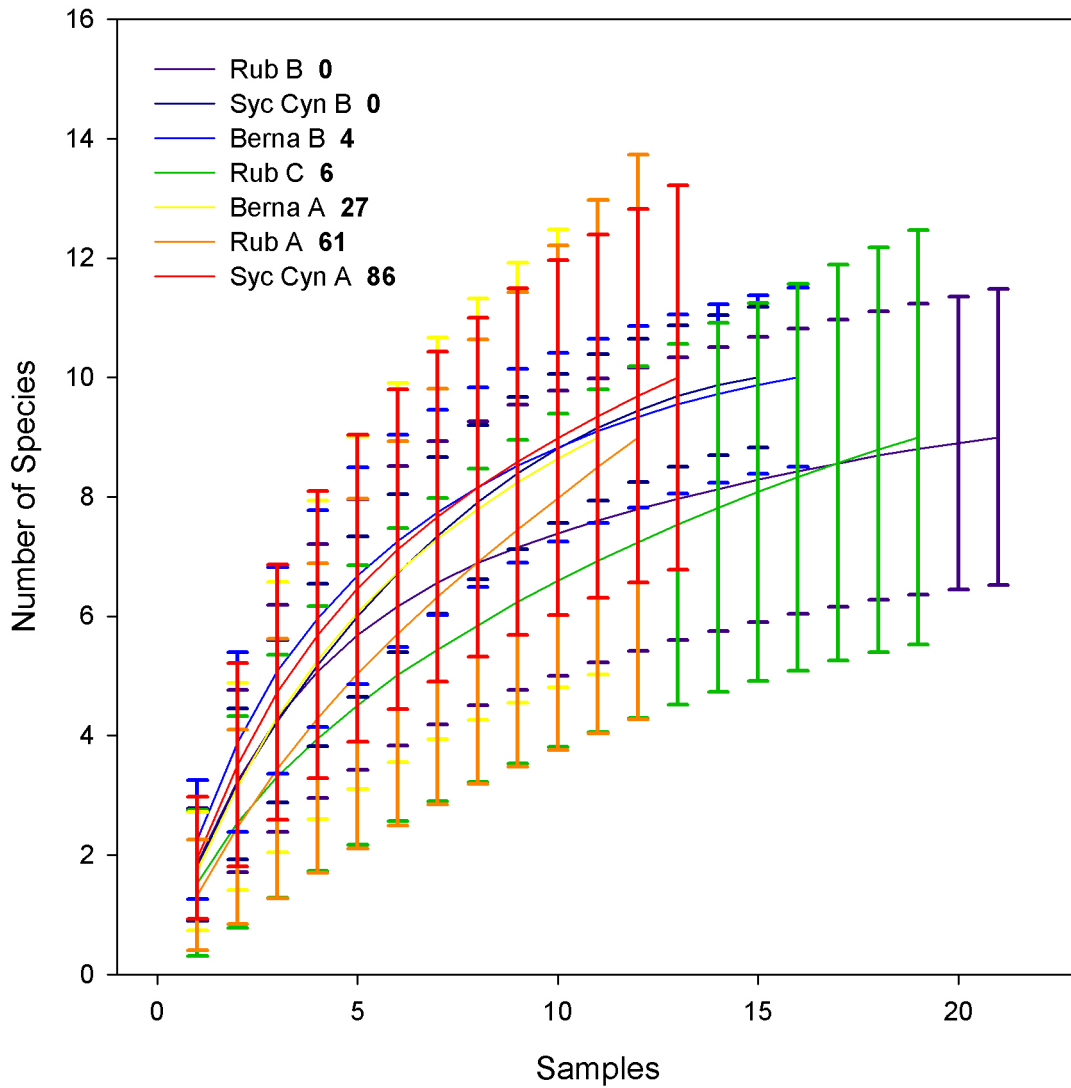
Figure 3.8. Rarefaction estimates of richness of native and exotic species, combined, based on Mau Tau observed species calculations (Sobs) of interpolated points (Colwell et al. 2004), based on outcrop samples in Riverside County. Samples are fractures in the rock where vegetation occurs. Bold numbers following site abbreviation in the key represent invasion index. Invasion index calculated as total number of fountain grass plants per meter squared on the outcrop divided by number of fractures per linear meter on the outcrop. See text for explanation of abbreviations.
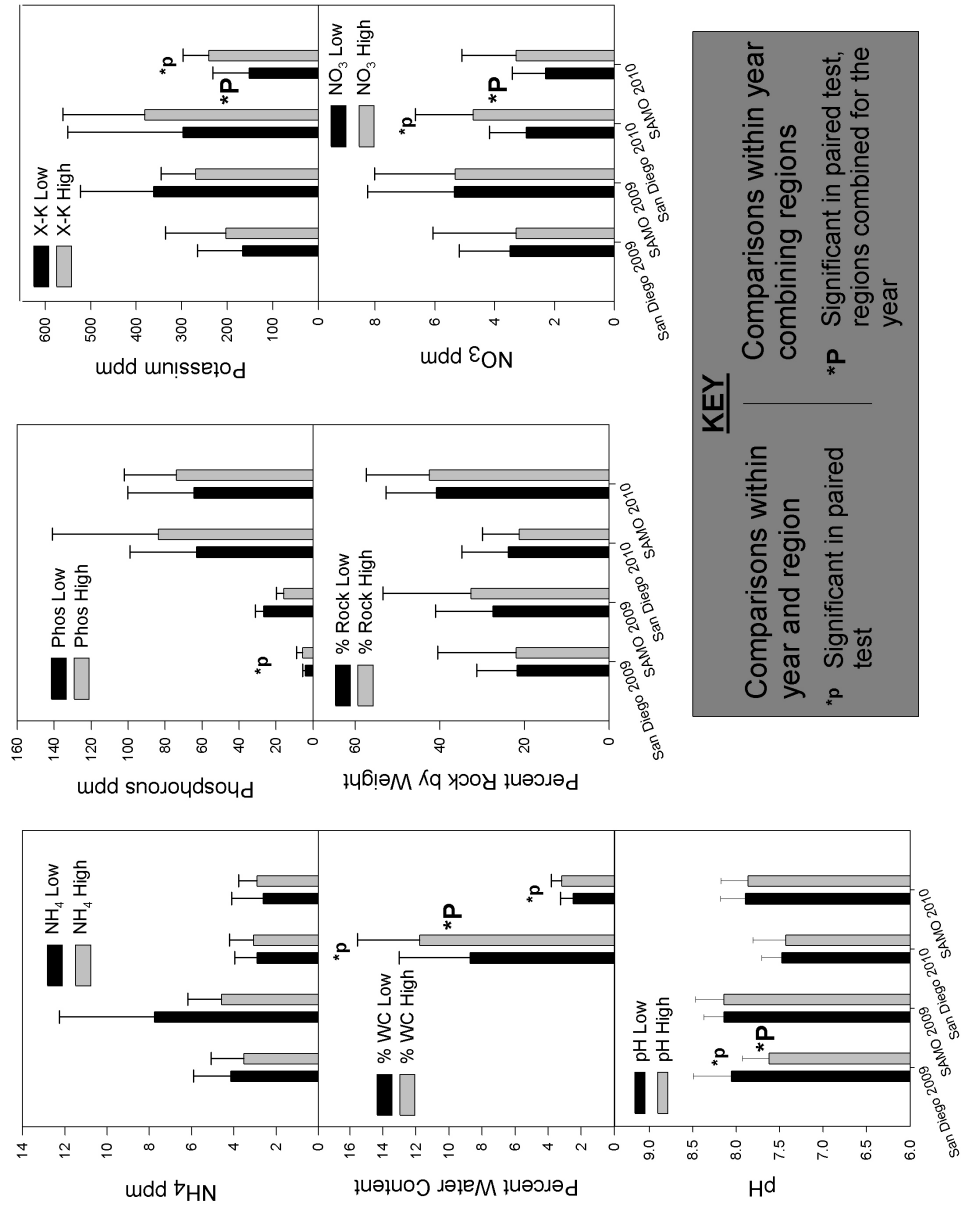
Figure 3.9. Soil characteristics from samples in low- and high- *P. setaceum* cover areas. Low- cover areas were 1-33% *P. setaceum* cover, and high-cover samples were taken in 67-100% cover of *P. setaceum*.
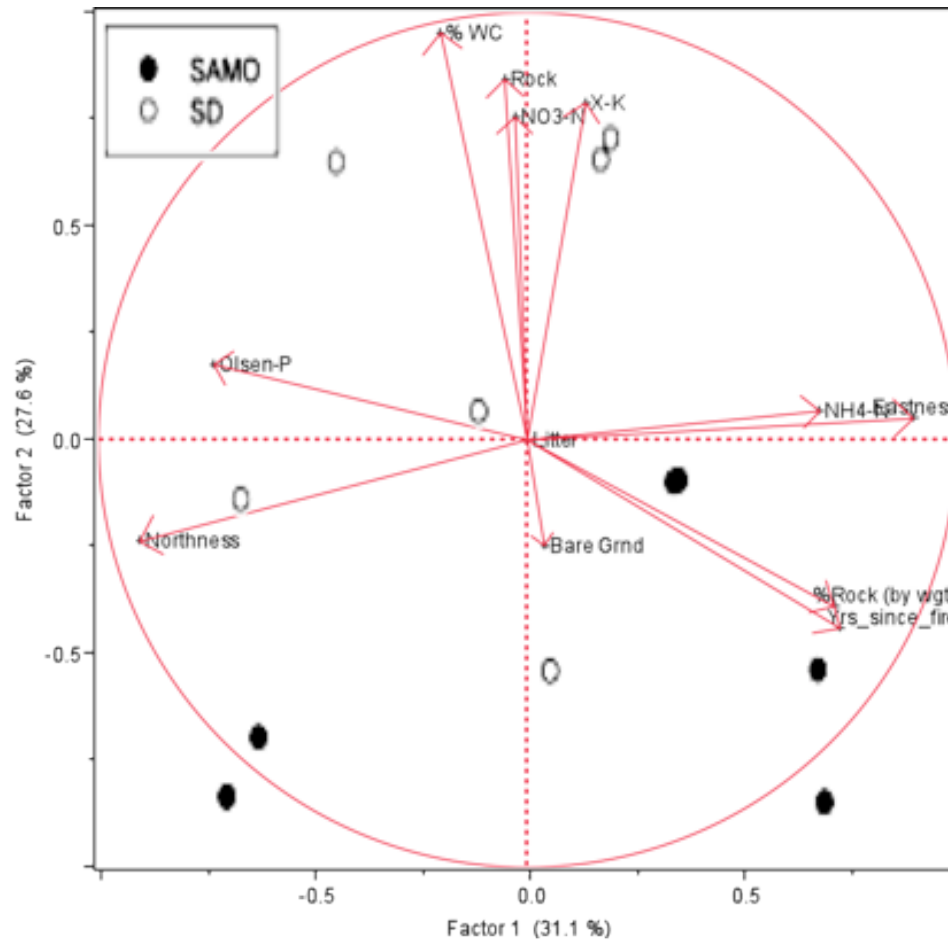
Figure 3.10. Principal components analysis score and loading plots with varimax rotation for sites in Santa Monica Mountains (SAMO) and San Diego (SD). Abiotic variables for PCA are shown in Table 3.2. Variables are described in the text. Scale is from the loading plot.

Site	Transect 1 length (m)	Transect 2 Length (m)	Total Outcrop Area (ellipse area, m^2)	Fractures sampled	Total *P. setaceum* (outcrop)	*P. setaceum* invasion index *100
Rubidoux A	14	13	142.94	12	39	61.39
Rubidoux B	22	9	155.51	21	0	0.00
Rubidoux C	19	14	208.92	19	7	5.82
Sycamore Cyn A	20	25	392.70	13	98	86.38
Sycamore Cyn B	11	15	129.59	15	0	0.00
Bernasconi A	13	15	153.15	11	16	26.59
Bernasconi B	10	12	94.25	16	3	4.38

Table 3.1. Length of transects, square area, and *P. setaceum* invasion index of outcrops sampled in Riverside County, California. Invasion index calculated as total number of fountain grass plants per meter squared on the outcrop divided by number of fractures per linear meter on the outcrop.

Table 3.2. Results of the ANOVA and Kruskal-Wallis analysis of plant percent cover and richness responses to categories of *P. setaceum* cover (cover classes, *see Methods*) for Santa Monica Mountains (SAMO) and San Diego County (SD) sites. Where transformation was necessary, square root or log(x+1) was used.

Year	Region	Variable	DF	ChiSquare	Prob>ChiSq	Sum of Squares	Mean Square	F Ratio	Prob > F
2009	SAMO	Exotic % Cover	3	9.7202	0.0211*				
		Native % Cover (transformed)	3			34.6514	11.5505	6.5206	0.0016*
		Exotic Richness	3	4.9916	0.1724	17.409722	5.80324	3.1807	0.0381*
		Native Richness	3			22.36111	7.4537	3.0383	0.0442*
		Total Richness	3						
	SD	Exotic % Cover (transformed)	3	9.2473	0.0262*				
		Native % Cover (transformed)	3			11.75368	3.91789	1.1353	0.3506
		Exotic Richness	3	2.7037	0.4396	2.576389	0.8588	0.5189	0.6725
		Native Richness	3			10.58333	3.5278	1.3948	0.2635
		Total Richness	3						
2010	SAMO	Exotic % Cover (transformed)	3	10.8817	0.0124*				
		Native % Cover	3	14.911	0.0019*	4317.1292	1439.04	9.8264	0.0001*
		Exotic Richness	3			31.409722	10.4699	9.1522	0.0002*
		Native Richness	3			74.63194	24.8773	12.0998	<.0001*
		Total Richness	3						
	SD	Exotic % Cover (transformed)	3			20.565721	6.85524	4.6248	0.0144*
		Native % Cover (transformed)	3			25.095425	8.36514	4.4702	0.0163*
		Exotic Richness (transformed)	3			0.890112	0.2967	4.1951	0.0204*
		Native Richness (tranformed)	3			0.5182041	0.172735	2.2979	0.1121
		Total Richness (tranformed)	3			0.7034667	0.23449	2.6676	0.0787

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Table 3.3. Regression results of functional group richness and cover by *P. setaceum* cover for both years and both regions. Functional groups not shown were not significant or near-significant in that year or region.

Variable	Functional Group	Site	Year 2009 R²	R	p-value	Year 2010 R²	R	p-value	Site	Year 2009 R²	R	p-value	Year 2010 R²	R	p-value
Cover	Exotic Total (excluding *P. setaceum*)	**SAMO**	0.06	-0.25	0.201	0.17	-0.42	0.0309*	**SD**	0.23	-0.48	0.0107*	0.20	-0.44	0.0297*
	Exotic Forbs		0.03	-0.16	0.423	0.18	-0.42	0.0282*		0.14	-0.37	0.057	0.06	-0.25	0.232
	Exotic Annuals		0.06	-0.25	0.211	0.17	-0.42	0.0309*		0.21	-0.46	0.0162*	0.20	-0.45	0.0264*
	Exotic Annual Forbs		0.11	-0.33	0.089	0.18	-0.42	0.0282*		0.12	-0.35	0.077	0.07	-0.27	0.207
	Native Total (transformed)		0.45	-0.67	0.0001***	0.38	-0.62	0.0006***		0.18	-0.42	0.0297*	0.38	-0.62	0.0012**
	Native Shrubs		0.11	-0.34	0.084	0.15	-0.38	0.0488*							
	Native Grass		0.31	-0.56	0.0024**	0.14	-0.38	0.052							
	Native Forbs (and Moss)		0.22	-0.47	0.0144*	0.12	-0.35	0.077		0.20	-0.45	0.0195*	0.12	-0.34	0.105
	Native Annual Forbs		0.17	-0.41	0.0325*	0.04	-0.19	0.332							
	Native Annual Grass		0.15	-0.38	0.0474*	0.11	-0.34	0.084							
	Total Native Annuals		0.26	-0.51	0.0071**	0.11	-0.33	0.098		0.17	-0.42	0.0314*	0.09	-0.30	0.159
	Native Perennial Forbs and Grass		0.14	-0.37	0.057	0.04	-0.19	0.341							
	Native Perennial Forbs and Shrubs		0.11	-0.34	0.087	0.04	-0.19	0.347		0.07	-0.26	0.198	0.27	-0.52	0.0091**
	Native Perenn Forbs									0.17	-0.41	0.0326*	0.11	-0.33	0.115
	Native Perennial Grass		0.18	-0.43	0.0262*	0.01	-0.07	0.721							
	Total Richness (Exotic and Native)		0.65	0.81	<.0001***	0.41	0.64	<.0001***		0.3	0.55	0.0004***	0.32	0.56	0.0008***
Richness	Total (excluding . *P. setaceum*)	**SAMO**	0.34	-0.59	0.0013**	0.64	-0.80	<.0001***	**SD**	0.14	-0.38	0.053	0.09	-0.30	0.157
	Exotic Total (excluding *P. setaceum*)		0.02	-0.15	0.465	0.17	-0.41	0.0345*							
	Exotic Forbs		0.04	-0.21	0.289	0.27	-0.52	0.0054**							
	Exotic Annuals		0.02	-0.14	0.494	0.17	-0.41	0.0345*							
	Exotic Annual Forbs		0.10	-0.31	0.113	0.27	-0.52	0.0054**							
	Native Total		0.50	-0.71	<.0001***	0.61	-0.78	<.0001***							
	Native Grass		0.27	-0.52	0.0058**	0.37	-0.61	0.0008***							
	Native Forbs (and Moss)		0.14	-0.37	0.055	0.25	-0.50	0.0074**							
	Native Annual Forbs		0.14	-0.38	0.050	0.04	-0.20	0.306							
	Native Annual Grass		0.14	-0.37	0.056	0.24	-0.49	0.0089**							
	Total Native Annuals		0.19	-0.43	0.0234*	0.09	-0.29	0.136		0.11	-0.33	0.096	0.01	-0.10	0.656
	Native Perennial Forbs and Grass									0.03	-0.17	0.400	0.12	-0.35	0.098
	Native Perennial Forbs									0.01	-0.10	0.605	0.12	-0.35	0.098
	Native Perennial Grass		0.20	-0.45	0.0181*	0.06	-0.24	0.227							

* P < 0.05; ** P < 0.01; *** P <0.001

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Region and Year	Variable	t-ratio or Sign-rank[1] (z)	df	p	Mean Difference	SE	Correlation	SD (difference)	Samples needed for α=0.05
2009 SAMO	% Rock	2[1]	3	0.625	0.011	-	-	0.1	788
	NO3	1.368066	3	0.265	0.930	0.680	0.927	1.4	20
	NH4	-1.66038	3	0.195	-3.675	2.213	0.198	4.4	14
	Phosphorous	-3[1]	3	0.375	-8.050	-	-	11.0	17
	Potassium	-0.79458	3	0.485	-92.000	115.784	-0.708	117.0	15
	pH	-0.16451	3	0.880	-0.048	0.289	-0.882	0.2	128
2009 SAN DIEGO	% Rock	-1.48415	5	0.198	-0.065	0.044	0.078	0.1	25
	NO3	-0.5[1]	5	1.000	0.217	-	-	2.5	1048
	NH4	-0.36265	5	0.732	-0.267	0.735	0.352	1.8	360
	Phosphorous	2.14492	5	0.085	1.900	0.886	0.903	2.2	13
	Potassium	1.405947	5	0.219	62.833	44.691	0.545	109.0	26
	pH	-3.08937	5	0.0272*	-0.467	0.151	0.569	0.4	7
2010 SAMO	% Water Content	3.411218	8	0.0092*	0.670	0.196	0.968	0.6	9
	% Rock	0.427245	8	0.681	1.642	3.843	0.653	12.0	422
	NH4	2.5[1]	8	0.820	0.291	-	-	11.0	11213
	NO3	14.5[1]	8	0.098	0.986	-	-	2.1	38
	Phosphorous	0.68728	8	0.511	0.944	1.374	0.652	4.1	150
	Potassium	2.380802	8	0.0445*	88.333	37.102	0.300	111.0	15
	pH	-0.26733	8	0.796	-0.028	0.104	0.469	0.3	979
2010 SAN DIEGO	% Water Content	2.089641	7	0.075	3.063	1.466	0.475	4.1	17
	% Rock	-0.65798	7	0.532	-2.602	3.954	0.373	11.0	143
	NH4	0.264752	7	0.799	0.173	0.652	-0.401	1.2	382
	NO3	13[1]	7	0.078	1.774	-	-	1.8	11
	Phosphorous	1.262404	7	0.247	2.063	1.634	0.594	4.6	42
	Potassium	1.084723	7	0.314	84.250	77.670	0.529	220.0	56
	pH	-0.28519	7	0.7838	-0.0462	0.16217	-0.1083	0.4	651

Table 3.4. Statistics from the soil analysis comparison of high and low *P. setaceum*-cover areas with power analysis for significance at alpha=0.05 for regular T-tests.

Variable	SAMO Average	StDev	San Diego Average	StDev
Years since fire	24.67	23.57	15.29	16.98
Aspect	190.00	35.50	175.00	17.73
% Water Content (by Wgt)	2.84	2.30	10.53	3.63
% Rock (by wgt)	41.64	12.53	25.06	9.70
NH_4	2.76	1.36	2.98	0.73
NO_3	2.79	1.76	3.25	1.65
Phosphorous	6.92	3.85	7.45	3.77
Potassium	196.39	94.02	325.29	207.76
% Bare Ground (plots)	17.91	8.37	19.52	13.90
% Rock (plots)	8.51	8.60	15.06	6.86
% Litter (plots	23.26	10.34	19.96	11.90
Dec. Precip	62.00	0.89	53.75	4.03
Jan. Avg. Precip	96.00	0.89	64.50	6.26
Feb. Avg. Precip	89.67	1.86	58.75	6.07
March Avg. Precip	66.33	2.88	67.75	6.52

Table 3.5. Average values for the physical variables measured at the Santa Monica Mountains and Eastern San Diego County sites. Aspect is in degrees, NO_3 and NH_4, potassium and phosophorous are parts per million, and average precipitation values are in millimeters.

		Rotated Factor Loading	
Variable		**Factor 1**	**Factor 2**
Yrs_since_fire		0.7293	-0.4406
Northness		-0.9041	-0.2374
Eastness		0.8996	0.0501
% WC		-0.2021	0.9531
%Rock (by wgt)		0.7142	-0.3895
NH4-N		0.6818	0.0677
NO3-N		-0.0285	0.7556
Olsen-P		-0.7309	0.1764
X-K		0.1364	0.7892
Bare Grnd		0.0396	-0.2471
Rock		-0.0529	0.8442
Litter		0	0
Region	**Site**	**Factor Scores**	
SAMO	MabCrk	-1.3811	-1.2019
SAMO	MabCrk	-1.2332	-0.9612
SAMO	MuguChu	0.6889	0.0756
SAMO	MuguChu	0.7146	0.0831
SAMO	MullCyn	1.3899	-1.2244
SAMO	MullCyn	1.3590	-0.6870
SD	CrestFlinn	-1.3160	0.0052
SD	CrestFlinn	-0.8724	1.3783
SD	CrestRios	0.1164	-0.6928
SD	CrestRios	-0.2152	0.3623
SD	SanMig	0.3980	1.4750
SD	SanMig	0.3509	1.3878

Table 3.6. Loading values for the variables in the principal components analysis of plot and geographic abiotic variables, and site factor scores on Factors 1 and 2. See text for explanation of abbreviations.

Discriminant Variable	F Ratio	Prob>F	Significance	Region Where Higher
Years since fire	3.87	0.0775		SAMO
Northness	0.007	0.9357		
Eastness	1.986	0.1891		
% Water Content (by Wgt)	19.207	0.0014	**	SD
% Rock (by wgt)	10.86	0.0081	**	SAMO
NH$_4$	0.121	0.7355		
NO$_3$	1.536	0.2436		
Phosphorous	0.017	0.8981		
K	3.148	0.1064		
% Bare Ground (plots)	0.663	0.4344		
% Rock (plots)	3.414	0.0944		SD
% Litter (plots	0.003	0.9552		
Dec. Precip	16.552	0.0023	**	SAMO
Jan. Avg. Precip	197.109	<0.0001	***	SAMO
Feb. Avg. Precip	103.22	<0.0001	***	SD
March Avg. Precip	0.157	0.6998		

* P < 0.05; ** P < 0.01; *** P <0.001

Table 3.7. Discriminate analysis for abiotic variable values for the sites in Santa Monica Mountains (SAMO) and San Diego (SD). See text for explanation of variables.

General Conclusions

These studies investigated the potential distribution and impacts of *Pennisetum setaceum* in California. I have shown that in Southern California, there likely remain many areas that are vulnerable to invasion by this exotic grass, especially coastal areas. With consideration of the impacts of *P. setaceum* in Hawaii (increased fine fuel loading and type conversion (Cuddihy 1990, Blackmore and Vitousek 2000)), the invasion of this grass in coastal sage scrub and desert systems may pose significant threats to native habitats and human communities at the wildland-urban interface.

Potential Distribution in California

P. setaceum, a C_4 (warm-season) grass, has a broad bioclimatic range within California, and it is known as a tolerant and plastic species, able to persist in a variety of habitats (Williams et al. 1995). Results of species distribution modeling in this study show that additional areas are vulnerable to invasion by this species in California. Suitable habitat in this region may be correlated with maximum December temperature, indicating that this species may grow best in places where the winter rainfall-season is warmest in this invasive range. Fine-scale distribution in the Colorado Desert Areas shows that *P. setaceum* is correlated geographically with increased or extended seasonal soil moisture, such as rock outcrops and washes. This indicates that desert areas may support summer growth as well as winter growth of *P. setaceum*, which is known to grow and flower opportunistically (Goergen and Daehler 2001). These results also

demonstrate the utility (along with some limitations) of species distribution modeling for invasive species.

Competition with Native Species

Since biotic factors such as competition with other species are known to affect species distribution, this portion of the research quantified competition of *P. setaceum* as compared to a native perennial grass in California. Results show that C_3 *S. pulchra* can slow initial growth of *P. setaceum*, but that late-season growth by *P. setaceum* can allow this species to overcome initial suppression to survive and reproduce at both low and high densities. This study showed that the barrier of a qualitative difference in life history may leave a phenological opening for the establishment of an exotic grass under some conditions. Thus, in recently burned grassland dominated by *S. pulchra*, we may expect arriving propagules of *P. setaceum* to experience intense competition in the cool season, but experience a release from this competition and an opportunity to thrive later in the season. Following up on these results, further investigation would reveal whether mature *S. pulchra* grassland would be able to suppress recruitment of an immature propagule of *P. setaceum*. With relevance to natural systems in Southern California, managers of *S. pulchra* grasslands should institute effective control of *P. setaceum*-dominated areas in close proximity to *S. pulchra*, especially post-disturbance, where maintenance of uninvaded grassland is a management goal.

Impact and Correlates in Coastal Sage Scrub

Documenting impacts of invasive plants is an important step in management (Parker et al. 1999, Gurevitch and Padilla 2004). This is the first documentation of the impact of *P. setaceum* in the Southern California Mediterranean ecosystem, which is different from other invaded ecosystems such as the Hawaiian dryland forest and the Sonoran Desert in the timing of precipitation. As shown here, *P. setaceum* can be implicated in community level changes in factors such as resource availability and species richness, although these were found to be smaller than expected.

To further investigate the differences seen here between invaded and uninvaded areas in terms of species richness and soil nutrients, longer-term monitoring approaches would be useful. Continued monitoring, larger-scale assessments of beta diversity, and follow up studies of nitrogen cycling at these sites through direct experimentation as well as experimental removal, addition, or recruitment studies would shed further light on the degree to which *P. setaceum* is impacting these communities.

Future Directions

The evaluation of distribution, potential spread, and impacts of invasive species is critical for the conservation and management of habitats. Species distribution modeling can be an informative tool for identifying either regions that are at-risk for invasion or local areas that may be targeted for monitoring and early detection efforts. Improvements in the prediction of invasive species distribution may focus on incorporating stochasticity and demography as well as other factors that help represent the dynamic process of invasion.

From a broader perspective, very recent discussion among ecologists (and even non-ecologists) has focused on whether exotic species are should *a priori* be considered undesirable (in addition to the ethics of controlling invasive species, as in T.C. Boyle, 2011), which emphasizes the need to evaluate species based on their impacts rather than simply accept a preconceived and implied assumption of impact based on exotic origins (Davis et al. 2011 and response by Simberloff and Signatories 2011). In view of these discussions it is imperative that ecologists establish quantitatively whether or not there exist impacts or potential for impacts of exotic species on native communities. These studies should also move beyond impacts of individual species on habitats towards informing broader meta-analyses that could shed light on patterns of impacts at a broader scale (Vila et al. 2011). In addition, investigation of invasive species life history and its relationship to biogeography and characteristics of recipient communities, these analyses may lead to greater insight into invasive species biology and ecology, as well as conservation as a whole.

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Appendix 1
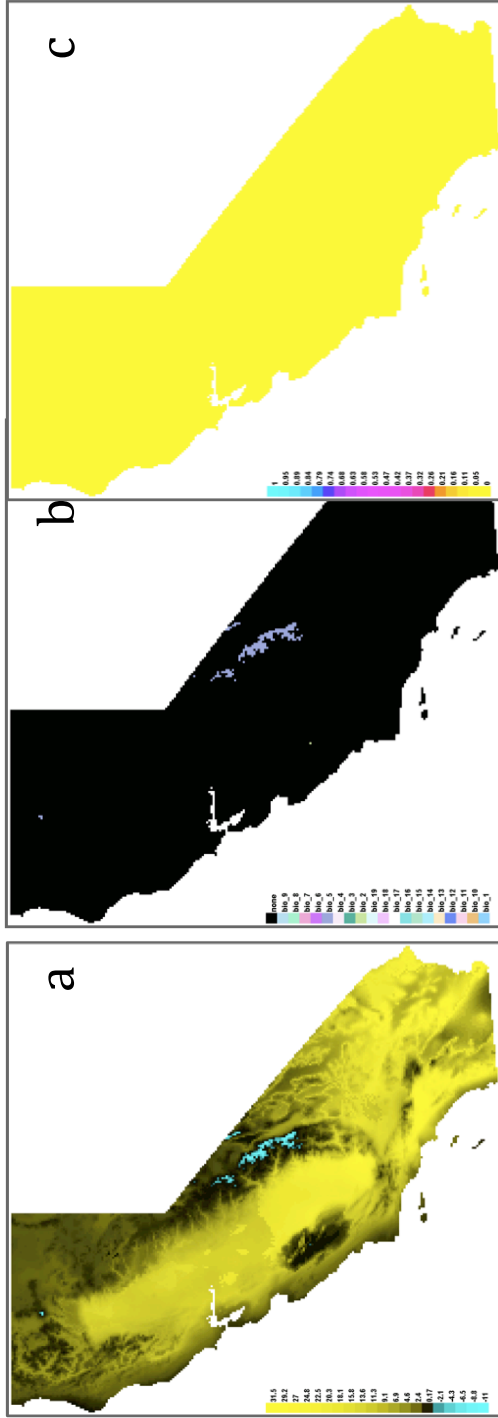
Appendix 1. Maps showing areas where clamping was a concern in California for the MaxEnt model of *Pennisetum setaceum* trained on bioclimatic environmental layers and native presence locations in Africa. **a)** The areas where the projected areas were most outside the range of the training data. **b)** Which variables were most outside the range of data used to train the model geographically. **c)** The difference in the models produced when the program did versus did not restrict the projection to the range of data encountered during training.

Appendix 2
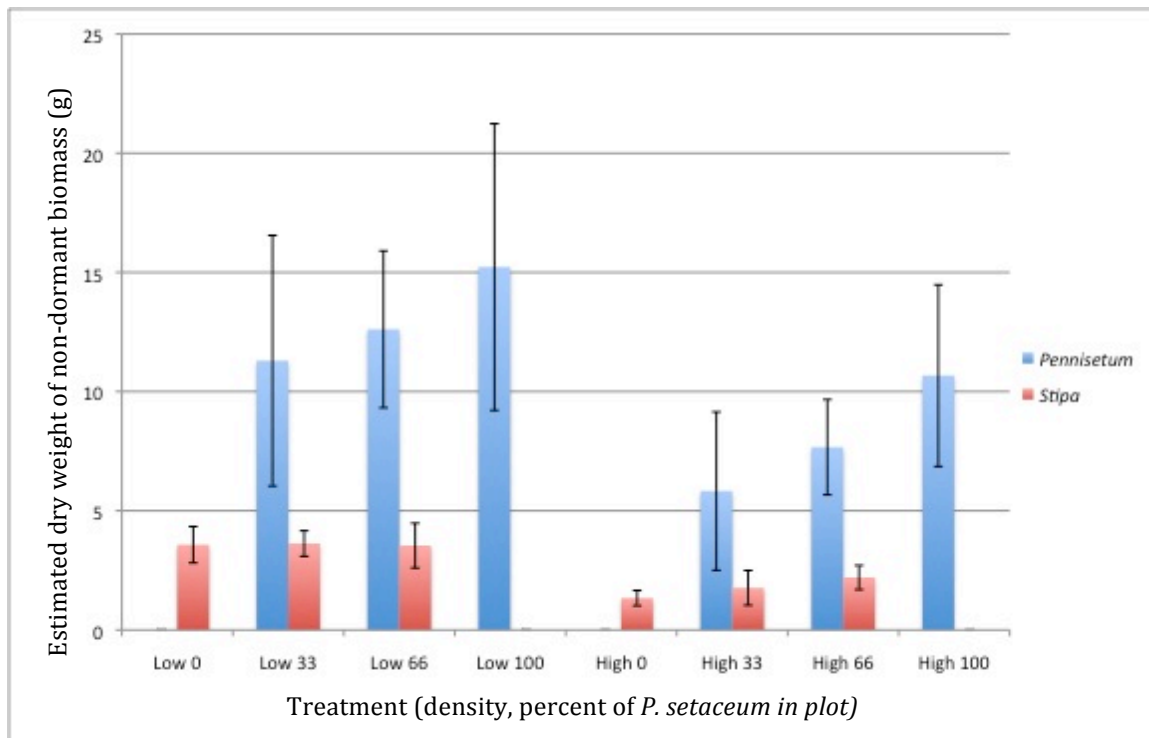
Appendix 2. Average dry weight per plant of non-dormant biomass for each treatment in the competition experiment (described in Chapter 2) in August for *Stipa pulchra* and *Pennisetum setaceum*. Percentage of non-dormant plant biomass was visually estimated after harvest, and total dry weights were multiplied by this percentage to obtain an estimate of live biomass. Error bars are one standard deviation for n=4 per treatment.

Appendix 3: Field site locations in the Southern California invasion study of

Pennisetum setaceum.

Appendix 4: Abiotic variables and litter associated with *Pennisetum setaceum* cover.

A small-scale study of abiotic variables (and litter) was performed in four cover classes of *Pennisetum setaceum* at a site containing coastal sage scrub vegetation along Mullholland Canyon Road, Santa Monica Mountains National Recreation Area in 2010 in association with the study described in Chapter 3. Cover Classes: 1=0%; 2=1-33%; 3=34-66%; 4=67-100%. Soil water content was taken using a portable moisture probe (Spectrum Technologies, Field Scout, TDR 200), temperature was measured with portable temperature probes (Forestry Suppliers), and percent cover readings were taken in 0.5 by 1m plots as described in Chapter 3.
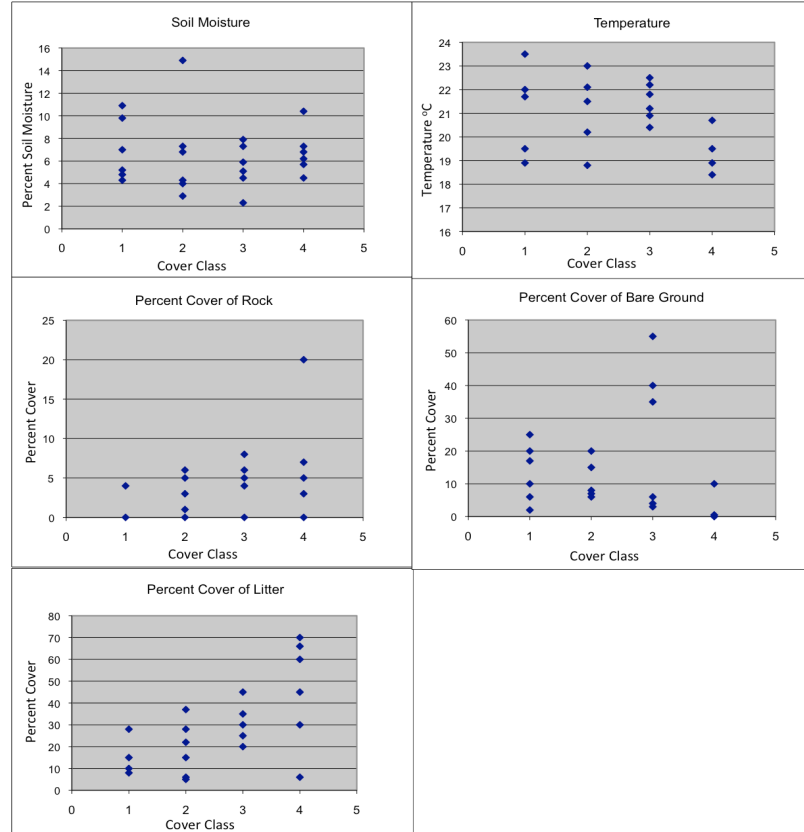
Appendix 5: Line-intercept and point-intercept richness data for coastal sage scrub sites in the Santa Monica Mountains and San Diego County (as described in Chapter 3).

Year	Site	Average Cover +/- 1m	Point-Intercept *P. setaceum*	Exotic Richness	Native Richness
2009	MullCyn	30		2	2
2009	MullCyn	80	1	0	1
2009	MullCyn	45		1	0
2009	MullCyn	20		1	1
2009	MullCyn	0		1	0
2009	MullCyn	30		1	2
2009	MullCyn	40	1	0	0
2009	MullCyn	0		1	1
2009	MullCyn	0		1	1
2009	MullCyn	55	1	1	0
2009	MullCyn	100	1	1	0
2009	MullCyn	100	1	0	0
2009	MullCyn	70	1	2	1
2009	MullCyn	25		2	1
2009	MullCyn	0		1	2
2009	MullCyn	35		0	2
2009	MullCyn	100	1	1	0
2009	MullCyn	60		0	0
2009	MullCyn	80	1	0	1
2009	MullCyn	0		2	2
2009	MuChu	10		0	1
2009	MuChu	10		0	2
2009	MuChu	15		0	2
2009	MuChu	35		0	1
2009	MuChu	100	1	0	1
2009	MuChu	85		0	1
2009	MuChu	70		0	0
2009	MuChu	45		0	1
2009	MuChu	0		0	1
2009	MuChu	35		1	3
2009	MuChu	20		0	0
2009	MuChu	75		0	1
2009	MuChu	10		0	0
2009	MuChu	30	1	1	0
2009	MuChu	0		0	1
2009	MuChu	15		0	1
2009	MuChu	30	1	0	1
2009	MuChu	65	1	0	1
2009	MuChu	60	1	0	1
2009	MuChu	55		0	0
2009	MuChu	100	1	0	0
2009	MuChu	90	1	0	1
2009	MuChu	62.5	1	0	0
2009	MuChu	0		0	1
2009	MuChu	0		0	0
2009	MuChu	0		0	3
2009	MuChu	20	1	0	2

Year	Site	Average Cover +/- 1m	Point-Intercept *P. setaceum*	Exotic Richness	Native Richness
2009	MuChu	0		0	2
2009	MuChu	0		0	1
2009	MuChu	0		0	1
2009	MuChu	50		0	2
2009	MuChu	70	1	0	2
2009	MuChu	25		0	1
2009	MuChu	0	1	0	2
2009	MuChu	45		1	0
2009	MabCrk	0		2	1
2009	MabCrk	0		2	3
2009	MabCrk	25	1	2	1
2009	MabCrk	10		2	1
2009	MabCrk	0		1	3
2009	MabCrk	55	1	1	3
2009	MabCrk	35		1	2
2009	MabCrk	0		1	3
2009	MabCrk	60	1	0	0
2009	MabCrk	100	1	1	1
2009	MabCrk	75		1	2
2009	MabCrk	25	1	0	1
2009	MabCrk	50		0	2
2009	MabCrk	25	1	0	4
2009	MabCrk	0		1	2
2009	MabCrk	55	1	0	1
2009	MabCrk	100	1	0	0
2009	MabCrk	95	1	0	2
2009	MabCrk	0	1	0	0
2009	MabCrk	0	1	0	1
2009	MabCrk	40		0	0
2009	MabCrk	90	1	0	1
2009	MabCrk	10		0	2
2009	MabCrk	0		2	0
2009	MabCrk	0		2	1
2009	MabCrk	75	1	3	0
2009	MabCrk	65	1	2	0
2009	MabCrk	85	1	0	2
2009	MabCrk	85	1	1	0
2009	MabCrk	10		2	0
2009	MabCrk	70	1	0	1
2009	MabCrk	80	1	0	0
2009	MabCrk	100	1	0	0
2009	MabCrk	95	1	0	0
2009	MabCrk	65	1	0	2
2009	MabCrk	100	1	1	0
2009	MabCrk	80	1	1	1
2009	MabCrk	90	1	0	0
2009	MabCrk	0		1	0

Appendix 5 (continued)

Year	Site	Average Cover +/- 1m	Point-Intercept *P. setaceum*	Exotic Richness	Native Richness	Year	Site	Average Cover +/- 1m	Point-Intercept *P. setaceum*	Exotic Richness	Native Richness
2009	CRR	0		2	2	2009	CRF	50	1	2	1
2009	CRR	0		0	0	2009	CRF	40	1	1	2
2009	CRR	0		1	2	2009	CRF	0		1	0
2009	CRR	0		1	1	2009	CRF	0		0	1
2009	CRR	10		1	2	2009	CRF	0		2	3
2009	CRR	50	1	0	1	2009	CRF	45		0	0
2009	CRR	0		0	0	2009	CRF	55	1	0	0
2009	CRR	0		0	0	2009	CRF	65	1	0	0
2009	CRR	65	1	1	2	2009	CRF	60	1	0	0
2009	CRR	65	1	0	0	2009	CRF	50	1	1	0
2009	CRR	85	1	2	1	2009	CRF	30		0	1
2009	CRR	85	1	1	0	2009	CRF	0		1	2
2009	CRR	60	1	0	0	2009	CRF	0		1	2
2009	CRR	0		0	0	2009	CRF	10	1	0	1
2009	CRR	0	1	0	0	2009	CRF	0		2	1
2009	CRR	0	1	0	0	2009	CRF	0		1	1
2009	CRR	0		0	0	2009	CRF	0		1	1
2009	CRR	15		0	1	2009	CRF	0	1	1	0
2009	CRR	35		0	2	2009	CRF	0		1	1
2009	CRR	0		0	0	2009	CRF	0		2	1
2009	CRR	0		1	1	2009	CRF	35	1	2	0
2009	CRR	45	1	1	0	2009	CRF	55		4	0
2009	CRR	35	1	0	0	2009	CRF	85	1	0	0
2009	CRR	70	1	1	1	2009	CRF	100	1	1	0
2009	CRR	100	1	0	0	2009	CRF	20	1	0	0
2009	CRR	35	1	0	1	2009	CRF	85		2	1
2009	CRR	25	1	0	1	2009	CRF	55	1	0	0
2009	CRR	0		1	1	2009	CRF	0	1	1	3
2009	CRR	75	1	0	1	2009	CRF	40		0	3
2009	CRR	72.5	1	0	0	2009	CRF	0		1	2
2009	CRR	0		1	2	2009	CRF	0		2	2
2009	CRR	0		0	1	2009	SDC	15		1	0
2009	CRR	0		1	2	2009	SDC	100	1	0	0
2009	CRR	65	1	0	0	2009	SDC	60	1	0	0
2009	CRR	15		0	1	2009	SDC	35	1	1	0
2009	CRR	70	1	0	1	2009	SDC	70	1	1	0
2009	CRR	70	1	1	1	2009	SDC	5		1	1
2009	CRR	80	1	1	1	2009	SDC	0		1	0
2009	CRR	70	1	1	0	2009	SDC	0		2	0
2009	CRR	55	1	2	0	2009	SDC	0		1	1
2009	CRF	35	1	1	2	2009	SDC	50	1	4	1
2009	CRF	40		0	1	2009	SDC	0		1	2
2009	CRF	60	1	0	0	2009	SDC	0		3	0
2009	CRF	40		1	1	2009	SDC	90	1	1	0
2009	CRF	100	1	0	0	2009	SDC	0		2	2
2009	CRF	25		1	1	2009	SDC	35		1	1
2009	CRF	0		4	1	2009	SDC	65	1	0	0

Appendix 5 (continued)

Year	Site	Average Cover +/- 1m	Point-Intercept *P. setaceum*	Exotic Richness	Native Richness
2009	SDC	60	1	0	1
2009	SDC	50	1	0	0
2009	SDC	50		0	0
2009	SDC	80	1	1	0
2010	MullCyn	50	2	1	1
2010	MullCyn	100	2	1	1
2010	MullCyn	75	2	1	1
2010	MullCyn	25	1	1	0
2010	MullCyn	100	0	0	0
2010	MullCyn	30	1	1	2
2010	MullCyn	0	0	0	0
2010	MullCyn	45	3	2	0
2010	MullCyn	100	1	0	0
2010	MullCyn	90	2	1	0
2010	MullCyn	85	1	0	1
2010	MullCyn	0	1	1	2
2010	MullCyn	0	2	2	1
2010	MullCyn	0	1	1	1
2010	MullCyn	0	1	1	1
2010	MullCyn	0	1	1	1
2010	MullCyn	15	0	0	3
2010	MullCyn	25	1	1	1
2010	MullCyn	45	1	1	1
2010	MullCyn	80	0	0	1
2010	MullCyn	0	0	0	1
2010	MullCyn	35	1	1	0
2010	MullCyn	0	0	0	0
2010	MullCyn	35	3	3	0
2010	MullCyn	90	1	0	1
2010	MullCyn	100	1	0	1
2010	MullCyn	65	1	0	1
2010	MullCyn	0	2	2	0
2010	MullCyn	0	2	2	1
2010	MuChu	30	0	0	1
2010	MuChu	55	0	0	2
2010	MuChu	100	1	0	1
2010	MuChu	95	1	0	2
2010	MuChu	100	1	0	0
2010	MuChu	70	1	0	3
2010	MuChu	65	2	1	3
2010	MuChu	0	0	0	2
2010	MuChu	10	0	0	1
2010	MuChu	40	0	0	1
2010	MuChu	0	0	0	2
2010	MuChu	0.5	1	0	1
2010	MuChu	65	1	0	2

Year	Site	Average Cover +/- 1m	Point-Intercept *P. setaceum*	Exotic Richness	Native Richness
2010	MuChu	100	1	0	0
2010	MuChu	95	1	0	1
2010	MuChu	60	0	0	1
2010	MuChu	100	1	0	0
2010	MuChu	85	1	0	1
2010	MuChu	70	1	0	0
2010	MuChu	10	0	0	1
2010	MuChu	0	0	0	0
2010	MuChu	0	0	0	2
2010	MuChu	75	1	0	0
2010	MuChu	0	0	0	0
2010	MuChu	45	1	0	3
2010	MuChu	0	0	0	3
2010	MuChu	65	1	0	1
2010	MuChu	40	0	0	0
2010	MuChu	100	1	0	2
2010	MuChu	50	1	0	1
2010	MuChu	0	2	2	2
2010	MabCrk	0	1	1	1
2010	MabCrk	0	3	3	1
2010	MabCrk	55	3	2	1
2010	MabCrk	10	2	2	2
2010	MabCrk	75	2	1	1
2010	MabCrk	60	3	2	1
2010	MabCrk	85	1	0	0
2010	MabCrk	95	1	0	1
2010	MabCrk	95	1	0	0
2010	MabCrk	55	2	1	1
2010	MabCrk	60	1	0	2
2010	MabCrk	70	2	1	2
2010	MabCrk	0	1	1	1
2010	MabCrk	0	1	1	2
2010	MabCrk	45	1	0	0
2010	MabCrk	90	1	0	1
2010	MabCrk	85	1	0	1
2010	MabCrk	95	1	0	2
2010	MabCrk	75	1	0	0
2010	MabCrk	5	1	0	0
2010	MabCrk	100	1	0	1
2010	MabCrk	0	1	1	2
2010	MabCrk	25	2	1	0
2010	MabCrk	90	1	1	1
2010	MabCrk	80	3	2	1
2010	MabCrk	40	2	1	2
2010	MabCrk	90	1	0	0
2010	MabCrk	30	1	1	1
2010	MabCrk	95	2	1	2

Appendix 5 (continued)

Year	Site	Average Cover +/- 1m	Point-Intercept *P. setaceum*	Exotic Richness	Native Richness	Year	Site	Average Cover +/- 1m	Point-Intercept *P. setaceum*	Exotic Richness	Native Richness
2010	MabCrk	80	1	0	1	2010	CRF	50	2	1	1
2010	MabCrk	90	1	0	0	2010	CRF	90	1	0	0
2010	MabCrk	95	1	0	1	2010	CRF	100	3	2	0
2010	MabCrk	90	1	0	2	2010	CRF	45	1	0	0
2010	MabCrk	35	0	0	1	2010	CRF	0	1	1	4
2010	CRR	0	2	2	1	2010	CRF	15	3	3	1
2010	CRR	80	2	1	0	2010	CRF	70	1	1	2
2010	CRR	30	0	0	2	2010	CRF	100	1	0	0
2010	CRR	15	1	1	1	2010	CRF	100	1	0	0
2010	CRR	35	0	0	2	2010	CRF	100	1	0	1
2010	CRR	15	2	1	1	2010	CRF	50	1	0	0
2010	CRR	0	2	2	2	2010	CRF	50	2	1	2
2010	CRR	0	0	0	0	2010	CRF	40	0	0	1
2010	CRR	5	0	0	0	2010	CRF	75	1	0	0
2010	CRR	72.5	1	0	1	2010	CRF	55	2	1	1
2010	CRR	30	1	0	0	2010	CRF	55	0	0	0
2010	CRR	95	1	0	0	2010	CRF	40	1	0	0
2010	CRR	20	1	0	1	2010	CRF	10	2	2	2
2010	CRR	60	0	0	1	2010	CRF	100	2	1	0
2010	CRR	65	1	0	0	2010	CRF	30	1	1	2
2010	CRR	40	1	1	1	2010	CRF	25	1	1	1
2010	CRR	Mowed	1	1	0	2010	CRF	50	1	1	2
2010	CRR	Mowed	2	1	1	2010	CRF	65	3	2	1
2010	CRR	Mowed	1	1	1	2010	CRF	100	1	0	0
2010	CRR	Mowed	0	0	0	2010	CRF	10	2	2	1
2010	CRR	Mowed	2	2	1	2010	CRF	0	2	2	1
2010	CRR	Mowed	1	1	0	2010	CRF	50	2	1	1
2010	CRR	Mowed	1	1	1	2010	CRF	80	1	0	0
2010	CRR	Mowed	1	0	2	2010	CRF	45	0	0	0
2010	CRR	Mowed	1	0	0	2010	CRF	70	1	0	1
2010	CRR	Mowed	1	0	1	2010	CRF	100	3	2	2
2010	CRR	Mowed	1	1	3	2010	CRF	50	2	1	4
2010	CRR	Mowed	0	0	4	2010	CRF	10	1	1	0
2010	CRR	Mowed	1	0	2	2010	CRF	65	1	0	0
2010	CRR	Mowed	1	0	1	2010	CRF	20	3	3	1
2010	CRR	Mowed	2	2	3	2010	CRF	15	1	1	2
2010	CRR	Mowed	1	0	4	2010	CRF	20	1	1	0
2010	CRR	0	2	2	1	2010	CRF	0	1	1	1
2010	CRR	55	2	1	2	2010	SMM	0	0	0	4
2010	CRR	60	0	0	0	2010	SMM	85	1	1	1
2010	CRR	0	1	1	2	2010	SMM	100	3	2	1
2010	CRR	10	1	1	1	2010	SMM	80	2	1	1
2010	CRR	55	0	0	1	2010	SMM	80	1	0	0
2010	CRR	80	2	1	1	2010	SMM	30	1	1	1
2010	CRR	50	2	1	0	2010	SMM	0	2	2	0
2010	CRR	0	0	0	0	2010	SMM	50	2	1	0
2010	CRR	0	1	1	1	2010	SMM	15	0	0	0

Appendix 5 (continued)

Year	Site	Average Cover +/- 1m	Point-Intercept *P. setaceum*	Exotic Richness	Native Richness
2010	SMM	100	3	2	0
2010	SMM	60	5	4	1
2010	SMM	55	2	1	2
2010	SMM	5	0	0	0
2010	SMM	60	2	1	1

Appendix 6: Total *Pennisetum setaceum* cover along transects at Southern California field sites over two years.

Overall *Pennisetum setaceum* cover in line-intercept measurements along transects in coastal sage scrub in Santa Monica Mountains (SAMO) and San Diego County (SD) in Southern California (as described in Chapter 3). *P. setaceum* cover is summed for the three transects per site for the two study years, except Rios Canyon where only two transects are compared (because part of one transect was mowed unexpectedly in the second year). Only the two sites in San Diego County that were included in both study years are shown.

		Overall Transect Cover (m)	
Region	**Site**	**2009**	**2010**
SAMO	Mullholland Canyon	10.7	13.2
SAMO	Point Mugu	12.45	15.21
SAMO	Malibu Creek	19.9	20.8
SD	Crestridge Rios Canyon	7.8	9.65
SD	Crestridge Flinn Springs	11.8	19.5

Appendix 7: *Pennisetum setaceum* growth and recruitment limitations in Riverside County.

Part 1: Recruitment of *Pennisetum setaceum* under natural rainfall conditions on type-converted exotic grassland slopes in Riverside, CA.
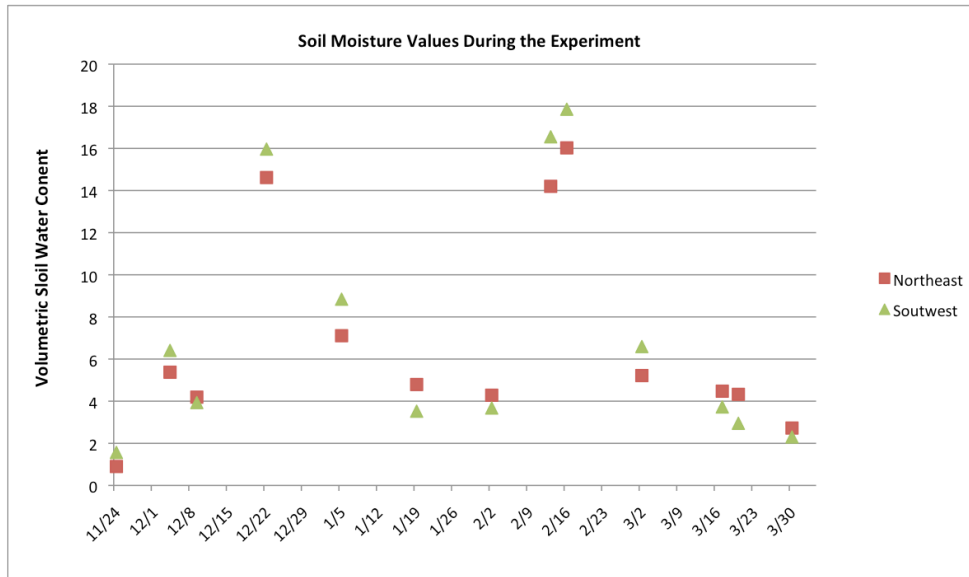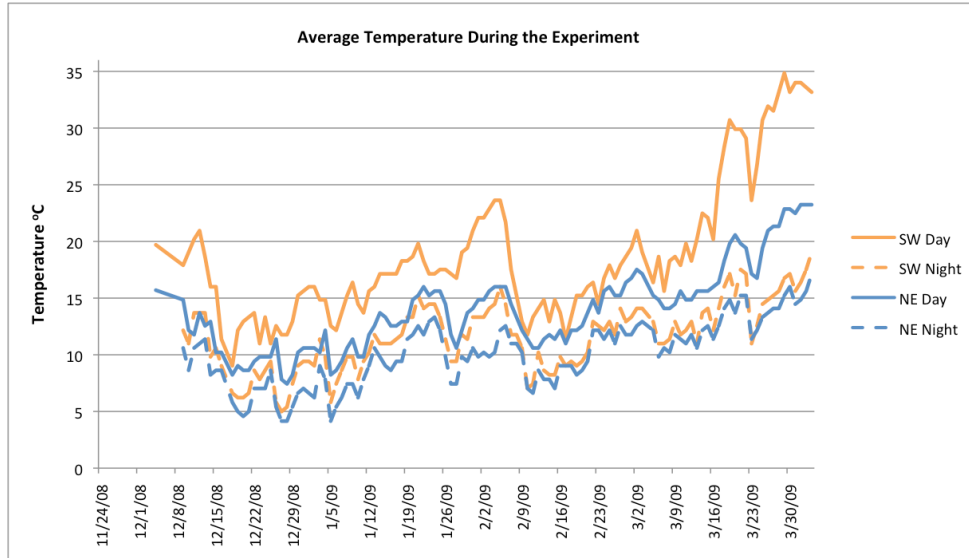

In 2008-2009, an experiment was established in Riverside, California (33.97°N, -117.32°W) in order to investigate the phenology of recruitment of *Pennisetum setaceum* in the Riverside area. Seeds harvested from greenhouse-grown plants were planted into replicated plots on southwest and northeast-facing slopes, in an area of degraded coastal sage scrub (heavily invaded by non-native grasses and *Brassica spp.*, with relic CSS diversity occurring on the rocky outcrops). Plots were situated only in areas lacking native shrubs, and dominated by non-native species. A total of 25 seeds was planted (within five cleared subplot areas) into 1x1m plots at roughly monthly intervals, with each plot being planted in consecutive months beginning in November of 2008. Plots were planted in 4 blocks in a randomized complete block design. The five 20x20cm sub-plots were cleared of vegetation and duff within each plot at the time of planting and five seeds were put in each of the five sub-plots within each plot, marked with a toothpick, and covered with a cage (plastic strawberry basket). Cages remained on each sub-plot for 1 month, or until growth reached the top of the cage (approximately 7cm), whichever occurred first. Monthly plantings were timed to coincide with a rain event within that month. Seeds were planted 1-3 days prior to the rain. All plots/cohorts were planted at least 2 weeks apart, depending on the rainfall. Sub-plots were censused for germination
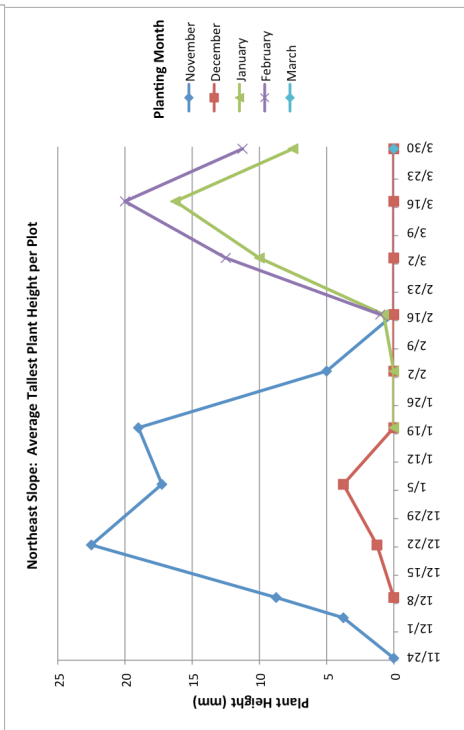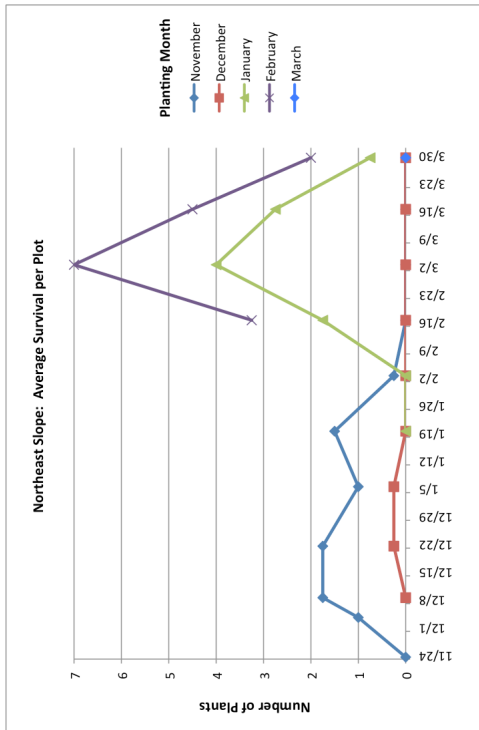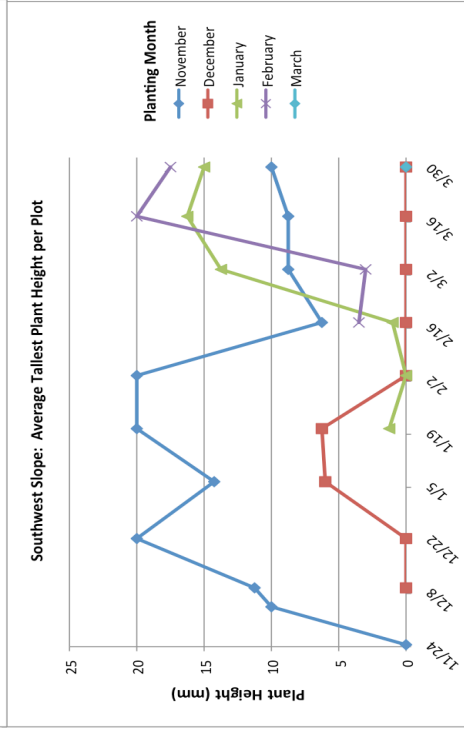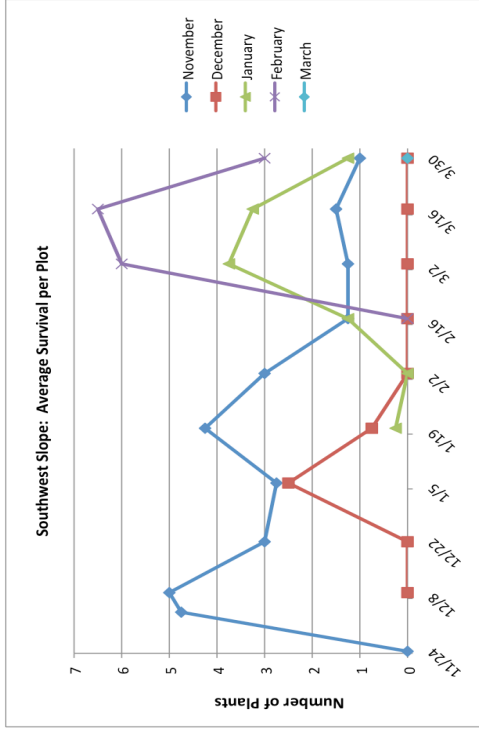
Appendix 7 (continued)

Part 1 (continued)

and growth 8 days post-rainfall. Subsequently, growth in all plots was measured in 2-week intervals, along with soil temperature and soil moisture. Height was measured to represent growth of fountain grass seedlings. Soil moisture (percent volumetric water content as a ratio of the volume of water in a given volume of soil to the total soil volume) and temperature were measured when seeds were planted, using a portable moisture probe (Spectrum Technologies, Field Scout, TDR 200), and portable temperature probes (Forestry Suppliers), respectively. Additionally, temperature was logged in 8-hour intervals daily using 2 HOBO devices (HOBO Pro-Series, Onset Computer Corp., www.onsetcomp.com/) placed 2.5cm beneath the soil surface. The experiment was terminated in March of 2009, after which no further substantial rain events occurred locally. Although germination and survival occurred for plants from several monthly planting cohorts, all plants died following the March 30th census and measurements. Increased germination and survival was observed on the southwest-facing slope, perhaps due to warmer temperatures. However, general censused numbers are low. Thus, several questions remain about the phenology of *P. setaceum* in Riverside, including whether there are other factors that regulate the establishment of this grass on open slopes.

Appendix 7 (continued)

Appendix 7 (continued)

Northeast Slope: Average Survival per Plot

Southwest Slope: Average Survival per Plot

Northeast Slope: Average Tallest Plant Height per Plot

Southwest Slope: Average Tallest Plant Height per Plot

Planting Month: November, December, January, February, March

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Part 2: Recruitment of *Pennisetum setaceum* under competition and added moisture conditions on type-converted exotic grassland slopes in Riverside, CA.

After the 2008-2009 experiment, which seemed to indicate that moisture or competition may be preventing establishment of *P. setaceum* at this site, an additional experiment was carried out. This experiment was conducted to investigate whether *P. setaceum* is limited from establishing on Riverside County slopes due to lack of moisture during the seedling stage or other resource limitation via competition with bromes/exotic grasses. In December 2010, an experiment was established on two degraded coastal sage scrub sites adjacent to the UC Riverside campus. Four blocks were established on each of the southwest- and northeast-facing slopes. The southwest-facing slope is now largely dominated by *Bromus rubens*, *Erodium cicutarium*, *Amsinckia menziesii*, *Cryptantha* spp. and *Pectocarya* spp. The Northeast slope is dominated by *Avena fatua* and *Bromus diandrus*. Each block contained each of the 5 treatments, arranged in a randomized complete block and factorial design. Treatments were the following: unweeded control (UC), control (C), added water (W), added bromes (B), and added water and bromes (W+B). All plots were established inside of 9.5cm wide x18cm deep pipe sunk to soil-level. Treatments were imposed 2 weeks after the pipes were installed to allow re-settling of soil. All plots (except the unweeded control) were weeded by hand where live plants were removed and duff was left in place. In all plots, five fountain grass seeds were planted and marked with wooden toothpicks. In the brome (B) plots, 20 seeds were

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also added (on the southwest-facing slope; the brome species used was *B. rubens*, and on the northeast-facing slope, *B. diandrus*). Plots receiving the water treatment were watered every two weeks. *P. setaceum* was weeded down to 1 surviving plant in each plot after establishment; however, very few plots had 2+ surviving plants past the two-leaf stage. The sources of plant material for this experiment were as follows: *P. setaceum* seeds were obtained from greenhouse-grown plants, and brome seeds were harvested in late-spring, derived from the field site. Pipes were made from 9.5cm diameter acrylonitrile-butadiene-styrene (ABS) plastic DWV pipe, cut to 18cm, with one end sanded slightly to an angle for ease of installation. Soil moisture and temperature were measured when seeds were planted, and weekly thereafter (pre-watering treatment) using a portable moisture probe (Spectrum Technologies, Field Scout, TDR 200), and portable temperature probes (Forestry Suppliers). Additionally, temperature was logged in 8-hour intervals daily using 2 HOBO devices (Onset Computer Corp., www.onsetcomp.com/) per slope, placed beneath the soil at 2.5 cm depth. Cover and density of species in unweeded plots were recorded at the time of planting. Subsequently, height of fountain grass in all plots was measured monthly, along with soil temperature and soil moisture. Density of brome species was inventoried monthly, and weeded to ensure even-density treatments across reps (approximately 8 plants per plot). At the end of the experiment in May, biomass was to be harvested; however, so little survival occurred of the *P. setaceum* that only height and number surviving were used to assess treatment differences. No *P. setaceum* plant survived past this date. ANOVA

Appendix 7 (continued)

showed no difference in height between survivors per treatment ($F_{4,17}=0.2570$, p=0.257).

Thus, other factors may be regulating establishment of *P. setaceum* at this location.

Appendix 7 (continued)

Table. 2010 establishment experiment raw data showing survival in May and plant height for surviving *Pennisetum setaceum* plants. Each replicate with a surviving plant is listed.

Treatment/Rep	Slope (NE or SW)	Surviving *P. setaceum* in May[1]	Tallest *P. setaceum* plant height (mm)
Unweeded Control	NE	1	30
Control (weeded)	SW	1	50
Control (weeded)	SW	1	55
Control (weeded)	NE	1	10
Control (weeded)	NE	1	15
Added Water	SW	2	20
Added Water	SW	1	35
Added Water	SW	1	20
Added Water	NE	1	20
Added Water	NE	1	25
Added Water	NE	1	25
Added *Bromus* seeds	SW	1	20
Added *Bromus* seeds	NE	1	40
Added Water and *Brome*	SW	1	35
Added Water and *Brome*	SW	1	20
Added Water and *Brome*	NE	1	40

[1] Treatments and replicates not listed had no surviving *P. setaceum* plants.