

Effects of Nitrogen Deposition on Multiple Ecosystem Services of the California Oak Savanna¹

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Abstract

The influence of enhanced nitrogen (N) deposition on key ecosystem services provided by oak woodlands was experimentally investigated. Fertilizer was applied for 2 years to paired plots in the oak understory and adjacent open grassland. Treatments simulated four N deposition levels and effects on forage productivity, biodiversity, and soil N supply were measured. At each treatment level, understory plots received twice the N fertilizer of paired open plots to simulate a deposition hotspot effect of the oak canopy. Soils in the open had lower inorganic N concentrations than the understory regardless of fertilizer level. Productivity largely did not respond to fertilization except at the highest level, where it declined by 34 percent and 25 percent relative to control plots in understory and open areas, respectively. Understory and open plots lost an average of two and one species under high N, respectively. These results indicate oak woodlands are resistant to the effects of N deposition on these ecosystem services up to 100 to 200 kg/ha/yr, which is a much higher level than currently received or expected. The different contributions by understory and open areas to these ecosystem services highlight the need to consider both habitats when predicting response to environmental change.

Key words: biodiversity, ecosystem services, nitrogen deposition, oak woodland, productivity, understory

Introduction

Oak woodlands provide many ecosystem services that benefit California, but understanding how these services may be altered in the face of environmental change is a challenge. Of particular importance are supporting services such as forage production and biodiversity. Forage production supports ranching operations, which is the primary use of oak woodlands (Huntsinger and others 2004). Biodiversity can support additional ecosystem functions such as decomposition, primary production, and nutrient cycling as well as support aesthetic or other cultural services in oak woodlands (Havstad and others 2007).

Nitrogen (N) deposition is one element of global change that may impact forage production, species diversity, and N cycling, in California oak woodlands. As agricultural land use intensifies and urban areas expand, N deposition to the adjacent oak woodlands is likely to increase (Grimm and others 2008). Nitrogen is often the limiting nutrient in oak woodland ecosystems (Harpole and others 2007a). Thus, N deposition may improve certain ecosystem services such as soil nutrient supply and productivity (Jones 1963). However, there may be tradeoffs as increasing levels of N deposition may negatively affect soils via nutrient loss and soil acidification (Likens

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and others 1996, Vitousek and others 1997). Diversity may also suffer as excess N has also been shown to lead to species loss and increased dominance of invasive species (Harpole and others 2007b). It is important to determine critical levels of N deposition in oak woodlands beyond which the system can no longer absorb additional inputs without negative consequences to ecosystem services (Fenn and others 2010).

Nitrogen deposition levels are low in California compared to areas in the eastern United States and Europe. Oak woodlands are exposed to N deposition rates ranging from two to seven kg/ha/yr, but with hotspots of 30 to 90 kg/ha/yr in areas near intensive agriculture or the Los Angeles air basin (Fenn and others 2003). About 40 percent of California oak woodlands may be in exceedance of a critical level of N deposition based on lichen indicator species (Fenn and others 2010). Despite successful efforts to curtail N emissions (McDonald and others 2012), oak woodlands remain susceptible to increasing N deposition because of the concentration of new urban and agricultural developments in the oak woodland range (Ferranto and others 2014).

In oak woodlands, the tree-grass mosaic vegetation structure introduces spatial heterogeneity to the ground layer ecosystem. Oak understory and open grassland areas make important, and unique, contributions to ecosystem functions at the landscape scale. Particularly in low canopy cover oak savannas, tree canopies are hotspots of atmospheric deposition compared to the adjacent open grassland and understories are recognized as islands of soil fertility in the landscape (Dahlgren and others 1997; Tulloss and Cadenasso, n.d.). Understory soils have greater nutrient and organic matter concentrations and the plant community is distinct from the open (Jackson and others 1990). Changes in forage productivity, plant community diversity and ecosystem N supply, in response to N deposition, may vary between understory and open areas in the savanna.

We focus on three oak woodland ecosystem services—*forage productivity, plant species diversity and soil N supply*—to investigate how N deposition will affect these heterogeneous landscapes. Specific objectives were to 1) quantify the effect of N deposition on the ecosystem services of forage productivity, plant species richness, and N supply and 2) compare those effects in understory and open environments. We expected productivity and diversity to increase with N deposition as more N resources become available to support more plants. We also expected N deposition to correlate with N supply. However, at high levels of N deposition the ecosystem will likely be N saturated leading to a saturation in productivity and diversity or a possible decrease in those functions. Because understory soils have greater N cycling rates, they will likely have the capacity to absorb excess N, and thus, we further expected the understory to reach a saturation point at a higher level of N deposition.

Methods

We simulated a range of N deposition rates using fertilizer treatments in a field experiment at Hopland Research and Extension Center (HREC) in Mendocino County. Hopland has low ambient N deposition rates of 2 to 5 kg/ha/yr (NADP 2014); the understory receives approximately twice the deposition of the open (Tulloss and Cadenasso, n.d.). The study site had a savanna-type vegetation structure where oak canopy cover was about 30 percent. Fertilizer levels simulated four different deposition scenarios: 1) “Low,” a deposition level that occurs in much of the California oak woodland region (equivalent to a doubling of HREC ambient levels), 2) “Medium-Low,” the highest level found across the California oak

woodland, 3) “Medium-High,” a potential increase above the highest level under increased N emissions, and 4) “High,” a very high level that corresponds to agricultural fertilization rates and is not anticipated (table 1). The treatments maintained the natural deposition hotspot effect beneath oaks meaning that within a single fertilizer treatment, the understory plots received double the fertilizer of the plots in the adjacent open.

Table 1—Application rates of ammonium nitrate fertilizer applied to open and understory plots. Each treatment level was divided into monthly applications. The division was unequal to mimic seasonal variation in inputs. To achieve the experimental deposition level, fertilizer was added assuming ambient deposition of two kg/ha in the open and four kg/ha in the understory based on previous site measurements (Tulloss and Cadenasso, n.d.)

Treatment	Position	Deposition (kg/ha/yr)	Monthly application rate (g/m ²)				
			Sep-Nov, Jul-Aug	Dec	Jan- Feb	Mar	Apr- Jun
Low	Open	5	0.04	0.22	0.13	0.25	0.09
	Understory	10	0.09	0.43	0.25	0.50	0.19
Med-Low	Open	10	0.11	0.57	0.34	0.67	0.25
	Understory	20	0.23	1.15	0.68	1.33	0.5
Med-High	Open	50	0.68	3.43	2.05	3.97	1.50
	Understory	100	1.38	6.93	4.16	8.03	3.05
High	Open	100	1.38	6.93	4.16	8.03	3.05
	Understory	200	2.8	14.00	8.40	16.23	6.16

Experimental design

Paired 2 x 2 m² fertilizer and control plots were established in the understory and adjacent open of 20 trees (fig. 1). The oak trees selected for the experiment were Blue oaks (*Quercus douglasii*) and Valley oaks (*Q. lobata*) with a canopy diameter of at least 10 m. Each tree/open area was randomly assigned to one of the four fertilizer treatments. Ammonium nitrate was mixed into 500 ml of water and sprayed onto fertilized plots starting in fall 2010 and continuing monthly until spring 2012. Equivalent water volume was sprayed onto control plots. To avoid both surface effects of the fertilizer and irrigation effects, application date was coordinated with rain events as much as possible so that fertilizer would quickly be washed into soil by rain. Plots were fenced to prevent grazing.

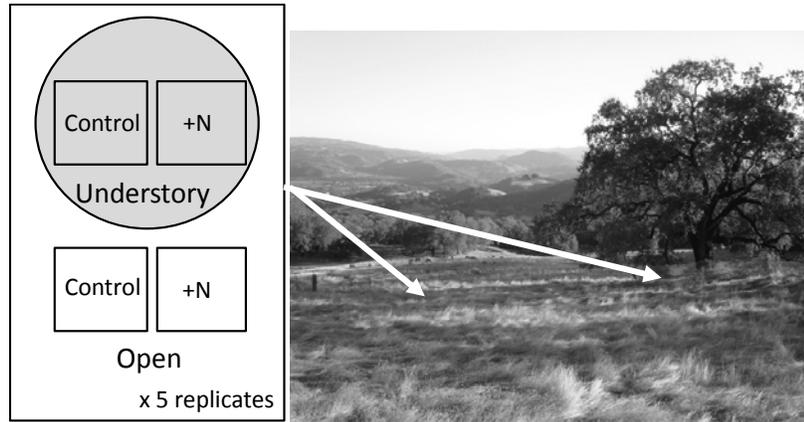


Figure 1—On left, experimental design for each fertilizer treatment level. There were five replicates for each of the four treatment levels for a total of 20 experimental tree/open units. Tree canopy indicated by grey shaded circle. Diagram is not to scale. On right, photo of study site with one replicate of plot exclosures.

Data collection and analysis

Productivity was determined by clipping plants at the soil surface from a 10 cm diameter ring randomly located in the outer 0.5 m of the plots. Plant biomass and litter were separated, dried, and weighed. Soil N supply was quantified by collecting 0 to 30 cm depth soil cores below each clipped ring and extracting inorganic N from soil cores with potassium chloride. Soil and plant biomass collections were made in the fall immediately following the first significant rains of the season and in the spring at peak biomass during the 2010-11 and 2011-12 seasons. To quantify diversity, a modified Daubenmire method was used to determine percent cover of all species present in the central m² of each plot in the spring of 2011 and 2012. From percent cover data, species richness was calculated for all plots (alpha diversity, α). Beta diversity was also calculated. Beta diversity, specifically Whittaker's β , measures the turnover, or differences in species richness among plots of each habitat type (i.e., understory and open). It was calculated as $\beta = \gamma_i/\alpha - 1$, where γ_i is the total species pool for the habitat type i (understory or open).

To analyze the data, we fit linear mixed effects models predicting forage productivity, alpha diversity, or soil N supply using N fertilizer level and landscape position (open versus understory) as fixed effects and plot and tree as nested random effects to account for spatial autocorrelation. Individual models were run for each sample date. Data was log transformed to meet homogeneity of variance assumptions except for species richness data from spring 2011. All analyses were performed in JMP 11 (SAS Institute Inc. 2013).

Results

Soil N

Soil inorganic N concentrations exhibited high variation from tree to tree. A significant positive effect of fertilizer on soil N concentration appeared to be driven by differences between paired control and fertilized plots at the highest treatment level (table 2, fig. 2). Soil N was significantly higher in the understory compared to

the open (fig. 2). With one exception in spring 2012, soil N in the open did not increase over understory levels, even when comparing across treatments. Fall 2011 soil N concentrations were higher than fall 2010 and 2011 and 2012 spring samples, indicating a potential year effect. The significant interaction between fertilizer level and position was due to a stronger positive response to N in open plots compared to the open.

Table 2—P-values for linear mixed effects models testing the effect of N fertilization and landscape position (open versus understory) on ecosystem services

Ecosystem Service	Season	Position (P)	N Level (N)	P x N
Forage productivity ^a	Fall 2010	0.889	0.647	0.743
	Spring 2011	0.023*	0.014*	0.0005**
	Fall 2011	0.017*	0.086	0.887
	Spring 2012	0.067	0.004*	0.961
Plant species diversity ^b	Spring 2011	<0.0001**	0.4093	0.2430
	Spring 2012	0.0005**	0.0307*	0.2524
Soil N supply ^c	Fall 2010	<0.0001**	0.0004**	0.2703
	Spring 2011	0.0002**	0.2195	0.8728
	Fall 2011	<0.0001**	<0.0001**	0.0220*
	Spring 2012	<0.0001**	<0.0001**	<0.0001**

^a aboveground productivity (g/m²), ^b species richness (i.e., alpha diversity), ^c Total inorganic N availability (ug/g)

*P < 0.05, **P < 0.001

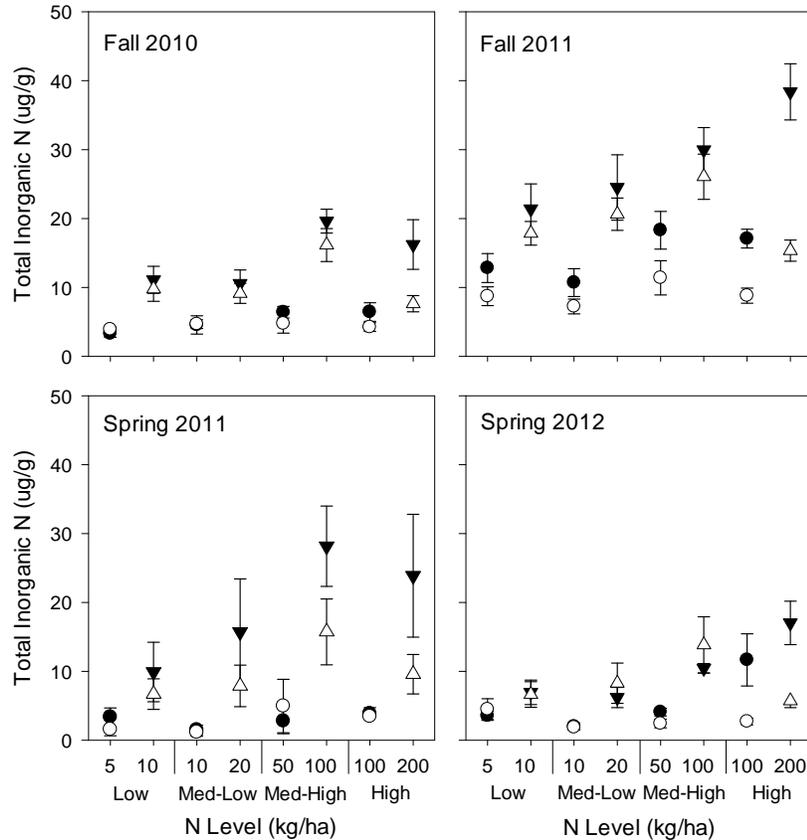


Figure 2—Total inorganic soil N response (mean \pm se) to N deposition level. Nitrogen deposition level is presented as a categorical treatment (in other words, y-axis is not a number line). Understory plots are triangles and open grassland plots are circles. Fertilized plots are filled symbols and paired control plots are open symbols.

Productivity

Similar to soil inorganic N concentrations, there was high variation in forage productivity among replicates. Productivity differed between understory and open only in spring 2011 and fall 2011. In both seasons, productivity was slightly greater in the understory compared to the open. In spring 2011, fertilization had a positive effect on productivity at low levels, but at the highest level productivity was reduced. At 100 kg/ha of fertilizer, productivity increased relative to control plots by 90 percent in the open and 65 percent in the understory, but decreased 30 percent in the understory at 200 kg/ha of fertilizer, giving an overall hump-shaped relationship between productivity and fertilization (fig. 3). In spring 2012, there were no positive effects of fertilizer on productivity. 2011-12 was a drought year, which may explain the lack of response to fertilizer in the spring compared with the previous year (fig 3, table 2). A significant interaction between fertilizer and landscape position in spring 2011 reflects the negative response to fertilizer in the understory at 200 kg/ha, while the open had a positive response up to 100 kg/ha. In spring 2012, plant productivity in both understory and open plots negatively responded to high fertilizer. Fall productivity showed no response to fertilizer (table 2).

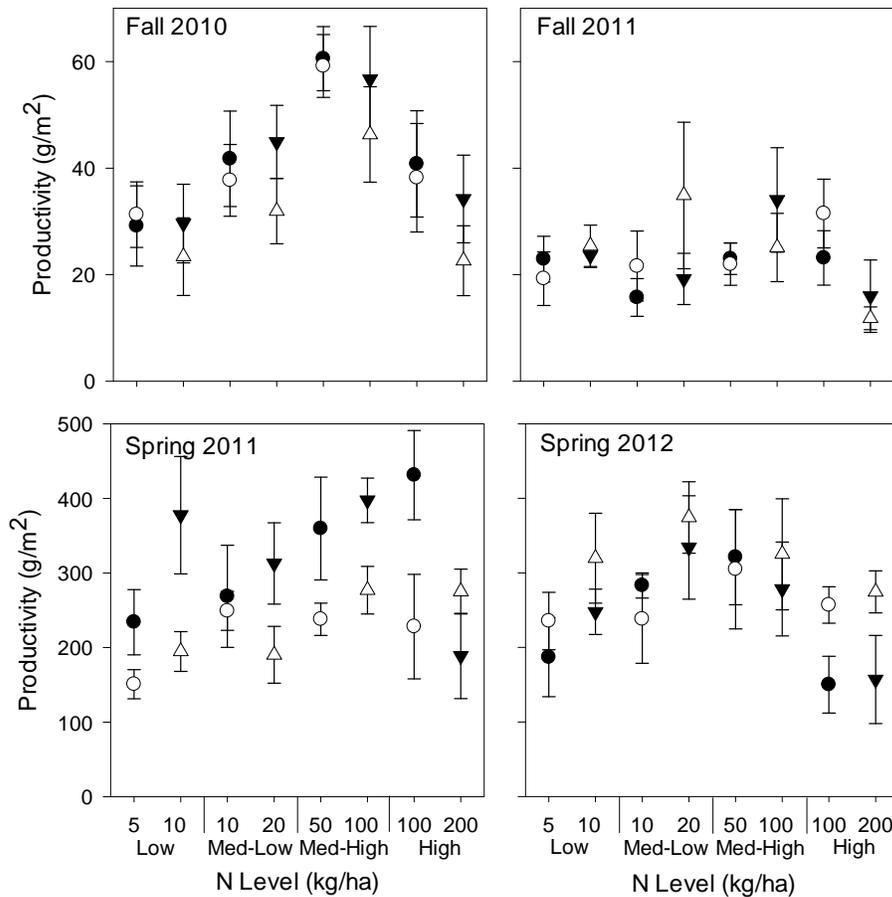


Figure 3—Productivity response (mean +/- se) to N deposition level. Nitrogen deposition level is presented as categorical treatment. Understory plots are triangles and open grassland plots are circles. Fertilized plots are filled symbols and paired control plots are open symbols. Note differences in y-axes between Fall and Spring.

Diversity

Species richness at the plot level (alpha diversity) was lower in the understory compared to the open. The understory was characterized by higher beta diversity, or in other words, greater species turnover among plots (table 3). In spring 2011, fertilizer treatments had no effect on species richness, but in spring 2012, fertilizer reduced species richness significantly (table 2). The high N treatment lost on average two species from understory plots and one from open plots compared to control plots (fig. 4).

Table 3—Alpha and beta diversity mean and standard error in understory and open landscape position

Position	Alpha diversity**	SE	Beta diversity*	SE
Open	9.3	0.4	4.2	0.2
Understory	5.5	0.2	5.7	0.3

*P<0.05, **P<0.001; asterisks indicate significant differences in those diversity measures between open and understory positions.

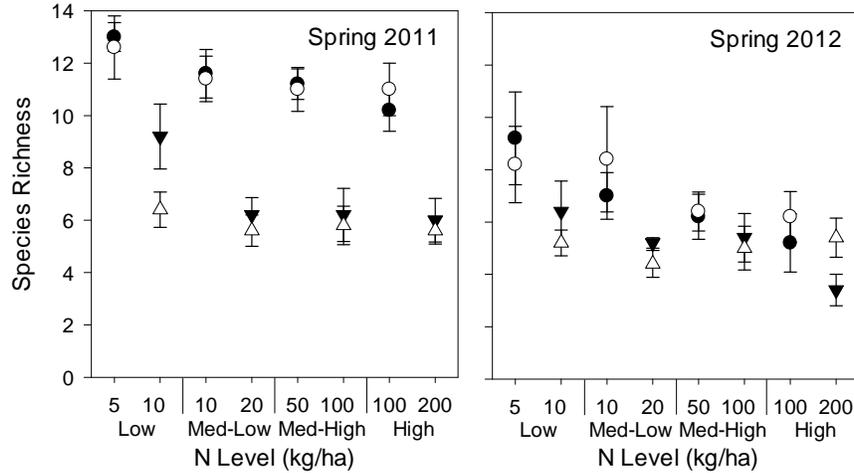


Figure 4—Species richness response (mean \pm se) to N deposition level. Nitrogen deposition level is presented as categorical treatment. Understory plots are triangles and open grassland plots are circles. Fertilized plots are filled symbols and paired control plots are open symbols.

Discussion and conclusions

At N deposition levels simulated here, little reduction to the key ecosystem services of forage productivity, biodiversity, and soil N supply was found. Some reduction in services was found when a rate of N deposition that is unrealistically high was applied. Therefore, California oak savannas may be resistant to N deposition. Soil N supply, which is logically a service expected to change under increased deposition, maintained levels comparable to control plots over a wide range of simulated deposition rates. In addition, N supply was consistently lower in the open than understory even where fertilizer in the open exceeded the rate in the understory. This could be due to higher plant uptake and microbial immobilization or to increased rates of N loss through leaching or volatilization and denitrification. The lack of a productivity response at low N levels supports the latter explanation and suggests N deposition in oak woodlands may have stronger impacts on downstream ecosystems than internal ecosystem functions. We are currently analyzing ion-exchange resin bags for evidence of N loss through leaching that would corroborate this.

Forage productivity and diversity services in the understory were more sensitive to the effects of N fertilization than open grasslands. Under a scenario where the understory continues to act as a deposition hotspot in the landscape, negative effects on these ecosystem services may appear first and be more severe in the understory than in the adjacent open within the same site. Understory and open grassland each make distinct contributions to the larger species pool and ecosystem N budget. A loss of productivity and especially of understory specialist species could represent an

important loss of resilience in the larger ecosystem. Fortunately, N deposition rates are much lower than the high fertilization rates that impacted ecosystem services and not expected to increase to those high levels in the future.

The results of this experiment emphasize the need to understand the effects of environmental changes on ecosystem services in spatially and temporally heterogeneous landscapes. Oak understories are important reservoirs of soil nitrogen, forage productivity, and species diversity in the landscape. They may be more susceptible to the effects of high N deposition. In addition, the seasonal and year effects we observed suggest that long-term N deposition may affect the ecosystem in ways that our two year experiment was not able to capture. In particular, the 2011-2012 drought may have reduced the positive productivity response to low fertilizer levels because plants were primarily water limited instead of N limited. The drought may also have exacerbated the negative effects of high fertilizer on productivity by increasing the amount of time fertilizer was exposed to dry plant surfaces and increased foliar scorching. Ecosystem services of the California oak woodland are expected to change in response to trends in N deposition, climate, and land use changes. Monitoring deposition and its effects at relevant spatial and temporal scales may be crucial for anticipating a critical deposition level that will disrupt ecosystem services. In particular, we suggest that capturing variation between understory and open environments will be important for predicting the effects of N deposition on oak woodlands.

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