

CALIFORNIA STATE UNIVERSITY SAN MARCOS

THESIS SIGNATURE PAGE

THESIS SUBMITTED IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE

MASTER OF SCIENCE

IN

BIOLOGICAL SCIENCES

THESIS TITLE: Vegetation responses to anthropogenic nitrogen
deposition and nitrogen fertilization in chaparral and
coastal sage scrub of southern California

AUTHOR: Sarah Cecilia Pasquini

DATE OF SUCCESSFUL DEFENSE: October 24, 2008

THE THESIS HAS BEEN ACCEPTED BY THE THESIS COMMITTEE IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE IN BIOLOGICAL SCIENCES

George L. Vourlitis
THESIS COMMITTEE CHAIR


SIGNATURE

12/5/08
DATE

Tracey K. Brown
THESIS COMMITTEE MEMBER

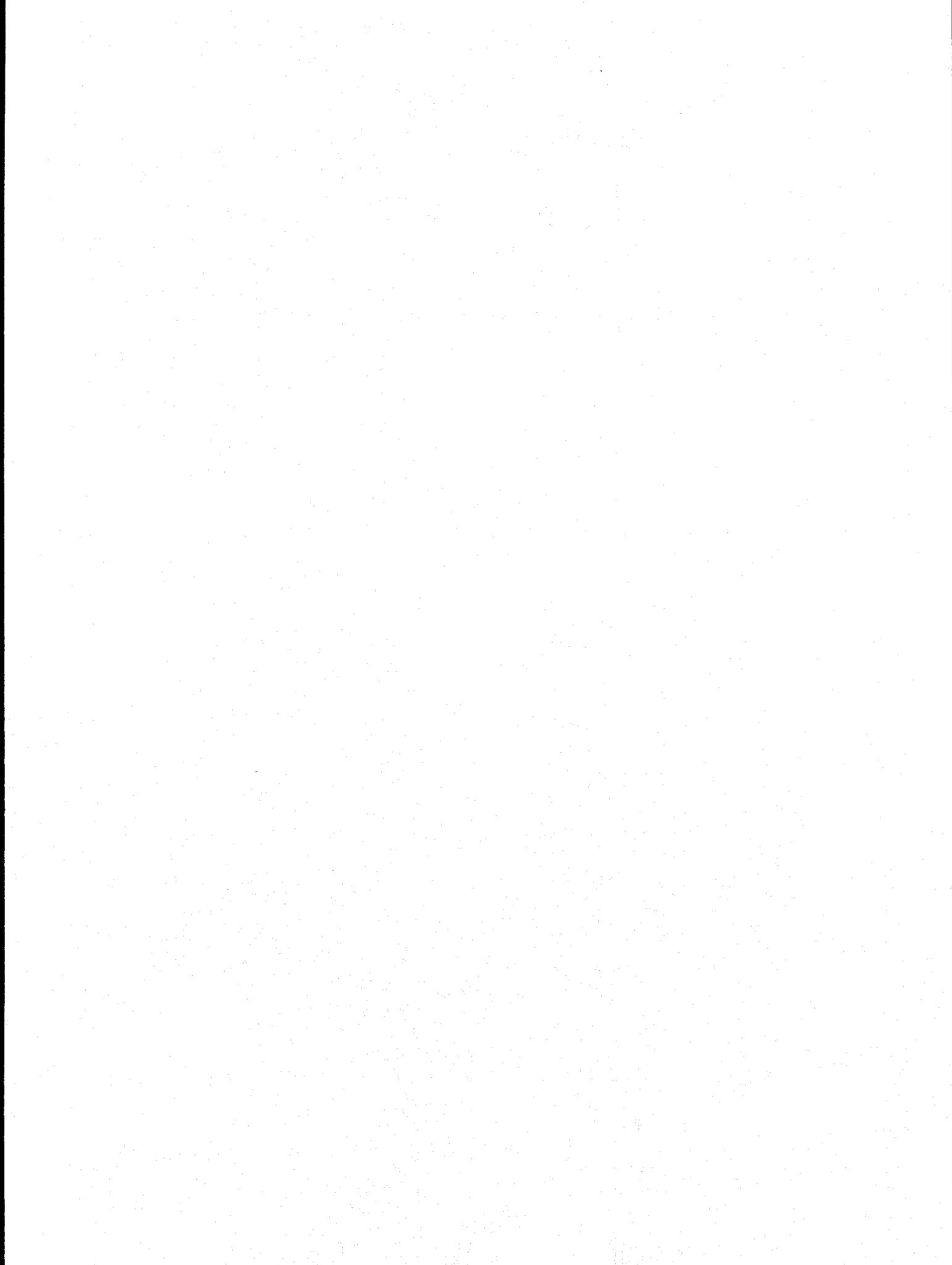

SIGNATURE

12/5/08
DATE

Louis S. Santiago
THESIS COMMITTEE MEMBER


SIGNATURE

10/24/2008
DATE



CALIFORNIA STATE UNIVERSITY

SAN MARCOS

Vegetation responses to anthropogenic nitrogen deposition and nitrogen
fertilization in chaparral and coastal sage scrub of southern California

A thesis submitted in partial satisfaction of the requirements for the degree
Master's of Science in Biological Sciences

by

Sarah Cecilia Pasquini

2008

ACKNOWLEDGEMENTS

There are many people that deserve my thanks for their support during my thesis work. First I would like to thank my advisor George Vourlitis for his guidance and support in my master's research and beyond and for the opportunity to attend graduate school. Thanks also to my other committee members Tracey Brown and my advisor at UC Riverside, Louis Santiago. Thanks so much to all the friends that helped me along the way especially Kerrie Sendall, Dave Faber, Andrew Lowe, Gypsi Zorba-Denison and Robert Bowers. I would like to thank all those who helped me with lengthy biomass measurements over the year including, but not limited to Rob Mustard, Zarela Guerrero, Sam Fernandez, Julie Kirker, Kimberly Davis, Sogand Tahiri, Kristen Falkner, Ryan Smith, Jaime Wilson, Raymond Hines and Chad Mitcham and any others that I have neglected to mention here. I would like to thank my parents Richard and Margaret Pasquini and my brother Vince for their love and support. Finally I must thank Blake Reemtsma for all his help ranging from field work to his spectacular editing skills, I love you. This thesis would not have been possible without the help and support of everyone mentioned above. Thank you all!

TABLE OF CONTENTS

SIGNATURE PAGE	i
TITLE PAGE	ii
ACKNOWLEDGEMENTS	iii
TABLE OF CONTENTS	iv
LIST OF TABLES AND FIGURES	v
THESIS ABSTRACT	vi
CHAPTER 1: INTRODUCTION	1
BACKGROUND	2
GENERAL METHODOLOGY	6
CHAPTER 2: NITROGEN ADDITION AND PRODUCTION	14
ABSTRACT	15
INTRODUCTION	16
HYPOTHESIS	18
METHODS	18
RESULTS	23
DISCUSSION	26
CHAPTER 3: NITROGEN DEPOSITION AND POST-FIRE RECOVERY	41
ABSTRACT	42
INTRODUCTION	43
HYPOTHESIS	45
METHODS	45
RESULTS	47
DISCUSSION	50
LITERATURE CITED	62

LIST OF TABLES AND FIGURES

FIGURES

1-1 Map of study sites	12
2-1 Total aboveground biomass	33
2-2 Leaf area index	34
2-3 Litterfall	35
2-4 Stem elongation	36
2-5 Net primary production	37
2-6 Species richness	38
2-7 Leaf mass ratio	39
2-8 Monthly precipitation for manipulation sites	40
3-1 Species composition	56
3-2 Total aboveground, shrub and average shrub biomass	57
3-3 Shrub biomass plotted as a function of shrub density	58
3-4 Annual grass biomass	59

TABLES

1-1 Site characteristics and locations of the study sites	13
2-1 Regression equations used to estimate biomass	32

APPENDICES

Appendix 1 Observed species at the chaparral study sites	60
Appendix 2 Observed species at the coastal sage scrub study site	61

THESIS ABSTRACT

Mediterranean-type ecosystems of southern California are exposed to atmospheric nitrogen deposition with some areas receiving 20-45 kg N ha⁻¹ annually. Although nitrogen is a limiting nutrient to plant growth, most nitrogen deposition in southern California occurs as dry deposition when plants are physiologically inactive due to seasonal drought. Due to this inactivity, it is unclear whether or not plants can utilize the additional nitrogen. The effects of nitrogen fertilization on aboveground plant production were tested in coastal sage scrub and chaparral ecosystems, and the effects of nitrogen deposition on post-fire recovery were observed in chaparral ecosystems. I found that experimentally added nitrogen did not result in increased production in either coastal sage scrub or chaparral sites. The vegetation did absorb added nitrogen but did not allocate aboveground production. Chaparral ecosystems did not respond to nitrogen deposition with increased rates of total or shrub biomass production post-fire but did show low density of large shrubs at high nitrogen deposition sites and high density of small shrubs at low nitrogen deposition sites. Since vegetation absorbs nitrogen but does not allocate it to increased production, it is important to discover the fate of the nitrogen because nitrogen deposition is projected to increase in southern California in future years.

Key words: disturbance, Mediterranean-type ecosystems, semi-arid ecosystems, *Adenostoma fasciculatum*, *Ceanothus*, air pollution

CHAPTER 1

INTRODUCTION

BACKGROUND

Air pollution is a growing problem in many urban areas (Vitousek et al. 1997), especially in southern California (Bytnerowicz et al. 1987, Fenn et al. 2003a). One of the consequences of air pollution is the deposition of nitrogen onto terrestrial and marine ecosystems (Vitousek et al. 1997). The South Coast Air Basin of southern California, which is comprised of portions of Los Angeles, Orange, Riverside and San Bernardino Counties, is exposed to some of the highest levels of nitrogen deposition in the world (Fenn et al. 1998, 2002, 2003a). South-facing slopes of the San Gabriel and San Bernardino Mountains are the most exposed areas and can receive inputs of nitrogen between 20-45 kg N ha⁻¹ per year (Fenn et al. 2003a), but some areas, especially at high elevation, can receive up to 145 kg N ha⁻¹ annually (Fenn and Poth 2004).

Atmospheric nitrogen pollution comes primarily from two sources: the use of fertilizer and the burning of fossil fuels (Boring et al. 1988, Vitousek et al. 1997, Fenn et al. 1998, Fenn et al. 2003a). It is estimated that the burning of fossil fuels contributes more than 25 Tg N per year (1 Tg = 10¹² g) and fertilizer production contributes more than 86 Tg N per year of nitrogen deposition (Galloway et al. 1994). Nitrogen deposition occurs in various chemical forms including nitrous oxide (N₂O), nitric oxide (NO), ammonium (NH₄⁺), ammonia (NH₃), nitric acid vapor (HNO₃), particulate (aerosol) nitrate (NO₃⁻) and peroxyacetyl nitrate (PAN), though oxidized forms (NO₂, HNO₃,

PAN) dominate in areas near photochemical smog sources resulting from the burning of fossil fuels (Bytnerowicz and Fenn 1996, Fenn et al. 2003a). In general, nitrogen oxides result from the burning of fossil fuels, and ammonia and ammonium result from fertilizer production and use (Bytnerowicz and Fenn 1996).

The effects of nitrogen deposition on aquatic ecosystems have been extensively studied. High nitrogen deposition can decrease water quality (Vitousek et al. 1997) and clarity (Jassby et al. 1994, Sickman et al. 2003) and increase toxic algae blooms (Burkholder et al. 1992). Nitrogen deposition causes elevated nitrate in runoff to aquatic ecosystems from chaparral in the southwestern Sierra Nevada (Williams et al. 1996, Fenn and Poth 1999, Fenn et al. 2003b).

Nitrogen deposition can also have impacts on human health. Nitrogen deposition has been shown to exacerbate asthma in children (McConnel et al. 1999) and indoor nitrous oxide (N_2O) pollution may cause as many as two million deaths per year in developing countries (Wolfe and Patz 2002, Townsend et al. 2003). Increased inorganic nitrogen in surface water may also increase the abundance and distribution of malaria carrying *Anopheles* mosquitoes (Rejmankova et al. 1991, Teng et al. 1998, Townsend et al. 2003) and *Culex* and *Aedes* mosquitoes which are vectors of La Crosse encephalitis, Japanese encephalitis and West Nile virus (Walker et al. 1991, Toth and Melton 2000, Sunish and Reuben 2001, Townsend et al. 2003).

Nitrate in drinking water from fertilizer runoff is a problem in both developing and developed countries and can cause health problems including reproductive damage, methemoglobinemia and cancer (Kramer et al. 1996, Townsend et al. 2003).

Although much is known about how anthropogenic nitrogen deposition affects aquatic ecosystems, less is known about how it affects terrestrial ecosystems. In general, nitrogen is a limiting factor in terrestrial plant growth (Kirkby 1981, Vitousek and Howarth 1991). Nitrogen deposition has been shown to increase net primary production in eastern (Boring et al. 1988), boreal (Vitousek 1982) and tropical forests (Giardina et al. 2003). However, for roots to be able to take up nitrogen from the soil, the nitrogen has to be in solution, and, without sufficient water, nitrogen will not be taken up by the plant (Larcher 2003). Most of the nitrogen in southern California (85-90%) is deposited in the late summer and early fall as dry deposition and becomes available as an ephemeral pulse following the first rainfall or heavy fog (Riggan et al. 1985, Bytnerowicz and Fenn 1996, Fenn et al. 1998, 2003a), when deposited nitrogen becomes available in solution. However, vegetation is largely dormant when atmospheric deposition is highest due to production limitations from seasonal drought (Poole and Miller 1975, Gray and Schlesinger 1981, Bytnerowicz and Fenn 1996, Larcher 2003), and it is unclear whether vegetation can utilize the brief pulse of available nitrogen.

Much research has been done on the effects of nitrogen deposition (wet and dry) in the northeastern United States and Europe (Bytnerowicz and Fenn 1996). Forests in these areas have shown nitrogen saturation in response to high nitrogen inputs (Aber et al. 1989, Bytnerowicz and Fenn 1996, Fenn et al. 1998), where levels of available nitrate and ammonium exceed plant and microbial nutrient demands (Aber et al. 1989). In the case of nitrogen saturation, continued nitrogen addition no longer causes an increase in productivity because the ecosystem is no longer nitrogen limited, but instead continued nitrogen input can cause limitation in other nutrients such as phosphorus (Mohren et al. 1986). Less is understood about how nitrogen deposition affects semi-arid ecosystems of the western United States and to what extent ecosystems may experience nitrogen saturation.

Chaparral and coastal sage scrub (CSS), or soft chaparral, ecosystems are Mediterranean-type ecosystems, which are characterized by warm, dry summers and mild, wet winters (Barbour et al. 1999). Most of the rainfall occurs in a few storms from November through April (Keeley 2000). Chaparral vegetation is generally evergreen and sclerophyllous (hard-leaved) such as *Adenostoma fasciculatum* Hook and Arn., *Adenostoma sparsifolium* Torr. and *Ceanothus* species, whereas coastal sage scrub vegetation is drought-deciduous and soft-leaved as is the case with *Artemisia californica* Less. and *Salvia mellifera* Greene (Barbour et al. 1999). Mediterranean-type ecosystems are areas of high biodiversity (Cowling et al. 1996) comprised of

woodlands, savanna, semi-desert and shrublands, and usually occur between the 30th and 40th parallels in each hemisphere (Barbour et al. 1999).

Mediterranean-type ecosystems are also heavily influenced by the frequent occurrence of fire (Barbour et al. 1999, Keeley 2000).

With the population of North America increasing, nitrogen deposition is expected to increase 25% by 2020 (Galloway et al. 2004). With the problem of anthropogenic nitrogen deposition not disappearing in the near future, increased understanding of the ability of coastal sage scrub and chaparral vegetation to utilize deposited nitrogen is crucial to further understanding of the terrestrial nitrogen and carbon cycles of these ecosystems. If terrestrial ecosystems are not able to utilize the deposited nitrogen, leaching of excess nitrogen could cause groundwater degradation (Riggan et al. 1985, Fenn et al. 1996, Vitousek et al. 1997), eutrophication of aquatic ecosystems (Vitousek et al. 1997, Townsend et al. 2003), and/or an increase in greenhouse gas emissions (Galloway 1994, Fenn et al. 1996, Fenn et al. 1998).

GENERAL METHODOLOGY

Chaparral and coastal sage scrub sites were selected along an established nitrogen deposition gradient (Padgett et al. 1999, Fenn et al. 2003a, Tonnesen et al. 2007) in southern California to determine how

atmospheric nitrogen deposition affects coastal sage scrub and chaparral production and chaparral post-fire recovery. The sites were sampled four times annually for three years to determine how atmospheric nitrogen deposition affects coastal sage scrub and chaparral production.

Site selection

In this study from December 2003 through November 2006, a total of four research sites in southern California were utilized (Figure 1-1): three were chaparral and one was coastal sage scrub. Within each ecosystem type, sites were selected based on similar characteristics including rainfall, elevation, soil texture, vegetation, slope, and logistical and security constraints (Table 1-1). The sites were designated as either high- or low-deposition on estimated nitrogen deposition. Low nitrogen deposition sites had nitrogen deposition levels similar to non-polluted coastal areas. One of the chaparral sites burned during this study, while the other two burned a year before, just prior to the study's initiation. All of the sites, however, burned within a 14-month period.

The Sky Oaks Field Station (SOFS) site is a low-deposition chaparral site located in northeastern San Diego County, California, within a research reserve managed by San Diego State University. The site is 1418 m above sea level, has a 4-10° slope with a SE-SW aspect and receives an average of 57 cm of precipitation annually which is comprised of about 90% rain. Using

data from a high-resolution (4 km²) Community Multiscale Air Quality (CMAQ) N-deposition model (Tonnesen et al. 2007) nitrogen deposition (wet + dry) is estimated at 8.1 kg N ha⁻¹ annually (Table 1-1). This site burned in July of 2003. Prior to burning, the site was a mature stand (50 years) dominated by the evergreen shrub *Adenostoma fasciculatum* (Table 1-1). Following the fire, the site was dominated by *A. fasciculatum* resprouts and seedlings, *Ceanothus greggii* A. Gray and herbaceous "fire followers" such as *Penstemon spectabilis* Thurb. and *Trichostema parishii* Vasey.

The San Dimas Experimental Forest (SDEF) site is a high-deposition chaparral site located in the San Gabriel Mountains within the Angeles National Forest of northern Los Angeles County, California, and is managed by the United States Forest Service. The site is 451 m above sea level, has a slope of 4-12° with a SE-SSW aspect and receives an average of 44 cm of rainfall annually. Nitrogen deposition (wet + dry) is estimated at 18.4 kg N ha⁻¹ annually (Table 1-1). Prior to burning in September of 2002, the site was a 42-year-old stand of primarily *Adenostoma fasciculatum*. Following fire, the site was dominated by *A. fasciculatum* and *Ceanothus crassifolius* Torr. with other shrubs such as *Malosma laurina* (Nutt.) Abrams and *Baccharis salicifolia* (Ruiz and Pav.) Pers., and invasive annuals such as *Hirschfeldia incana* Lagr.-Fossat, *Bromus tectorum* L. and *Avena fatua* L.

The San Bernardino National Forest (SBNF) site is a high-deposition chaparral site located in the San Bernardino Mountains of San Bernardino

County, California. The site is 807 m above sea level, receives on average 56 cm of rainfall annually and is located on a 4-10° slope with a SE-SW aspect. Nitrogen deposition (wet + dry) is estimated at 11.9 kg N ha⁻¹ annually (Table 1-1). Prior to burning in October of 2003, the site was a 35-year-old stand dominated by *Adenostoma fasciculatum* but had more open space than SOFS and SDEF. Following the fire, the site was dominated by *A. fasciculatum* and *Ceanothus crassifolius* with other shrubs such as *Dendromecon rigida* Benth and *Eriodictyon trichocalyx* A. Heller and invasive annuals including *Bromus tectorum*.

The Santa Margarita Ecological Reserve (SMER) is a low-deposition coastal sage scrub site located in southern Riverside County, California, and is within a research reserve managed by San Diego State University. The site is 338 m above sea level, receives on average 33 cm rainfall annually and is located on a 9-11° slope with a S-SW aspect. Nitrogen deposition (wet + dry) is estimated at 6.3 kg N ha⁻¹ annually (Table 1-1). The site is a 35-year-old stand dominated by *Artemisia californica* and *Salvia mellifera*. There is little other vegetation, which consists primarily of *Gutierrezia californica* (DC.) Torr. and A. Gray, *Yucca whipplei* Torr. and several *Gnaphalium* species.

Experimental Design

This study had a manipulative and an observational component. For the manipulative portion of the study, eight 10 x 10 m (100 m²) plots were set up at the two low-deposition sites (SOFS and SMER). At these sites, four of the eight plots were randomly selected to receive *in-situ* nitrogen addition in the form of ammonium nitrate (NH₄NO₃) fertilizer in the fall of each year beginning in 2004, and four unfertilized plots served as unmanipulated controls. The fertilizer was added in an amount equivalent to 50 kg N ha⁻¹ to simulate atmospheric nitrogen deposition levels consistent with areas of highest deposition in the South Coast air basin of southern California and future deposition projected by increases in population and fossil fuel emissions (Riggan et al. 1985, Galloway et al. 1994, Bytnerowicz and Fenn 1996, Fenn et al. 2003a). NH₄NO₃ was used because NH₃ and NO_x are the primary forms of dry nitrogen deposition in southern California (Fenn et al. 2003a). At each of the eight plots per site, the measurements outlined in the following chapters were performed four times per year in the winter (December-January), spring (March-April), summer (June-July) and fall (September-October). Results from the measurements were used to compare added nitrogen and control plots within each ecosystem type to determine the effects of the nitrogen deposition on the vegetation.

For the observational portion of the study, post-fire recovery at the low-deposition chaparral site SOFS was compared to two high-deposition sites,

SBNF and SDEF. All three chaparral sites burned within a 14-month period in the 2002-2003 fire season. At each of the high-deposition sites, four 100 m² plots were set up and measurements were performed as described in the manipulation portion above. The measurements were compared between the control plots of the low-deposition chaparral site SOFS and the high-deposition sites SBNF and SDEF to determine how nitrogen deposition affected post-fire recovery.

Taxonomy

To ensure accuracy and reflect the most recent information, the Jepson Flora Project's Online Interchange (2007) was used for all plant species treatments and designations of California native and non-native species.

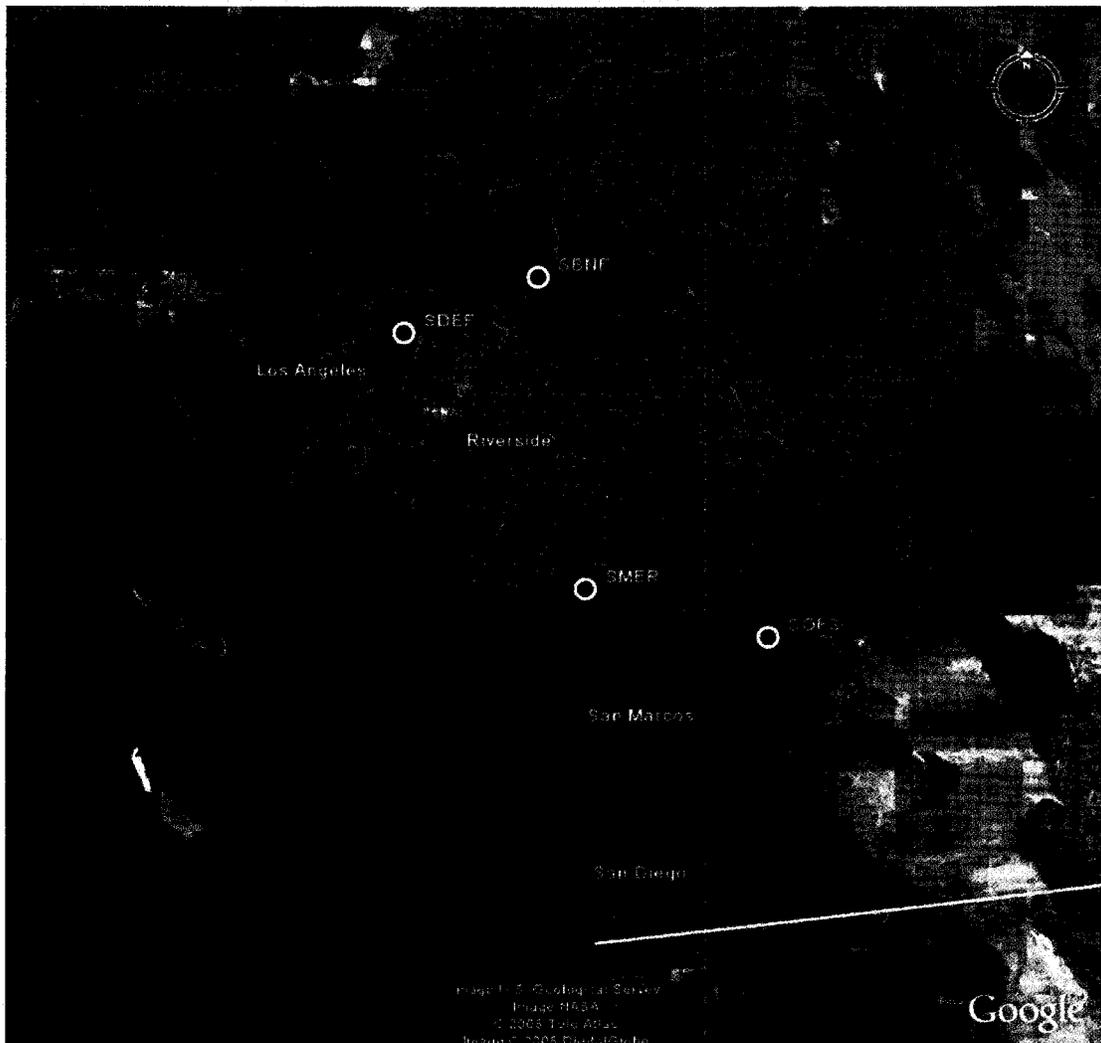


Figure 1-1. Map showing locations of study sites: Sky Oaks Field Station (SOFS), San Bernardino National Forest (SBNF), San Dimas Experimental Forest (SDEF) and Santa Margarita Ecological Reserve (SMER). Image courtesy of Google Earth.

Table 1-1. Site characteristics and locations of the study sites. Total nitrogen deposition (wet + dry) were estimated from a high-resolution Community Multiscale Air Quality (CMAQ) nitrogen deposition model from Tonnesen et al. (2007). Rainfall data were from the Western Regional Climate Center (www.wrcc.dri.edu, verified 29 March 2007) for locations near the study sites and represent over 50-year averages (Vourlitis et al. 2007b). Data for soil texture and bulk density for SOFS, SDEF and SMER are for the upper 0-10 cm soil layer from Vourlitis et al. (2007c). Soil texture and bulk density data for SBNF are for the upper 0-10 cm soil Vourlitis and Pasquini (2008). Fire occurrences for SOFS, SBNF and SDEF are from personal observations. Stand age for SMER from Santa Margarita Ecological Reserve website (<http://fs.sdsu.edu/kf/reserves/smer/>).

Characteristic	Sky Oaks Field Station (SOFS)	San Bernardino National Forest (SBNF)	San Dimas Experimental Forest (SDEF)	Santa Margarita Ecological Reserve (SMER)
Latitude and longitude (N:W)	33°21':116°34'	34°19':117°18'	34°10':117°44'	33°29':117°09'
California county	San Diego	San Bernardino	Los Angeles	Riverside
Vegetation type	Chaparral	Chaparral	Chaparral	Coastal sage scrub
Nitrogen deposition (kg N ha ⁻¹ y ⁻¹)	8.1	11.9	18.4	6.3
Elevation (m)	1418	807	451	338
Annual Rainfall (cm)	57	56	44	33
Sand, silt, clay (%)	78, 14, 8	78, 16, 6	71, 18, 11	68, 19, 13
Soil texture class	Sandy loam	Loamy sand	Sandy loam	Sandy loam
Soil nomenclature [†]	Ultic haploxeroll	Typic xerorthent	Typic xerorthent	Lithic haploxeroll
Bulk Density (g cm ⁻³)	1.34	1.28	1.26	1.22
Dominant species ^{††}	<i>Af</i> , <i>As</i> , <i>Cg</i> , <i>Qd</i> ¹	<i>Af</i> , <i>Cc</i>	<i>Af</i> , <i>Cc</i> , <i>Qd</i> ²	<i>Ac</i> , <i>Sm</i>
Slope/aspect	4-10°/SE-SW	4-10°/SE-SW	4-12°/SE-SSW	9-11°/S-SW
Burned	July 2003	October 2003	September 2002	> 35 years ago
Stand age prior to burn	50 years	35 years	42 years	N/A

[†]Soil nomenclature for SOFS from Moreno and Oechel (1992), for SDEF from Riggan et al. (1985), and for SMER from Knecht (1971).

^{††}*Ac* = *Artemisia californica*; *Af* = *Adenostoma fasciculatum*; *As* = *Adenostoma sparsifolium*; *Cg* = *Ceanothus greggii*; *Cc* = *Ceanothus crassifolius*; *Qd*¹ = *Quercus dumosa*; *Qd*² = *Quercus durata*; *Sm* = *Salvia mellifera*.

CHAPTER 2

NITROGEN ADDITION AND PRODUCTION

ABSTRACT

Terrestrial ecosystems of southern California receive some of the highest levels of nitrogen deposition in the world due to air pollution. Some exposed areas in the mountains can routinely receive inputs of 20-45 kg N ha⁻¹ per year. Because Mediterranean-type ecosystems of southern California are typically nutrient poor and nitrogen is a limiting nutrient in plant production, it was hypothesized that increases in nitrogen availability would result in increased production. To test this hypothesis, measures of aboveground production were compared between nitrogen fertilized and control plots at a coastal sage scrub and a chaparral site with low atmospheric deposition. Results showed no effect of nitrogen addition on aboveground production at either site. Data indicate that the vegetation is taking up experimentally deposited nitrogen, but it appears that the nitrogen is not being used for aboveground production. Explanations that may account for this are: 1) vegetation at these sites are "luxury consuming" nitrogen (uptake in excess of biotic demand), 2) production at these sites is either not nitrogen limited, or is co-limited by nitrogen and another resource (likely water), or 3) the nitrogen is being used in another way (e. g. increased photosynthesis for plant defense and/or carbon storage, and/or increased belowground production). Since nitrogen deposition in southern California is projected to increase 25% by the year 2020, it is important to determine the extent to which these ecosystems can utilize deposited nitrogen.

INTRODUCTION

Nitrogen is a limiting factor in plant growth, and increases in nitrogen availability typically increase growth (Kirkby 1981, Vitousek and Howarth 1991). Nitrogen has been shown to increase net primary production (NPP) as demonstrated by increased litterfall mass in eastern (Boring et al. 1988) boreal (Vitousek 1982) and tropical forests (Giardina et al. 2003). Increased nitrogen availability increases aboveground and belowground biomass in temperate forests (Nadelhoffer et al. 1985), root length in Chilean matorral (Kummerow et al. 1982), and root and shoot biomass in a coastal dune-slack community of southern California (Vourlitis 1991). Increased production in response to nitrogen deposition may cause terrestrial ecosystems to act as a greater sink for anthropogenic CO₂ (Peterson and Melillo 1985, Schindler and Bayley 1993). Nitrogen deposition may not result in increased production if ecosystems are already nitrogen saturated where nitrogen input is in excess of biotic demand (Aber et al. 1991, Fenn et al. 1998), or if other mineral nutrients such as phosphorus are or become limiting (Mohren et al. 1986). Nitrogen deposition can also lead to changes in species composition. In Europe, nitrogen deposition causes shrublands to convert to grasslands (Bobbink 1991), and, in the Great Plains of the United States, nitrogen deposition is implicated in the expansion of forests (Köchy and Wilson 2001). Nitrogen deposition can also alter forest carbon cycling and fire cycles by fuel

accumulation (Grulke and Balduman 1999, Fenn and Poth 2001). Whether or not these patterns hold true for chaparral and coastal sage scrub is less clear.

In Mediterranean shrub ecosystems, including chaparral and coastal sage scrub, shrub growth has been shown to be limited by low soil nutrient availability, and shrub production has been stimulated by nitrogen fertilization (Kummerow et al. 1982). Nitrogen addition resulted in increased production of *Adenostoma fasciculatum* and *Ceanothus greggii* (Hellmers et al. 1955, McMaster et al. 1982). Other research indicates that *Adenostoma fasciculatum* experiences most of its nutrient uptake in the winter during rainfall when plants were not experiencing aboveground growth (Mooney and Rundel 1979, Shaver 1981). These results suggest that evergreen plants store nutrients in old tissue (leaves and stems) during the non-growth period for use in subsequent growth periods when nutrient demands are greater (Mooney and Rundel 1979, Shaver 1981). In coastal sage scrub ecosystems, nitrogen addition resulted in increased biomass of *Salvia leucophylla* and *Ceanothus megacarpus* (Gray and Schlesinger 1983) and increased shoot yield of *Artemisia californica*, *Encelia farinosa* and *Eriogonum fasciculatum* (Padgett and Allen 1999). Although nitrogen addition generally stimulates production, nitrogen deposition has also been shown to cause declines in coastal sage scrub vegetation through conversion to grasslands (Westman 1981, Allen et al. 1998, Padgett and Allen 1999) and increases in non-native vegetation (Allen et al. 1998, Minnich and Dezzani 1998). This increase in

non-native vegetation may be caused by greater relative responses to nitrogen by non-native annuals than the responses of native shrubs (McMaster et al. 1982, Padgett and Allen 1999).

Because nitrogen deposition in southern California is primarily (85-90%) dry deposition in the late summer and early fall when vegetation is largely dormant due to drought, it is unclear whether and to what extent deposited nitrogen is utilized by vegetation when it becomes available as a brief pulse following the first rainfall (Riggan et al. 1985, Bytnerowicz and Fenn 1996, Fenn et al. 1998, 2003a).

HYPOTHESIS

Coastal sage scrub and chaparral vegetation will show increased aboveground production in response to experimental dry-season nitrogen deposition.

METHODS

Aboveground biomass

Aboveground biomass was estimated at chaparral and coastal sage scrub sites (Table 1-1) that contained nitrogen fertilized and control plots four times per year, seasonally, using non-destructive dimensional analysis (Bonham 1989). Vegetation at least 20 cm in height was measured within a 2

m radius (12.57 m²) circular subplot located in the center of each plot.

Vegetation under 20 cm was measured within a 0.5 x 0.5 m (0.25 m²) subplot in the center of the plot. Plant volume was quantified by measuring the crown width at the widest point, the perpendicular width and the plant height, and calculated as shown in the following equation (Bonham 1989):

$$V = \frac{\pi D^2}{4} \bullet h \quad (1)$$

where V is plant volume, D is average plant diameter and h is plant height.

Plant volume was calculated assuming a cylindrical shape (Bonham 1989).

Vegetation biomass was estimated from volume using regression equations that were developed for each species by harvesting measured plants of various sizes (Table 1-1). The shrubs were then dried at 80°C for at least one week and weighed. Shrub weight and volume data were natural log transformed to reduce variation. For species that did not occur frequently and/or lacking regression equations, generalized shrub and herbaceous plant equations were used (Table 1-1). In seasons where many annuals and grasses were present in the 0.25 m² subplot, all herbaceous vegetation within the subplot was harvested, dried and weighed to directly measure biomass.

Leaf area index

Leaf area index (LAI) was calculated from measurements of photosynthetically active radiation (PAR) using a linear PAR/LAI ceptometer

(Decagon model PAR-80, Decagon Devices, Inc., Pullman, WA). PAR is the solar radiation between 400 and 700 nm in wavelength that plants use for photosynthesis (Decagon Devices, Inc. 2004). LAI of the canopy was calculated from differences in above- and below-canopy PAR using a method described in Goudriaan (1988) and the software provided by Decagon Devices, Inc.

Measurements of LAI were performed four times per year, seasonally, at the center of each plot to coincide with the estimates of aboveground biomass. Measurements were performed at or near solar noon during periods of uniform light conditions (e.g. full sun or full cloud). When periods of non-uniform light were present, additional above canopy measurements of PAR were performed to adjust for changing light conditions. These data were used along with aboveground biomass regression equations to obtain a secondary estimate of leaf biomass.

Litterfall

Litterfall is plant leaves, twigs and other organic matter that falls to the ground to make up a litter layer. Litterfall was collected using four 25.4 x 25.4 cm (0.0645 m²) mesh traps that were randomly placed within each plot. Litterfall accumulated in these traps was collected four times per year, seasonally. In the field, rocks and soil were removed through the mesh of the traps. In the laboratory, litterfall was oven dried at 80°C for at least one week,

sorted a second time using a 1 mm mesh sieve to remove any additional non-organic matter, and then weighed to the nearest 0.1 mg.

Net primary productivity (NPP)

Net primary productivity (NPP) was calculated for each year using production and litterfall as shown in the following equations (Gower et al. 1999):

$$P_i = B_t - B_{t-1} \quad (2)$$

$$NPP = \sum (P_i + D_i) \quad (3)$$

where P_i is production over seasonal interval i , B_t is the current aboveground biomass, B_{t-1} is the previous aboveground biomass measured three months earlier, NPP is net annual aboveground primary production and D_i is litterfall at seasonal interval i . In equation 2 if $B_t - B_{t-1}$ was not greater than zero, then $P_i = 0$. P_i and D_i were then summed over the year to calculate NPP .

Shoot elongation

Shoot elongation was also measured to provide an additional index of shrub growth. Apical shoots of *Adenostoma fasciculatum* and *Ceanothus crassifolius* and *greggii* (chaparral) and *Salvia mellifera* and *Artemisia californica* (coastal sage scrub) were tagged, and the length of the shoot from the tag to the tip of the shoot was measured. At least six shoots per species were tagged in each plot. The tagged stems were measured at each of the

four seasonal collection periods. Shoot elongation was considered the difference between consecutive measurements. If tags became lost or fell off during the course of the study, they were replaced at the next collection period.

Species richness

Because all plants measured for biomass were also identified, species richness was also examined. Species richness for each plot was simply the number of species that occurred during each collection in the 2 m radius circular subplot.

Statistical analysis and derived quantities

Aboveground biomass and litterfall were estimated for the entire 10 x 10 m (100 m²) plots based on the measurements within the subplots by dividing the total by the area of the subplot. All data presented in figures represent an average of four plots at each site ($n = 4$). Differences between control and added nitrogen plots were tested using repeated measures analysis of variance (RMANOVA). RMANOVAs were performed on data for each plot ($n = 4$) for each season. The factors used in the RMANOVA were nitrogen (i. e. control and added nitrogen) and time (i. e. season, year or time interval). If the distribution of data was non-normal, the data were either natural log or square root transformed to produce a normal distribution. In

cases where transformation did not result in a normal distribution, the RMANOVA was performed on non-transformed data since RMANOVA is robust to violations of normality (Zar 1999). Linear regressions to estimate aboveground biomass from plant volume, leaf biomass proportion as a function of the natural log of shrub volume, and RMANOVAs were performed using NCSS (NCSS version 2004, NCSS, Kaysville, Utah, USA). Statistical difference was accepted at an alpha of 0.05 (Zar 1999).

RESULTS

Total aboveground biomass

Nitrogen addition did not affect total aboveground biomass for chaparral or coastal sage scrub manipulation plots, however, time was a significant factor in total aboveground biomass for control and added nitrogen plots for both ecosystems types (Figure 2-1). For the chaparral site (SOFS), aboveground biomass increased over the course of the study from winter 2004 through fall 2006 to reach a peak biomass of $666.4 \pm 200.3 \text{ g m}^{-2}$ for the control plots and $343.9 \pm 127.2 \text{ g m}^{-2}$ for the added nitrogen plots (Figure 2-1). For the coastal sage scrub site (SMER), total biomass also increased over time and peaked in 2005 in spring and summer and reached a high in fall 2006 of $631.2 \pm 51.50 \text{ g m}^{-2}$ for the control and $805.3 \pm 153.6 \text{ g m}^{-2}$ for the added nitrogen plots (Figure 2-1).

Leaf area index (LAI)

Nitrogen addition also did not affect leaf area index (LAI) for chaparral or coastal sage scrub manipulation plots; although, there were significant differences in LAI over time for both ecosystem types (Figure 2-2). For the chaparral site, LAI generally increased between summer 2004 and fall 2006 from $0.09 \pm 0.12 \text{ m}^2 \text{ m}^{-2}$ to $0.25 \pm 0.04 \text{ m}^2 \text{ m}^{-2}$ for control and from $0.16 \pm 0.06 \text{ m}^2 \text{ m}^{-2}$ to $0.32 \pm 0.11 \text{ m}^2 \text{ m}^{-2}$ for added nitrogen plots (Figure 2-2). LAI was at an annual low in winter 2005 and spring 2006 and at a high in summer 2005 and fall 2006 for SOFS. For the coastal sage scrub site, LAI varied from a low of $0.89 \pm 0.04 \text{ m}^2 \text{ m}^{-2}$ in fall 2006 to a high of $2.07 \pm 0.52 \text{ m}^2 \text{ m}^{-2}$ in summer 2005 in the control plots and from a low of $0.92 \pm 0.20 \text{ m}^2 \text{ m}^{-2}$ in fall 2006 to a high of $1.75 \pm 0.07 \text{ m}^2 \text{ m}^{-2}$ in spring 2006 in the added nitrogen plots (Figure 2-2). In general, LAI reached an annual peak in the spring or summer and an annual low in the fall.

Litterfall

There was no effect of nitrogen addition on litterfall production for chaparral or coastal sage scrub manipulation plots. Litterfall did differ significantly over time (Figure 2-3). For the chaparral site, litterfall generally declined until summer 2004 then increased to a peak of approximately 20 g m^{-2} in winter 2006 (Figure 2-3). For coastal sage scrub, litterfall generally increased during the fall and winter of 2003 and 2004, but, in 2005, added

nitrogen plots exhibited a peak of 63.8 ± 33.3 in summer 2005 that was on average nearly two times that observed for control plots (Figure 2-3).

Stem elongation

Stem elongation was not affected by nitrogen addition for chaparral or coastal sage scrub manipulation plots. Significant annual variations in stem elongation were seen in the chaparral manipulation plots however (Figure 2-4). For SOFS, stem elongation was greatest for both control and added nitrogen plots from winter 2004 to winter 2005, and stem elongation for control plots was nearly two-fold higher than added nitrogen plots (Figure 2-4). Stem elongation was substantially lower for drier years with no difference between control and added nitrogen plots (Figure 2-4). There was no significant manipulation or temporal trends for stem elongation in the coastal sage scrub manipulation plots, and on average stem elongation varied between 2-17 cm year⁻¹ for both control and added nitrogen plots over the 3-year study period (Figure 2-4).

Net primary production (NPP)

Net primary production (NPP) was also unaffected by nitrogen addition for chaparral or coastal sage scrub manipulation plots, but there were significant differences in NPP over time for both ecosystem types (Figure 2-5). For SOFS, NPP from 2004 to 2005 increased from 259.3 to 492.0 g m⁻² in

the control plots and from 94.5 to 340.4 g m⁻² in the added nitrogen plots, corresponding to a 2.5 and 3-fold increase in NPP for control and added nitrogen plots, respectively (Figure 2-5). Between 2005 and 2006, there was little change in NPP for both the control and added nitrogen SOFS plots (Figure 2-5). For SMER, NPP increased almost linearly between 2004 and 2006 from 547.3 to 1140.3 g m⁻² for the added nitrogen plots, while NPP for control plots changed little between 2004 and 2005 then increased to 1209.5 g m⁻² in 2006 (Figure 2-5).

Species richness

Although species richness was not affected by nitrogen addition for chaparral or coastal sage scrub manipulation plots, there were significant seasonal variations in species richness (Figure 2-6). For SOFS, species richness was generally greatest in the spring and summer and lowest in the winter and fall (Figure 2-6). For SMER, species richness was fairly constant throughout the year with peaks in the spring (Figure 2-6).

DISCUSSION

Due to nitrogen being a limiting nutrient in plant production, and since semi-arid, Mediterranean-type ecosystems of southern California have low soil and plant nitrogen (Kummerow et al. 1982), it was hypothesized that

experimental nitrogen deposition would result in increased production. However, in this study, there were no significant effects of nitrogen deposition on any measure of chaparral or coastal sage scrub productivity, including total aboveground biomass, leaf area index, litterfall production, stem elongation or net primary production. The only significant trends were temporal which can be attributed to seasonal rainfall patterns. These results are in contrast to other studies where nitrogen addition significantly increased biomass production of chaparral (Hellmers et al. 1955, McMaster et al. 1982) and increased biomass and shoot production of coastal sage scrub (Gray and Schlesinger 1983, Padgett and Allen 1999).

There are a few possibilities why this study did not show significant increases in production in response to experimental nitrogen deposition. One possibility is that these sites are nitrogen saturated and therefore do not absorb experimentally deposited nitrogen. This explanation is not supported, however, by other data from these sites showing that plant tissue nitrogen is significantly higher in added nitrogen plots compared to control plots at both sites (Vourlitis et al. 2007a). Because vegetation is taking up added nitrogen, the plants are not nitrogen saturated. Another explanation is that plants at these sites are not nitrogen limited and are "luxury consuming" nitrogen (uptake in excess of demand; Driessche 1974, Chapin 1980). Vegetation may also be "luxury consuming" nitrogen to store for future growth when conditions are more favorable to growth. Storing nutrients for future growth

has been observed in plant growing in nutrient-poor soils (Rundel and Parsons 1980). This is important because nutrient availability often does not correspond with the growing season. Previous studies in chaparral have shown that growth and nutrient availability is uncoupled, but coastal sage scrub vegetation showed a linear growth response to increasing nutrient concentration (Gray and Schlesinger 1983). Plants at these sites also may not show increased production in response to nitrogen addition because plants in nutrient-poor sites often have low growth rates (Grundon 1972, Grime and Hunt 1975) and the length of this study was insufficient to see effects of added nitrogen. Finally, plants at these sites may be co-limited by nitrogen and another nutrient such as potassium or limited by water. Since these two sites are semi-arid ecosystems, they are likely limited by water. Because nitrogen fertilization was done in the fall to correspond with the season in which most anthropogenic nitrogen is deposited, plant physiological activity was minimal due to seasonal drought. During this period, no growth was occurring in either site. When the spring rains came, the vegetation grew, but there was no significant difference between the control and added nitrogen plots. This lack of significant difference in growth between control and added nitrogen plots following the spring rains seems to indicate that plant growth at these sites is at least partially regulated by water because maximum growth occurred when water was available. Other studies that found increased production with nitrogen addition added dry nitrogen to

irrigated shrubs (Hellmers et al. 1955) or in the spring (McMaster et al. 1982) during periods of greater water availability.

Although there were no significant effects of nitrogen found by this study, some interesting trends were suggested by the data. At the chaparral site SOFS, nitrogen appeared to negatively affect total aboveground biomass, litterfall production, net primary productivity and stem elongation but positively affect leaf area index. These trends may be due to differences between the plots rather than nitrogen addition. When SOFS burned in 2003, the added nitrogen plots seemed to have been more intensely burned than the control plots. When aboveground biomass was measured for the first time after the fire in winter 2004, the control plots had 6.5 times greater biomass on average than the added nitrogen plots. Since fire intensity can affect a number of aspects of post-fire recovery such as soil nutrients (DeBano and Conrad 1978), resprouting and the seed bank (Moreno and Oechel 1991), this may help to explain the seeming negative effect of nitrogen addition at SOFS. The seemingly negative effect of nitrogen on measures of productivity at SOFS contrast the trend suggested that leaf area index somewhat increased with nitrogen. This increase in leaf area index, although insignificant, supports previous findings by Knops and Reinhard (2000) that nitrogen caused increased leaf area index in perennial grasses and of Pierce et al. (1994) that leaf area index increased as leaf nitrogen content increased. Since leaf area index is proportional to productivity (Monsi et al. 1973),

productivity and leaf area index should show the same trend. This may be explained by the relationship between leaf biomass and shrub size described by Black (1987) where older (i. e. larger) chaparral shrubs had a lower proportion of leaf weight compared to younger (i. e. smaller) shrubs. When all shrubs for which leaf biomass was available in this study were pooled and the leaf mass ratio (LMR) was plotted as a function of shrub volume, the proportion of leaf biomass significantly decreased as volume increased (Figure 2-7), supporting the findings of Black (1987). Due to the leaf mass ratio, plots with smaller shrubs should have greater LAI than plots with larger shrubs. In the case of SOFS in the fall 2006, the average shrub volume was 1.2 times greater for the control plots compared to the added nitrogen plots, $0.052 \pm 0.003 \text{ m}^3$ and $0.042 \pm 0.017 \text{ m}^3$, respectively.

If vegetation at these sites is taking up nitrogen but not allocating it to increased production due to water or other limitation, what are the plants doing with the nitrogen? Is the vegetation storing the additional nitrogen for possible future biomass if there is an especially wet year? Net primary production data somewhat supports this prediction. In 2005, southern California experienced above average precipitation. SOFS and SMER experienced rainfall of 70 and 57 cm, respectively, compared to averages of 57 and 33 cm, respectively, for 50-year averages (Figure 2-8). In 2005, SOFS showed increased total aboveground biomass in control plots compared to added nitrogen, which may be explained by uneven burning

during in the 2003 fire. SMER, an unburned site, experienced the greatest total biomass in the added nitrogen plots in this year, which suggests that, given greater water availability, nitrogen absorbed in this site may be allocated to increased production. To fully test this prediction, these sites would have to receive an additional experimental treatment of water and nitrogen in a factorial design. It is also possible that the vegetation is allocating the additional nitrogen to other physiological processes such as increasing allocation to photosynthetic machinery or greater belowground production. Further study is needed to determine the fate of added nitrogen at these sites.

Table 2-1. Regression equations used to estimate aboveground biomass. Developed from plant volume (area for grass) and total biomass measurements. Total biomass and volume (area for grass) data were natural log transformed to reduce variance. Equations are in the form $y = a*x+b$, where variable a represents slope and b represents the y-intercept. Also shown are the coefficients of determination (r^2), the F -ratios (mean square divided by the error mean square), the degrees of freedom (df) and the P -values. The three general equations were developed by combining all data for shrubs, herbaceous vegetation, and grasses, respectively. A portion of the data from the *A. fasciculatum*, *A. californica* and *S. mellifera* equations were from Hines and Mitcham (*unpublished data*).

Species name	a	b	r^2	F	df	p
<i>Adenostoma fasciculatum</i>	0.8831	-4.7844	0.99	1223.27	1,19	<0.0001
<i>Artemisia californica</i>	0.8606	-5.7531	0.99	2428.09	1,24	<0.0001
<i>Hirschfeldia incana</i>	1.1490	-11.5250	0.78	29.03	1,8	0.0007
<i>Camissonia spp.</i>	0.4092	-2.7481	0.80	32.25	1,8	0.0005
<i>Ceanothus spp.</i>	0.7162	-4.1991	0.95	351.07	1,19	<0.0001
<i>Cryptantha spp.</i>	0.7362	-5.4398	0.87	52.91	1,8	0.0001
<i>Dendromecon rigida</i>	0.5899	-3.1105	0.96	210.91	1,8	<0.0001
<i>Eriodictyon trichocalyx</i>	0.7628	-4.5410	0.94	120.93	1,8	<0.0001
<i>Eriogonum fasciculatum</i>	0.7870	-4.9588	0.99	139.01	1,3	0.0071
<i>Gnaphalium spp.</i>	0.7162	-4.1991	0.93	153.65	1,12	<0.0001
<i>Heliathemum scoparium</i>	0.6619	-3.8972	0.72	20.36	1,8	0.0020
<i>Phacelia spp.</i>	0.7164	-5.1923	0.95	162.45	1,8	<0.0001
<i>Salvia mellifera</i>	0.9353	-6.4553	0.99	1938.70	1,16	<0.0001
<i>Stephanomeria virgata</i>	0.4213	-3.0902	0.89	62.31	1,8	<0.0001
Shrubs (general)	0.8704	-5.4883	0.97	3195.39	1,116	<0.0001
Herbaceous (general)	0.7201	-5.0866	0.79	234.25	1,62	<0.0001
Grass by area (general)	1.0513	-4.1304	0.97	83.56	1,4	0.0028

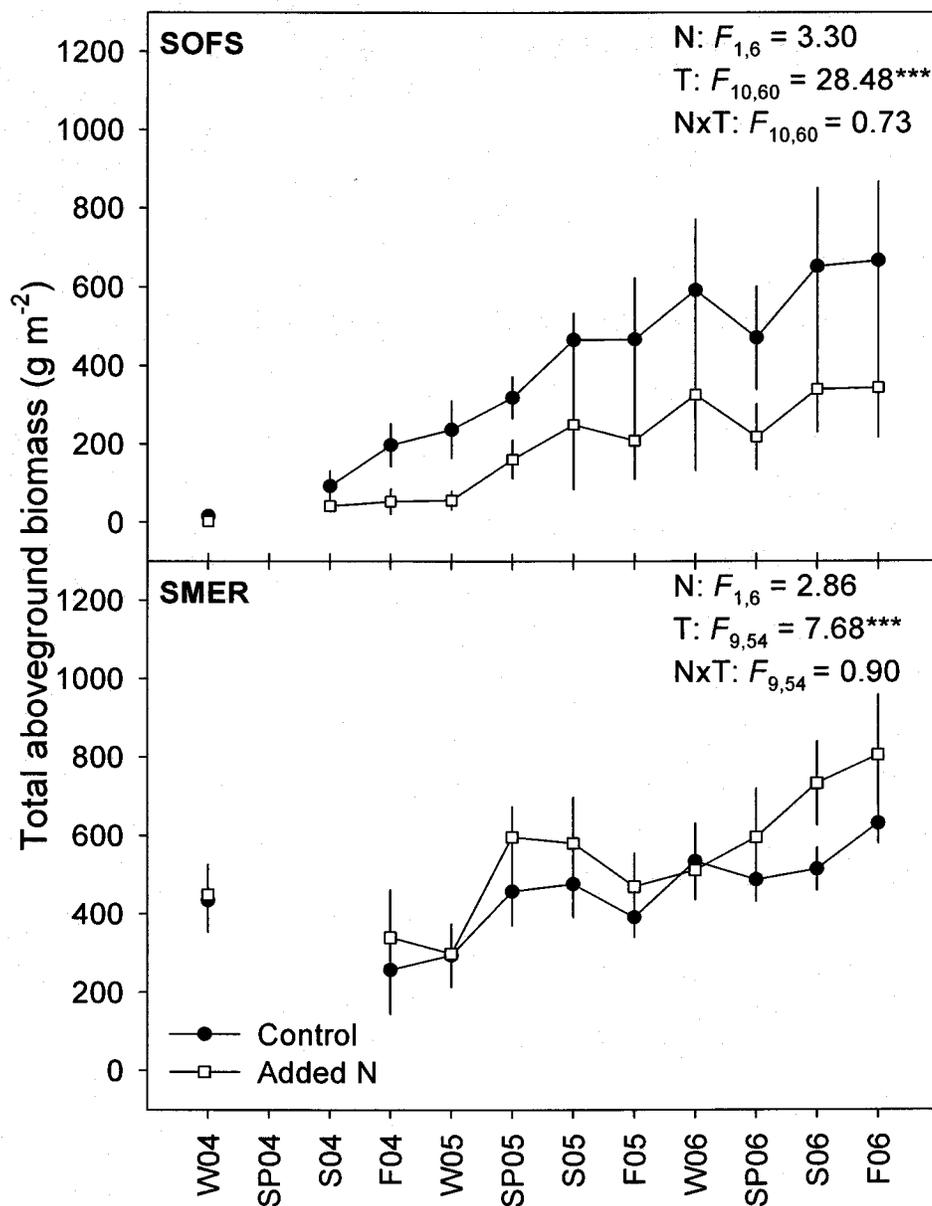


Figure 2-1. Total aboveground biomass for manipulation portion of study for the chaparral site Sky Oaks Field Station (SOFS) and the coastal sage scrub site Santa Margarita Ecological Reserve (SMER). Data represent the mean \pm 1 standard error ($n = 4$). Results are shown for a repeated measures analysis of variance (RMANOVA). N represents comparisons between control and added nitrogen plots, T represents seasonal comparisons and NxT represents the interaction of nitrogen and seasonal components. Statistical significance is indicated by * = $p < 0.05$, ** = $p < 0.001$, and *** = $p < 0.0001$. Missing data points represent seasons in which aboveground biomass was not measured.

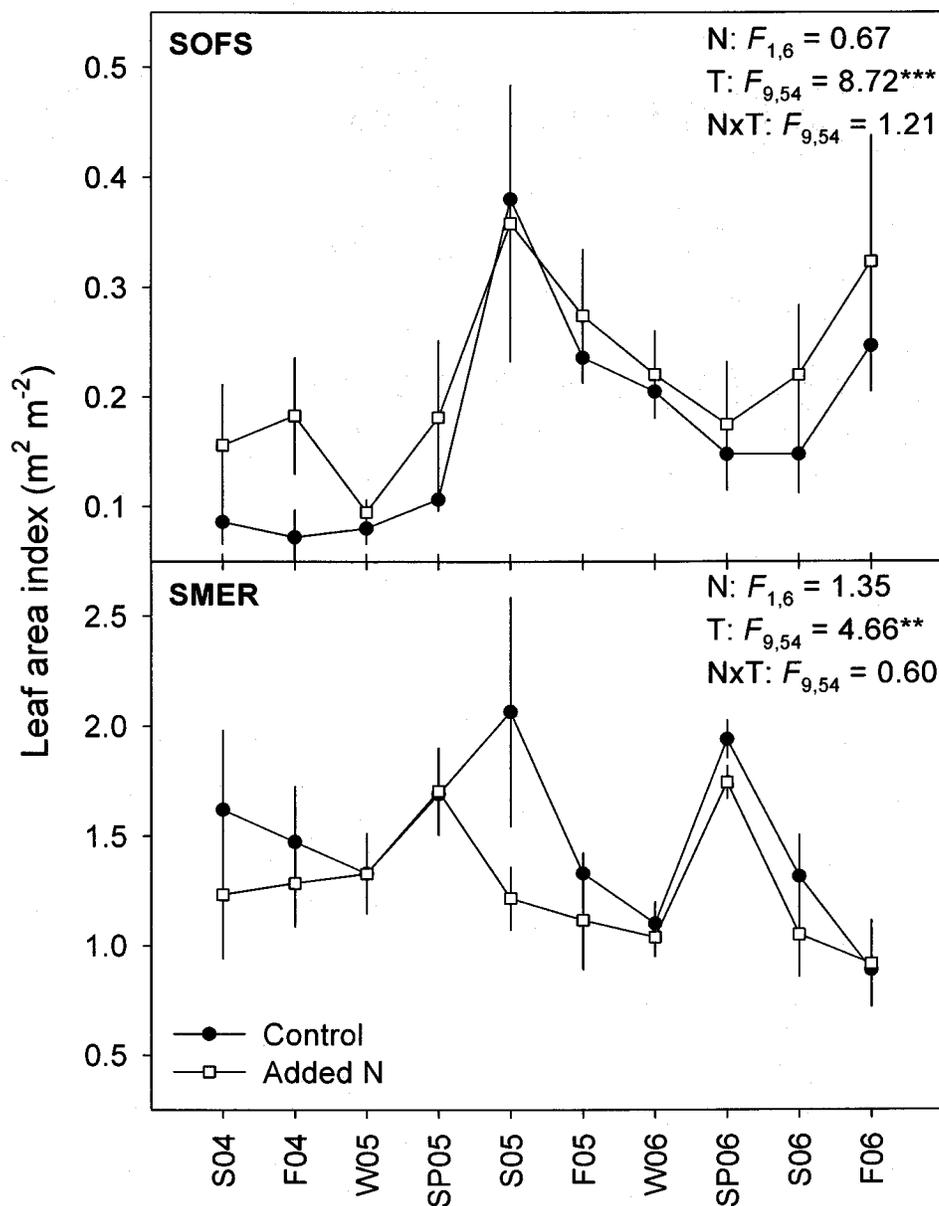


Figure 2-2. Leaf area index (LAI) for manipulation portion of the study for the chaparral site Sky Oaks Field Station (SOFS) and the coastal sage scrub site Santa Margarita Ecological Reserve (SMER). Data represent the mean \pm 1 standard error ($n = 4$). Results are shown for a repeated measures analysis of variance (RMANOVA). N represents comparisons between control and added nitrogen plots, T represents seasonal comparisons and NxT represents the interaction of nitrogen and seasonal components. Statistical significance is indicated by * = $p < 0.05$, ** = $p < 0.001$, and *** = $p < 0.0001$.

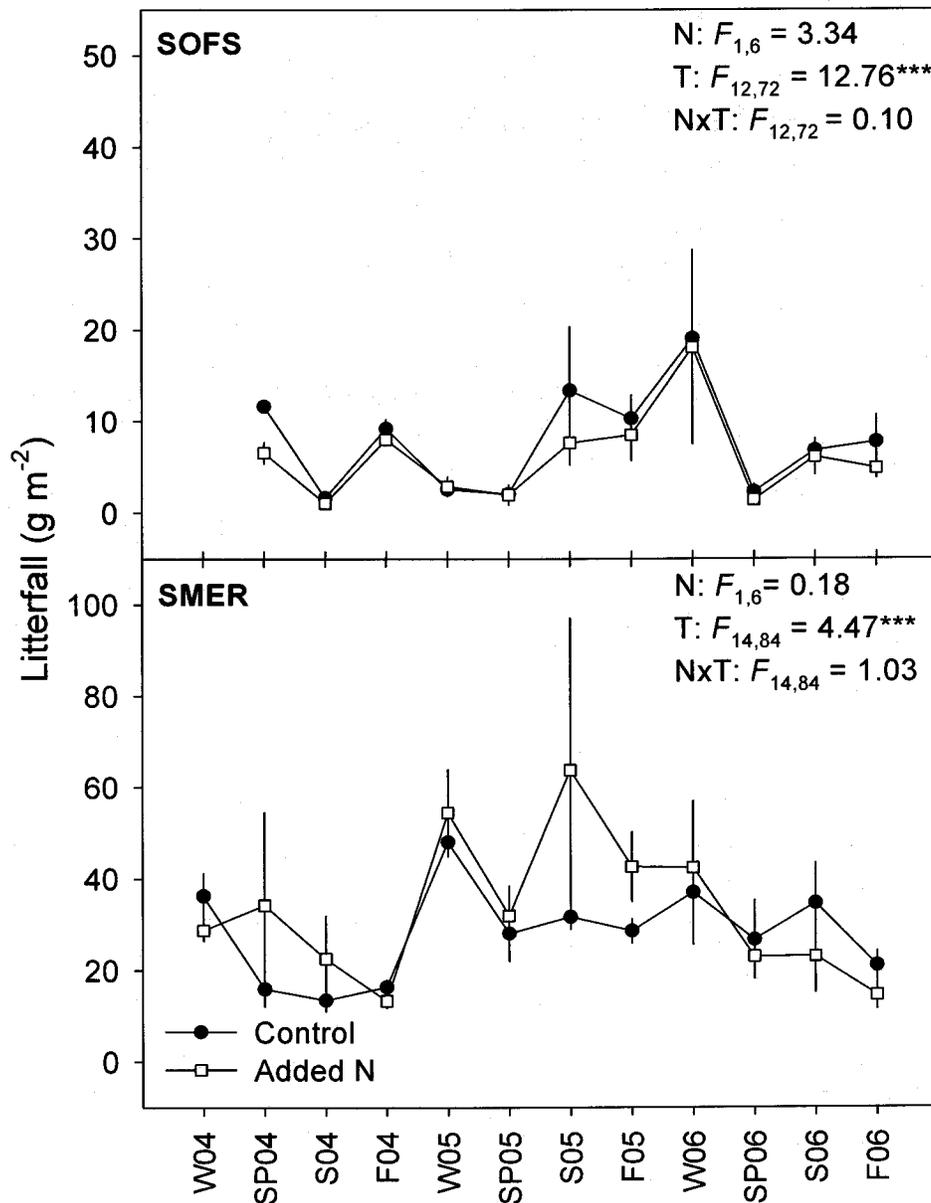


Figure 2-3. Litterfall for manipulation portion of study for the chaparral site Sky Oaks Field Station (SOFS) and the coastal sage scrub site Santa Margarita Ecological Reserve (SMER). Data represent the mean \pm 1 standard error ($n = 4$). Results are shown for a repeated measures analysis of variance (RMANOVA). N represents comparisons between control and added nitrogen plots, T represents seasonal comparisons and NxT represents the interaction of nitrogen and seasonal components. Statistical significance is indicated by * = $p < 0.05$, ** = $p < 0.001$, and *** = $p < 0.0001$.

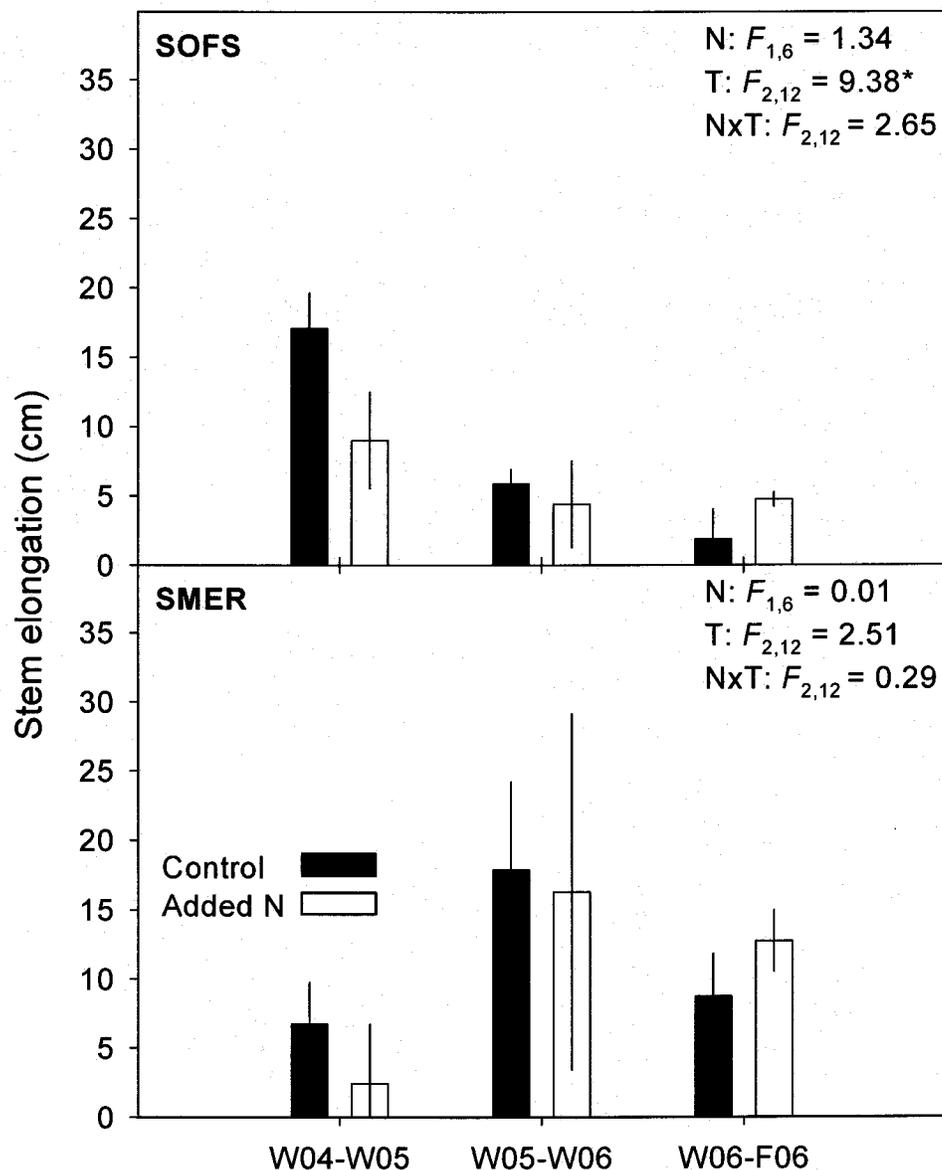


Figure 2-4. Stem elongation for manipulation portion of study for the chaparral site Sky Oaks Field Station (SOFS) and the coastal sage scrub site Santa Margarita Ecological Reserve (SMER). Data represent the mean \pm 1 standard error ($n = 4$). Results are shown for a repeated measures analysis of variance (RMANOVA). N represents comparisons between control and added nitrogen plots, T represents seasonal comparisons and NxT represents the interaction of nitrogen and seasonal components. Statistical significance is indicated by * = $p < 0.05$, ** = $p < 0.001$, and *** = $p < 0.0001$.

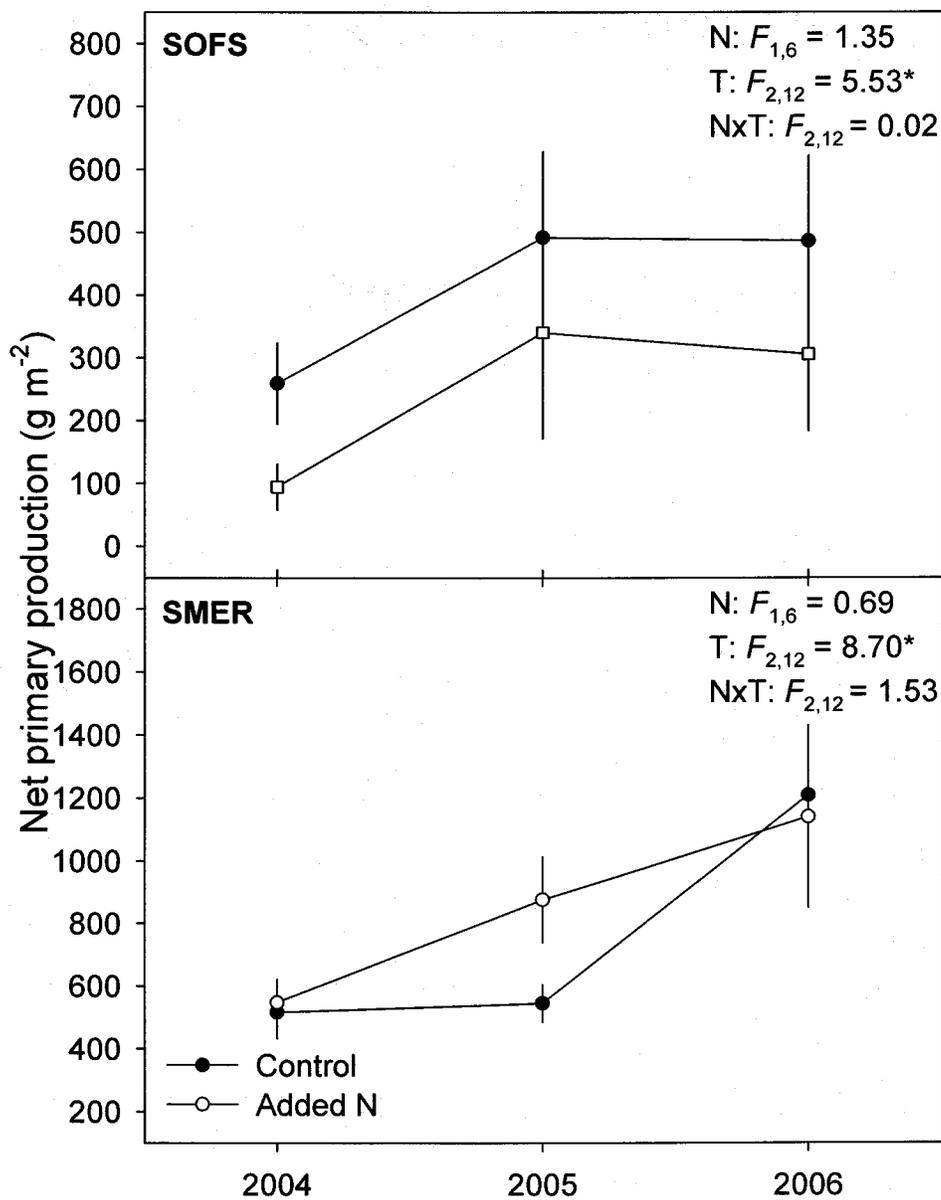


Figure 2-5. Net primary production (NPP) for manipulation portion of study for the chaparral site Sky Oaks Field Station (SOFS) and the coastal sage scrub site Santa Margarita Ecological Reserve (SMER). Data represent the mean \pm 1 standard error ($n = 4$). Results are shown for a repeated measures analysis of variance (RMANOVA). N represents comparisons between control and added nitrogen plots, T represents seasonal comparisons and NxT represents the interaction of nitrogen and seasonal components. Statistical significance is indicated by * = $p < 0.05$, ** = $p < 0.001$, and *** = $p < 0.0001$.

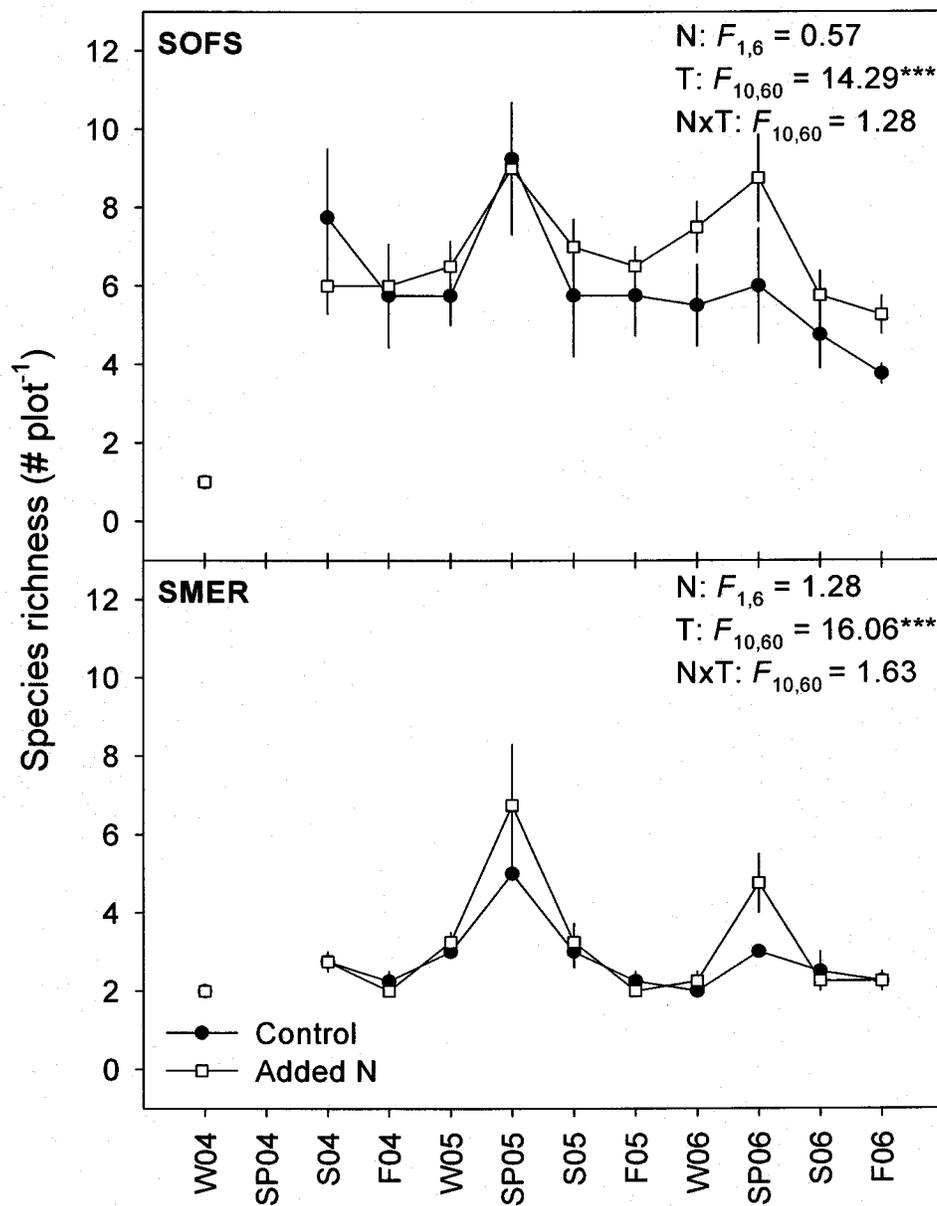


Figure 2-6. Species richness for manipulation portion of study for the chaparral site Sky Oaks Field Station (SOFS) and the coastal sage scrub site Santa Margarita Ecological Reserve (SMER). Data represent the mean \pm 1 standard error ($n = 4$). Results are shown for a repeated measures analysis of variance (RMANOVA). N represents comparisons between control and added nitrogen plots, T represents seasonal comparisons and NxT represents the interaction of nitrogen and seasonal components. Statistical significance is indicated by * = $p < 0.05$, ** = $p < 0.001$, and *** = $p < 0.0001$.

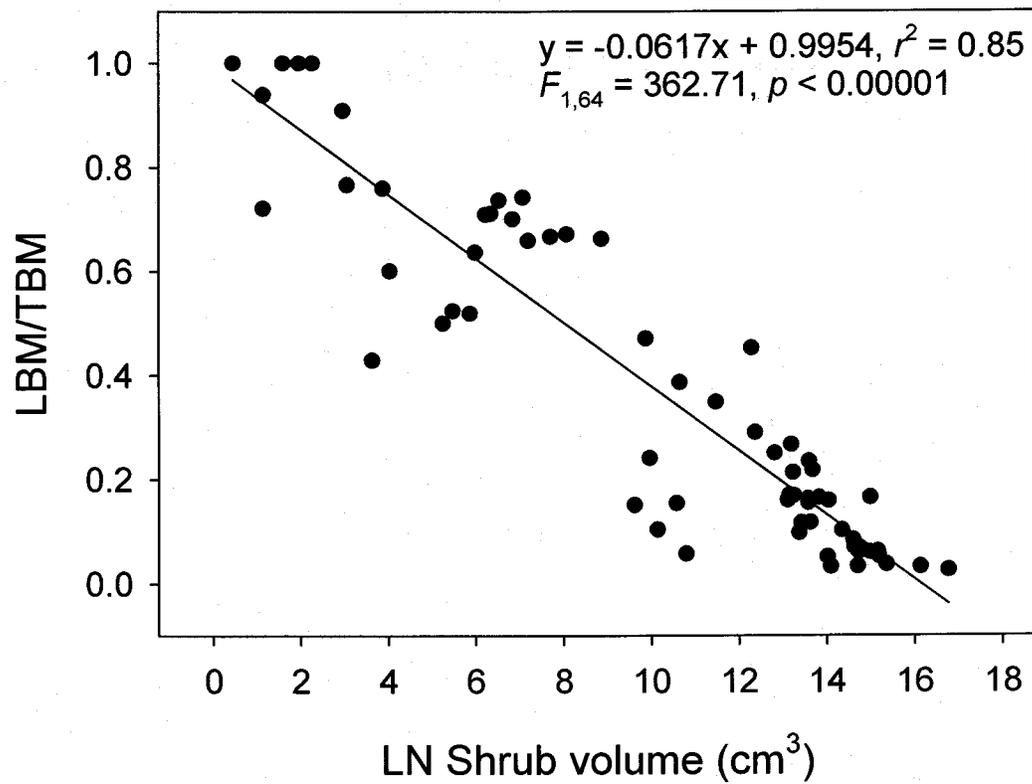


Figure 2-7. Leaf mass ratio (LMR) plotted as a function of the natural log of shrub volume for *A. fasciculatum*, *A. californica* and *S. mellifera*. Results of linear regression are shown.

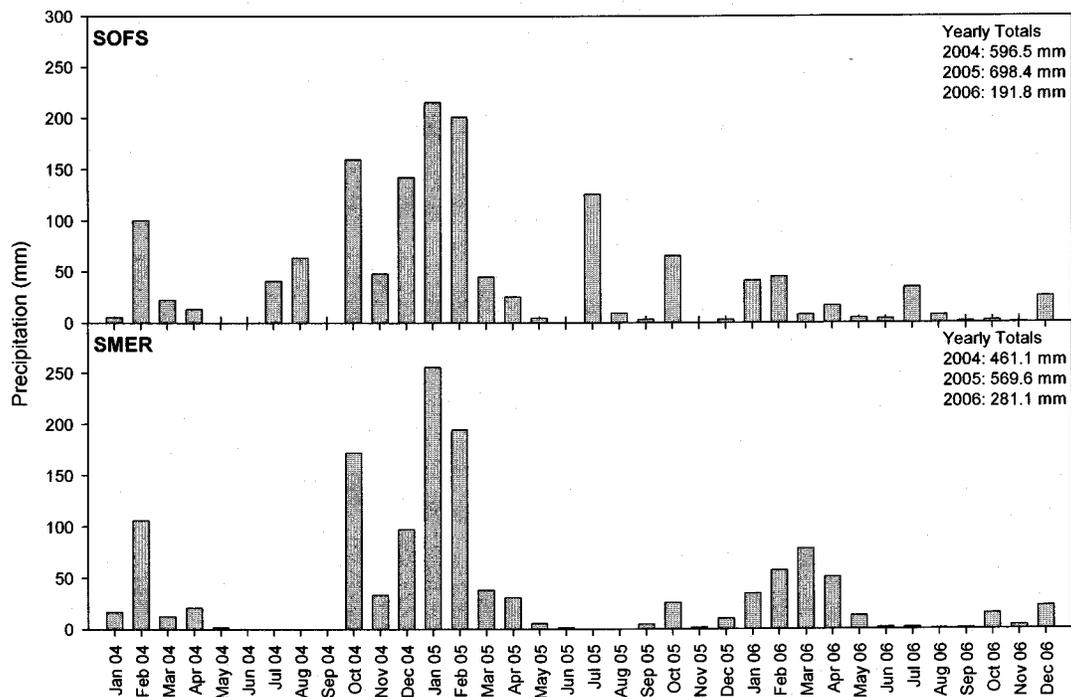


Figure 2-8. Monthly precipitation in mm for the manipulation sites from 2004 to 2006. The chaparral site is Sky Oaks Field Station (SOFS) and the coastal sage scrub site is Santa Margarita Ecological Reserve (SMER). Precipitation data for SOFS 2004 to 2005 and for SMER from Vourlitis *unpublished data*. Precipitation data for SOFS 2006 is from a San Diego State University weather station located on the reserve.

CHAPTER 3

NITROGEN DEPOSITION AND POST-FIRE RECOVERY

ABSTRACT

Chaparral ecosystems in exposed areas of southern California can receive nitrogen inputs from air pollution ranging from 20–45 kg N ha⁻¹ per year. In these same ecosystems, fire is an important disturbance agent with a frequency of 20–40 years. Nitrogen deposition may interact with fire to affect post-fire ecosystem recovery in terms of production and species composition. Whereas nitrogen deposition increases nitrogen availability to these ecosystems, fire can either increase or decrease nitrogen availability depending upon fire intensity. Because chaparral ecosystems of southern California are nutrient-poor, it was hypothesized that nitrogen deposition may increase rates of post fire recovery. To test this hypothesis, aboveground productivity was compared during the first three years post-fire at three chaparral sites located along an established nitrogen deposition gradient that burned within a 14-month period. Results showed that aboveground shrub and total biomass did not increase with nitrogen deposition but that high nitrogen deposition resulted in a lower density of large shrubs compared to a high density of small shrubs with low nitrogen deposition. Although non-significant, high nitrogen deposition sites also seemed to have increased herbaceous biomass. Since nitrogen deposition in southern California is projected to increase in the future, there is the potential to significantly alter post-fire recovery and species composition of these ecosystems.

INTRODUCTION

Southern California chaparral ecosystems are located in a region of Mediterranean-type climate that is characterized by hot, dry summers and cool wet winters where the majority of the rainfall occurs in a few storms from November through April (Keeley 2000). In chaparral ecosystems of southern California, fire is an important agent of disturbance that occurs at a frequency of 20-40 years depending on the site (Kummerow and Lantz 1983).

Chaparral ecosystems are composed of sclerophyllous shrubs that are closely spaced and form a nearly continuous cover. Herbaceous shrubs are mostly absent, except after fire (Keeley 2000). Following fire, chaparral ecosystems generally continue to accumulate biomass for 50 years, after which production levels off (Black 1987).

Fire can substantially alter nitrogen availability and storage depending on intensity. For example, substantial nitrogen loss (both total nitrogen and NO_3^-) from volatilization can follow high intensity fires (DeBano and Conrad 1978, DeBano et al. 1979, Dunn et al. 1979, Boerner 1982, Grogan et al. 2000), but deposition of NH_4^+ in ash and incomplete burning of vegetation and detritus can also increase available nitrogen (DeBano et al. 1979, Dunn et al. 1979, Gray and Schlesinger 1981, Boerner 1982, Grogan et al. 2000). Although fire can cause increases in available and total nitrogen (DeBano et al. 1979, Dunn et al. 1979, Grogan et al. 2000), nitrogen can be quickly lost due to erosion during the first post-fire rain (DeBano and Conrad 1978).

Following fire, chaparral ecosystems experience growth of many herbaceous and suffrutescent plants with plant diversity being greatest the first year after fire (Keeley 2000). Many species occurring immediately following the fire are "fire followers" that either require high heat or smoke for seed germination. In addition, some shrub species such as *Adenostoma fasciculatum*, *Quercus dumosa* Nutt., *Quercus durata* Jeps. (scrub oak) and *Malosma laurina* (Nutt.) Abrams (laurel sumac) are facultative seeders that are able to germinate from seeds or resprout from basal burls or root crowns depending on fire intensity, soil moisture, plant size and condition (Moreno and Oechel 1992, Sparks et al. 1993, Keeley 2000). Other shrubs, such as *Ceanothus* and *Arctostaphylos*, are obligate seeders that do not resprout and require seed germination (Moreno and Oechel 1992, Sparks et al. 1993, Keeley 2000). There may also be a large seed bank of shrub species that may survive depending on the same factors stated above. Seedlings and resprouts following fire show increased photosynthetic rates compared to mature vegetation due to favorable post-fire water conditions resulting from biomass removal (Hastings et al. 1989).

Nitrogen deposition may shorten the time between fire intervals or increase fire intensity due to higher shrub density (Fenn et al. 2003b) and increased fuel loads (Fenn et al. 2003a). Increased nitrogen availability from atmospheric deposition could also result in more rapid ecosystem recovery if systems are nitrogen limited during post-fire recovery despite possible

increased nitrogen availability due to ash and incomplete burning. Changes in community composition from shrublands to grasslands due to nitrogen deposition could also increase the fire frequency (D'Antonio and Vitousek 1992). Furthermore, following fire, ecosystems exposed to high anthropogenic nitrogen deposition may be in even greater danger of changes in community composition by invasion of non-native annuals, especially grasses (Allen et al. 1998, Minnich and Dezzani 1998), as removal of native vegetation may allow invasive annuals to enter the ecosystem and out-compete native vegetation for nutrients (McMaster et al. 1982, Padgett and Allen 1999).

HYPOTHESIS

Chaparral ecosystems exposed to high levels of atmospheric nitrogen deposition will show increased rates of post-fire recovery and increased non-native vegetation.

METHODS

Total aboveground biomass

Aboveground biomass was estimated at three chaparral sites that burned within a 14-month period. These sites were located along a nitrogen deposition gradient and were either designated high- or low-nitrogen

deposition. San Dimas Experimental Forest (SDEF) is a high-nitrogen deposition site that burned in September 2002, Sky Oaks Field Station (SOFS) is a low-nitrogen deposition site that burned in July 2003 and San Bernardino National Forest (SBNF) is a high-nitrogen deposition site that burned in October 2003 (Table 1-1).

Aboveground biomass was estimated four times per year, seasonally, using plant volume to biomass regression equations (Table 2-1) to allow for repeated non-destructive measurements and bulk harvests of spring annuals and grasses as described in Chapter 2.

Species composition

All plants that were measured to estimate aboveground biomass in this study were identified. This allowed changes in species composition over time with nitrogen deposition to be examined. Species were categorized as either *Adenostoma fasciculatum* (pre-burn dominant shrub), *Ceanothus greggii* or *crassifolius*, other shrubs, or herbaceous vegetation (herbaceous annuals and perennials including grasses).

Statistical analysis and derived quantities

Aboveground and shrub biomass were estimated for the entire 10 x 10 m (100 m²) plots based on the measurements within the subplots by dividing the total by the area of the subplot. All data presented in figures represent an

average of four plots at each site ($n = 4$). Linear regression equations for biomass estimation from plant volume, total aboveground, shrub, and average shrub biomass as a function of time post fire, and shrub biomass as a function of shrub density were performed using NCSS (NCSS version 2004, NCSS, Kaysville, Utah, USA). Differences between slopes were tested using curve inequality randomization tests using NCSS. Differences between grass biomass for the sites was tested using analysis of variance (ANOVA) with NCSS, and differences between species composition was tested using chi-square analysis with Minitab (Minitab version 14, Minitab, Inc., State College, Pennsylvania, USA). Statistical difference was accepted at an alpha of 0.05 (Zar 1999).

RESULTS

Species composition

When species composition was compared at 1, 2, and 3 years post-fire for the three sites, there was no significant difference between years or sites (Figure 2-1). For SOFS and SBNF, the greatest proportion of biomass was comprised of *Adenostoma fasciculatum*, which was an average of $84.0 \pm 1.8\%$ and $81.7 \pm 5.6\%$, respectively, for the three years combined. At SDEF, *A. fasciculatum* and *Ceanothus crassifolius* were the most dominant vegetation (Figure 3-1) and were on average $47.4 \pm 10.3\%$ and $21.8 \pm 4.5\%$,

respectively, for the two years combined. Both SBNF and SDEF seemed to have higher average percentages of other shrub species ($11.9 \pm 5.4\%$ and $11.6 \pm 2.5\%$) than SOFS ($2.3 \pm 2.1\%$), although there was no significant difference. At SBNF, the majority of the species grouped as other shrubs were *Dendromecon rigida* and *Eriodictyon trichocalyx* with a small amount of *Yucca whipplei* (Appendix 1). At SDEF, most other shrubs were *Malosma laurina*, *Quercus durata* with a small amount of *Baccharis salicifolia* and *Ericameria parishii* (Appendix 1). At SOFS, there was little shrub vegetation besides *Adenostoma fasciculatum* and *Ceanothus greggii*, and the other shrub vegetation was comprised mostly of small amounts of *Eriogonum fasciculatum*, *Solanum xanti* and *Trichostemma parishii* (Appendix 1). The highest nitrogen deposition site, SDEF, also had the highest percentage of herbaceous vegetation ($19.2 \pm 3.4\%$) for the two years (Figure 3-1). At SDEF, most of the herbaceous vegetation was *Brassica geniculata*, *Lotus scoparius* and grasses. At SBNF, it was *Helianthemum scoparium*, *Lotus scoparius* and grasses (Appendix 1). At SOFS, there was a greater variety of herbaceous species including *Eriogonum davidsonii*, *Stephanomeria virgata*, *Penstemon spectabilis*, *Helianthemum scoparium* and *Gutierrezia californica* (Appendix 1).

Aboveground biomass

Total aboveground biomass recovered from fire at a significantly greater rate for SBNF ($32.4 \text{ g m}^{-2} \text{ month}^{-1}$) than for SOFS ($16.8 \text{ g m}^{-2} \text{ month}^{-1}$) and SDEF ($18.5 \text{ g m}^{-2} \text{ month}^{-1}$), and there was not a significant difference in the rate of total biomass increase since fire between the lowest deposition site SOFS and the highest deposition site SDEF (Figure 3-2A). By the end of the study period, total aboveground biomass was $1269.7 \pm 178.9 \text{ g m}^{-2}$, $651.3 \pm 119.2 \text{ g m}^{-2}$ and $717.7 \pm 122.0 \text{ g m}^{-2}$ for SBNF, SDEF and SOFS, respectively (Figure 3-2A).

Post-fire shrub biomass recovery showed the same results as total biomass where the greatest recovery was seen at SBNF ($30.9 \text{ g m}^{-2} \text{ month}^{-1}$), and there was no difference between the lowest deposition site SOFS ($16.0 \text{ g m}^{-2} \text{ month}^{-1}$) and the highest deposition site SDEF ($14.8 \text{ g m}^{-2} \text{ month}^{-1}$), (Figure 3-2B). At the end of the study period, shrub biomass was $1211.3 \pm 193.1 \text{ g m}^{-2}$, $697.7 \pm 119.1 \text{ g m}^{-2}$ and $631.6 \pm 200.6 \text{ g m}^{-2}$ for SBNF, SDEF and SOFS, respectively (Figure 3-2B).

Post-fire average shrub biomass was greater at the high nitrogen deposition sites, SDEF ($13.4 \text{ g plant}^{-1} \text{ month}^{-1}$) and SBNF ($11.9 \text{ g plant}^{-1} \text{ month}^{-1}$), than at the low nitrogen deposition site SOFS ($2.8 \text{ g plant}^{-1} \text{ month}^{-1}$), and there was not a significant difference in post-fire average shrub biomass recovery between SDEF and SBNF (Figure 3-2C). This indicated that shrubs at the two high nitrogen deposition sites (SDEF and SBNF) were significantly

larger than those at the low nitrogen deposition site (SOFS). At the end of the study period, average shrub biomass was $599.3 \pm 118.6 \text{ g m}^{-2}$, $462.9 \pm 93.8 \text{ g m}^{-2}$ and $80.1 \pm 30.4 \text{ g m}^{-2}$ for SDEF, SBNF and SOFS, respectively (Figure 3-2C).

When shrub biomass was plotted as a function of shrub density, the highest nitrogen deposition site, SDEF, had the largest shrubs overall ($227.8 \text{ g plant}^{-1}$), followed by the second highest nitrogen deposition site, SBNF ($109.4 \text{ g plant}^{-1}$), and the lowest nitrogen deposition site, SOFS ($28.0 \text{ g plant}^{-1}$), with the smallest shrubs throughout the study period (Figure 3-3). All three sites were significantly different from each other in terms of shrub size (Figure 3-3).

DISCUSSION

Because southern California chaparral ecosystems are nutrient-poor (Kummerow et al. 1982), it was hypothesized that nitrogen deposition would result in increased production following fire. It was also hypothesized that, in addition to increased post-fire recovery, nitrogen deposition would result in increased non-native vegetation due to removal of native vegetation and non-native annuals out-competing native species.

The lack of significant differences between the three sites and years in species composition was likely due to the high proportion of *Adenostoma*

fasciculatum at all sites. Although non-significant, the species composition data seem to suggest greater diversity of plant types at the highest nitrogen deposition site SDEF. Nitrogen deposition seemed to result in a shift away from the pre-fire dominant species, *Adenostoma fasciculatum*. The species composition data seem to support prior findings of Bobbink et al. (1998) that nitrogen deposition cause increases in species diversity in nutrient-poor European shrublands due to invasions of species intolerant to the original nutrient-poor conditions. Although the trend suggests that there was greatest number of plant types in the highest deposition site SDEF, more species appeared overall at SOFS (38), followed by SDEF (16) and SBNF (15) (Appendix 1). The highest nitrogen deposition site, SDEF, also had the highest percentage of biomass as herbaceous vegetation. Previous studies of Westman (1981), Allen et al. (1998) and Padgett et al. (1999) found that nitrogen deposition caused declines in native shrublands by conversion to grassland. Eventually, the invasive grasses replace the original shrubland vegetation and lead to loss of diversity (Westman 1981, Allen et al. 1998, Padgett and Allen 1999). This conversion from shrubland to grassland may also be facilitated by fire through the removal of original vegetation (Minnich and Dezanni 1998). In addition, increased grass biomass can also cause fires to occur more frequently through increased fuel loads (D'Antonio and Vitousek 1992), which can exacerbate the problem. Although the biomass of grasses was not measured specifically throughout the course of this study, in

the spring of 2005 for SDEF and 2006 for SOFS and SBNF, grass biomass was $7.8 \pm 6.2 \text{ g m}^{-2}$, $10.6 \pm 8.1 \text{ g m}^{-2}$ and $116.6 \pm 67.4 \text{ g m}^{-2}$ for SOFS, SBNF and SDEF, respectively (Figure 3-4). Although grass biomass was not significantly different between the three sites, the data suggest a trend of increased grass biomass with increased nitrogen deposition. In addition, the composition of grass was the non-native *Bromus tectorum* at SOFS and SBNF and a mixture of *B. tectorum*, non-native *Avena fatua* and non-native *Ehrharta calycina* at SDEF (Figure 3-4). This suggests that nitrogen may not only increase grass biomass but also increase the biomass of invasive, non-native grasses. These data seem to support the hypothesis that nitrogen deposition causes increases in non-native vegetation, but, due to the results being non-significant, no conclusions can be made.

In terms of total and shrub biomass recovery, there was not a clear trend of increased rate of production with nitrogen. Although one of the high nitrogen deposition sites (SBNF) showed the highest rate of recovery for both shrub and total biomass, the highest (SDEF) and lowest (SOFS) nitrogen deposition sites had nearly the same rates of recovery. It is unclear why shrub and total biomass production were not correlated to nitrogen deposition, but one explanation may be differences in fire intensity among the sites. Because the fires at these sites were natural and therefore unplanned, the intensities of the fires were neither controlled nor measured. Fire intensity can be estimated, however, using changes between pre- and post-fire soil

carbon and nitrogen (DeBano and Conrad 1978, DeBano et al. 1979).

Vourlitis and Pasquini (2008) found that soil carbon and nitrogen decreased at SOFS and SDEF and increased at SBNF from a period pre-fire to one year post-fire. This indicated that fire intensity at SOFS and SDEF was likely more intense than at SBNF. The fire at SBNF may have been less intense due to the site being located on the top of a ridge with less fuel present on the surrounding rocky slopes. Since increased fire intensity can cause more volatilization of nitrogen from biomass and negatively affect seed germination of species such as *A. fasciculatum* (Moreno and Oechel 1991), increased fire intensity may explain why the total and shrub biomass recovery rates did not increase with nitrogen deposition as hypothesized. Another explanation for production not increasing with nitrogen deposition is that, because fire may cause increased nitrogen availability from burned biomass (DeBano et al. 1979, Dunn et al. 1979, Gray and Schlesinger 1981, Boerner 1982, Grogan et al. 2000), these sites may have not been in a state of nitrogen limitation following fire. Additionally, nitrogen deposition may have not yielded increased production because evergreen vegetation characteristic of chaparral is slower growing than other vegetation such as coastal sage scrub and herbaceous annuals (Chapin 1980, Gray and Schlesinger 1981) and may not necessarily allocate nutrients to immediate growth but may instead "luxury consume," where nutrients are taken up in excess of current demand (Driessche 1974, Chapin 1980). Plants in nutrient-poor environments will

often take advantage of nutrient flushes by taking up nutrients when they are briefly available and store them for later use when conditions are more favorable to growth (Chapin 1980). This is important for fire-adapted vegetation in nutrient-poor environments. These plants can utilize increased nutrients released by fire and store the nutrients for future growth (Rundel and Parsons 1980).

Shrub size did show increases in response to nitrogen deposition. Following fire, the two high nitrogen deposition sites (SDEF and SBNF) showed greater increases in average shrub biomass over time than the low nitrogen deposition site (SOFS). Thus, overall, nitrogen deposition lead to increased individual shrub size and these sites. In addition to nitrogen deposition resulting in increased shrub size, when shrub biomass was plotted as a function of shrub density, a clear relationship was seen with larger shrubs being present at the highest nitrogen deposition site (SDEF) followed by SBNF and the lowest deposition site SOFS. This is likely due to "self-thinning," where density decreases as plant size increases (Harper and McNaughton 1962). Looking at the results from these figures (Figure 3-2C and 3-3), it is demonstrated that nitrogen deposition leads to fewer larger shrubs at the high deposition sites (SDEF and SBNF) as opposed to many smaller shrubs at the low deposition site (SOFS).

Although this study compared sites with differences in elevation, aspects and rainfall, it yielded some interesting findings about how nitrogen

deposition affects post-fire ecosystem recovery. While there was no clear trend in terms of ecosystem production, shrub size increased with nitrogen deposition while density decreased. So, nitrogen deposition led to large shrubs with low density as opposed to many small shrubs. Nitrogen deposition also seemed to result in a shift away from the dominant pre-fire vegetation and an increase in other shrubs and herbaceous vegetation including grasses. Despite the limitations of this study, the results indicate alteration of ecosystem fire recovery along a nitrogen deposition gradient.

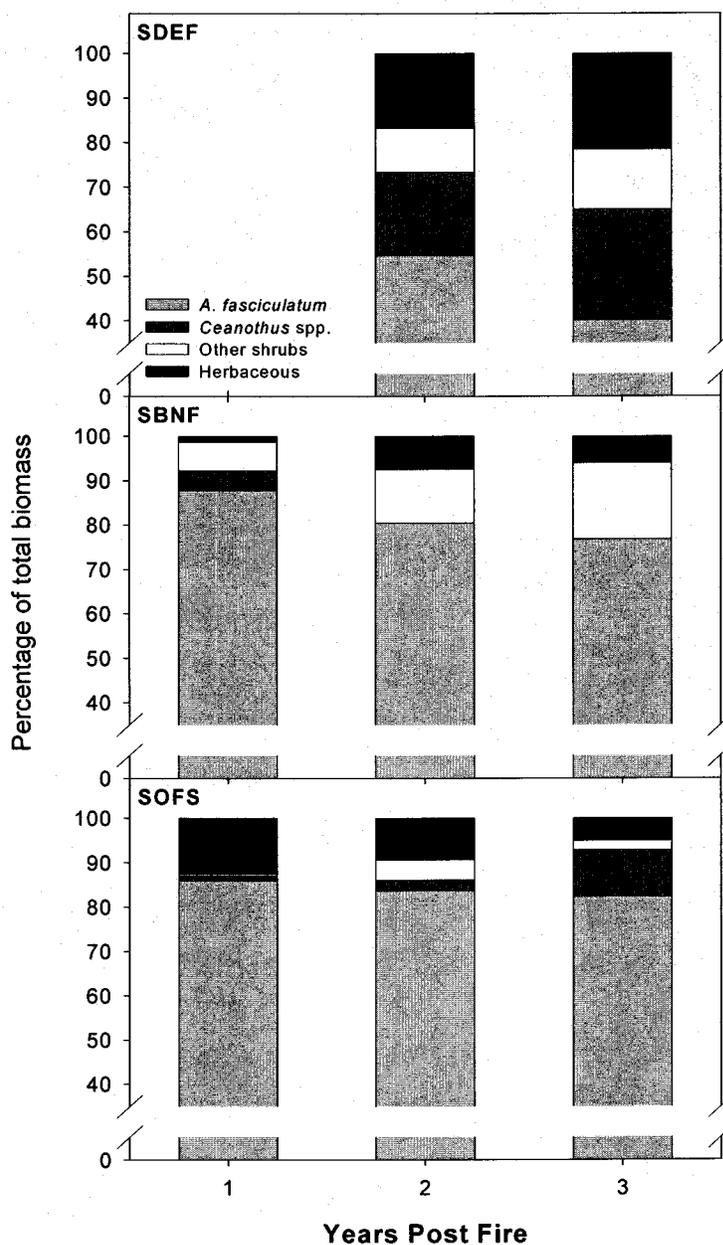


Figure 3-1. Percentage of the total aboveground biomass of *A. fasciculatum*, *Ceanothus* spp., other shrubs and herbaceous vegetation for the three study sites, San Dimas Experimental Forest (SDEF), San Bernardino National Forest (SBNF) and Sky Oaks Field Station (SOFS). Each bar represents the mean ($n = 4$) annual percentages. There were no significant differences between sites or years in biomass composition. Only years 2 and 3 post-fire are presented for SDEF due to a gap in post-fire sampling.

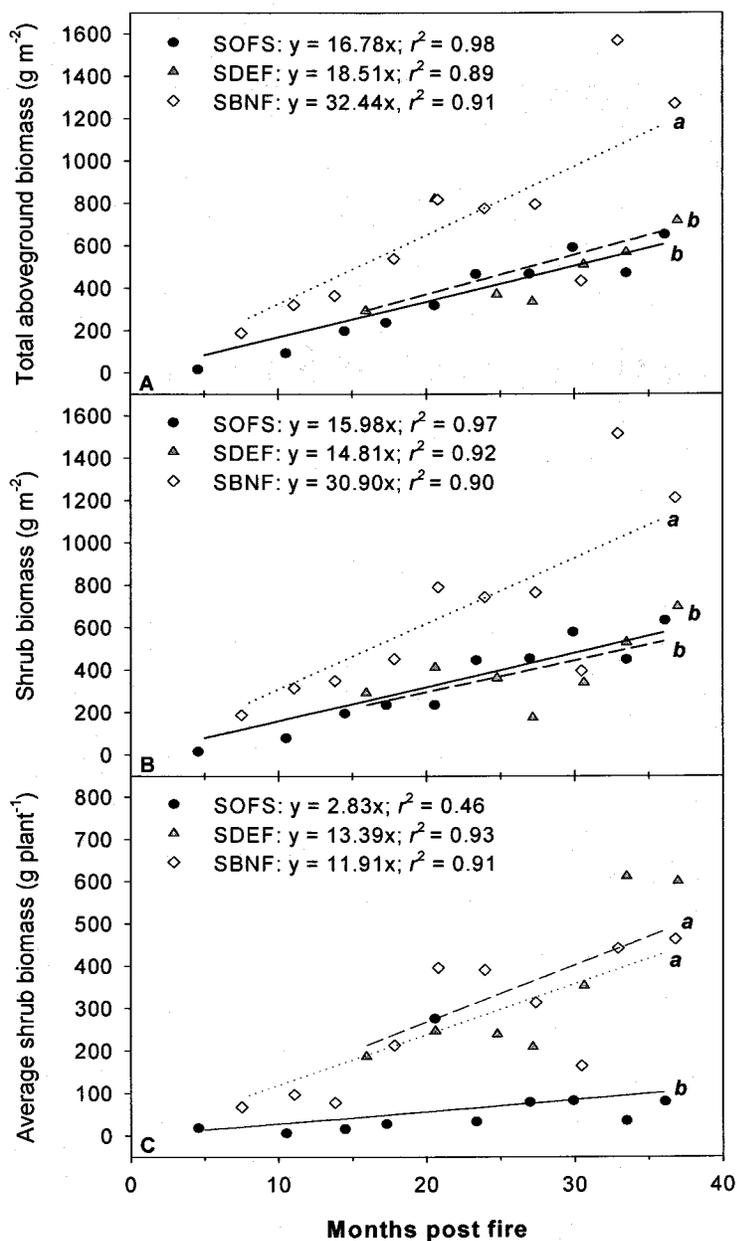


Figure 3-2. Total aboveground (shrub + herbaceous) biomass (A), shrub biomass (B) and average shrub biomass (C) for the three study sites, Sky Oaks Field Station (SOFS), San Dimas Experimental Forest (SDEF) and San Bernardino National Forest (SBNF). Each data point represents the mean ($n = 4$). Lines were fit to the data using linear regression. Regressions were forced through the origin to assume zero biomass at time zero post fire. The regressions for SOFS, SDEF and SBNF are represented by solid, dashed and dotted lines, respectively. All regression equations were statistically significant ($p < 0.05$). Differences between regressions were tested using curve inequality randomization tests ($p < 0.05$) and statistically significant differences are designated a and b (e.g. in panel A, SBNF is statistically different from SOFS and SDEF but SDEF and SOFS are not statistically different).

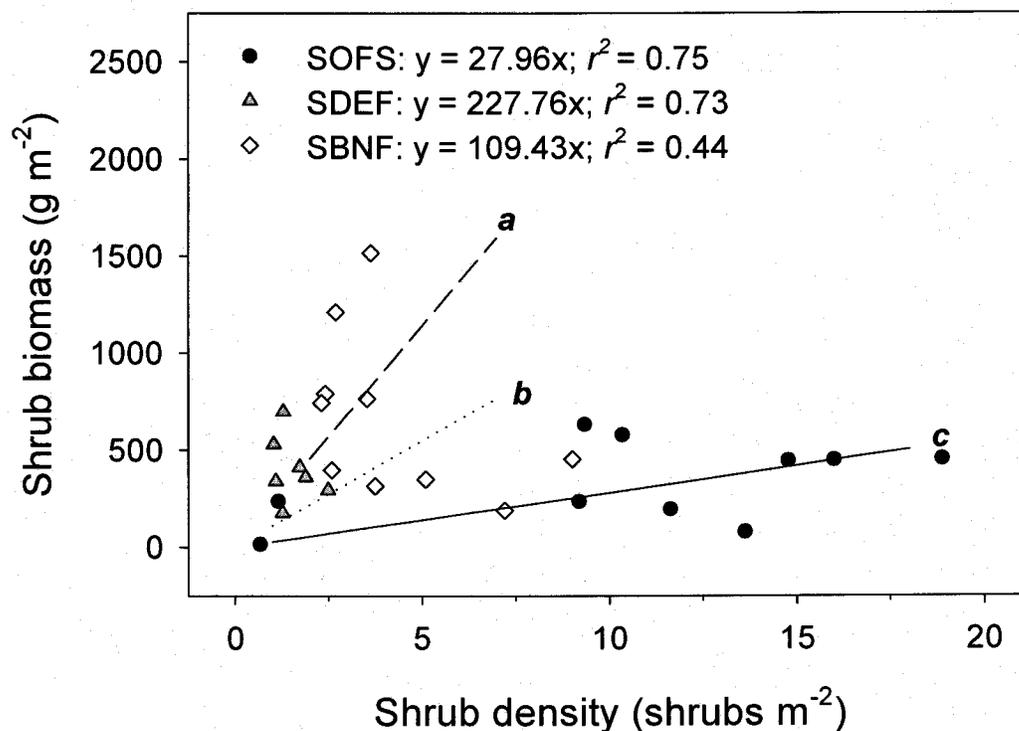


Figure 3-3. Shrub biomass plotted as a function of shrub density for the three study sites, Sky Oaks Field Station (SOFS), San Dimas Experimental Forest (SDEF) and San Bernardino National Forest (SBNF). Data represent three years post-fire. Each data point represents the mean ($n = 4$). Lines were fit to the data using linear regression. Regressions were forced through the origin to assume zero biomass at a shrub density of zero. The regressions for SOFS, SDEF and SBNF are represented by solid, dashed and dotted lines, respectively. All regression equations were statistically significant ($p < 0.05$). Differences between regressions were tested using curve inequality randomization tests ($p < 0.05$) and statistically significant differences are designated *a*, *b* and *c* (e. g. all three sites are significantly different from on another).

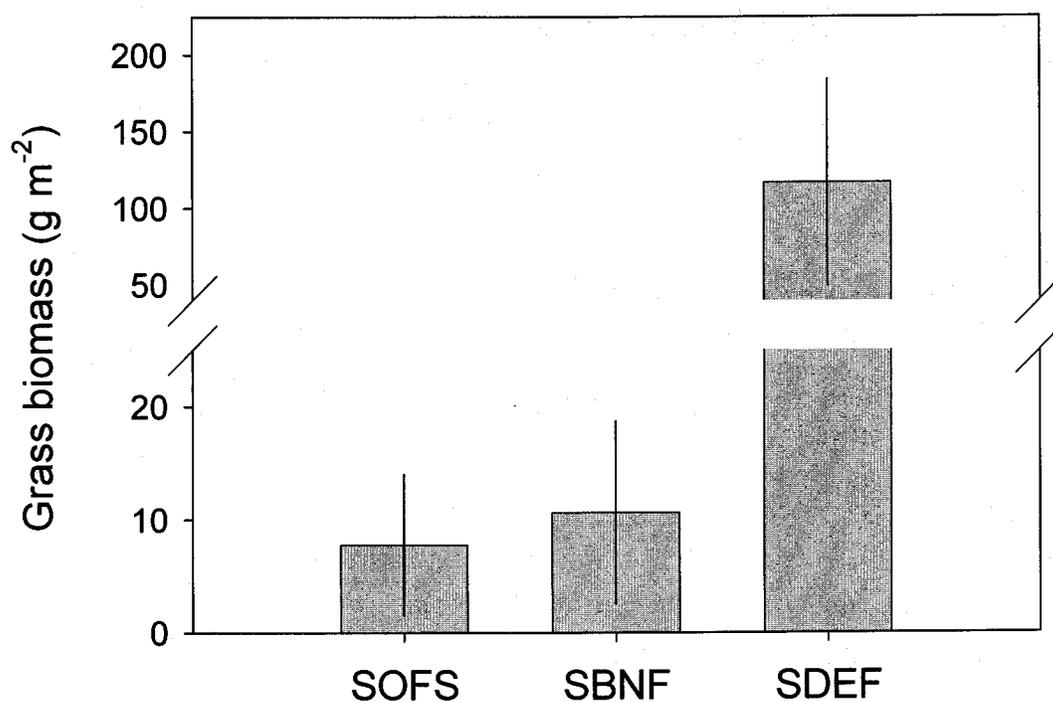


Figure 3-4. Annual grass biomass for the three study sites, Sky Oaks Field Station (SOFS), San Bernardino National Forest (SBNF) and San Dimas Experimental Forest (SDEF). Data presented are for spring 2005 (SDEF) and spring 2006 (SOFS and SBNF). These seasons represent 33.5, 30.5 and 33.5 months post-fire for SOFS, SBNF and SDEF, respectively. Each bar represents the mean \pm 1 standard error ($n = 4$) annual percentages. At SOFS and SBNF 100% of the grass was *B. tectorum* (non-native) and at SDEF 0.4% was *A. fatua*, 42.0% was *B. tectorum* and 57.6% was *E. calycina* (all non-native).

Appendix 1. Observed species at the chaparral study sites, Sky Oaks Field Station (SOFS), San Dimas Experimental Forest (SDEF) and San Bernardino National Forest (SBNF).

SOFS			
Perennial shrubs		Herbaceous (continued)	
<i>Adenostoma fasciculatum</i> Hook. & Arn.	ROSA	<i>Cryptantha muricata</i> (Hook. & Arn.) A. Nelson & J. F. Macbr.	BORA
<i>Artemisia californica</i> Less.	ASTE	<i>Dichelostemma capitatum</i> (Benth.) A. W. Wood	THEM
<i>Ceanothus greggii</i> A. Gray	RHAM	<i>Eriogonum davidsonii</i> Greene	POLG
<i>Eriogonum fasciculatum</i> Benth.	POLG	<i>Erodium cicutarium</i> (L.) L'Hér. Ex Aiton*	GERA
<i>Opuntia basilaris</i> Engelm. & J. M. Bigelow	CACT	<i>Euphorbia peplus</i> L. *	EUPH
<i>Salvia leucophylla</i> Greene	LAMI	<i>Gilia</i> sp.	POLE
<i>Solanum xanti</i> A. Gray	SOLA	<i>Gutierrezia californica</i> (DC.) Torr. & A. Gray	ASTE
<i>Trichostema parishii</i> Vasey	LAMI	<i>Helianthemum scoparium</i> Nutt.	CIST
<i>Yucca whipplei</i> Torr.	AGAV	<i>Logfia filaginoides</i> (Hook. & Arn.) Morefield	ASTE
Herbaceous		<i>Lotus strigosus</i> (Nutt.) Greene	FABA
<i>Amsinckia</i> sp.	BORA	<i>Penstemon spectabilis</i> Thurb.	PLAN
<i>Bromus diandrus</i> Roth*	POAC	<i>Phacelia</i> sp.	BORA
<i>Bromus madritensis</i> L. subsp. <i>rubens</i> (L.) Husn. *	POAC	<i>Plagiobothrys collinus</i> (Phil.) I. M. Johnst.	BORA
<i>Bromus tectorum</i> L. *	POAC	<i>Pseudognaphalium canescens</i> (DC.) Anderb.	ASTE
<i>Calyptidium monandrum</i> Nutt.	PORT	<i>Schismus barbatus</i> (L.) Thell. *	POAC
<i>Camissonia hirtella</i> (Green) P. H. Raven	ONOG	<i>Stephanomeria virgata</i> Benth.	ASTE
<i>Chaenactis artemisiifolia</i> (A. Gray) A. Gray	ASTE	<i>Stylocline gnaphaloides</i> Nutt.	ASTE
<i>Conyza canadensis</i> (L.) Cronquist	ASTE	<i>Vulpia myuros</i> (L.) C. C. Gmel. *	POAC
<i>Cordylanthus rigidus</i> (Benth.) Jeps.	SCRO	<i>Vulpia octoflora</i> (Walter) Rydb.	POAC
<i>Crassula connata</i> (Ruiz & Pav.) A. Berger	CRAS		
SDEF		SBNF	
Perennial shrubs		Perennial shrubs	
<i>Adenostoma fasciculatum</i> Hook. & Arn.	ROSA	<i>Adenostoma fasciculatum</i> Hook. & Arn.	ROSA
<i>Baccharis salicifolia</i> (Ruiz & Pav.) Pers.	ASTE	<i>Arctostaphylos glandulosa</i> Eastw.	ERIC
<i>Ceanothus crassifolius</i> Torr.	RHAM	<i>Ceanothus crassifolius</i> Torr.	RHAM
<i>Ericameria parishii</i> (Greene) H. M. Hall	ASTE	<i>Dendromecon rigida</i> Benth	PAPA
<i>Hazardia squarrosa</i> (Hook & Arn.) Greene	ASTE	<i>Eriodictyon trichocalyx</i> A. Heller	BORA
<i>Malosma laurina</i> (Nutt.) Abrams	ANAC	<i>Salvia mellifera</i> Greene	LAMI
<i>Quercus durata</i> Jeps.	FAGA	<i>Yucca whipplei</i> Torr.	AGAV
Herbaceous		Herbaceous	
<i>Avena fatua</i> L. *	POAC	<i>Bromus tectorum</i> L. *	POAC
<i>Bromus tectorum</i> L. *	POAC	<i>Calystegia occidentalis</i> (A. Gray) Brummitt	CONV
<i>Carduus pycnocephalus</i> L. *	ASTE	<i>Camissonia</i> sp.	ONOG
<i>Cryptantha</i> sp.	BORA	<i>Helianthemum scoparium</i> Nutt.	CIST
<i>Ehrharta calycina</i> Sm. *	POAC	<i>Logfia filaginoides</i> (Hook. & Arn.) Morefield	ASTE
<i>Galium angustifolium</i> Nutt. Ex A. Gray	RUBI	<i>Lotus scoparius</i> (Nutt.) Ottley	FABA
<i>Gnaphalium californicum</i> DC.	ASTE	<i>Marah macrocarpus</i> (Greene) Greene	CUCU
<i>Helianthemum scoparium</i> Nutt.	CIST	<i>Vicia villosa</i> Roth*	FABA
<i>Hirschfeldia incana</i> (L.) Lagr.-Fossat	BRAS		
<i>Lotus scoparius</i> (Nutt.) Ottley	FABA		
<i>Marah macrocarpus</i> (Greene) Greene	CUCU		
<i>Stephanomeria</i> sp.	ASTE		

*Plant species non-native to California.

Plant family abbreviations: AGAV = Agavaceae; ANAC = Anacardiaceae; ASTE = Asteraceae; BORA = Boraginaceae; BRAS = Brassicaceae; CIST = Cistaceae; CONV = Convolvulaceae; CUCU = Cucurbitaceae; ERIC = Ericaceae; EUPH = Euphorbiaceae; FABA = Fabaceae; LAMI = Lamiaceae; NYCT = Nyctaginaceae; ONOG = Onograceae; PAPA = Papaveraceae; PHRY = Phymaceae; POAC = Poaceae; ROSA = Rosaceae; RUBI = Rubiaceae.

Appendix 2. Observed species at the coastal sage scrub study site, Santa Margarita Ecological Reserve (SMER).

SMER

Perennial shrubs	
<i>Artemisia californica</i> Less.	ASTE
<i>Salvia mellifera</i> Greene	LAMI
<i>Yucca whipplei</i> Torr.	AGAV
Herbaceous	
<i>Chamaesyce polycarpa</i> (Benth.) Millsp.	EUPH
<i>Cryptantha</i> sp. BORA	BORA
<i>Deinandra paniculata</i> (A. Gray) Davidson & Moxley	ASTE
<i>Eucrypta chrysanthemifolia</i> (Benth.) Greene	BORA
<i>Gnaphalium californicum</i> DC.	ASTE
<i>Gnaphalium palustre</i> Nutt.	ASTE
<i>Gnaphalium stramineum</i> Kunth	ASTE
<i>Gutierrezia californica</i> (DC.) Torr. & A. Gray	ASTE
<i>Hirschfeldia incana</i> (L.) Lagr.-Fossat *	BRAS
<i>Marah macrocarpus</i> (Greene) Greene	CUCU
<i>Mimulus</i> sp.	PHRY
<i>Mirabilis laevis</i> (Benth.) Curran	NYCT
<i>Stylocline gnaphaloides</i> Nutt.	ASTE

*Plant species non-native to California.

Plant family abbreviations: AGAV = Agavaceae; ASTE = Asteraceae; BORA = Boraginaceae; BRAS = Brassicaceae; CUCU = Cucurbitaceae; EUPH = Euphorbiaceae; LAMI = Lamiaceae; NYCT = Nyctaginaceae; PHRY = Phrymaceae.

LITERATURE CITED

- Aber, J. D., K. J. Nadelhoffer, P. Steudler and J. M. Melillo. 1989. Nitrogen saturation in northern forest ecosystems. *Bioscience* 39: 378-386.
- Aber, J. D., J. M. Melillo, K. J. Nadelhoffer, J. Pastor and R. D. Boone. 1991. Factors controlling nitrogen cycling and nitrogen saturation in northern temperate forest ecosystems. *Ecological Applications* 1: 303-315.
- Allen, E. B., P. E. Padgett, A. Bytnerowicz and R. Minnich. 1998. Nitrogen deposition effects on coastal sage scrub vegetation of southern California. United States Department of Agriculture Forest Service, General Technical Report PSW-GTR-166.
- Barbour, M. G., J. H. Burk and W. D. Pitts, F. S. Gilliam and M. W. Schwartz. 1999. *Terrestrial plant ecology*, 3rd edition. Benjamin Cummings Publishing Company, Inc., Menlo Park, California, USA.
- Black, C. H. 1987. Biomass, nitrogen, and phosphorus accumulation over a southern California fire cycle chronosequence. In: Tenhunen J. D., et al. (eds) *Plant response to stress*. NATO ASI series, vol. G15. Springer-Verlag, Berlin Heidelberg New York, pp. 445-458.
- Bobbink, R. 1991. Effects of nutrient enrichment in Dutch chalk grassland. *Journal of Applied Ecology* 28: 24-41.
- Bobbink, R., M. Hornung and J. G. M. Roelofs. 1998. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *Journal of Ecology* 86: 717-738.
- Boerner, R. E. J. 1982. Fire and nutrient cycling in temperate ecosystems. *Bioscience* 32:187-192.
- Bonham, C. D. 1989. *Measurements for terrestrial vegetation*. Wiley, New York.
- Boring, L. R., W. T. Swank, J. B. Waide and G. S. Henderson. 1988. Sources, fates, and impacts of nitrogen inputs to terrestrial ecosystems: review and synthesis. *Biogeochemistry* 6: 119-159.
- Burkholder, J. E., E. Noga, C. Hobbs and H. Glasgow. 1992. New "phantom" dinoflagellate is the causative agent of major estuarine fish kills. *Nature* 353: 407-410.

- Bytnerowicz, A., P. R. Miller, D. M. Olszyk, P. J. Dawson and C. A. Fox. 1987. Gaseous and particulate air pollution in the San Gabriel Mountains of southern California. *Atmospheric Environment* 21: 1805-1814.
- Bytnerowicz, A. and M. E. Fenn. 1996. Nitrogen deposition in California forests: a review. *Environmental Pollution* 92: 127-146.
- Chapin III, F. S. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* 11: 233-260.
- Cowling, R. W., P. W. Rundel, B. B. Lamont, M. K. Arroyo and M. Arianoutsou. 1996. Plant diversity in mediterranean-climate regions. *Trends in Ecology and Evolution* 11: 362-366.
- D'Antonio, C. M. and P. M. Vitousek. 1992. Biological invasions by exotic grasses: the grass-fire cycle and global change. *Annual Review of Ecology and Systematics* 23:63-87.
- DeBano, L. F. and C. E. Conrad. 1978. The effect of fire on nutrients in a chaparral ecosystem. *Ecology* 59:489-497.
- DeBano, L. F., G. E. Eberlein and P. H. Dunn. 1979. Effects of burning chaparral soils: I. soil nitrogen. *Soil Science Society of America Journal* 43:504-509.
- Driessche, R van den. 1974. Prediction of mineral nutrient status of trees by foliar analysis. *Botanical Review* 40: 347-394.
- Dunn, P. H., L. F. DeBano and G. E. Eberlein. 1979. Effects of burning chaparral soils: II. soil microbes and nitrogen mineralization. *Soil Science Society of America Journal* 43:509-514.
- Fenn, M. E., M. A. Poth and D. W. Johnson. 1996. Evidence for nitrogen saturation in the San Bernardino Mountains in southern California. *Forest Ecology and Management* 82: 211-230.
- Fenn, M. E., M. A. Poth, J. D. Aber, J. S. Baron, B. T. Bormann, D. W. Johnson, D. Lemly, S. G. McNulty, D. F. Ryan and R. Stottlemyer. 1998. Nitrogen excess in North American ecosystems: predisposing factors, ecosystem responses, and management strategies. *Ecological Applications* 8: 706-733.

- Fenn, M. E. and M. A. Poth. 1999. Temporal and spatial trends in streamwater nitrate concentrations in the San Bernardino Mountains, southern California. *Journal of Environmental Quality* 28: 822-836.
- Fenn, M. E. and M. A. Poth. 2001. A case study of nitrogen saturation in western U. S. forests. Pages 433-439 in Galloway, J., E. Cowling, J. W. Erisman, J. Wisniewski and C. Jordan, eds. *Optimizing Nitrogen Management in Food and Energy Production and Environmental Protection: Proceedings of the 2nd International Nitrogen Conference on Science and Policy*, Lisse (Netherlands): A. A. Balkema Publishers. (4 March 2003; www.thescientificworld.com).
- Fenn, M. E., M. A. Poth and M. J. Arbaugh. 2002. A throughfall collection method using mixed bed ion exchange resin columns. In *Proceedings of the International Symposium on Passive Sampling of Gaseous Air Pollutants in Ecological Effects Research*. *TheScientificWorld* 2: 122-130. (4 March 2003, www.thescientificworld.com).
- Fenn, M. E., R. Haeuber, G. S. Tonnensen, J. S. Baron, S. Grossman-Clarke, D. Hope, D. A. Jaffe, S. Copeland, L. Geiser, H. M. Rueth and J. O. Sickman. 2003a. Nitrogen emissions, deposition and monitoring in the western United States. *Bioscience* 53: 391-403.
- Fenn, M. E., J. S. Baron, E. B. Allen, H. M. Rueth, K. R. Nydick, L. Geiser, W. D. Bowman, J. O. Sickman, T. Meixner, D. W. Johnson and P. Neitlich. 2003b. Ecological effects of nitrogen deposition in the western United States. *Bioscience* 53: 404-420.
- Fenn, M.E. and M. A. Poth. 2004. Monitoring nitrogen deposition in throughfall using ion exchange resin columns: a field test in the San Bernardino Mountains. *Journal of Environmental Quality* 33: 2007-2014.
- Galloway J. N., F. J. Dentener, D. G. Capone, E. W. Boyer, R. W. Howarth, S. P. Seitzinger, G. P. Asner, C. C. Cleveland, P. A. Green, E. A. Holland, D. M. Karl, A. F. Michaels, J. H. Porter, A. R. Townsend and C. J. Vörösmarty. 2004. Nitrogen cycles: past present and future. *Biogeochemistry* 70: 153-226.
- Giardina, C. P., M. G. Ryan, D. Binkley and J. H. Fownes. 2003. Primary production and carbon allocation in relation to nutrient supply in a tropical experimental forest. *Global Change Biology* 9: 1438-1450.

- Goudriaan, J. 1988. The bare bones of leaf-angle distribution in radiation models for canopy photosynthesis and energy exchange. *Agricultural and Forest Meteorology* 43: 155-169.
- Gower, S. T., C. J. Kucharik and J. M. Norman. 1999. Direct and indirect estimation of leaf area index, fAPAR and net primary production of terrestrial ecosystems. *Remote Sensing of Environment* 70: 29-51.
- Gray, J. T. and W. H. Schlesinger. 1981. Biomass, production, and litterfall in the coastal sage scrub of southern California. *American Journal of Botany* 68: 24-33.
- Gray, J. T. and W. H. Schlesinger. 1983. Nutrient use by evergreen and deciduous shrubs in southern California: II. experimental investigations of the relationship between growth, nitrogen uptake and nitrogen availability. *Journal of Ecology* 71: 43-56.
- Grime, J. P. and R. Hunt. 1975. Relative growth rate: its range and adaptive significance in a local flora. *Journal of Ecology* 63: 339-344.
- Grogen, P., T. D. Bruns and F. S. Chapin III. 2000. Fire effects on ecosystem nitrogen cycling in a Californian bishop pine forest. *Oecologia* 122:537-544.
- Grulke, N. E. and L. Balduman. 1999. Deciduous conifers: high N deposition and O₃ exposure effects on growth and biomass allocation in ponderosa pine. *Water, Air and Soil Pollution* 116: 235-248.
- Grundon, N. J. 1972. Mineral nutrition of some Queensland heath plants. *Journal of Ecology* 60: 171-181.
- Harper, J. L. and I. H. McNaughton. 1962. The comparative biology of closely related species living in the same area. VII. Interference between individuals in pure and mixed populations of *Papaver* species. *New Phytologist* 61:175-188.
- Hastings, S. J., W. C. Oechel and N. Sionit. 1989. Water relations and photosynthesis of chaparral resprouts and seedlings following fire and hand clearing. In: Keeley, S. C. (ed.) *The California chaparral: paradigms reexamined*. Science series, no. 34. Natural History Museum of Los Angeles County, Los Angeles, pp.107-113.

- Hellmers, H., J. F. Bonner and J. M. Kelleher. 1955. Soil fertility: a watershed management problem in the San Gabriel Mountains of southern California. *Soil Science* 80: 189-197.
- Hines, R. J. and C. Mitcham. Ray and Chad's shitty paper. Unpublished.
- Jassby, A. D., J. E. Reuter, R. P. Azler, C. R. Goldman and S. H. Hackley. 1994. Atmospheric deposition of nitrogen and phosphorus in the annual nutrient load of Lake Tahoe (California-Nevada). *Water Resources Research* 30: 2207-2216.
- Jepson Online Interchange. 2007. The Jepson Project, University of California, Berkeley http://ucjeps.berkeley.edu/interchange/about_interchange.html. Cited 26 April 2007.
- Keeley, J. E. 2000. Chaparral. In: Barbour, M. G. and W. D. Billings (eds.) *North American terrestrial vegetation*. Cambridge University Press, Cambridge Madrid Melbourne New York, pp. 203-254.
- Kirkby, E. A. 1981. Plant growth in relation to nitrogen supply. *Terrestrial Nitrogen Cycles* 33: 249-267.
- Knecht, A. A. 1971. Soil survey for western Riverside area, California. Soil Conservation Service, Washington, D. C.
- Knops, J. M. H. and K. Reinhard. 2000. Specific leaf area along a nitrogen fertilization gradient. *American Midland Naturalist* 144: 265-272.
- Köchy M. and S. D. Wilson. 2001. Nitrogen deposition and forest expansion in the northern Great Plains. *Journal of Ecology* 89: 807-817.
- Kramer, M. H., B. L. Herwaldt, G. F. Craun, R. L. Calderon and D. D. Juranek. 1996. Surveillance of waterborne-disease outbreaks – United States, 1993-1994. *CDC Surveillance Summaries, MMWR Surveillance Summaries* 45: 1-33.
- Kummerow, J., G. Avila, M. E. Aljaro, S. Araya and G. Montenegro. 1982. Effect of fertilizer on fine root density and shoot growth in Chilean matorral. *Botanical Gazette* 143: 498-504.
- Kummerow, J. and R. K. Lantz. 1983. Effect of fire on fine root density in red shank (*Adenostoma sparsifolium* Torr.) chaparral. *Plant and Soil* 70: 347-352.

- Larcher, W. 2003. Physiological plant ecology: ecophysiology and stress physiology of functional groups. Springer-Verlag, New York, New York, USA.
- McConnel, R. K., K. Berhane, F. Gilliland, S. J. London, H. Vora, E. Avol, W. J. Gunderman, H. G. Marsolis, F. Lurmann, D. C. Thomas and J. M. Peters. 1999. Air pollution and bronchitic symptoms in southern California children with asthma. *Environmental Health Perspectives* 107: 757-760.
- McMaster, G. S., W. M. Jow and J. Kummerow. 1982. Response of *Adenostoma fasciculatum* and *Ceanothus greggii* chaparral to nutrient additions. *Journal of Ecology* 70: 745-756.
- Minnich, R. A. and R. J. Dezzani. 1998. Historical decline of coastal sage scrub in the Riverside-Perris Plain, California. *West Birds* 29:366-391.
- Mohren, G. M. J., J. Van Den Burg and F. W. Burger. 1986. Phosphorus deficiency induced by nitrogen input in Douglas fir in the Netherlands. *Plant and Soil* 95: 191-200.
- Monsi, M., Z. Uchijima and T. Oikawa. 1973. Structure of foliage canopies and photosynthesis. *Annual Review of Ecology and Systematics* 4: 301-327.
- Mooney, H. A. and P. W. Rundel. 1979. Nutrient relations of the evergreen shrub, *Adenostoma fasciculatum*, in the California chaparral. *Botanical Gazette* 140: 109-113.
- Moreno, J. M. and W. C. Oechel. 1991. Fire intensity effects on germination of shrubs and herbs in southern California chaparral. *Ecology* 72: 1993-2004.
- Moreno, J. M. and W. C. Oechel. 1992. Factors controlling postfire seedling establishment in southern California chaparral. *Oecologia* 90:50-60.
- Nadelhoffer, K. J., J. D. Aber and J. M. Melillo. 1985. Fine roots, net primary production, and soil nitrogen availability: a new hypothesis. *Ecology* 66: 1377-1390.
- Padgett, P. E. and E. B. Allen. 1999. Differential responses to nitrogen fertilization in native shrubs and exotic annuals common to Mediterranean coastal sage scrub of California. *Plant Ecology* 144: 93-101.

- Padgett, P. E., E. B. Allen, A. Bytnerowicz and R. A. Minnich. 1999. Changes in soil inorganic nitrogen as related to atmospheric nitrogenous pollutants in southern California. *Atmospheric Environment* 33: 769-781.
- Pasquini, S. C. and G. L. Vourlitis. 2008. Early post-fire biomass accumulation of chaparral stands exposed to varying levels of nitrogen deposition. *Plant Ecology* *submitted*.
- Peterson, B. J. and J. M. Melillo. 1985. The potential storage of carbon caused by eutrophication of the biosphere. *Tellus* 37B: 117-127.
- Pierce, L. L., S. W. Running and J. Walker. 1994. Regional-scale relationships of leaf area index to specific leaf area and leaf nitrogen content. *Ecological Applications* 4: 313-321.
- Poole, D. K. and P. C. Miller. 1975. Water relations of selected species of chaparral and coastal sage communities. *Ecology* 56:1118-1128.
- Rejmankova, E., H. M. Savage, M. Rejmanek, J. I. Arredondo-Jimenez and D. R. Roberts. 1991. Multivariate analysis of relationships between habitats, environmental factors and occurrence of Anopheline mosquito larvae *Anopheles albimanus* and *A pseudopunctipennis* in southern Chiapas, Mexico. *Journal of Applied Ecology* 28: 827-841.
- Riggan, P. J., R. N. Lockwood and E. N. Lopez. 1985. Deposition and processing of airborne nitrogen pollutants in Mediterranean-type ecosystems of southern California. *Environmental Science and Technology* 19: 781-789.
- Rundel, P. W. and D. J. Parsons. 1980. Nutrient changes in two chaparral shrubs along a fire-induced age gradient. *American Journal of Botany* 67: 51-58.
- Schindler, D. W. and S. E. Bayley. 1993. The biosphere as an increasing sink for atmospheric carbon: estimates from increased nitrogen deposition. *Global Biogeochemical Cycles* 7: 717-733.
- Shaver, G. R. 1981. Mineral nutrition and nonstructural carbon utilization. In: Miller, P. C. (ed.) *Resource use by chaparral and matorral*. Springer-Verlag, New York Heidelberg Berlin, pp. 237-257.

- Sickman, J. O., J. M. Melack and D. W. Clow. 2003. Evidence for nutrient enrichment of high-elevation lakes in the Sierra Nevada, California. *Limnology and Oceanography* 48: 1885-1892.
- Sparks, S. R., W. C. Oechel and Y. Mauffette. 1993. Photosynthate allocation patterns along a fire-induced age sequence in two shrub species from the California chaparral. *International Journal of Wildland Fire* 3:21-30.
- Sunish I. P. and R. Reuben. 2001. Factors influencing the abundance of Japanese encephalitis vectors in rice fields in India – I. abiotic. *Medical and Veterinary Entomology* 15: 381-392.
- Teng, H. J., Y. L. Wu and C. Lin. 1998. Effects of environmental factors on abundance of *Anopheles minimus* larvae and their seasonal fluctuations in Taiwan. *Environmental Health Perspectives* 110: 665-670.
- Tonnesen, G., Z. Wang, M. Omary and C. J. Chien. 2007. Assessment of nitrogen deposition: modeling and habitat assessment. California Energy Commission, PIER Energy-Related Environmental Research. CEC-500-2005-032.
- Toth, S. J. and T. A. Melton. 2000. North Carolina Pest News, North Carolina Coop Ext. Serv., 16.
- Townsend, A. R., R. W. Howarth, F. A. Bazzaz, M. S. Booth, C. C. Cleveland, S. K. Collinge, A. P. Dobson, P. R. Epstein, E. A. Holland, D. R. Keeney, M. A. Mallin, C. A. Rogers, P. Wayne and A. H. Wolfe. 2003. Human health effects of a changing global nitrogen cycle. *Frontiers in Ecology and the Environment* 1: 240-246.
- Vitousek, P. 1982. Nutrient cycling and nutrient use efficiency. *American Naturalist* 119: 553-572.
- Vitousek, P. M. and R. W. Howarth. 1991. Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry* 13: 87-115.
- Vitousek, P., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger and D. G. Tilman. 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* 7: 737-750.

- Vourlitis, G. L. 1991. The importance of nitrogen in a southern California coastal dune-slack community. Master's thesis, San Diego State University. 105 pages.
- Vourlitis, G. L., S. Pasquini and G. Zorba. 2007a. Plant and soil N response of southern Californian semi-arid shrublands after 1 year of experimental N deposition. *Ecosystems* 10: 263-279.
- Vourlitis, G. L., G. Zorba, S. C. Pasquini and R. Mustard. 2007b. Chronic nitrogen deposition enhances nitrogen mineralization potential of semiarid shrubland soils. *Soil Science Society of America Journal* 71: 836-842.
- Vourlitis, G. L., G. Zorba, S. C. Pasquini and R. Mustard. 2007c. Carbon and nitrogen storage in soil and litter of southern Californian semi-arid shrublands. *Journal of Arid Environments* 70: 164-173.
- Vourlitis, G. L. and S. Pasquini. 2008. Carbon and nitrogen dynamics of pre- and post-fire chaparral exposed to varying atmospheric N deposition. *Journal of Arid Environments* 72: 1448-1463.
- Walker, E. D., D. L. Lawson, R. W. Merritt, W. T. Morgan and K. J. Klug. 1991. Nutrient dynamics, bacterial populations and mosquito productivity in tree-hole ecosystems and microcosms. *Ecology* 72: 1529-1546.
- Westman, W. E. 1981. Diversity relations and succession in California coastal sage scrub. *Ecology* 62: 737-750.
- Williams, M. W., J. S. Baron, N. Caine, R. Sommerfeld and R. Sanford. 1996. Nitrogen saturation in the Rocky Mountains. *Environmental Science and Technology* 30: 640-646.
- Wolfe, A. H. and J. A. Patz. 2002. Reactive nitrogen and human health: acute and long-term implications. *Ambio* 31: 120-125.
- Zar, J. H. 1999. *Biostatistical Analysis*, 4th, editor. Prentice-Hall, New Jersey, USA.