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Imprint of oaks on nitrogen availability and δ^{15}N in California grassland-savanna: a case of enhanced N inputs?

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Abstract Woody vegetation is distributed patchily in many arid and semi-arid ecosystems, where it is often associated with elevated nitrogen (N) pools and availability in islands of fertility. We measured N availability and δ^{15}N in paired blue-oak versus annual grass dominated patches to characterize the causes and consequences of spatial variation in N dynamics of grassland-savanna in Sequoia-Kings Canyon National Park. We found significantly greater surface soil N pools (0–20 cm) in oak patches compared to adjacent grass areas across a 700 m elevation gradient from foothills to the savanna-forest boundary. N accumulation under oaks was associated with a 0.6‰ depletion in soil δ^{15}N relative to grass patches. Results from a simple δ^{15}N mass balance simulation model, constrained by surface soil N and δ^{15}N measured in the field, suggest that the development of islands of N fertility under oaks can be traced primarily to enhanced N inputs. Net N mineralization and percent nitrification in laboratory incubations were consistently higher under oaks across a range of experimental soil moisture regimes, suggesting a scenario whereby greater N inputs to oak patches result in net N accumulation and enhanced N cycling, with a potential for greater nitrate loss as well. N concentrations of three common herbaceous annual plants were nearly 50% greater under oak than in adjacent grass patches, with community composition shifted towards more N-demanding species under oaks. We find that oaks imprint distinct N-rich islands of fertility that foster local feedback between soil N cycling, plant N uptake, and herbaceous community composition. Such patch-scale differences in N inputs and plant–soil interactions increase biogeochemical heterogeneity in grassland-savanna ecosystems and may shape watershed-level responses to chronic N deposition.

Keywords Nitrogen cycle · Mineralization · Nitrification · Natural abundance isotopes · Blue oak savanna

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Introduction

Patchily distributed vegetation is a common feature of arid and semi-arid ecosystems and is often associated with spatial variations in soil fertility. In semi-arid savanna systems, contrasting woody and herbaceous life forms codominate to create a mosaic of continuous plant cover (Breshears 2006). Woody canopies frequently promote the development of ''islands of fertility'' characterized by higher local soil nutrient pools and availability. The development of nitrogen (N)-rich islands of fertility under woody vegetation may have several causes, including the scavenging of atmospheric N by tree canopies and associated epiphytes, lateral redistribution of N away from herbaceous areas towards woody patches by roots, vertical redistribution from deep to shallow soils, and low rates of N leaching due to slow decay of woody litter and intensive root foraging beneath woody vegetation (Scholes and Archer 1997). In very arid regions, the development of islands of fertility can also result from accelerated nutrient losses by overland flow and erosion in barren inter-canopy patches, and nutrient trapping in woody plant patches (Abrahams and Parsons 1991).

In the grassland-savanna of California, long-lived oaks (175–450 years) occur as individuals to small groves in a background matrix of herbaceous vegetation dominated primarily by non-native annual grasses. Oak islands in these systems contain larger pools of soil carbon (C) and N (e.g., Jackson et al. 1990; Dahlgren et al. 1997) and higher rates of C and N turnover (Davidson et al. 1990) than adjacent grass dominated areas. Such oak-patch properties are also reversible; when oaks are removed, soil N pools and N availability decline within decades (Herman et al. 2003). This reversibility suggests that oaks directly foster local N accumulation, and do not simply occupy the most inherently N-rich patches within the grassland-tree mosaic.

Both greater N inputs and stronger N retention have been advanced to explain greater N accumulation under oaks. The physical prominence of oaks in grassland-savanna ecosystems provides a structural basis for enhancing N inputs in local patches. Oaks support epiphytic N-fixing lichens (Knops et al. 1996), and non N-fixing epiphytes that scavenge reactive forms of atmospheric N in dry deposition (Boonpragob et al. 1989). Oaks may also foster local N accumulation by direct and indirect effects on N retention. It has been suggested that oaks reduce leaching losses of N from deep soils via root uptake (Dahlgren et al. 1997). Such retention may be particularly important at the onset of fall rains when soils display high concentrations of inorganic N, but before annual plants have germinated to provide an additional N sink (Jackson et al. 1990). Oaks can also promote N retention indirectly by reducing summer soil temperatures and increasing soil moisture (Rice and Nagy 2000; Millikin Ishikawa and Bledsoe 2000), resulting in greater N immobilization by soil microbial communities under oaks (Davidson et al. 1990).

Although several studies have reported a pattern of accelerated N cycling under blue oak in California savanna (e.g., Jackson et al. 1990; Herman et al. 2003), the ultimate cause of greater overall N under oaks remains elusive. Natural abundance δ^{15}N stable isotope approaches have potential to resolve this question. In other arid and semi-arid ecosystems, the δ^{15}N of surface soils are depleted beneath woody plants, which is attributed to local deposition of δ^{15}N depleted woody litter (Shearer and Kohl 1988). While such an interpretation is internally consistent, it cannot fully resolve the δ^{15}N depletion of entire plant-soil systems in woody patches relative to non-woody patches. A different idea that has received attention primarily at the level of watersheds and whole-ecosystems is the use of plant-soil δ^{15}N signatures to infer N input–output balances (Högberg 1997). Could patch-scale differences in N input–output budgets lead to the development of δ^{15}N signatures in ways that are analogous to whole-ecosystem patterns?

We measured N and δ^{15}N variations in plants and soils of paired oak and grass patches within blue oak (*Quercus douglasii* Hook. & Arn.) savanna of Sequoia National Park to gain insight into input–output processes that influence patch-scale N accumulation and development of islands of fertility under oaks. A simple iterative simulation model was used to evaluate whether inputs or losses were more important controls over

differences in soil N and $\delta^{15}N$ in oak versus grass patches. Laboratory incubations of soils under various moisture regimes were used to evaluate patch-based differences in the production and potential leaching of N. We also measured biomass and composition of herbaceous vegetation in our plots to understand potential relationships between patch-scale N economies and plant community dynamics.

Methods

Site description

We conducted this study in deciduous blue oak grassland-savannah in the foothills of the Sierra Nevada, in Sequoia-Kings Canyon National Park. Climate is Mediterranean with a distinct summer drought. Long-term records from the Ash Mountain climate station (500 m elevation) show mean annual precipitation of 66 cm. Precipitation for the water years (Nov–Oct) of this study were 52 cm in 2001/2002 and 71 cm in 2002/2003, with more than 98% of these totals recorded by the time of our May sampling. The mean maximum temperature of all months averages 24.6°C (range 14.2–36.6°C), and mean minimum temperature of all months averages 10.2°C (range 2.4–19.8°C). Soils are fine, thermic, schistose Ultic Haploxeralfs (Huntington and Akeson 1987).

Sample collection

We sampled twelve sites between 500 and 1200 m, ranging from the lower elevation foothills up to closed-canopy mixed broadleaf-conifer forest. Six sites were sampled in May 2002 and six additional sites were sampled in May 2003, synchronous with the senescence of herbaceous vegetation. At each site, we collected samples from adjacent pairs of oak and grassland areas. Oak areas were sampled beneath the canopy of individual blue oak trees within 1 m of the bole. Grass areas were sampled at least 50 m from the nearest woody vegetation. In May 2002, we collected 0–10 cm mineral soil from oak and grass patches. In May 2003 we sampled both surface and deeper soils and vegetation from six additional oak-grass paired sites. Soils were sampled from 0 cm to 10 cm depth using a 6.8 cm diameter corer, and below that in 10 cm increments to 70 cm using a 3 cm diameter corer. Depth to bedrock was between 70 cm and 80 cm in all but one site. Herbaceous vegetation was collected in three 177 cm^2 circular subplots in each patch by clipping stems within 1 cm of the ground surface. At least five individuals each of *Bromus diandrus* and *B. hordeaceus* (non-native annual grasses) and *Torilis nodosa* (non-native annual forb) were also collected as index species common to all sites for N and $\delta^{15}N$ determination. At least five fully expanded sun leaves were collected from each blue oak using a pruner.

Sample processing and analysis

Soil samples were kept cool in the field, sieved (2 mm), and extracted within 8 h for inorganic N concentrations. Available NH_4^+ and NO_3^- were assayed by extracting 7 g soil with 35 ml 2 M KCl for 1 h. Total soluble C and N were extracted from 7 g soil for 1 h with 35 ml 0.5 M K_2SO_4. Chloroform labile microbial C and N were determined by exposing 7 g soil to $CHCl_3$ vapor for 24 h, followed by extraction with 35 ml 0.5 M K_2SO_4. All suspensions were filtered through Whatman 42 filters. Potential N mineralization over 28 days in the laboratory was determined on 10 g subsamples of 0–10 cm soils incubated at 25°C and 60% water holding capacity (WHC). Soil pH was determined in 1:2 mixture of soil:water. Moisture content was determined by drying at 105°C for 48 h. Soil and foliage were dried at 65°C and ground to fine powder prior to elemental and isotopic analysis. Total C and N in solid samples were analyzed on a Costech ECS 4010 elemental analyzer. $\delta^{15}N$ was analyzed on a Finnigan Delta C Mass Spectrometer with Carlo Erba NA1500 Combustion at the Stable Isotope Laboratory of the University of Georgia Institute of Ecology. NH_4^+ and NO_3^- in soil extracts were analyzed colorimetrically using a Lachat RFA 5000A.

Drydown experiment

We conducted a laboratory experiment on soils (0–10 cm) collected in May 2003 to examine

effects of soil moisture regimes on net N production and nitrification. Subsamples (10 g) were moistened with deionized water to 60% WHC in specimen containers prior to incubation at 25°C. We evaluated six moisture regimes overall. Three of these regimes were designed to evaluate how short-term soil moisture variations influenced N production, and were extracted for inorganic N after 28 day incubations. The remaining three regimes were designed to evaluate how longer-term dry-down (resembling summer drought) influenced N availability, whereby 28 day incubations were followed by 4 month extended dry-down prior to extraction. In each of the short- and long-term incubations, we evaluated three moisture regimes: wet, wet-dry, and dry. All moisture regimes were initiated at 60% WHC. ''Wet'' treatments were maintained at constant 60% WHC for the 28 day incubation by covering specimen containers with parafilm, poking multiple tiny holes for air exchange, and replenishing moisture loss weekly (average weekly water loss = 0.04 ml g^{-1} dry soil). ''Wet-dry'' treatments remained uncovered, which allowed soils to dry-down in between weekly remoistening to 60% WHC (average weekly water loss = 0.27 ml g^{-1}). ''Dry'' treatments also remained uncovered, with no remoistening (water loss in week 1 = 0.28 ml g^{-1}, and 0.01 ml g^{-1} after week 4). At the end of short-term (28 day) and long-term (28 day plus 4 month dry-down) incubations, we extracted soils with KCl for available NH_4^+ and NO_3^-. Net N mineralization in all treatments was corrected for N in initial extracts and blanks.

Simulation model

We constructed a simple iterative one-pool simulation model in an Excel spreadsheet to evaluate soil N accumulation and $\delta^{15}N$ abundances in oak versus grass dominated patches. The model was initialized with grassland parameters of N input, loss and pool sizes. Rates of N input and loss were then altered to simulate the effects of oak establishment on N balances over time. The model considers changes only for 0–10 cm soils, since observed N and $\delta^{15}N$ differences in oak versus grass patches were confined to surface soils. Soils were initialized using the average pool of soil N in 0–10 cm grass areas (115 g N m^{-2}, see Results) at 1.8‰ $\delta^{15}N$. N inputs to grass areas were initialized at wet deposition values of 0.5 g N m^{-2} yr^{-1} (Stohlgren and Parsons 1987), not at higher rates of throughfall N measured under tree canopies (1.0 g N m^{-2} yr^{-1}, Fenn et al. 2003b), since our model seeks to evaluate independently how trees influence N inputs to this ecosystem. The isotopic composition of N inputs was set to 0‰, based on nearby measurements in a high elevation catchment (Sickman et al. 2003). Nitrate dominates hydrologic N losses from these soils under a range of hydrologic conditions (Perakis et al. in preparation), and nitrate-leaching losses were initialized at 0.3 g m^{-2} yr^{-1} (Fenn et al. 2003b), with nitrate 7‰ depleted relative to bulk soil N (Herman and Rundel 1989). In simulations, we first satisfied N mass balance by manipulating rates of N input and output over 200 years, until differences in N accumulation between oak versus grass simulations matched actual differences measured in the field. We then used $\delta^{15}N$ balances as an additional constraint to evaluate whether oaks fostered patch-scale N accumulation primarily by affecting rates of N input or loss to the system.

Calculations and statistics

Total soil C and N were estimated based on bulk density and chemical concentrations of the <2 mm fraction. Microbial C and N were calculated as chloroform labile C and N minus total soluble C and N, with no correction factor. Potential N mineralization rates were corrected for initial NH_4^+ and NO_3^- concentrations. Natural abundance ^{15}N stable isotopic data are presented using standard delta notation (Högberg 1997). Isotopic enrichment span of plants relative to soil ($\varepsilon_{s\text{-}p}$) was calculated as $\delta^{15}N$ of 0–10 cm soil minus plant. Data were analyzed using analysis of variance (ANOVA) with vegetation type as a main effect, blocked by collection site. Moisture incubations were analyzed with factorial ANOVA, blocked by collection site, with vegetation type, moisture level, and extended dry-down as main effects. Block effects were often significant, but were unrelated to elevation or other measured factors. All statistical tests were performed

using SYSTAT 11 (Richmond, CA) and considered significant at $\alpha = 0.05$.

Results

Herbaceous vegetation

Standing biomass of herbaceous vegetation was similar in grass (306 g m^{-2}) and oak (334 g m^{-2}) patches (Table 1). Species richness in grass patches (5.4 spp./sample) was significantly greater than beneath oak canopies (4.4 spp./sample). *Bromus diandrus* accounted for a significantly greater proportion of biomass under oaks (45%) than in open areas (18%). *Bromus hordeaceus* dominated in open areas (27% of total biomass), but was less abundant under oaks (2% of total biomass). *Torilis nodosa*, a common non-native forb, was the third most abundant species and accounted for a significantly greater fraction of biomass under oaks (13%) than in grass areas (3%). *Carduus pycnocephalus*, a prominent non-native thistle, occasionally dominated entire samples under oaks yet was completely absent from grass patches.

N concentrations of the three most abundant herbaceous species common to both oak and grass areas (*B. diandrus*, *B. hordeaceus*, and *T. nodosa*) were significantly greater under oaks (all $P < 0.05$) (Fig. 1a). Biomass-weighted average tissue %N from these herbaceous species was 47% greater under oak. These species tended towards more $\delta^{15}N$ depleted values under oak, but no significant differences were observed ($P > 0.2$, Fig. 1b). However, within oak patches, oak foliage $\delta^{15}N$ (average = –1.5‰, s.e. = 0.3, $n = 6$) was significantly more enriched (ANOVA, $P = 0.01$) than the pooled $\delta^{15}N$ of herbaceous vegetation (range of average herbaceous values: –2.3 to –2.8‰). The $\delta^{15}N$ enrichment span ($\varepsilon_{s\text{-}p}$) of 0–10 cm soil minus plants differed significantly by patch type only for *B. hordeaceus*

Table 1 Total biomass, species richness, and percent contribution of the five most abundant species in the herbaceous layer of oak and grass cover types in 2003 (mean ± s.e.)

Characteristic	2003	
	Oak	Grass
Species richness (number of species)	**4.4 ± 0.2**	**5.4 ± 0.2**
Total biomass (g/m^2)	334 ± 24	306 ± 20
Bromus diandrus (% of total biomass)	**45.1 ± 4.2**	**17.8 ± 2.0**
Bromus hordeaceus (% of total biomass)	**1.7 ± 0.4**	**27.1 ± 1.6**
Torilis nodosa (% of total biomass)	**12.8 ± 1.5**	**2.8 ± 0.4**
Carduus pycnocephalus (% of total biomass)	**13.1 ± 4.1**	**0 ± 0**
Avena fatua (% of total biomass)	**9.5 ± 3.6**	**0.1 ± 0.0**

Significant differences ($P \leq 0.05$) between grass and oak cover types identified in bold.

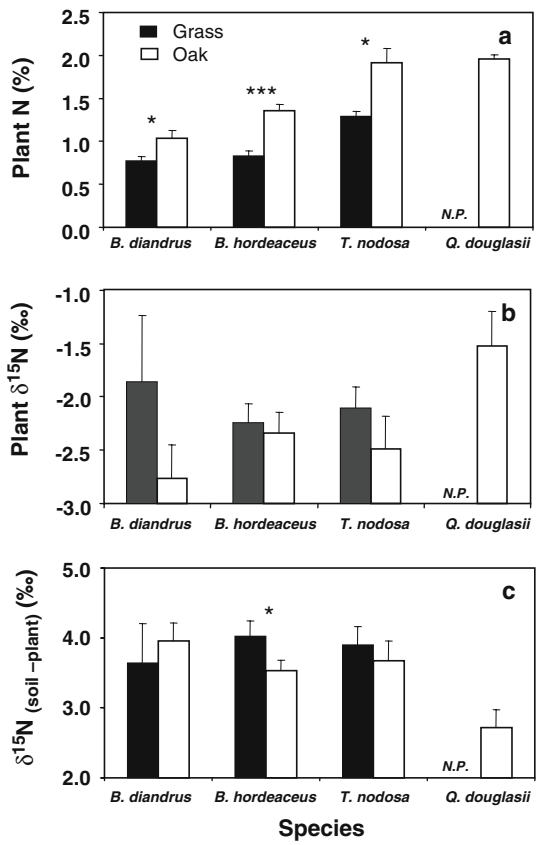

Fig. 1 Average (**a**) %N, (**b**) $\delta^{15}N$, and (**c**) $\delta^{15}N$ difference between plant and soil of the three dominant herbaceous annuals, and of oak foliage, collected in May 2003. Asterisks indicate significant differences (*$P < 0.05$, ***$P < 0.001$) of values for herbaceous species collected in oak versus grass patches. NP signifies oaks are not present in grass patches

(Fig. 1c), and narrowed with increased N mineralization both within oak patches ($r^2 = 0.69$, $P < 0.05$) and aggregated across both patch types ($r^2 = 0.37$, $P < 0.05$), but no other species $\varepsilon_{s\text{-}p}$ exhibited significant relationships to N mineralization.

Soils

We found higher soil C, N, C:N, and N availability under oaks compared to grass patches. In surface 0–10 cm, soil C and N content (g m^{-2}), and C:N ratios were greater under oaks than grasses (Table 2). Concentrations of soil N were greater under oaks only in 0–10 cm and 10–20 cm depths, and converged at depth (Fig. 2a). Oak soils were significantly $\delta^{15}N$ depleted relative to grass soils by 0.6‰ at both 0–10 and 10–20 cm, and converged with depth (Fig. 2b). The relationship between soil %N and $\delta^{15}N$ was similar in oak and grass patches, and described by the equation $\delta^{15}N = 6.5e^{-9.15soil\%N}$ ($r^2 = 0.73$, $n = 72$) (Fig. 2 inset).

Surface soil moisture at the time of sampling was three times higher in 2003 than 2002, yet in both years was significantly greater under oaks, corresponding to higher soil %C under oaks (Table 2). Microbial biomass C and N, measured only in 2003, were greater under oaks. pH was one full unit higher in surface soil under oak (pH = 7.0) compared to grass areas (pH = 6.0). Ammonium was the dominant form of extractable inorganic N in field soils of both patches types, with higher extractable ammonium and nitrate under oak than grass.

Oak soils displayed significantly higher net N mineralization than grass soils across every experimental wetting and drying regime in the laboratory ($P < 0.001$, Table 3). Oak soils also displayed significantly higher percent nitrification overall relative to grass soils ($P < 0.001$), with the most pronounced differences under the most intense drying regimes. Extended four month dry-down after the initial 28 day incubation produced significantly more mineralized N relative to incubations extracted at 28 days. Overall, nitrate was the most important endproduct of net N production when soil moisture was high, and accounted for a declining fraction of mineralized N with more intense drying (Table 3).

Simulation modeling of patch-scale $\delta^{15}N$ development, constrained by soil N and $\delta^{15}N$ observations in the field, indicated that oaks fostered N

Table 2 Characteristics of surface soils (0–10 cm) in oak and grass cover types in May 2002 and May 2003 (mean ± s.e.)

Soil characteristic	2002		2003	
	Oak	Grass	Oak	Grass
Bulk density (<2 mm)	**0.68 ± 0.06**	**0.88 ± 0.04**	**0.68 ± 0.02**	**0.87 ± 0.05**
Water content (%)	**8.6 ± 0.5**	**5.2 ± 0.3**	**22.6 ± 1.3**	**17.2 ± 1.5**
pH	**7.0 ± 0.2**	**5.9 ± 0.1**	**6.9 ± 0.1**	**6.0 ± 0.1**
% C	**3.50 ± 0.23**	**1.86 ± 0.11**	**2.33 ± 0.12**	**1.29 ± 0.16**
% N	**0.26 ± 0.02**	**0.16 ± 0.01**	**0.19 ± 0.01**	**0.11 ± 0.01**
C content (g/m^2)	**2390 ± 202**	**1631 ± 130**	**1579 ± 99**	**1109 ± 96**
N content (g/m^2)	**181 ± 14**	**137 ± 10**	**127 ± 7**	**94 ± 9**
C:N	**13.3 ± 0.1**	**11.9 ± 0.1**	**12.1 ± 0.3**	**10.7 ± 0.2**
Extractable NH_4^+ (μg/g)	**2.2 ± 0.4**	**0.5 ± 0.1**	**1.4 ± 0.1**	**1.1 ± 0.2**
Extractable NO_3^- (μg/g)	**1.3 ± 0.3**	**0.1 ± 0.1**	0.5 ± 0.1	0.3 ± 0.2
Extractable % NO_3^-	**38 ± 4**	**17 ± 8**	26 ± 4	18 ± 6
Mineralizable NH_4^+ (μg/g 28 day)	**0.0 ± 0.0**	**0.3 ± 0.1**	0 ± 0	0 ± 0
Mineralizable NO_3^- (μg/g 28 day)	**25.9 ± 3.9**	**10.5 ± 0.7**	**28.9 ± 2.7**	**18.2 ± 1.1**
Mineralizable % NO_3^-	**100 ± 0**	**97 ± 1**	100 ± 0	100 ± 0
Microbial carbon (μg/g)	n.d.	n.d.	**236 ± 30**	**167 ± 8**
Microbial nitrogen (μg/g)	n.d.	n.d.	**47 ± 5**	**30 ± 1**
Microbial C:N (by mass)	n.d.	n.d.	4.7 ± 0.7	5.5 ± 0.1

Bold text indicates significant differences ($P \leq 0.05$) between grass and oak cover types within years. Missing data indicated by n.d.

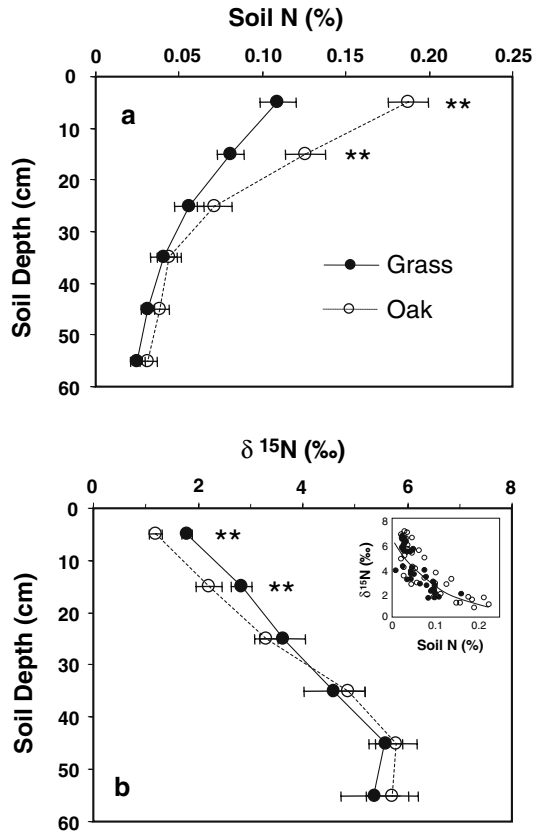

Fig. 2 Average (**a**) %N and (**b**) δ^{15}N of soil profiles from samples collected in May 2003. Asterisks indicate significant differences (**$P < 0.01$) between oak versus grass patches within each soil depth

accumulation primarily by enhancing N inputs, and only marginally by enhancing N retention. We show in Fig. 3 the change in soil δ^{15}N of oak minus grass patches over 200 years of simulated increase in N capital under oaks. Using literature values for N and δ^{15}N inputs and losses (see Methods), base-case simulations of grassland soil δ^{15}N increased from 1.8‰ to 3.1‰ over 200 years (not shown). We required oak simulations to accumulate 38 g N m^{-2} more than grass simulations (Table 2), and distributed this extra N evenly as 0.19 g N m^{-2} yr^{-1} over 200 years. Different simulations were evaluated for δ^{15}N response as a function of either increased N inputs, decreased N outputs, or both, and simulation output was compared to the observed 0.6‰ depletion of oak minus grass soil δ^{15}N in the field (Fig. 2). When N inputs alone were increased to satisfy N accumulation under oak (i.e., from 0.50 to 0.69 g N m^{-2} yr^{-1}), simulated oak soil became 0.5‰ depleted relative to grass soil after 200 years (Fig. 3, dotted line), very close to the 0.6‰ depletion observed in the field. However, if N retention alone was increased under oaks (i.e., decreased N output from 0.30 to 0.11 g N m^{-2} yr^{-1}), then simulated oak soil δ^{15}N was 1.4‰ depleted relative to grass soils after 200 years (dashed line), which overshoots field observations. A mixture of these processes that assigned 90% of net N accumulation to greater inputs under oak (increase from 0.50 to 0.67 g N m^{-2} yr^{-1}) and the remaining 10% as increased retention (decreased outputs from 0.30 to 0.28 g N m^{-2} yr^{-1}) simulated the 0.6‰ relative depletion of oak minus grass soil in concordance with field observations (Fig. 3, solid line).

Table 3 Net N mineralization and percent nitrification in 28 day laboratory incubations of 0–10 cm soil collected in May 2003

	N Mineralization (μg N / kg)		% Nitrification	
	Oak	Grass	Oak	Grass
28 day incubation				
Wet	**36.3 ± 3.4**	**21.9 ± 1.4**	100 ± 0	100 ± 0
Wet-dry	**18.1 ± 1.4**	**7.0 ± 0.9**	66 ± 4	55 ± 8
Dry	**10.6 ± 0.9**	**5.0 ± 0.9**	**68 ± 4**	**45 ± 6**
28 day ± extended dry down				
Wet	**54.4 ± 6.5**	**35.1 ± 1.5**	**86 ± 3**	**75 ± 2**
Wet-dry	**24.6 ± 2.1**	**14.7 ± 0.8**	**55 ± 5**	**26 ± 6**
Dry	**19.3 ± 2.4**	**11.9 ± 1.1**	**43 ± 5**	**19 ± 5**

Significant overall effects ($P < 0.001$) were observed for vegetation patch type, soil moisture, and four month extended dry-down. Bold values denote significant differences ($P < 0.05$) between oak and grass soils in pairwise comparisons within rows. See Methods for details of moisture regime variations. All values are means ± standard errors ($n = 6$)

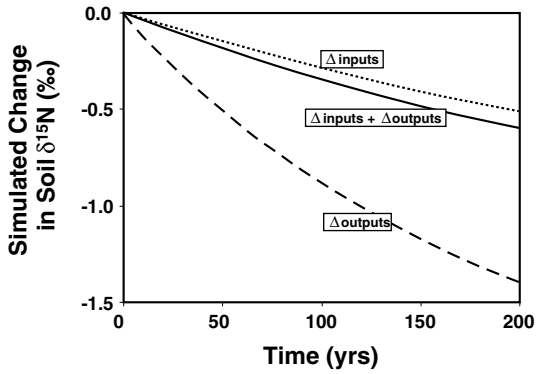

Fig. 3 Model output showing depletion in soil δ^{15}N of oak patches relative to grass patches during 200 years of simulated N accumulation under oaks. See Methods for details. Dotted line shows change in soil δ^{15}N due to simulated increases in N input to oak patches, with no change in output. Dashed line shows change due to decreased N output from oak patches, with no change in input. Solid line matches observed field differences in soil N and δ^{15}N of oak versus grass patches, and partitions N accumulation to 90% greater N input and 10% decreased N output under oaks

Discussion

We found several lines of evidence for higher N availability under oak trees relative to grass areas, including larger standing pools of total N, inorganic N, and microbial N in field soils and higher rates of N mineralization under a range of moisture conditions in the laboratory. Despite reports from elsewhere in the Sierra Nevada of higher aboveground herbaceous production under oaks (Frost and Edinger 1991), we found no significant differences by patch type (Jackson et al. 1990). This is surprising, since herbaceous vegetation in grass patches of this ecosystem is strongly N-limited (Perakis et al. in preparation). Competition for available N by oaks may limit herbaceous production in oak patches, while promoting higher productivity overall in these patches. Local inputs of woody litter are consistent with the higher C content and C:N of surface soils observed under oaks, as well as their lower bulk density (Table 2). Effects of shade cast by oaks, microclimate differences, and the effect of oak litter of herbaceous plant germination may also account for the lack of difference in herbaceous biomass among canopy types.

Dominance patterns of herbaceous species varied by patch type in a manner consistent with greater N supply under oaks. *Bromus diandrus*, which accounted for half of herbaceous biomass under oaks, responds more to N additions than *B. hordeaceus* in these sites (Perakis et al. in preparation). *Bromus hordeaceus*, on the other hand, is better adapted to low N soils characteristic of open grass areas (Rice and Nagy 2000). The invasive Italian thistle *Carduus pycnocephalus* was present only in oak patches, where it accounted for 47% of biomass in the five samples where it occurred, and averaged 13% of herbaceous biomass across all oak plots. Higher N availability under oaks may contribute to the near-complete dominance of this species in some plots due to its superior competitive ability at high N supply (Moore and Williams 1983) and suggests that oak patches may serve as local hotspots of continued Italian thistle invasion in this ecosystem.

Our natural abundance δ^{15}N data do not provide strong evidence for a shift in plant N foraging strategies among patch-types at our sites. Foliar δ^{15}N are often used to provide insight into variations in N foraging by form, depth, timing, mycorrhizal activity, and other factors (Robinson 2001), but we did not observe any significant patch effects on δ^{15}N of three common annual plants (Fig. 1b). It is possible that multiple competing processes kept plant δ^{15}N relatively constant across patches despite differences in N availability and foraging behavior that resulted in nearly 50% greater plant tissue N under oaks. The isotopic enrichment span $\varepsilon_{s\text{-}p}$ of surface soil (0–10 cm) minus plant tissue varied across patches for only *B. hordeaceus* (narrower under oaks, Fig. 1c) and was related positively to N mineralization, suggesting a possible shift to shallower foraging and/or greater reliance on δ^{15}N depleted nitrate under oaks. Oak foliage was significantly more enriched (average = –1.5‰, s.e. = 0.3, n = 6) than annuals (range of species: –2.3 to –2.8‰) and displayed δ^{15}N values closer to soils (i.e., lower $\varepsilon_{s\text{-}p}$). These oak δ^{15}N enrichment patterns are consistent with deeper foraging and/or evidence that oaks rely more on organic sources of soil N for nutrition than annuals (Cheng and Bledsoe 2004).

Soil moisture may interact with patch variations in soil N fertility to enhance N production and mobility under oaks. Oak soils displayed higher inherent N availability and nitrification across a range of moisture conditions in laboratory incubations, and often have greater field moisture due to shading and hydraulic lift by oaks (Millikin Ishikawa and Bledsoe 2000). Taken together, high moisture and N fertility are likely to accelerate N cycling and nitrification in oak soils across a wide range of field conditions, and may explain why oak soils exhibit higher rates of gross nitrate immobilization (Herman et al. 2003), while also possessing larger standing nitrate pools (Table 2) than grass soils. As a consequence, oak patches may be more susceptible to nitrate leaching than grass patches, at least from surface soils. Nitrate leaching losses may be especially important at the onset of fall rains, before nitrate-demanding annual plants have established (Jackson et al. 1990, 2006). Significantly higher rates of nitrous oxide gas loss have been shown to occur from oak rather than grass soils (Herman et al. 2003), consistent with the idea that oak patches may have potential for higher losses of available N than grass patches.

If N-rich conditions and favorable soil moisture under oaks increase the potential for N loss, then how do oak patches maintain larger total soil N pools over the long-term? Furthermore, if hydrologic and gaseous N losses are typically δ^{15}N depleted and thus enrich residual soil δ^{15}N in dry to mesic systems, then why are surface soils under oaks more depleted than comparable grass soils?

^{15}N-depletion of surface soils under woody vegetation is often attributed to accelerated N inputs from litter from woody plants (e.g., Shearer and Kohl 1988). Oak foliage is δ^{15}N depleted relative to 0–10 cm soil at our sites (average depletion = 2.7‰, s.e. = 0.3, n = 6), and large inputs of oak litter could plausibly drive depletion of surface soil N under oaks, but this process must also leave an enriched pool of N elsewhere in the ecosystem to satisfy whole-system δ^{15}N mass balance. However, mechanisms that invoke substantial vertical translocation of N from deep to shallow soils, or lateral translocation of N from grass to oak patches, are readily falsified by N and δ^{15}N mass balance constraints. A large vertical translocation of deep N to shallow horizons by oaks is unlikely, because soils under oak and grass display similar N concentrations at depth (Fig. 1a, see also Dahlgren et al. 1997). Moreover, δ^{15}N balances fail to support vertical translocation, since deep soil δ^{15}N under oak and grass are similar despite significant differences at the surface (Fig. 2b). Lateral transport of N from grass to oak areas is also inconsistent with observed δ^{15}N patterns. Fine roots of blue oak are concentrated in surface horizons and can extend 5 m beyond the crown (Millikin and Bledsoe 1999). Oak foliage was significantly more enriched than grass tissue and lateral transport of enriched N by oaks should leave behind depleted δ^{15}N in grass patches, but the opposite pattern was observed (Fig. 2b). Blue oak roots do not exploit nutrient rich (i.e., N–P–K) soil patches as effectively as herbaceous fine roots, suggesting that lateral oak roots may instead function primarily to obtain water (Cheng and Bledsoe 2002). Although some spatial redistribution of N by oaks may occur in our study sites, this effect appears to be relatively small, and is not a viable explanation for N and δ^{15}N differences observed between oak and grass patches in the field.

Changes in N inputs and/or retention due to oaks are further possible explanations for the development of islands of N fertility under oaks. Results from our simple δ^{15}N mass balance simulation model, constrained by surface soil N and δ^{15}N measured in the field, suggest that oaks promote local N accumulation and surface soil δ^{15}N depletion primarily by fostering greater N inputs, with only slight effects on nitrate outputs. To satisfy the additional 38 g N m^{-2} that accumulates under oaks relative to grass patches in the field (Table 2), we simulated N accumulation in oak patches at a rate 0.19 g N m^{-2} yr^{-1} greater than grass patches for 200 years. Simulation results matched the 0.6‰ δ^{15}N field difference between oak and grass soils perfectly when the required N accumulation under oaks was partitioned 90% to greater N inputs, and 10% to lower N losses (solid line, Fig. 3). This conclusion is consistent qualitatively with results from mid-western USA grassland-savanna showing that oak and grass patches have similar soil water nitrate fluxes at 60 cm depth (Dijkstra et al. 2006). Our

model $\delta^{15}N$ results are not sensitive to the selection of a 200 year simulation interval, which falls within the age span of blue oak at our sites (50–250 years, Brooks 1969), provided that total N accumulation under oaks was constrained to 38 g N m^{-2} greater than grass patches. Consideration of additional soil N in the model (e.g., 10–20 cm) would only increase the role of inputs as a driver of N accumulation under oaks. Our estimate of enhanced N input attributable to oaks (<0.2 g N m^{-2} yr^{-1}) is conservative compared to an estimate of ~ 0.5 g N m^{-2} yr^{-1} additional input from dry and fog deposition for our site, calculated as the difference between throughfall (1 g N m^{-2} yr^{-1}, Fenn et al. 2003a) and wet deposition (0.5 g N m^{-2} yr^{-1}, Stohlgren and Parsons 1987). Detailed isotopic information on fog and dry deposition inputs, as well as other N fluxes at our sites, could refine our model calculations of the role of oak tree canopies in concentrating N inputs to local soils patches. Overall, our N isotope and mass balance results indicate that oaks foster the development of N islands of fertility at the patch scale primarily by increasing rates of N input, with less effect of oaks on attenuating N losses.

Scavenging of atmospherically deposited N by oak canopies appears to be a significant source of local N accumulation in blue oak grassland-savanna ecosystems, and may be enhanced by anthropogenic contributions to N deposition in the region. Both dry deposition and fog are significant contributors (~50%) to total atmospheric N loading to the western slope of the Sierra Nevada (Fenn et al. 2003a), and can be especially important N sources in sites such as ours, where high summer aridity restricts the growth of canopy N fixers (Jovan and McCune 2004). Fog and dry deposited N that is intercepted by tree canopies is transferred to soils as throughfall and stemflow, or is assimilated directly by stomata with subsequent movement into the plant or transfer to soils via litterfall (Hanson and Lindberg 1991; Bytnerowicz et al. 1999). The majority of the dry deposited N at our sites occurs in reduced forms (i.e., NH_x), originating from agriculture in the nearby San Joaquin Valley (Bytnerowicz et al. 2002), and is probably $\delta^{15}N$ depleted relative to bulk deposition (Russell et al. 1998; Schulz et al. 2001) depending on the source, and the time and distance of transport to our site. Fog is also quantitatively important at our site and elsewhere in southern California, and can rival wet N deposition rates of both nitrate and ammonium (Collett et al. 1990; Fenn et al. 2000). Accelerated N deposition can foster soil acidification in extreme cases, but the significantly higher pH observed under oak than grass patches raises the possibility that oak trees may buffer such acidification effects in heterogeneous savanna, perhaps by recycling of base cations from deeper to shallow soil horizons (Dahlgren et al. 1997). Higher soil pH under oaks may also foster recycling and nitrification of locally deposited N, thus accelerating N cycling at the scale of individual patches. Watersheds of Sequoia National Park exhibit incipient N saturation (Fenn et al. 2003b). Our results raise the possibility that N effects observed at the scale of entire watersheds may not fully reflect local-scale impacts where different vegetation types shape N input, availability, and loss.

Conclusions

Oak trees support consistently higher N pools and N availability than adjacent grass dominated patches in California blue oak grassland-savanna. Higher N pools and $\delta^{15}N$ depletion of surface soil under blue oak can be explained primarily by greater inputs of N to oak patches, plus a small effect of increased N retention under oaks. Higher N availability at the oak patch scale leads to greater N uptake by herbaceous communities, and may also foster success of N-demanding invasive plants such as Italian thistle. The enhancement of N inputs by oaks appears to imprint localized effects on N balances in this spatially heterogeneous ecosystem. In turn, this fosters predictable yet distinct spatial variation in feedbacks between soil N cycling, plant N uptake, and herbaceous community composition that increase biogeochemical heterogeneity in California grassland-savanna.

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