

Risk-based determination of critical nitrogen deposition loads for fire spread in southern California deserts

LEELA E. RAO,^{1,4} EDITH B. ALLEN,^{1,2} AND THOMAS MEIXNER³

¹Center for Conservation Biology, University of California–Riverside, 900 University Avenue, Riverside, California 92521 USA

²Department of Botany and Plant Sciences, University of California–Riverside, 900 University Avenue, Riverside, California 92521 USA

³Department of Hydrology and Water Resources, University of Arizona, 1133 East James E. Rogers Way, Tucson, Arizona 85721 USA

Abstract. Fire risk in deserts is increased by high production of annual forbs and invasive grasses that create a continuous fine fuel bed in the interspaces between shrubs. Interspace production is influenced by water, nitrogen (N) availability, and soil texture, and in some areas N availability is increasing due to anthropogenic N deposition. The DayCent model was used to investigate how production of herbaceous annuals changes along gradients of precipitation, N availability, and soil texture, and to develop risk-based critical N loads. DayCent was parameterized for two vegetation types within Joshua Tree National Park, California, USA: creosote bush (CB) and piñon–juniper (PJ). The model was successfully calibrated in both vegetation types, but validation showed that the model is sensitive to soil clay content. Despite this fact, DayCent (the daily version of the biogeochemical model CENTURY) performed well in predicting the relative response of production to N fertilization and was used to determine estimates of fire risk for these ecosystems. Fire risk, the probability that annual biomass exceeds the fire threshold of 1000 kg/ha, was determined for each vegetation type and began to increase when N deposition increased 0.05 g/m² above background levels (0.1 g/m²). Critical loads were calculated as the amount of N deposition at the point when fire risk began to increase exponentially. Mean critical loads for all soil types and precipitation <21 cm/yr, representing the majority of our study region, were 0.32 ± 0.07 and 0.39 ± 0.09 g N/m² for CB and PJ, respectively. Critical loads decreased with increasing soil clay content and increasing precipitation, such that the wettest areas with clay contents of 6–14% may have critical loads as low as 0.15 g N/m². Mean fire risks approached their maximum at 0.93 ± 0.21 and 0.87 ± 0.17 g N/m² in CB and PJ, indicating that precipitation is the driver of fire above these N deposition levels, which are currently observed in some areas of the Sonoran and Mojave Deserts. Overall, this analysis demonstrates the importance of considering both N deposition and precipitation when evaluating fire risk across arid landscapes.

Key words: arid; biogeochemical model; *Bromus*; CENTURY; climate change; desert; exotic grasses; fire risk; fuel load; Joshua Tree National Park, California, USA; *Larrea tridentata*; *Schismus*.

INTRODUCTION

In the United States there is growing interest in managing atmospheric nitrogen (N) deposition using critical loads, which are defined as the amount of one or more pollutants below which there are no adverse ecological effects (Nilsson and Grennfelt 1988, Fisher et al. 2007, Burns et al. 2008). The European Union regulates N deposition using critical loads based on both acidification and fertilization effects (Nilsson and Grennfelt 1988). In the United States, recent research has improved our understanding of ecosystem thresholds for effects of N deposition, resulting in increased

support for implementing critical loads on federal lands (Porter et al. 2005, Porter and Johnson 2007, Burns et al. 2008). In arid regions, acidification effects are limited due to low rainfall, lack of surface water bodies, and high soil buffering capacity. Instead, the primary effect of N deposition is chronic fertilization. Nitrogen fertilization can alter soil microbial processes, promote exotic species growth that would otherwise be N limited, and increase the growth of rapidly responding annual species above the threshold for carrying fire (Minnich and Dezzani 1998, Brooks 2003, Fenn et al. 2003a). In this paper, we applied a biogeochemical process model to determine critical loads for N deposition for its effects on increasing fire risk in the arid lands of southern California, USA.

Fires in the arid regions of southern California have increased in frequency during the last several decades due in large part to a period of increased numbers of above-normal precipitation years and increased cover of

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⁴ Present address: CA Air Resources Board, Mobile Source Control Division, 9480 Telstar Avenue, No. 4, El Monte, California 91731 USA. E-mail: lr Rao@arb.ca.gov

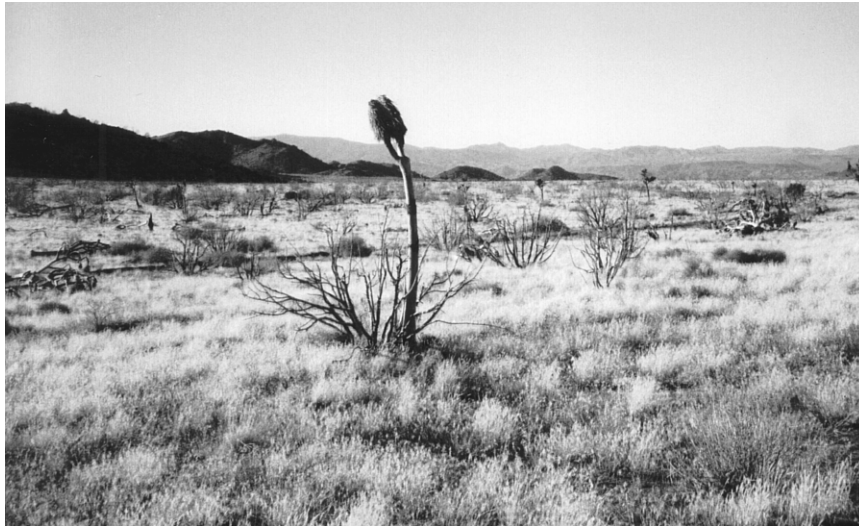


PLATE 1. Region of Lower Covington Flats in Joshua Tree National Park, California, USA, that burned in 1999. Taken in 2004, this photograph illustrates the lack of native species recovery after fire; five years after the fire the landscape is dominated by burnt-out shrub skeletons and the exotic grasses *Bromus tectorum* and *B. madritensis*. Photo credit: L. E. Rao.

exotic annual grasses (Brown and Minnich 1986, Brooks and Berry 2006, Brooks and Minnich 2006). The exotic grass litter does not break down as rapidly as most native herbaceous litter, thus creating a highly flammable continuous fine fuel load during the dry season (Brooks and Minnich 2006). The threshold of biomass necessary to carry fire has been reported to range from 700 to 1500 kg/ha of continuous fine fuel (Anderson 1982, Scifres and Hamilton 1993, Minnich and Dezzani 1998, Fenn et al. 2003a), although the exact amount of native forb and exotic grass biomass needed to carry fire in the desert is still unknown. In creosote bush scrub, the small amount of discontinuous woody fuel is believed to have hindered fire spread resulting in long fire-return intervals (Brooks and Minnich 2006), while in areas with greater woody biomass such as piñon-juniper woodland, fire cycle periods have been estimated at 480 years (Wangler and Minnich 1996). Because of the relative rarity of fire in these arid systems, shrubs are not fire adapted and suffer large-scale mortality during most fire events and are slow to reestablish (McLaughlin and Bowers 1982, Brown and Minnich 1986). Slow recovery of shrubs coupled with rapid recovery of exotic grasses can result in increased fire frequency and a shift in the plant community from a shrub-dominated to exotic-grass-dominated system (D'Antonio and Vitousek 1992, D'Antonio 2000, Brooks et al. 2004, Steers 2008; see Plate 1).

Exotic grasses promote landscape conversion by invading the interspaces between shrubs and creating a continuous fine fuel bed. However, the interspaces are harsh environments that are low in nutrients (Kieft et al. 1998, Schlesinger and Pilmanis 1998, Schade and Hobbie 2005), have high sand and gravel contents (Pake and Venable 1995, Kieft et al. 1998), and have

more extreme temperatures than under shrubs (Pake and Venable 1995). These factors limit interspace productivity in comparison to the under shrub "islands of fertility" (Halvorson and Patten 1975, Hadley and Szarek 1981), such that release from limiting factors should increase interspace production. The foremost limiting factor of productivity is water (Noy-Meir 1973), with secondary limitation by N (Romney et al. 1978, Gutierrez et al. 1988, 1992). Arid land production has been observed to increase with increased precipitation (Patten 1978, Romney et al. 1978, Bowers 2005) and N fertilization (Romney et al. 1974, 1978, Salo et al. 2005, Allen et al. 2009). Additionally, in some cases there are interactions between increased N and water availability such that exotic and native annuals increase more with added N in high rainfall years than in low rainfall years (Gutierrez et al. 1992, Hooper and Johnson 1999, Brooks 2003).

The N and hydrologic cycles are closely linked through the effects of soil water content on mineralization, denitrification, and leaching, making it extremely difficult to separate out the effects of one from the other in the field (Burke et al. 1997, Schimel et al. 1997). Additionally, soil texture influences ecosystem responses to precipitation and N by affecting water holding capacity, infiltration, and hydraulic conductivity (Austin et al. 2004, Schwinning et al. 2004). As a result of the complex interactions between N, precipitation, and soil texture, the effects of each factor on annual production using field observations and measurements can be difficult to differentiate. Instead, it has been suggested that mechanistic process models, such as the biogeochemical model CENTURY, be employed in the hopes of understanding ecosystem functioning, especially with respect to temporal processes like changes in

TABLE 1. Selected characteristics for the creosote bush (CB) and piñon-juniper (PJ) calibration (C) and validation (V) sites in Joshua Tree National Park, California, USA.

Site	MAP (cm)	N deposition (g·m ⁻² ·yr ⁻¹)	Sand-silt-clay (%)	Rock (%)	Bulk density (g/cm ³)	pH	Field capacity (% volume)	Wilting point (% volume)	Hydraulic conductivity (cm/s)
CB-C	10.34	0.3	83-11-6	29	1.63	8.3	15.99	5.61	0.0039
CB-V	13.7	0.7	88-10-2	25	1.61	7.1	9.47	2.68	0.0081
PJ-C	12.57	0.8	78-13-9	11	1.39	6.9	16.16	6.07	0.0024
PJ-V	16.77	0.4	71-25-4	42	1.63	7.7	10.46	3.11	0.0042

Notes: Soil characteristic values represent the actual values used in the soil parameterization files. MAP is mean annual precipitation. Field capacity, wilting point, and hydraulic conductivity values were determined using the Saxton model (Saxton et al. 1986) using soil texture and rock content as input values.

precipitation patterns and N deposition (Schimel et al. 1997).

While the CENTURY model was originally developed for the grasslands of the United States (Parton et al. 1987, 1988), it has since been applied to numerous ecosystems including forests (Kelly et al. 1997, Peng et al. 1998), tundra (Baron et al. 1994, Conley et al. 2000), and chaparral (Li et al. 2006). However, few applications of the daily version of CENTURY (DayCent) or the original CENTURY model have been conducted in desert ecosystems (Kemp et al. 2003). Thus the objectives of this study are to (1) determine the extent to which DayCent can model annual production and nutrient cycling in the desert under a range of N-fertilization scenarios and (2) use DayCent to gain an understanding of how fire risk in the deserts of southern California changes with increasing N deposition. To accomplish these objectives we parameterized DayCent for two vegetation types found at Joshua Tree National Park (JTNP), creosote bush scrub and piñon-juniper woodland. The model was then used to evaluate the risk of exceeding a threshold amount of interspace herbaceous biomass believed to enhance the spread of fire and determine critical N loads across a precipitation transect and a range of soil clay contents. This simulated landscape allows for a risk-based approach to determining critical loads for N deposition across southern California deserts.

METHODS

Site description

We modeled the interspace vegetation from two vegetation types characteristic of the arid lands of southern California, creosote bush scrub (CB) and piñon-juniper woodland (PJ). Winter annual interspace vegetation was the focus of the modeling effort because the interspace vegetation connects shrubs with a fine fuel layer enabling fire to spread readily through the ecosystem. Without a sufficient fine fuel load, fire is unlikely to carry in CB ecosystems, although fire may still spread through PJ due to larger shrub size, density, and woody fuel load (Brooks and Matchett 2006). At the CB sites modeled in this study, live shrub cover ranged between 9.5% $\pm$ 2.7% and 18.1% $\pm$ 3.8%. At the PJ sites live tree + shrub cover ranged between 20.8% $\pm$

0.9% and 22.7% $\pm$ 1.4% (all data presented are mean $\pm$ SE).

Soil and vegetation data were collected from two low-elevation CB sites in Joshua Tree National Park (JTNP) located in the Colorado Desert portion of the Sonoran Desert and two PJ sites located in the Mojave Desert portion of JTNP. One site in each vegetation type was used for model calibration, while the other was used for model validation. Site characteristics are presented in Table 1 and site-specific vegetation data are in Allen et al. (2009), with general descriptions in Keeler-Wolfe (2007) and Schoenherr and Burk (2007). The dominant shrub on the CB sites was *Larrea tridentata* with an understory of native forbs and the exotic annual grasses *Schismus arabicus* and *Schismus barbatus* (hereafter *Schismus* spp.). The dominant trees/shrubs on the PJ sites were *Juniperus californica* and *Pinus monophylla*, with an understory of shrubs, native forbs, and the exotic annual grasses *Bromus madritensis* ssp. *rubens*, *Bromus tectorum*, and *Schismus* spp. Annual exotic forbs were not a major component of the herbaceous cover at any of these sites (Allen et al. 2009).

Fire has never been observed at the CB sites since the establishment of Joshua Tree National Monument in 1936, although wetter areas outside of JTNP have burned once or even twice since 1980 (Brown and Minnich 1986, Brooks and Matchett 2006, Steers 2008). The PJ sites were assumed to have a fire return interval of 300 and 500 years for the more and less productive calibration and validation sites respectively, with grazing at both sites occurring from the 1870s to 1945 (Schmid and Rogers 1988, Wangler and Minnich 1996, Brooks and Minnich 2006).

Site-specific data collection

Ten experimental blocks were established at each site in 2002 to evaluate the effects of N fertilization on the native and exotic annual plants (Allen et al. 2009). The vegetation and soils at the experimental blocks within the CB and PJ sites have been measured annually since 2003. Plots were fertilized with 0, 0.5, and 3.0 g N/m² each December, surveyed for percent cover of annual forbs and grasses each spring, and surface soils (5 cm deep cores) collected each July for analysis of extractable N. Biomass was calculated from the percent cover data

using equations developed for one CB site and one PJ site relating percent cover to biomass using 0.25×0.5 m clipped plots in fertilized and unfertilized plots from both a wet (2005) and dry (2008) year (Allen et al. 2009). Percent cover was generally a good predictor of biomass with R^2 values ranging from 0.77 to 0.97 (2005 regressions $n = 11$ plots; 2008 regressions $n = 21$ plots).

At one CB and one PJ site, a one-time sampling of annual forbs and exotic grasses from each of the 10 control and 3.0 g N/m^2 fertilized plots was made for determination of aboveground tissue C, N, and lignin content. Soil cores to a 1 m depth were taken from control and 3.0 g N/m^2 fertilized plots. Soil samples were collected from six depths (0–5, 10–15, 20–25, 45–50, 70–75, and 95–100 cm) using a bucket sand auger and sieved for determination of percentage of rock and gravel ($>2\text{mm}$) content. Sieved samples were sent to the University of California Division of Agriculture and Natural Resources Analytical Laboratory (Davis, California, USA) for analysis of total C and N by combustion, extractable inorganic N, and soil texture. Samples were also analyzed for soil pH on a 1:1 soil:water slurry and $\text{CO}_3\text{-C}$ via a modified manometer method (Allison and Moodie 1965). Bulk density was determined for the surface layer only (0–5 cm).

Daily maximum and minimum temperature and precipitation data were obtained from a weather station placed at each site. Because on-site weather station data were only available for the years 2005–2008, climate data from the nearest weather station were obtained from National Oceanic and Atmospheric Administration's online National Climate Data Center. Daily temperature and precipitation data were scaled to the site data based on regressions between actual site and weather station data. Daily weather data from the long-term stations were available from 1936 to 2005, with actual site data used from 2005 to 2008.

Model description

The CENTURY model was developed to simulate plant production, soil nutrient dynamics, and soil water in natural and managed ecosystems, with an emphasis on soil organic matter as an integrator of production and decomposition over time (Parton et al. 1987, 1988). A daily time-step version of CENTURY (DayCent) was developed to model trace gas (CO_2 , CH_4 , N_2O , and NO) exchange between the soil and atmosphere (Parton et al. 2001, Del Grosso et al. 2005). As these models have been thoroughly described elsewhere (Parton et al. 1987, 1988, 1998, 2001, Del Grosso et al. 2005), we provide only a brief description here.

The model used in these simulations was DayCent version 4.5. The model was constructed with multiple sub-models: decomposition and soil organic matter, water budget, and plant production. The soil organic matter (SOM) sub-model simulated the dynamics of C, N, P, and S in the soil. Shoot and root litter of plants were divided into structural and metabolic C pools

based on lignin:N ratios. N inputs were from atmospheric deposition and N fixation, and N losses from NO_3 leaching, denitrification, and nitrification. The water budget sub-model calculated evaporation and transpiration water loss, water content of the soil layers, and flow of water between soil layers. Once water moved into the soil profile, it could be lost via transpiration, evaporation, or exit the profile as outflow or water storage. Because there was no stream flow at these desert sites, all excess water in the soil profile was assumed to be lost to deep water storage where it became inaccessible to the biota. The plant production sub-model may be used to simulate production for herbaceous annuals (crops) and perennials (grasses), forests, or mixed tree-grass (savanna) systems. Because the purpose of this experiment was to determine the ability of DayCent to model interspace annual grass and forb production under natural and increased N-deposition scenarios, only the herbaceous annual vegetation was simulated for this study.

Parameterization and simulations

Model calibration.—Most of the parameters in DayCent are intended to remain constant in the majority of applications and are referred to as fixed parameters. All default values of fixed parameters for herbaceous crop/grassland simulations were used here. The site-specific parameters were daily precipitation, daily maximum and minimum air temperatures, soil profile information, and plant characteristics.

Background N inputs were set as constant annual values of $0.07 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ from fixation (Rychert et al. 1978) and $0.1 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ from wet + dry deposition (Vitousek et al. 1997, Holland et al. 1999). Models were run to equilibrium by simulating the system from year 0 to 1900; at that point N deposition was increased linearly to a value of 0.3 and $0.8 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ by 1980 based on current estimates of deposition at the creosote bush calibration (CB-C) and piñon-juniper calibration (PJ-C) sites respectively (M. E. Fenn, *personal communication*). N deposition measurements were made using ion exchange resin collectors (Fenn et al. 2002, Fenn and Poth 2004) that were placed in the interspaces (CB and PJ) and under piñon pines (PJ only). CB deposition estimates were bulk deposition measurements from the interspace areas and PJ deposition estimates were based on throughfall and interspace measurements averaged across the landscape based on percent cover of PJ tree and shrub cover and interspace areas.

Default soil profile layering structure was used to ensure proper operation of the soil water sub-model. Values for soil texture, pH, C, and N were obtained from 1-m soil cores taken at each site. Because bulk density measures were not available for each depth, the surface bulk density (0–5 cm) was applied to each layer. The uniform use of surface bulk density through the profile was considered appropriate given that there were no significant changes in soil texture or rock content

observed through the 1-m soil cores. Saturated hydraulic conductivity, wilting point, and field capacity were determined using soil texture and rock content data from each layer and Saxton equations modified for use in the DayCent model (Saxton et al. 1986). While values of soil C and N are not required, providing initial values reduces the time needed for the model to reach equilibrium. The model was considered to have reached equilibrium if the difference in the 25-year mean for soil organic matter (SOM) carbon for the last 125 years of the spin-up period (i.e., mean SOM C from 1775 to 1800 compared to mean SOM C from 1875 to 1900) was less than 5%.

Because DayCent cannot model species mixtures, the mixture of winter annual grasses and forbs found at CB-C and PJ-C were parameterized as a generalized herbaceous vegetation type. The primary inputs for plant parameterization were root:shoot ratios, above and belowground C:N ratios, changes in the C:N ratios with precipitation, and percentage lignin. Plant data were determined from a combination of greenhouse (Rao 2008) and field measurements on dominant exotic grasses and native forbs from each vegetation type. For each vegetation type, the value assigned to each input parameter was weighted based on the mean percent cover of the exotic grass (*Schismus* spp. for CB and *B. madritensis* for PJ) and the native forbs measured at our sites.

The model was run until the last six years of output corresponded to the actual weather years of 2003 through 2008. The model was calibrated using observations of plant production and soil organic C from each study site. Input variables were altered as necessary to obtain adequate (within $\pm$ SD) agreement between simulated and observed production and soil C under background conditions. To determine the overall ability of the model to simulate the C and N dynamics in an arid ecosystem, modeled soil inorganic N, soil C:N ratio, N mineralization, and plant C:N ratio were compared to field observations and gaseous N flux was compared to literature values.

Modeled production response to N fertilization was tested by simulating the field N-fertilization experiment conducted at each site. As in the field, fertilizer was added as a one-time application each December in DayCent. The modeled N fertilizer application was in addition to the current N deposition in the model. Model performance was evaluated by regressing simulated production against measured production.

Model validation.—The model was validated on sites with similar vegetation to that at CB-C and PJ-C, but different current N deposition, climate, and soils (Table 1). As with the calibration sites, the model was run for 1900 years using background N fixation and N deposition (0.07 and $0.1 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, respectively). Starting in 1900, N deposition was increased linearly to the observed values of 0.7 and $0.4 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for the

CB-validation (CB-V) and PJ-validation (PJ-V) sites respectively (M. E. Fenn, *personal communication*).

Surface soil measurements of C, N, soil texture, pH, and bulk density were used to initialize DayCent. Information regarding the soil profile to a 1 m depth was not collected because high rock content at both validation sites prohibited coring, so surface (0–5 cm) data were used uniformly throughout the default layering structure. Uniform application of soil properties was deemed appropriate since soil C and N are used only to reduce the time needed for the model to reach equilibrium and cores from the calibration sites indicate no significant differences in soil texture between surface and one meter depths. The vegetation input files developed for the calibration sites were not altered for the validation simulations.

The model was validated on the parameters of annual biomass production, total soil organic C and N, soil C:N, surface soil inorganic N, N mineralization, and gaseous-N fluxes. All comparison data were collected from the sites except gaseous-N fluxes, which were obtained from literature sources. As with the calibration sites, the ability of the model to respond to N fertilization was tested by simulating the field N-fertilization experiment conducted from 2002 to 2008 and comparing simulated to observed annual production.

Statistical analyses.—Robust regression was used to compare production for both calibration and validation sites because at several sites the production data did not conform to the assumptions of ordinary least squares regression. Additionally, the creosote bush (CB) production data contained outliers (i.e., unexpectedly large or small data points), while the piñon-juniper (PJ) data sets contained both outliers and points with high leverage (i.e., the observed response played a large role in the value of the predicted response). Least squares regression is sensitive to outliers and gives heavier weights to large residuals. Robust regression techniques are not as sensitive to the presence of outliers because different mathematical functions are used to quantify residual variation (Gotelli and Ellison 2004). We used the appropriate robust regression method for the type of data deviation present in the CB (Huber-M estimator) and PJ (least median of squares) production data using Systat 12 (2007; Cranes Software, Chicago, Illinois, USA).

DayCent model performance was considered to be satisfactory if modeled inorganic soil N and soil organic C and N were within ± 1 SD of the observed value. Because of the high temporal variability of soil parameters, the mean of the last 25 years of model data was compared to the mean observed value.

Fire-risk simulations

The parameterized DayCent model was used to determine the risk of exceeding the fire-carrying threshold by obtaining an annual output of production

for each year in the simulation. Simulations were run for a combination of six precipitation regimes $\times$ six soil clay textures $\times$ 30 N-deposition levels to test the effects of the interactions between soil texture, water availability, and N availability on production. The threshold of biomass production needed to carry fire was set at 1000 kg/ha (42 g C/m²) because this amount of grass biomass has been shown as the minimum to carry fires in grasslands during the dry season (Anderson 1982) as well as in grass-invaded coastal sage scrub vegetation located in nearby Riverside, California (R. A. Minnich, *personal communication*). Fire risk was calculated as the fraction of years in which production exceeded this threshold at a given precipitation $\times$ clay $\times$ N deposition level. The critical load was defined as the amount of annual N deposition when the fire risk began to increase exponentially above background levels and was calculated as the maximum of the second derivative of the fire-risk probability curve. We also determined the amount of annual N deposition when fire risk no longer increased. Above this fire-risk-stabilization load, increased N inputs did not increase the probability that biomass would exceed the fire threshold, although additional N inputs may increase biomass. The fire-risk-stabilization load was calculated as the amount of N deposition at 95% of the modeled maximum fire-risk probability; the actual theoretical maximum fire-risk probability cannot be used because it is not possible to mathematically evaluate N deposition at the maximum value.

The daily temperatures for the calibration sites (CB-C and PJ-C) were used in all simulations for a vegetation type in an effort to eliminate confounding effects of temperature on nutrient cycling and production. Actual precipitation records spanning a range of mean annual precipitation (MAP) found in California deserts were used in the risk simulations. Precipitation records were obtained from across the 200-km precipitation gradient in this region of the Mojave and Sonoran Deserts from six sites with >75 years of precipitation data. MAP (defined as the rain year spanning 1 October–30 September) for the six sites ranged from 9.6 to 43.3 cm. As with most arid climates, the precipitation at these sites is skewed with more dry than wet years (Bowers 2005) and high interannual variability (mean $\pm$ SD for all sites: 9.6 ± 5.5 , 10.3 ± 8.2 , 12.6 ± 8.4 , 14.4 ± 10.6 , 21.6 ± 10.4 , and 43.3 ± 20.9 cm/yr).

The six soil clay levels used were 1%, 2%, 3%, 6%, 9%, and 14% and were based on the range of soil clay values observed from sampling across Joshua Tree National Park (JTNP). Because soil texture is correlated with a number of other parameters including rock content, pH, and bulk density (Wood et al. 2005), the sensitivity of modeled production to changes in bulk density, rock content, saturated hydraulic conductivity (K_{sat}), and pH was evaluated. Production under the mean observed value for each parameter was compared to the production under the maximum and minimum observed

value to evaluate model sensitivity. While a given parameter was being tested, all other parameters were set to mean values.

The sensitivity analysis indicated that production was greatly influenced by variations in bulk density and rock content (Appendix A); therefore mean values of these soil parameters were used in all soil input files during the fire risk simulations. Production was also sensitive to K_{sat} , which was a function of soil clay texture and was being tested by the range of soil clay content. The Saxton equations were used to calculate field capacities, wilting points, and K_{sat} for each clay content based on the soil texture and the mean rock content. Uniform soil profiles were created using the default DayCent layering structure.

The effect of N deposition on production at each precipitation and soil texture was evaluated by first running the simulation for 1000 years at background N-deposition levels (0.1 g/m²) to achieve equilibrium of SOM pools. N deposition was then increased by 0.05 g/m² every 100 years to a maximum of 1.5 g/m². The range of N deposition values bracketed observed deposition across JTNP with the maximum approximately double that of 0.8 g/m² observed (Sullivan et al. 2001) and modeled (Tonnesen et al. 2007) for the more polluted areas of JTNP.

RESULTS

Parameterization

Regression on the simulated and observed interspace production at the creosote bush calibration site (CB-C) resulted in a slope <1 and intercept >0, indicating that modeled production for this site was overestimated when production was low (dry years) but underestimated when production was high (wet years; Fig. 1). At the validation site (CB-V), production was generally overestimated by the model, although the year to year variation in production was well described (slope = 1.0, intercept = 10.5). At CB-C, the soil organic matter C and N were effectively modeled, as was the inorganic N content through the soil profile (Table 2). There was a small amount of annual nitrate leaching loss below the soil profile (>120 cm) that was on the low end of loss determined for other arid sites (Table 2). Gaseous N loss was dominated by nitric oxide (NO) loss via nitrification with no loss via the denitrification pathway. Modeled NO loss from nitrification was >five times that observed in the literature, while nitrous oxide (N₂O) loss (0.010 g·m⁻²·yr⁻¹) was slightly less than the lower fluxes observed in semi-arid sagebrush steppe (0.013 g·m⁻²·yr⁻¹; Matson et al. 1991).

The same pattern in leaching and gaseous N loss occurred for the CB-V simulations (Table 2). However, the model did not accurately represent the organic C and N pools as evidenced by the fact that the modeled soil C pool was just outside -1 SD of observed soil C and modeled soil N was significantly lower than observed. These inaccuracies in soil pool sizes resulted in a much

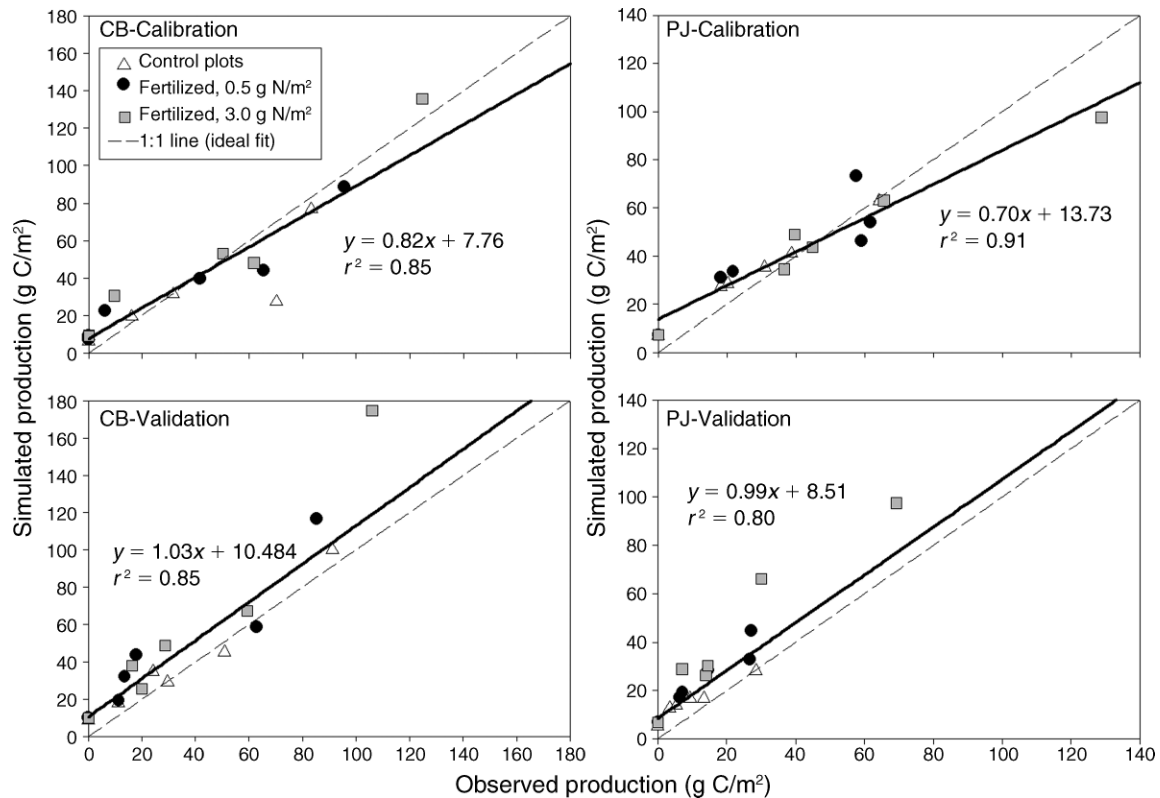


FIG. 1. Robust regressions of observed vs. simulated production for the calibration (C) and validation (V) sites in two vegetation types within Joshua Tree National Park, California, USA: creosote bush scrub (CB) and piñon-juniper woodland (PJ). Production was simulated using DayCent, the daily time-step version of the CENTURY biogeochemical model. Each regression was run on peak interspace production for all control and fertilized plots combined. Plots were fertilized each winter, and production was measured the following spring from December 2002 to April 2008. In 2007 there was insufficient precipitation for germination in the field at all sites, although the DayCent model simulated a small amount of production in that year. Statistical tests indicate that only the slopes for CB-V and PJ-V do not differ from 1.0 ($P > 0.9$ for validation sites and $P < 0.002$ for calibration sites); all intercepts are statistically different from 0 ($P < 0.015$ in all cases). Ideal fit (1:1) is shown as a dashed line.

higher modeled C:N ratio and lower inorganic N pools than observed. The modeled annual net mineralization was less than half the mineralization potential determined for the site. Leaching loss of nitrate was 1.6 times as high as that in the CB-C simulations, but within the range reported in the literature.

Regressions on piñon-juniper (PJ) interspace vegetation indicated that, as with the CB simulations, the production at the calibration site (PJ-C) was overestimated in dry years and underestimated in wet years, while at the validation site (PJ-V) year to year variation in production was well modeled (slope = 0.99) but shifted up by 8.5 g C/m² (Fig. 1). Although the slope of the regression line for PJ-C was much less than 1 (slope = 0.70), for all fertilization levels and years when germination in the field occurred, simulated production was within ± 1 SD of observed production.

For both PJ-C and PJ-V, soil organic C was modeled reasonably well, but simulated soil organic N was lower than observed by >1 SD (Table 2). As a result, modeled soil C:N was generally too high. At PJ-C, the soil inorganic N through the profile was well modeled, but at

PJ-V the observed surface (0–10 cm) soil N was equivalent to the simulated soil N in the total profile (0–120 cm). Gaseous N loss at both sites was dominated by NO nitrification, which was about an order of magnitude greater than values reported in the literature (Table 2). N₂O loss appeared to be slightly underestimated in both the PJ-C and PJ-V simulations but was within the same order of magnitude measured in other sites. Unlike the CB simulations, there was denitrification loss in the PJ simulations within the range of observations in other arid regions. Mean annual leaching loss at both PJ sites was low, but within the range of observed values (Table 2).

Fire-risk simulations

Fire risk was determined for the calibration sites of each vegetation type (Fig. 2). Fire risk rapidly increased with increasing N inputs from deposition in both vegetation types above the calculated critical loads (0.22 and 0.36 g·m⁻²·yr⁻¹ for CB-C and PJ-C, respectively), stabilizing at a fire risk of 0.31 under 0.55 g N/m² at CB-C and 0.35 under 0.88 g N/m² at PJ-C. Because

the model was run for 100 years at each N deposition increment and the length of the precipitation record was ~ 75 years, the probability of exceeding the fire threshold for each N deposition level was calculated using a different set of the precipitation record. Precipitation variability resulted in scatter around the maximum fire risk (Fig. 2). Above the calculated fire-stabilization loads, fire risk did not substantially increase with increasing N deposition and instead was governed by year to year variations in precipitation.

The values of the critical loads and fire-stabilization loads in Fig. 2 are specific to the calibration sites, but should be useful across a landscape scale since the fire risk in each vegetation type was evaluated across the range of soil clay content and mean annual precipitation (MAP) observed from this region of the Mojave and Sonoran Deserts. Results from the CB risk analysis showed that in sandy soils ($\leq 2\%$ clay) there was a greater vegetation response to N fertilization, which resulted in higher fire risk across all MAP levels at the maximum N loading (Fig. 3a). However, when MAP was < 21 cm, maximum fire risk was lower in sandy soils (Fig. 3a) than in soils with $\geq 3\%$ clay (Fig. 3b, c). When MAP and clay content were intermediate (6–9% clay and 21 cm MAP) there was a nonzero fire risk at the background N deposition level of 0.1 g/m^2 that all but disappeared at greater or lesser clay contents (Fig. 3b and Appendix B, part 1). Mean landscape critical loads and fire-risk-stabilization loads were calculated by averaging the calculated loads from all evaluated soil textures at two precipitation regimes: < 21 cm MAP representing the majority of CB desert areas and > 21 cm MAP representing only the wettest portions of the western Colorado Desert or possible shifts in precipitation due to climate change. Under the < 21 cm MAP category ($n = 24$ samples), the mean critical load was $0.32 \pm 0.09 \text{ g/m}^2$ at a fire probability of 0.03 ± 0.007 and fire risk stabilization occurred with $0.93 \pm 0.21 \text{ g/m}^2$ N deposition at a fire probability of 0.46 ± 0.14 . When MAP ≥ 21 cm ($n = 12$ samples), the critical load was $0.21 \pm 0.05 \text{ g/m}^2$ at a fire probability of 0.08 ± 0.02 and fire-risk stabilization occurred with $0.58 \pm 0.13 \text{ g/m}^2$ at a fire probability of 0.87 ± 0.05 .

Fire risk for PJ interspace vegetation was generally lower and the critical loads higher than for CB vegetation. Additionally, there was little difference in the response of the vegetation between 9 and 10 cm MAP, with a large jump in production between 10 and 12.5 cm MAP (Fig. 3d–f). As with the CB vegetation, the sites with more clay (Fig. 3e, f) reached fire-risk stabilization at a lower deposition level than sandier sites (Fig. 3d), but the absolute fire risk at this point was higher in sandier soils. Fire risk remained near 0 until N deposition reached 0.15 g/m^2 , and increased first in soils with intermediate clay and intermediate MAP levels (Fig. 3e and Appendix B, part 2). The critical load when MAP < 21 cm ($n = 24$ samples) was $0.39 \pm 0.07 \text{ g/m}^2$ at a fire probability of 0.03 ± 0.01 and fire-risk stabiliza-

tion occurred under $0.87 \pm 0.17 \text{ g/m}^2$ N deposition at a fire probability of 0.37 ± 0.14 . When MAP ≥ 21 cm ($n = 12$) the critical load was $0.30 \pm 0.03 \text{ g/m}^2$ at a fire probability of 0.07 ± 0.007 and fire risk stabilization occurred with $0.63 \pm 0.08 \text{ g/m}^2$ at a fire probability of 0.86 ± 0.06 .

DISCUSSION

Risk-based critical loads

Placing critical loads in a risk-based framework is one way to allow policymakers and land managers to determine when an effect is considered “adverse.” To our knowledge such an approach has not been previously taken with respect to N deposition and fire risk in any ecosystem type. The results from our fire-risk simulations indicate that the interspace vegetation in both creosote bush scrub (CB) and piñon-juniper woodland (PJ) is strongly limited by water and N and thus will be susceptible to increases in N deposition as well as changes in climate. There are few differences in fire risk between systems dominated by PJ or CB when mean annual precipitation (MAP) is greater than 21 cm. However, below 21 cm the production potential of annuals in CB is greater than in PJ. As a result, at a given clay $\times$ N input when MAP < 21 cm the probability that herbaceous annual biomass will exceed the fire threshold at the critical load and fire-risk-stabilization load is generally higher for CB vegetation than for PJ vegetation.

This finding of greater production potential in CB is supported by studies on the dominant exotic grasses found at our CB and PJ sites (*Schismus* spp. and *B. madritensis*, respectively). These studies show that *B. madritensis* has high water requirements and is not particularly plastic in its response to N inputs (Brooks 2003, DeFalco et al. 2003), with production showing no interactive effects of combined water and N inputs (Rao 2008). In contrast, *Schismus* spp. biomass responds more to added N and water than to either alone (Gutierrez et al. 1992, Rao 2008), and may be as productive as *B. madritensis* under high N and water availability (Rao 2008). However, this does not mean that CB is more likely to burn than PJ since PJ contains more woody biomass than CB and is more likely to burn on this basis alone (Brooks and Minnich 2006). Because fire risk in PJ has been found to be greater in years of high production of winter annual vegetation (Brooks and Matchett 2006), it is instructive to examine how the annuals in this area respond to changes in precipitation regime and N deposition, particularly since some PJ regions in southern California, including PJ-C, experience N deposition near the fire-risk-stabilization load of $0.87 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (Tonnesen et al. 2007).

A large portion of the CB and PJ desert ecosystems in southern California are also above the critical loads calculated through our analyses (Tonnesen et al. 2007). We defined the critical load as the amount of N deposition where the fire risk begins to increase

TABLE 2. Comparison of observed (obs.) and 25-year simulated (sim.) plant, soil nutrient, and gaseous loss characteristics (mean $\pm$ SD) from each calibration (C) and validation (V) site located in creosote bush scrub (CB) and piñon-juniper woodland (PJ).

Parameter	Creosote bush scrub			
	C, obs.†,‡	C, sim.†	V, obs.†,§	V, sim.†
Aboveground C:N	23.40 $\pm$ 6.66	23.76 $\pm$ 6.10	NA	18.47 $\pm$ 5.63
Total SOM C (g/m ²)	915.55 $\pm$ 356.96	923.51 $\pm$ 18.47	668.54 $\pm$ 199.55	455.79 $\pm$ 14.19
Total SOM N (g/m ²)	100.8 $\pm$ 52.1	71.70 $\pm$ 1.09	110.34 $\pm$ 36.75	36.42 $\pm$ 1.04
Soil C:N	9.62 $\pm$ 1.73	12.09 $\pm$ 0.04	6.49 $\pm$ 2.94	12.31 $\pm$ 0.24
Mean total annual N mineralization (g/m ²)	2.46	1.56 $\pm$ 0.59	4.58	1.78 $\pm$ 0.64
Total mineral N in soil profile (g/m ²)	1.31 $\pm$ 0.636	1.20 $\pm$ 0.31	NA	0.752 $\pm$ 0.312
Soil mineral N, 0–10 cm (g/m ²)	0.575 $\pm$ 0.087	0.493 $\pm$ 0.126	0.834 $\pm$ 0.373	0.450 $\pm$ 0.181
Soil mineral N, 10–30 cm (g/m ²)	0.324 $\pm$ 0.191	0.082 $\pm$ 0.056	NA	0.101 $\pm$ 0.078
Soil mineral N, 30–45 cm (g/m ²)	0.118 $\pm$ 0.137	0.027 $\pm$ 0.021	NA	0.022 $\pm$ 0.027
Soil mineral N, 45–60 cm (g/m ²)	0.051 $\pm$ 0.025	0.016 $\pm$ 0.018	NA	0.004 $\pm$ 0.015
Soil mineral N, 60–90 cm (g/m ²)	0.100 $\pm$ 0.049	0.133 $\pm$ 0.081	NA	0.061 $\pm$ 0.036
Soil mineral N, 90–120 cm (g/m ²)	0.106 $\pm$ 0.064	0.447 $\pm$ 0.205	NA	0.110 $\pm$ 0.093
Soil mineral N, below 120 cm (g·m ⁻² ·yr ⁻¹)¶	0.003–0.172	0.008	0.003–0.172	0.013
NO ₃ -N loss (nitrification; g·m ⁻² ·yr ⁻¹)#	0.002–0.038	0.084 $\pm$ 0.043	0.002–0.038	0.214 $\pm$ 0.108
N ₂ O-N loss (g·m ⁻² ·yr ⁻¹)	0.013–0.04	0.010 $\pm$ 0.005	0.013–0.04	0.016 $\pm$ 0.008
N loss (denitrification; mg·m ⁻² ·h ⁻¹)††	6.7–21.7	0	6.7–21.7	0
Total gaseous loss (g·m ⁻² ·yr ⁻¹)	unknown	0.094 $\pm$ 0.048	unknown	0.230 $\pm$ 0.116

Notes: Soil profile data are only available for the two calibration sites. All gaseous-loss simulated values are compared to literature values. SOM is soil organic matter. The 25-year mean of the simulated values is the last 25 years of the simulation run to create the data. NA indicates that data are unavailable.

† Observed data (“obs.”) show either mean $\pm$ SD (values measured in the field) or ranges from literature values that represent the range of values obtained from studies conducted by others. Simulation results (“sim.”) are means $\pm$ SD of the last 25 years of the simulation.

‡ Soil data were collected from deep cores taken October 2006; vegetation data are from spring 2005; soil mineralization is potential from laboratory incubation.

§ Soil data were collected from surface cores (0–5 cm depth) taken in 2005 (spring and summer) for total C and N and extrapolated to 20 cm based on proportional decrease in depth from C sites; surface cores (0–5 cm depth) were taken each July for mineral N and extrapolated to 10 cm depth; soil mineralization is potential from laboratory incubation.

¶ Validation leaching data are minimum and maximum values provided by Walvoord et al. (2003) and Hartsough et al. (2001); simulated values are the cumulative N leaching loss divided by the total number of years in the simulation.

Validation NO₃-N loss data are from Barger et al. (2005) and Hartley and Schlesinger (2000).

|| Validation N₂O loss data are from Matson et al. (1991) and Guilbault and Matthias (1998); simulated CB N₂O loss is only from nitrification, and simulated PJ N₂O loss is a total of denitrification and nitrification loss.

†† Validation denitrification N loss from Schaeffer and Evans (2005) and Billings et al. (2002); simulated values are the mean of only the days with denitrification (PJ-C, $n = 77$; PJ-V, $n = 5$).

exponentially above background levels. Thus, small increases in N inputs above our calculated critical loads result in large increases in fire risk up to the fire-risk-stabilization point. For example, in CB when MAP < 21 cm, the fire risk increases from 0.03 to 0.46 from the critical load to the fire-risk-stabilization load, indicating that tripling N deposition increases the fire risk by a factor of 15. Fire risk in PJ similarly increases 10 times from the critical load to the fire-risk-stabilization load, which is a doubling of the annual atmospheric N input. Although it is unlikely that N deposition in highly polluted areas will be brought down to below our calculated critical loads, our results indicate that there is a high potential to reduce fire risk if deposition is brought down below the fire-risk-stabilization load.

Because fire risk in CB has historically been much lower than in PJ due to the low amount of woody biomass and the large distances between shrubs (Brooks and Minnich 2006), the potential to reduce fire risk in CB by reducing deposition is particularly high. The critical loads for CB ranged from 0.15 to 0.50 g N/m² depending on soil texture and precipitation, and fire-risk stabilization ranged from 0.43 to 1.34 g N/m². Averaging across soil types, with MAP $\geq$ 21 cm, the

fire-stabilization load was 0.58 g N/m² but increased to 0.93 g N/m² with MAP < 21 cm. MAP in the south-central Mojave Desert of southern California ranges between 10 and 25 cm, while MAP in the western Colorado Desert ranges between 5 and 38 cm, with most CB sites receiving <20 cm/yr of rain in both deserts (Rowlands 1995). Thus, although areas of CB in California experience N deposition around the lower fire-stabilization load of 0.58 g N·m⁻²·yr⁻¹ (Sullivan et al. 2001, Tonnesen et al. 2007), fire risk will generally be low due to the primary limitation on production by water availability, with the fire threshold exceeded only in years of above-mean precipitation. Fires have been observed in CB sites near Palm Desert, California, adjacent to the southwest border of Joshua Tree National Park (JTNP; 33°53' N, 116°40' W; MAP = 13.8 cm) and were correlated with periods of above-mean precipitation (Brown and Minnich 1986, Steers 2008), supporting the findings of the fire-risk model. If N deposition increases due to greater urban or agricultural development (Fenn et al. 2003b) and mean precipitation increases due to climate change or shifts in sea surface temperatures (Mo and Higgins 1998, Swetnam and Betancourt 1998, Norman and Taylor 2003), then fire

TABLE 2. Extended.

Piñon-juniper woodland			
C, obs. ^{†,‡}	C, sim. [†]	V, obs. ^{†,§}	V, sim. [†]
33.79 ± 7.48	20.09 ± 4.80	NA	20.84 ± 5.19
1121.93 ± 245.41	945.12 ± 29.13	939.04 ± 633.33	498.60 ± 12.46
109.18 ± 38.69	52.98 ± 2.52	92.48 ± 62.04	29.16 ± 1.06
12.09 ± 6.98	17.80 ± 0.30	11.47 ± 3.56	16.99 ± 0.18
1.68	1.21 ± 0.47	1.42	1.06 ± 0.29
0.833 ± 0.295	0.828 ± 0.413	NA	0.729 ± 0.230
0.553 ± 0.207	0.507 ± 0.217	0.734 ± 0.396	0.160 ± 0.129
0.135 ± 0.091	0.108 ± 0.085	NA	0.047 ± 0.040
0.068 ± 0.056	0.027 ± 0.018	NA	0.011 ± 0.014
0.031 ± 0.036	0.013 ± 0.008	NA	0.003 ± 0.007
0.023 ± 0.093	0.082 ± 0.111	NA	0.070 ± 0.065
0.022 ± 0.006	0.092 ± 0.173	NA	0.436 ± 0.185
0.003–0.172	0.005	0.003–0.172	0.012
0.002–0.038	0.174 ± 0.082	0.002–0.038	0.141 ± 0.058
0.013–0.04	0.014 ± 0.007	0.013–0.04	0.010 ± 0.003
6.7–21.7	73.2 ± 50.0	6.7–21.7	67.9 ± 19.6
unknown	0.187 ± 0.085	unknown	0.151 ± 0.062

risk is likely to increase in CB areas throughout this region.

The information on fire risk generated using the DayCent model can be combined with land-cover data, soil surveys, spatially explicit N-deposition models, and climate models to determine the fire risk across the landscape. Landscape-scale fire risk could then be evaluated under various climate change scenarios and nitrogen emission control policies. As an example, we can consider the effects of a 50% reduction in N deposition on fire risk in Palm Desert (CB vegetation) and Yucca Valley (PJ vegetation, adjacent to the northwest border of JTNP). Both sites are located in areas subject to high N deposition (Allen et al. 2009, Rao et al. 2009) and may receive as much as 0.8 g N·m⁻²·yr⁻¹ of total N deposition (Sullivan et al. 2001, Tonnesen et al. 2007). For Palm Desert, current fire risk ranges between 0.52 and 0.64 g/m² (Fig. 3a–c), indicating a fairly high risk of fire in years with mean to above-mean precipitation. If N deposition were decreased to 0.4 g/m², fire risk would be substantially decreased to 0.17–0.35 across the landscape. For PJ, the current fire risk for Yucca Valley ranges between 0.29 and 0.45 (Fig. 3d–f). Halving N deposition would theoretically decrease fire risk to 0.01–0.11, although the fuel load provided by woody vegetation would keep the baseline fire risk higher than in CB.

While this study is the first, to our knowledge, that investigates the fire risk due to interactions of atmospheric N deposition and precipitation, other investigators have used risk-based approaches to assess the risk of atmospheric pollution to ecosystems (Church and van Sickle 1999, Tao et al. 2002, Lawler et al. 2005, Semenov et al. 2006). Using metrics of sensitivity and vulnerability of soils to loss of base saturation and cation exchange capacity from acid deposition, Tao et al. (2002) estimated the risk of problems from acid deposition by

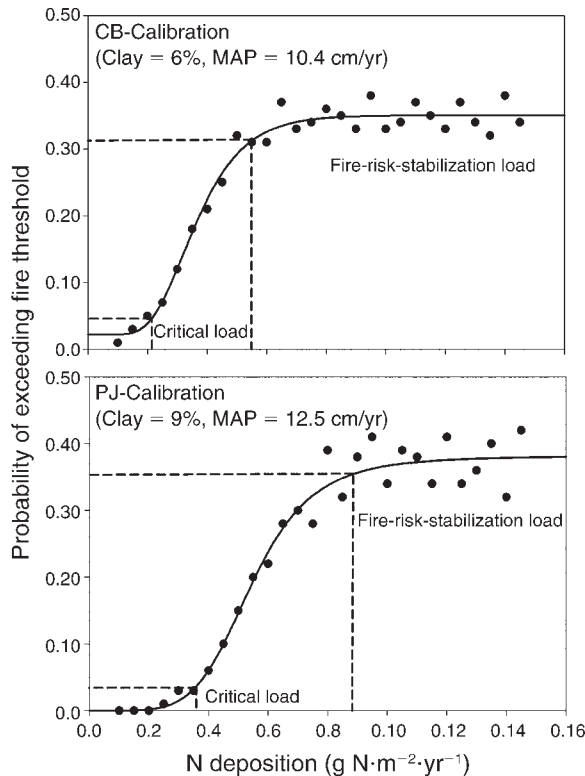


FIG. 2. Fire risk for each vegetation type in southern California deserts calculated as the probability that annual biomass will exceed the fire threshold (1000 kg/ha) under a given N-deposition load. The fire risk was calculated for each site using the site-specific soil parameters (e.g., percentage clay) and precipitation regimes. The critical load, the point at which fire risk begins to increase exponentially, is 0.21 and 0.36 g/m² of N deposition for CB-C and PJ-C, respectively. The fire risk begins to level out at the fire-risk-stabilization load, which is 0.55 and 0.88 g/m² of N deposition for CB-C and PJ-C, respectively. Between the critical load and fire-risk-stabilization load, the fire risk changes very rapidly with increases or decreases in N deposition. MAP is mean annual precipitation.

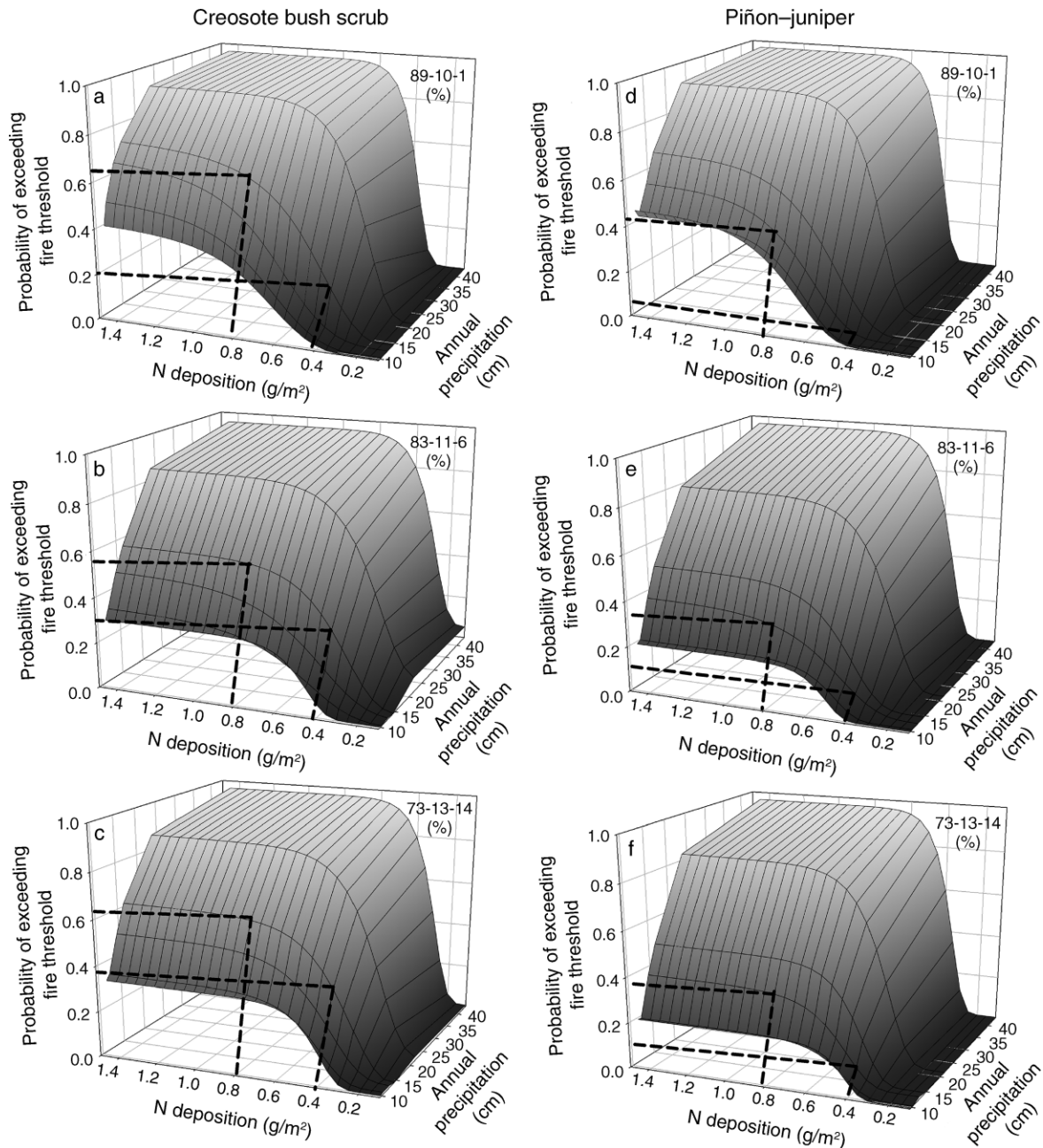


FIG. 3. Fire-risk analysis for (a–c) creosote bush scrub and (d–f) piñon-juniper across three soil textures and six precipitation regimes. The percentage “sand-silt-clay” content used in each modeling run is indicated in the upper right corner of each graph. See Appendix B for the full array of soil texture fire-risk analyses. Dashed lines indicate fire risk under current N deposition and 50% reduction in N deposition (from $0.8 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ to $0.4 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) for two sites: Palm Desert, California, USA (creosote bush scrub) and Yucca Valley, California (piñon-juniper woodland).

combining vulnerability and sensitivity maps with a map of sulfur deposition in China. Church and van Sickle (1999) successfully showed that N deposition represented a greater risk to stream and lake acidification in the Adirondack region, USA than sulfur deposition. Their study also assessed risk using a probabilistic fraction of lakes that would drop below acid neutralizing capacity (ANC) of 0, thus threatening fish populations. Similarly,

here we identify thresholds by the possibility that exceeding some level of N deposition leads to changes in fire regime.

DayCent for arid-land production

Because DayCent was developed for more mesic ecosystems and has not been applied extensively in hot deserts, one objective of our study was to evaluate the

ability of DayCent to model production and nutrient cycling for the Mojave and Sonoran Desert regions of California. By simulating a six-year multi-site field fertilization experiment, we were able to calibrate and validate the model at different sites and evaluate the production response under a range of N fertilization. Comparison of simulated and observed production at all fertilization levels shows that at the calibration sites the model fits well, with simulated production falling within ± 1 SD of observed production in most years.

The primary cause of the lack of model fit in both the calibration and validation sites was the very low precipitation amounts that occurred in 2006 and 2007. At the creosote-bush calibration site (CB-C) there was insufficient precipitation for germination during 2006 and 2007, resulting in 0 production in those years; the same was true at all sites in 2007. DayCent does not limit germination based on precipitation and thus produces some small amount of biomass even in extremely dry years, resulting in poor regression fits between observed and simulated production. Additionally, because the Sonoran and Mojave Deserts are characterized by high precipitation variability and are skewed toward more dry than wet years (Bowers 2005), this model trait potentially results in an excess of C moving into the soil pool.

Simulated and observed soil C are within close agreement at the calibration sites, but not at the validation sites. We would expect simulated soil C to be somewhat different from the observed values because the model parameterization is for a mean winter annual species growing alone in the interspaces. In reality, the interspaces are characterized by a mixture of forbs and grasses as well as shrub roots that extend out into the interspace soils (Chew and Chew 1965). Shrub roots contribute organic matter to the soils, as well as compete with annuals for nutrients and moisture. Thus, if the effect of shrub roots were included in the model it is likely that soil organic matter (SOM) C would increase and annual production decrease, resulting in a better model fit at the validation sites. Additionally, no summer annual growth was included in the model although summer precipitation can result in significant growth of summer grasses and forbs (R. Steers, *personal communication*), which would contribute additional C to the soil as they decompose and may increase the probability of fire. However, the western Mojave and Sonoran Deserts primarily have winter precipitation, and summer precipitation occurs sporadically.

Another possible source of both SOM C and production discrepancies between the models and field data is that winter annuals change in community composition and densities with changes in timing and amounts of precipitation (Beatley 1974, Salo 2004, Brooks and Berry 2006). Such changes in community composition result in changes in the C:N and lignin:N ratios of decomposable substrate added to the soil each spring. These shifts in community composition and thus

quality of organic input to the soils are not represented in DayCent. The model cannot automatically determine when one species group will be dominant over another, making it necessary for us to use one single vegetation type throughout the simulation.

Not only can shifts in community composition result in differences in C and N cycling, but different species groups have different growth patterns that can result in very different levels of peak biomass depending on the dominant species. The main winter annual vegetation groups at our sampling sites in Joshua Tree National Park (JTNP) are exotic annual grasses and native annual forbs. As an example of shifting dominance, at CB-C exotic grasses were dominant during 2003–2005. After a two-year drought and no germination of winter annual plants, the native forbs became dominant in 2008 with very few exotic grasses present. The observed production that year was 60–80 g C/m², but simulated production was only 20–40 g C/m², resulting in several “outlier” points where simulated production was outside $\pm$ SD of observed production.

The greatest source of model uncertainty is gaseous N loss, which has not been measured at our field sites and has not been widely studied in arid systems (Seitzinger et al. 2006). Comparison of model output to the limited literature data suggests that the magnitude of total N loss is relatively accurate, although the ratio of loss by the different N compounds may not be as accurate. One study in the Mojave Desert suggests that ~ 30 –40% of N inputs may be lost via NO and NH₃ loss, with the majority of the loss coming from ammonia following water pulses (McCalley and Sparks 2008). Ammonia loss is not explicitly represented in the DayCent model, although given that our soils trend toward neutral (Table 1), it is not likely that ammonia loss in our soils is as substantial as reported by McCalley and Sparks (2008), where soil pH ranged from 9 to 11.

Our model results indicate that 24–37% of N inputs from deposition and fixation were lost through gaseous N loss with NO an order of magnitude greater than N₂O loss and little to no denitrification loss. The magnitude of N₂O loss is similar to that reported in the literature, although at the low end of the range averaging 0.012 g N·m⁻²·yr⁻¹. In contrast, modeled NO loss was up to an order of magnitude greater than that reported for other arid and semi-arid sites. Estimates of annual NO flux use several seasonal “point-in-time” measurements to scale up to an annual loss (Barger et al. 2005, McCalley and Sparks 2008), resulting in uncertainty around the estimates. The NO fluxes predicted by the DayCent simulations for the four sites in JTNP indicate that annual NO loss in arid systems may be greater than what has been estimated to date. However, given the wide discrepancy between observed and simulated NO loss, it is unclear as to what degree NO loss is being overestimated by DayCent or underestimated in field studies.

Some additional uncertainty comes from the requirement for extensive input data by DayCent, much of which was not available for the sites. When site-specific data were not available, literature values were used, followed by expert-informed estimates. For the soil water characteristic parameters (i.e., wilting point [WP], field capacity [FC], and saturated hydraulic conductivity [K_{sat}]), the Saxton model was used (Saxton et al. 1986). Soil mineralization, gaseous N loss, and soil N leaching are largely a function of the soil water characteristic parameters (Parton et al. 1998), and discrepancies between simulated and field-collected data indicate that the model is not effective when soils are highly sandy and rocky (Table 2). However, without site-specific field validation data on the soil water characteristic parameters, it is unclear why DayCent is not as effective under these conditions. Despite the uncertainty in model input and validation data, the model performs well in its ability to simulate production under a range of chronic N-fertilization conditions.

In fact, the model results conform to the general principles of arid land production and mineralization as outlined in the inverse texture hypothesis. The inverse texture hypothesis posited by Noy-Meir (1973) and later modified by Austin et al. (2004) suggests that in arid systems, sandy soils will have greater productivity but lower mineralization rates than finer textured soils due to the effect of soil texture on water-holding capacity. Because of these confounding effects, one would expect production to have the greatest boost from N deposition in the sandier soils that have the lowest mineralization rates but highest productivity potentials. Both the soil-sensitivity analysis (Appendix A) and the fire-risk analyses (Fig. 3) show that, as N input increases, the sandier soils then have greater production than soils with more clay. Austin et al. (2004) also predicted that the effects of soil texture on mineralization would be maximal at intermediate precipitation ranges. This effect can be best observed in the CB simulations (Fig. 3b, c), which show that when the clay content is $>6\%$, there is a nonzero risk of exceeding the fire threshold at the lowest N-deposition level of 0.1 g/m^2 , with maximum risk observed at the 20 cm MAP level.

CONCLUSIONS

As global population increases, so will the production of reactive N and the distribution of that N via atmospheric and hydrologic pathways (Galloway et al. 2004). Thus, it is imperative to determine where ecosystems currently stand with respect to changes due to N deposition and if the critical loads for various environmental indicators have already been exceeded. Here we used the biogeochemical process model, DayCent, to quantify the relationship between N deposition and the ecosystem response of annual production in the southern Mojave and western Sonoran Deserts. We then determined the critical loads of N deposition for vegetation associations present in

these arid systems by calculating the probability that production would exceed the fire-carrying threshold. Although there are numerous other sensitive indicators of chronic N fertilization, such as loss of species diversity and changes in nutrient cycling (Vitousek et al. 1997, Baron et al. 2000, Egerton-Warburton and Allen 2000, Suding et al. 2005, Bowman et al. 2006, Rao et al. 2009), we considered only fire risk here due to its wide-ranging and long-term impacts in arid environments not adapted to fire (O'Leary and Minnich 1981, Koniak 1985, Brooks et al. 2004), and the large economic cost at the federal and state level associated with fighting fires in this region (California Legislative Analyst's Office 2008).

The DayCent model was generally effective at modeling production of winter annuals found in CB and piñon-juniper (PJ). However, the model appears to be sensitive to soil clay content such that soil C and N cycling may not be accurately represented in extremely sandy soils. Critical loads averaged across all soil types and mean annual precipitation levels $< 21 \text{ cm}$ were 0.39 and 0.32 g N/m^2 for PJ and CB vegetation, respectively, and decreased to 0.30 and 0.21 g N/m^2 for $\text{MAP} \geq 21 \text{ cm}$ for PJ and CB, respectively. Critical loads decreased with increasing soil clay content and increasing precipitation, such that the wettest areas with clay contents of $6\text{--}14\%$ may have critical loads as low as 0.15 g N/m^2 . These results suggest that these vegetation types are sensitive to both climate change and N deposition. Fire risk stabilized at a maximum value in both vegetation types at N deposition loads two to three times above the critical loads; these fire-risk-stabilization loads are currently met or exceeded in some areas of the Mojave and Sonoran Deserts, including two of our four sampling sites in JTNP. As a result, changes to N inputs from deposition and/or changes in the precipitation regime from climate change are likely to significantly affect the ecological and socioeconomic impacts of fire in these deserts.

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LITERATURE CITED

- Allen, E. B., L. E. Rao, R. J. Steers, A. Bytnerowicz, and M. E. Fenn. 2009. Impacts of atmospheric nitrogen deposition on vegetation and soils in Joshua Tree National Park. Pages 78–100 in R. H. Webb, L. F. Fenstermaker, J. S. Heaton, D. L. Hughson, E. V. McDonald, and D. M. Miller, editors. *The Mojave Desert: ecosystem processes and sustainability*. University of Nevada Press, Las Vegas, Nevada, USA.
- Allison, L. E., and C. D. Moodie. 1965. Carbonate. Pages 1388–1389 in C. A. Black, D. D. Evans, J. L. White, L. E.

- Ensminger, and F. E. Clark, editors. Methods of soil analysis, part 2. American Society of Agronomy, Madison, Wisconsin, USA.
- Anderson, H. E. 1982. Aids to determining fuel models for estimating fire behavior. General Technical Report INT-122. USDA Forest Service Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.
- Austin, A. T., L. Yahdjian, J. M. Stark, J. Belnap, A. Porporato, U. Norton, D. A. Ravetta, and S. M. Schaeffer. 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia* 141:221–235.
- Barger, N. N., J. Belnap, D. S. Ojima, and A. Mosier. 2005. NO gas loss from biologically crusted soils in Canyonlands National Park, Utah. *Biogeochemistry* 75:373–391.
- Baron, J. S., D. S. Ojima, E. A. Holland, and W. J. Parton. 1994. Analysis of nitrogen saturation potential in Rocky Mountain tundra and forest: Implications for aquatic systems. *Biogeochemistry* 27:61–82.
- Baron, J. S., H. M. Rueth, A. M. Wolfe, K. R. Nydick, E. J. Allstott, J. T. Minear, and B. Moraska. 2000. Ecosystem responses to nitrogen deposition in the Colorado Front Range. *Ecosystems* 3:352–368.
- Beatley, J. C. 1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. *Ecology* 55:856–863.
- Billings, S. A., S. M. Schaeffer, and R. D. Evans. 2002. Trace N gas losses and N mineralization in Mojave Desert soils exposed to elevated CO₂. *Soil Biology and Biochemistry* 34:1777–1784.
- Bowers, J. E. 2005. El Niño and displays of spring-flowering annuals in the Mojave and Sonoran deserts. *Journal of the Torrey Botanical Society* 132:38–49.
- Bowman, W. D., J. R. Gartner, K. Holland, and M. Wiedermann. 2006. Nitrogen critical loads for alpine vegetation and terrestrial ecosystem response: Are we there yet? *Ecological Applications* 16:1183–1193.
- Brooks, M. L. 2003. Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. *Journal of Applied Ecology* 40:344–353.
- Brooks, M. L., and K. H. Berry. 2006. Dominance and environmental correlates of alien annual plants in the Mojave Desert, USA. *Journal of Arid Environments* 67:100–124.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54:677–688.
- Brooks, M. L., and J. R. Matchett. 2006. Spatial and temporal patterns of wildfires in the Mojave Desert, 1980–2004. *Journal of Arid Environments* 67:148–164.
- Brooks, M. L., and R. A. Minnich. 2006. Southeastern deserts bioregion. Pages 391–414 in N. G. Sugihara, J. W. V. Wagtendonk, K. E. Shaffer, J. Fites-Kaufman, and A. E. Thode, editors. *Fire in California's Ecosystems*. University of California Press, Berkeley, California, USA.
- Brown, D. E., and R. A. Minnich. 1986. Fire and changes in creosote bush scrub of the Western Sonoran Desert, California. *American Midland Naturalist* 116:411–422.
- Burke, I. C., W. K. Lauenroth, and W. J. Parton. 1997. Regional and temporal variation in net primary production and nitrogen mineralization in grasslands. *Ecology* 78:1330–1340.
- Burns, D. A., T. Blett, R. Haeuber, and L. H. Pardo. 2008. Critical loads as a policy tool for protecting ecosystems from the effects of air pollutants. *Frontiers in Ecology and the Environment* 6:156–159.
- California Legislative Analyst's Office. 2008. Analysis of the 2008–09 budget bill: resources. E. G. Hill, editor. California Legislative Analyst's Office, Sacramento, California, USA. (http://www.lao.ca.gov/analysis_2008/resources/resource_anl08.pdf)
- Chew, R. M., and A. E. Chew. 1965. The primary productivity of a desert-shrub (*Larrea tridentata*) community. *Ecological Monographs* 35:355–375.
- Church, M. R., and J. van Sickle. 1999. Potential relative future effects of sulfur and nitrogen deposition on lake chemistry in the Adirondack Mountains, United States. *Water Resources Research* 35:2199–2211.
- Conley, A. H., E. A. Holland, T. R. Seastedt, and W. J. Parton. 2000. Simulation of carbon and nitrogen cycling in an alpine tundra. *Arctic, Antarctic, and Alpine Research* 32:147–154.
- D'Antonio, C. M. 2000. Fire, plant invasions, and global changes. Pages 65–93 in H. A. Mooney and R. J. Hobbs, editors. *Invasive species in a changing world*. Island Press, Washington, D.C., USA.
- 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.
- DeFalco, L. A., D. R. Bryla, V. Smith-Longozo, and R. S. Nowak. 2003. Are Mojave Desert annual species equal? Resource acquisition and allocation for the invasive grass *Bromus madritensis* subsp. *rubens* (Poaceae) and two native species. *American Journal of Botany* 90:1045–1053.
- Del Grosso, S. J., A. R. Mosier, W. J. Parton, and D. S. Ojima. 2005. DAYCENT model analysis of past and contemporary soil N₂O and net greenhouse gas flux for major crops in the USA. *Soil and Tillage Research* 83:9–24.
- Egerton-Warburton, L., and E. B. Allen. 2000. Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. *Ecological Applications* 10:484–496.
- 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. 2003a. Ecological effects of nitrogen deposition in the western United States. *BioScience* 53:404–420.
- Fenn, M. E., R. Haeuber, G. S. Tonnesen, J. S. Baron, S. Grossman-Clarke, D. Hope, D. A. Jaffe, S. Copeland, L. Geiser, and H. M. Rueth. 2003b. Nitrogen emissions, deposition, and monitoring in the western United States. *BioScience* 53:391–403.
- 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.
- Fenn, M. E., M. A. Poth, and M. J. Arbaugh. 2002. A throughfall collection method using mixed bed ion exchange resin columns. *TheScientificWorldJOURNAL* 2:122–130.
- Fisher, L. S., P. A. Mays, and C. L. Wylie. 2007. An overview of nitrogen critical loads for policy makers, stakeholders, and industries in the United States. *Water, Air, and Soil Pollution* 179:3–18.
- Galloway, J. N., et al. 2004. Nitrogen cycles: past, present, and future. *Biogeochemistry* 70:153–226.
- Gotelli, N. J., and A. M. Ellison. 2004. *A primer of ecological statistics*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Guilbault, M. R., and A. D. Matthias. 1998. Emissions of N₂O from Sonoran Desert and effluent-irrigated grass ecosystems. *Journal of Arid Environments* 38:87–98.
- Gutierrez, J. R., L. E. Aguilera, and J. J. Armesto. 1992. The effects of water and macronutrients addition on aboveground biomass production of annual plants in an old field from a coastal desert site of North-Central Chile. *Revista Chilena de Historia Natural* 65:83–90.
- Gutierrez, J. R., O. A. Dasilva, M. I. Pagani, D. Weems, and W. G. Whitford. 1988. Effects of different patterns of supplemental water and nitrogen-fertilization on productivity and composition of Chihuahuan Desert annual plants. *American Midland Naturalist* 119:336–343.
- Hadley, N. F., and S. R. Szarek. 1981. Productivity of desert ecosystems. *BioScience* 31:747–753.

- Halvorson, W. L., and D. T. Patten. 1975. Productivity and flowering of winter ephemerals in relation to Sonoran Desert shrubs. *American Midland Naturalist* 93:311–319.
- Hartley, A. E., and W. H. Schlesinger. 2000. Environmental controls on nitric oxide emission from northern Chihuahuan Desert soils. *Biogeochemistry* 50:279–300.
- Hartsough, P., S. W. Tyler, J. Sterling, and M. Walvoord. 2001. A 14.6 kyr record of nitrogen flux from desert soil profiles as inferred from vadose zone pore waters. *Geophysical Research Letters* 28:2955–2958.
- Holland, E. A., F. J. Dentener, B. H. Braswell, and J. M. Sulzman. 1999. Contemporary and pre-industrial global reactive nitrogen budgets. *Biogeochemistry* 46:7–43.
- Hooper, D. U., and L. Johnson. 1999. Nitrogen limitation in dryland ecosystems: responses to geographical and temporal variation in precipitation. *Biogeochemistry* 46:247–293.
- Keeler-Wolfe, T. 2007. Mojave Desert scrub vegetation. Pages 609–656 in M. G. Barbour, T. Keeler-Wolfe, and A. A. Schoenherr, editors. *Terrestrial vegetation of California*. Third edition. University of California Press, Berkeley, California, USA.
- Kelly, R. H., W. J. Parton, G. J. Crocker, P. R. Grace, J. Klir, M. Korschens, P. R. Poulton, and D. D. Richter. 1997. Simulating trends in soil organic carbon in long-term experiments using the century model. *Geoderma* 81:75–90.
- Kemp, P. R., J. F. Reynolds, R. A. Virginia, and W. G. Whitford. 2003. Decomposition of leaf and root litter of Chihuahuan Desert shrubs: effects of three years of summer drought. *Journal of Arid Environments* 53:21–39.
- Kieft, T. L., C. S. White, S. R. Loftin, R. Aguilar, J. A. Craig, and D. A. Skaar. 1998. Temporal dynamics in soil carbon and nitrogen resources at a grassland-shrubland ecotone. *Ecology* 79:671–683.
- Koniak, S. 1985. Succession in pinyon-juniper woodlands following wildfire in the Great Basin. *Great Basin Naturalist* 45:556–566.
- Lawler, J. J., J. Rubin, B. J. Cosby, I. J. Fernandez, J. S. Kahl, and S. A. Norton. 2005. Predicting recovery from acidic deposition: applying a modified TAF (tracking and analysis framework) model to Maine (USA) high elevation lakes. *Water, Air, and Soil Pollution* 164:383–399.
- Li, X. Y., T. Meixner, J. O. Sickman, A. E. Miller, J. P. Schimel, and J. M. Melack. 2006. Decadal-scale dynamics of water, carbon and nitrogen in a California chaparral ecosystem: DAYCENT modeling results. *Biogeochemistry* 77:217–245.
- Matson, P. A., C. Volkman, K. Copping, and W. A. Reiners. 1991. Annual nitrous-oxide flux and soil-nitrogen characteristics in sagebrush steppe ecosystems. *Biogeochemistry* 14:1–12.
- McCalley, C. K., and J. P. Sparks. 2008. Controls over nitric oxide and ammonia emissions from Mojave Desert soils. *Oecologia* 156:871–881.
- McLaughlin, S. P., and J. E. Bowers. 1982. Effects of wildfire on a Sonoran Desert plant community. *Ecology* 63:246–248.
- Minnich, R. A., and R. J. Dezzani. 1998. Historical decline of coastal sage scrub in the Riverside-Perris Plain, California. *Western Birds* 29:366–391.
- Mo, K. C., and R. W. Higgins. 1998. Tropical influences on California precipitation. *Journal of Climate* 11:412–430.
- Nilsson, J., and P. Grennfelt. 1988. Critical loads for sulfur and nitrogen. Report number Nord 1988:97. Nordic Council of Ministers, Copenhagen, Denmark.
- Norman, S. P., and A. H. Taylor. 2003. Tropical and north Pacific teleconnections influence fire regimes in pine-dominated forests of north-eastern California, USA. *Journal of Biogeography* 30:1081–1092.
- Noy-Meir, I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4: 25–51.
- O'Leary, J. F., and R. A. Minnich. 1981. Postfire recovery of creosote bush scrub vegetation in the western Colorado Desert. *Madroño* 28:61–66.
- Pake, C. E., and D. L. Venable. 1995. Is coexistence of Sonoran Desert annuals mediated by temporal variability in reproductive success? *Ecology* 76:246–261.
- Parton, W. J., M. Hartman, D. Ojima, and D. Schimel. 1998. DAYCENT and its land surface submodel: description and testing. *Global and Planetary Change* 19:35–48.
- Parton, W. J., E. A. Holland, S. J. Del Grosso, M. D. Hartman, R. E. Martin, A. R. Mosier, D. S. Ojima, and D. S. Schimel. 2001. Generalized model for NO_x and N₂O emissions from soils. *Journal of Geophysical Research—Atmospheres* 106: 17403–17419.
- Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima. 1987. Analysis of factors controlling soil organic-matter levels in Great Plains grasslands. *Soil Science Society of America Journal* 51:1173–1179.
- Parton, W. J., J. W. B. Stewart, and C. V. Cole. 1988. Dynamics of C, N, P and S in grassland soils: a model. *Biogeochemistry* 5:109–131.
- Patten, D. T. 1978. Productivity and production efficiency of an upper Sonoran Desert ephemeral community. *American Journal of Botany* 65:891–895.
- Peng, C. H., M. J. Apps, D. T. Price, I. A. Nalder, and D. H. Halliwell. 1998. Simulating carbon dynamics along the Boreal Forest Transect Case Study (BFTCS) in central Canada. 1. Model testing. *Global Biogeochemical Cycles* 12: 381–392.
- Porter, E., T. Blett, D. U. Potter, and C. Huber. 2005. Protecting resources on federal lands: implications of critical loads for atmospheric deposition of nitrogen and sulfur. *BioScience* 55:603–612.
- Porter, E., and S. Johnson. 2007. Translating science into policy: using ecosystem thresholds to protect resources in Rocky Mountain National Park. *Environmental Pollution* 149:268–280.
- Rao, L. E. 2008. Nitrogen deposition and its effects on the soils, vegetation, and fire risk in southern California deserts. Dissertation. University of California, Riverside, California, USA.
- Rao, L. E., D. R. Parker, A. Bytnerowicz, and E. B. Allen. 2009. Nitrogen mineralization across an atmospheric nitrogen deposition gradient in southern California deserts. *Journal of Arid Environments* 73:920–930.
- Romney, E. M., A. Wallace, J. E. Childress, J. E. Kinneer, H. Kaaz, P. A. T. Wieland, M. Lee, and T. L. Ackerman. 1974. Responses and interactions in desert plants as influenced by irrigation and nitrogen applications. Report number 74-17. Utah State University, Logan, Utah, USA.
- Romney, E. M., A. Wallace, and R. B. Hunter. 1978. Plant response to nitrogen fertilization in the northern Mohave Desert and its relationship to water manipulation. Pages 232–243 in N. E. West and J. J. Skujins, editors. *Nitrogen in desert ecosystems*. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, USA.
- Rowlands, P. G. 1995. Regional bioclimatology of the California desert. Pages 95–134 in J. Latting and P. G. Rowlands, editors. *The California desert: an introduction to natural resources and man's impact*. University of California, Riverside Press, Riverside, California, USA.
- Rychert, R., J. J. Skujins, D. Sorensen, and D. Porcella. 1978. Nitrogen fixation by lichens and free-living microorganisms in deserts. Pages 20–30 in N. E. West and J. J. Skujins, editors. *Nitrogen in desert ecosystems*. Dowden, Hutchinson, and Ross, Stroudsburg, Pennsylvania, USA.
- Saló, L. F. 2004. Population dynamics of red brome (*Bromus madritensis* subsp. *rubens*): times for concern, opportunities for management. *Journal of Arid Environments* 57:291–296.
- Saló, L. F., G. R. McPherson, and D. G. Williams. 2005. Sonoran Desert winter annuals affected by density of red

- brome and soil nitrogen. *American Midland Naturalist* 153: 95–109.
- Saxton, K. E., W. J. Rawls, J. S. Romberger, and R. I. Papendick. 1986. Estimating generalized soil-water characteristics from texture. *Soil Science Society of America Journal* 50:1031–1036.
- Schade, J. D., and S. E. Hobbie. 2005. Spatial and temporal variation in islands of fertility in the Sonoran Desert. *Biogeochemistry* 73:541–553.
- Schaeffer, S. M., and R. D. Evans. 2005. Pulse additions of soil carbon and nitrogen affect soil nitrogen dynamics in an arid Colorado plateau shrubland. *Oecologia* 145:425–433.
- Schimmel, D. S., B. H. Braswell, and W. J. Parton. 1997. Equilibration of the terrestrial water, nitrogen, and carbon cycles. *Proceedings of the National Academy of Sciences (USA)* 94:8280–8283.
- Schlesinger, W. H., and A. M. Pilmanis. 1998. Plant–soil interactions in deserts. *Biogeochemistry* 42:169–187.
- Schmid, M. K., and G. F. Rogers. 1988. Trends in fire occurrence in the Arizona Upland Subdivision of the Sonoran Desert, 1955 to 1983. *The Southwestern Naturalist* 33:437–444.
- Schoenherr, A. A., and J. H. Burk. 2007. Colorado desert vegetation. Pages 657–682 in M. G. Barbour, T. Keeler-Wolfe, and A. A. Schoenherr, editors. *Terrestrial vegetation of California*. Third edition. University of California Press, Berkeley, California, USA.
- Schwinning, S., O. E. Sala, M. E. Loik, and J. R. Ehleringer. 2004. Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. *Oecologia* 141: 191–193.
- Scifres, C. J., and W. T. Hamilton. 1993. *Prescribed burning for brushland management: the south Texas example*. Texas A&M University Press, College Station, Texas, USA.
- Seitzinger, S., J. A. Harrison, J. K. Bohlke, A. F. Bouwman, R. Lowrance, B. Peterson, C. Tobias, and G. V. Dreht. 2006. Denitrification across landscapes and waterscapes: a synthesis. *Ecological Applications* 16:2064–2090.
- Semenov, M. Y., T. V. Khodzher, V. A. Obolkin, V. M. Domysheva, L. P. Golobokova, N. A. Kobeleva, O. G. Netsvetaeva, V. L. Potemkin, R. van Grieken, and N. Fukuzaki. 2006. Assessing the acidification risk in the Lake Baikal region. *Chemistry and Ecology* 22:1–11.
- Steers, R. J. 2008. *Invasive plants, fire succession, and restoration of creosote bush scrub in southern California*. Dissertation. University of California, Riverside, California, USA.
- Suding, K. N., S. L. Collins, L. Gough, C. Clark, E. E. Cleland, K. L. Gross, D. G. Milchunas, and S. Pennings. 2005. Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences (USA)* 102:4387–4392.
- Sullivan, T. J., C. L. Peterson, C. L. Blanchard, and S. J. Tanenbaum. 2001. Assessment of quality and air pollutant impacts in class I national parks of California. National Park Service, Air Resources Division, Denver, Colorado, USA.
- Swetnam, T. W., and J. L. Betancourt. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *Journal of Climate* 11:3128–3147.
- Tao, F. L., Y. Hayashi, and E. D. Lin. 2002. Soil vulnerability and sensitivity to acid deposition in China. *Water, Air, and Soil Pollution* 140:247–260.
- Tonnesen, G. S., Z. Wang, M. Omary, and C. J. Chien. 2007. Assessment of nitrogen deposition: modeling and habitat assessment. Report number CEC-500-2006-032. California Energy Commission, PIER Energy-Related Environmental Research. (<http://www.energy.ca.gov/2006publications/CEC-500-2006-032/CEC-500-2006-032.PDF>)
- Vitousek, P. M., 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.
- Walvoord, M. A., F. M. Phillips, D. A. Stonestrom, R. D. Evans, P. C. Hartsough, B. D. Newman, and R. G. Striegl. 2003. A reservoir of nitrate beneath desert soils. *Science* 302: 1021–1024.
- Wangler, M. J., and R. A. Minnich. 1996. Fire and succession in pinyon–juniper woodlands of the San Bernardino Mountains, California. *Madroño* 43:493–514.
- Wood, Y. A., R. C. Graham, and S. G. Wells. 2005. Surface control of desert pavement pedologic process and landscape function, Cima volcanic field, Mojave Desert, California. *Catena* 59:205–230.

APPENDIX A

Results from sensitivity analysis (*Ecological Archives* A020-045-A1).

APPENDIX B

Full presentation of fire-risk analysis for creosote bush scrub and piñon–juniper woodland across six soil textures and six precipitation regimes (*Ecological Archives* A020-045-A2).