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Oak tree and grazing impacts on soil properties and nutrients in a California oak woodland

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Abstract. There is great interest in understanding how rangeland management practices affect the long-term sustainability of California oak woodland ecosystems through their influence on nutrient cycling. This study examines the effects of oak trees and low to moderate intensity grazing on soil properties and nutrient pools in a blue oak (*Quercus douglasii* H.&A.) woodland in the Sierra Nevada foothills of northern California. Four combinations of vegetation and management were investigated: oak with grazing, oak without grazing, open grasslands with grazing, and open grasslands without grazing. Results indicate that oak trees create islands of enhanced fertility through organic matter incorporation and nutrient cycling. Compared to adjacent grasslands, soils beneath the oak canopy have a lower bulk density, higher pH, and greater concentrations of organic carbon, nitrogen, total and available P, and exchangeable Ca, Mg, and K, especially in the upper soil horizons (0–35 cm). In contrast, the light grazing utilized at this site had minimal effects on soil properties which included an increase in the bulk density of the surface horizon and an increase in available P throughout the entire soil profile. While low to moderate intensity grazing has little effect at this study site, there could be much larger impacts under the more intensive grazing practices utilized on many rangelands. The lack of oak regeneration and oak tree removal to enhance forage production may eventually lead to large losses of nutrients and soil fertility from these ecosystems. Results of this study have important implications for predicting how management practices may potentially affect oak regeneration, water quality, and ecosystem sustainability.

Introduction

Soil properties and nutrient pools can vary dramatically within certain plant communities (e.g., Holland 1973; Lajtha & Schlesinger 1986; Klopatek 1987; Burke 1989; Jackson et al. 1990; Belsky et al. 1993; Belsky & Canham 1994). Soil nutrient concentrations, pH, and organic matter content have been shown to vary by more than an order of magnitude at spatial scales of 5 m or less (e.g., Downes & Beckwith 1951; Raupach 1951; Trangmar et al. 1987; Robertson et al. 1988). In California oak woodlands and savanna, scattered trees create a mosaic of open grasslands and oak/understory plant communities. Evidence indicates that oaks create islands of enhanced fertility beneath their canopy due to processes associated with nutrient cycling (Holland 1973; Kay 1987;

Jackson et al. 1990; Callaway et al. 1991; Klemmedson 1991). Such results suggest that nutrient cycling in these ecosystems is spatially complex and may be strongly influenced by rangeland management practices. These spatial patterns of nutrient availability may in turn influence future regeneration success and plant community structure (Robertson et al. 1988).

Blue oak (*Quercus douglasii*, H.&A.) is the dominant tree species on an estimated 3 million ha of woodlands and savanna in the interior valleys and foothills of Central California (Griffin 1977). These ecosystems are used extensively for cattle grazing, firewood production, wildlife habitat, and watersheds. Many oak populations do not appear to be regenerating at rates capable of maintaining current distributions and densities, causing great concern over sustainability of these ecosystems (Griffin 1971, 1976; Muick & Bartolome 1987). No clear evidence exists as to why oak regeneration may be hindered; however, rangeland management practices have been implicated as a possible contributing factor. As a result, there is great interest in understanding how management practices affect long-term ecosystem sustainability, oak regeneration, and water quality through their influence on nutrient cycling.

Comparisons of forage productivity beneath blue oak canopies and adjacent open grasslands give conflicting results in California oak woodland rangelands. Several studies report lower forage production under blue oak canopies (Murphy & Crampton 1964; Kay & Leonard 1980; Kay 1987; McClaran & Bartolome 1989); however, other studies indicate higher yields under the oak canopy than in open grasslands (Holland 1980; Holland & Morton 1980). Total and available soil nutrients are generally shown to be higher beneath the oak canopy than in surrounding grasslands. To exploit the greater nutrient pools beneath oak canopies, tree removal has been advocated as a means of decreasing competition for water, nutrients, and light, presumably leading to increased forage production. The results of oak clearing trials on forage production are not consistent and appear to depend on canopy density and annual precipitation (Standiford & Howitt 1993). In some cases, oak tree removal resulted in 65–650% increases in forage production compared to adjacent open grassland areas in the short-term following tree removal (Johnson et al. 1959; Murphy & Crampton 1964; Kay 1987). However, long-term assessments indicate that the benefits of tree removal declined to levels similar to that of the adjacent grasslands within 15 years (Kay 1987). Similarly, the effects of grazing on soil properties show no consistent trend. An analysis of a worldwide data set containing data from 236 sites showed no relationship between grazing and soil organic matter, nitrogen, phosphorus, or pH (Milchunas & Lauenroth 1993).

To date, there has been no comprehensive study of nutrient cycling in California oak woodlands at the ecosystem scale. This study serves as the foundation for a larger nutrient cycling investigation of ecosystem-scale nutrient pools and fluxes in managed and non-managed oak woodlands. The primary objective of this paper is to examine the effects of oak trees and grazing on nutrient cycling through their influence on soil properties and nutrient pools. The study focuses on grazing and oak tree effects because grazing and oak removal are the two management practices having the greatest potential impact on nutrient cycling in most California oak woodlands. Results of this study have important implications for understanding how these management practices may potentially affect oak regeneration, water quality, and ecosystem sustainability.

Materials and methods

Study site

The investigation was conducted in the northern Sierra Nevada foothills at the University of California Sierra Foothill Research and Extension Center, approximately 30 km east of Marysville, CA (39°15′ N, 121°17′ W). The climate is Mediterranean, with cool moist winters and hot dry summers; mean annual precipitation is 73 cm and mean annual temperature is 15 °C. Soil water potentials remain below −1.5 MPa at the 0–30 cm depth for approximately five months each year (Jackson et al. 1988). The dominant tree species is blue oak (*Quercus douglasii* H.&A.), a winter-deciduous oak, with associated interior live oak (*Quercus wislizenii* A. DC.), an evergreen oak. The oak stocking ranges from 90–200 trees per hectare with an average canopy coverage for the watershed of approximately 70%. Major forbs include filaree (*Erodium sp.*), annual clovers (*Trifolium sp.*), and geranium (*Geranium sp.*). Common annual grass species are soft chess (*Bromus hordeaceus*), ripgut brome (*Bromus diandrus*), red brome (*Bromus madritensis spp. rubens*), annual fescue (*Vulpia sp.*), wild oats (*Avena fatua* and *Avena barbata*), and medusahead (*Taeniantherum caput-medusae*). The oak understory community has lower species richness and a somewhat different group of plant taxa than the open grasslands (Jackson et al. 1990). Nitrogen fixing clovers are found only in the open grasslands. A complete description of the vascular plant species and their distribution are reported by Jackson et al. (1990). Soils within the study area formed in basic metavolcanic (greenstone) bedrock and are classified as fine, mixed, thermic Typic Haploxeralfs.

Study sites were selected within a 10 ha parcel of the Schubert watershed (200 m elevation) having uniform site factors with the exception of grazing. One portion of the study area was grazed by beef cattle at low to moderate intensity (∼0.5 animals/ha) for between 4 and 8 weeks per year during the

January to June period. Over the past 20 years, grazing intensity has remained consistent within the low to moderate range. The other tract has been preserved as a natural area with no livestock grazing for 20 years prior to sampling. Slopes within the study area range between 5 and 20%. Sites for twenty soil pits were randomly selected using a quadrat map (10 m $\times$ 10 m) of the study area to obtain five replicates each from the following combination of vegetation and management: (i) oak with grazing (Ok/Gz), (ii) oak without grazing (Ok/Ng), (iii) open grasslands with grazing (Gs/Gz), and (iv) open grasslands without grazing (Gs/Ng). Soil pits were excavated with a backhoe to the depth of consolidated bedrock (80–120 cm). Soil pits beneath the oak canopy were excavated perpendicular to the bole of the tree while pits in the open grasslands were located a minimum of three meters from the edge of the oak canopy. The age of the trees from beneath which soils were sampled was estimated to be 80 to 100 years. Each pedon was described and bulk soil samples were collected from across the entire 2 m pit face for each morphological horizon. Soil samples were collected during the month of July following the death of the annual grasses.

Methods

Soil samples were air-dried, gently crushed, and passed through a 2 mm sieve; roots passing through the sieve were removed with a forceps. The air-dried, $<$2 mm soil was used for the analyses which follow, unless otherwise noted. Soil pH was measured potentiometrically in water (1:2, soil:water) following a 15 min equilibration period. Cation exchange capacity and exchangeable cations were measured using 1 *M* NH_4OAc (pH = 7) (Soil Survey Staff 1984). Bulk density in the A and AB horizons was determined by coring while field moist, paraffin-coated clods (two clods per horizon) were used in the B horizons (Soil Survey Staff 1984). Organic carbon and nitrogen were determined on ground samples ($<$250 μm) by dry combustion with a C/N analyzer. Total digestible phosphorus was measured using a modified Kjeldahl digestion with phosphorus quantification by ICP (Parkinson & Allen 1975). An index of plant-available phosphorus was determined using the Bray No. 2 extraction (Olsen & Sommers 1982).

Soil nutrient pools were calculated for each soil profile by summing the nutrient content of all horizons within the solum. Nutrient concentrations for each horizon were determined from the nutrient concentration in the $<$2 mm fraction, mean horizon thickness, and bulk density of each horizon, correcting for the coarse fragment ($>$2 mm) volume.

The experimental design was a split-plot; the management regime (grazing versus non-grazed) was the whole-plot treatment factor and the vegetation (oak versus grass) was the split-plot treatment factor. Tests for the main effects and interactions were performed using ANOVA and a post-hoc Fisher's least-significant-difference test was used for pair-wise comparisons among means. All statistical analyses were performed using SYSTAT for Windows, Version 5 (SYSTAT Inc., Evanston, IL) at a $p = 0.05$ significance level.

Results and discussion

Solum depth and bulk density

The soil textures range from clay loam in the A horizons to clay in the B horizons (Table 1). The soils display a well developed argillic horizon that effectively restricts root penetration and saturated water flow. Coarse fragment content increases from 15% gravel in the A horizon to 60–65% rock and cobble in the subsurface horizons. Grass roots are found nearly exclusively in the A and AB horizons, their growth into the B horizons limited by the dense argillic horizon. Approximately 85% of the grass roots have been found in the upper 10 cm of the soil profile (Jackson et al. 1988). In contrast, oak roots were found preferentially in the B horizons where they presumably avoid the severe desiccation that occurs in the A and AB horizons during the summer.

There were no differences in the depth of the soil profile as a function of management or vegetation. The soil depth was 107 ± 8 cm (Mean $\pm$ SD; range 82–116 cm). These soil profiles were underlain by consolidated bedrock that we were not able to dig through with a backhoe. Oak roots were limited by the bedrock, with the possible exception of some roots exploiting joints within the bedrock. The depth of the soil profile strongly affected oak regeneration under a similar Mediterranean-type climate in France where soil profiles <40 cm displayed nearly complete seedling mortality while soils deeper than 80 cm were required for good growth conditions (Meredieu et al. 1996).

Soils beneath the oak canopy had a thicker A horizon and thinner AB horizon suggesting that oak trees promote the development of thicker A horizons at the expense of the AB horizon (Figure 1). There are considerably greater inputs of litterfall beneath the oak canopy that provides the additional organic matter necessary for development of A horizons (Dahlgren & Singer 1994). The A horizons were also thicker in the natural area as compared to the pasture suggesting that grazing practices result in the destruction of A horizons. A greater bulk density of A horizons in grazed soils could account for approximately a 10% ($\sim$1 cm) decrease in thickness compared to the 2–3 cm decrease measured. Other factors that could possibly influence A horizon thickness are changes in above- and below-ground detritus inputs and enhanced erosion. In spite of grazing, peak standing live biomass of the

Table 1. Soil profile description for a representative soil beneath the blue oak canopy.

Horizon	Depth (cm)	Color (moist)	Texture	Structure	Consistence	Roots	Boundary	>2 mm (%)
A	0–10	5YR 3/4	cl	3 f-m cr	sh fr so po	3vf,2f	cs	15
AB	10–35	5YR 4/4	gcl	1 f-m sbk	h f ss ps	2vf,2f,1m	cw	30
Bt1	35–62	2.5YR 4/4	xkc	3 c-vc pr → 1 m-c sbk	vh f s p	2f,2m,2co	gw	60
Bt2	62–84	2.5YR 4/6	xkc	2 c-vc pr → 1 m-c sbk	vh f s p	1f,2m,2co	gw	60
BC	84–109	10YR 5/4	xkcl	1 m sbk	vh f ss ps	1f,2m,2co	cw	65
Cr/R	>109	10YR 3/3		M		1m,1co		

Abbreviations:
Texture: cl – clay loam; c – clay; g – gravel; xk – extremely cobbly
Structure: 1 – weak; 2 – moderate; 3 – strong; f – fine; m – medium; c – coarse; vc – very coarse; cr – crumb; sbk – subangular blocky; pr – prism; M – massive; → – breaking to
Consistence: (Dry) sh – slightly hard; h – hard; vh – very hard; (Moist) fr – friable; f – firm; (Wet) so-nonsticky; ss – slightly sticky; s – sticky; po – nonplastic; ps – slightly plastic; p – plastic
Roots: 1 – few; 2 – common; 3 – many; vf – very fine; f – fine; m – medium; co – coarse
Boundary: c – clear; g – gradual; s – smooth; w – wavy

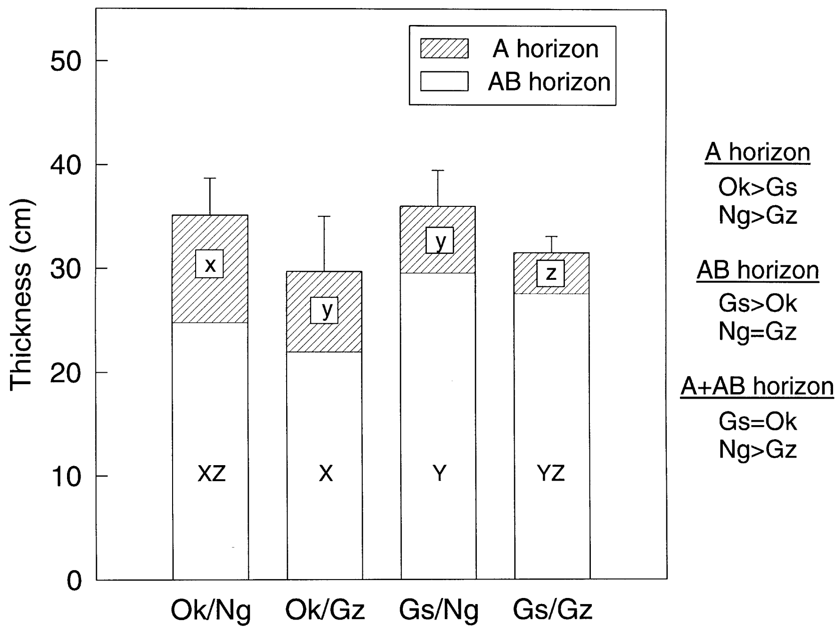

Figure 1. Thickness of A and AB soil horizons as related to grazing and oak canopy effects. Treatment designations are oak (Ok), open grasslands (Gs), grazed (Gz), and non-grazed (Ng). Bars with the same lower and upper case letters are not statistically different for A and AB horizons, respectively. All statistical differences between treatments were determined at the $p = 0.05$ significance level.

annual grasses was similar in both grazed (oak = 1794; grass = 2983 kg/ha) and non-grazed (oak = 1721; grass = 2839 kg/ha) sites (Dahlgren & Singer 1994). Therefore, the amount of detritus returned to the organic matter pool at the soil surface was similar for both treatments. While we did not measure grass root biomass in this study, grazing was shown to increase root mass by an average of 20% in a worldwide grazing comparison (Milchunas & Lauenroth 1993). This suggests that grazing could increase organic matter inputs into the A horizon and enhance A horizon formation, a response opposite of that measured in this study. Enhanced erosion in the grazed area was not observed or measured in the suspended sediment concentrations of the stream draining the grazed watershed (suspended sediments ∼30 kg/ha/yr; Dahlgren & Singer 1994). Thus, erosion is not believed to be the primary cause of the thinner A horizons in the grazed treatment.

Oak regeneration studies on soils similar to those in our study area suggest that the argillic horizon may impede oak seedling tap root establishment into deeper horizons resulting in summer desiccation and death of the seedling (McCreary 1995). Thus, the thickness of the soil above the argillic horizon

Table 2. Mean (±SD) bulk density (g/cm^3) and statistical analysis comparing the effects of vegetation (Ok-oak versus Gs-grass) and management practices (Gz-grazed versus Ng-nongrazed) on bulk density.

Treatment	Horizon A	AB	Bt1	Bt2	BC
Ok/Ng	0.92 (0.08)a[†]	1.29 (0.07)a	1.42 (0.08)a	1.49 (0.09)a	1.64 (0.17)a
Ok/Gz	1.07 (0.12)b	1.25 (0.11)a	1.35 (0.10)a	1.46 (0.12)a	1.56 (0.13)a
Gs/Ng	1.12 (0.04)b	1.29 (0.10)a	1.39 (0.07)a	1.53 (0.08)a	1.65 (0.07)a
Gs/Gz	1.17 (0.09)b	1.30 (0.11)a	1.43 (0.12)a	1.50 (0.09)a	1.62 (0.11)a
Vegetation	Gs>Ok[‡]	Gs=Ok	Gs=Ok	Gs=Ok	Gs=Ok
Management	Gz>Ng	Ng=Gz	Ng=Gz	Ng=Gz	Ng=Gz

[†] Means in each column with the same letter are not statistically different at $p < 0.05$.
[‡] Statistical differences determined at a significance level of $p = 0.05$.

(i.e., A and AB horizons) may influence seedling establishment. The thickness of the combined A and AB horizons did not differ between oak and grassland sites (Figure 1). Because no oak seedlings were found to survive during the five years of investigation, we have no direct evidence for site conditions that favor oak seedling establishment.

Bulk density in the A horizon was different for both vegetation and grazing treatments; however, this difference did not extend below the A horizon (Table 2). Soils beneath the oak canopy had a lower bulk density by 0.1–0.2 g/cm^3. This is most likely due to the higher soil organic matter concentrations found beneath the oak canopy (65 versus 41 g C/kg) which result in a porous crumb soil structure. Grazed sites had a bulk density 0.05 to 0.15 g/cm^3 greater than non-grazed sites. This is likely due to the tramping effect of cattle, especially during wet soil conditions, which creates a “hoof pan” at the soil surface. While the non-grazed site has not been grazed since 1972, this time period (20 years) may not be sufficient for bulk density to recover from the previous grazing regime. While grazing effects on bulk density appear minor, they may result in lower infiltration rates that in turn could induce surface runoff and erosion during high intensity rainfall events.

Soil pH

Soil pH was greater in the A and AB horizons and less in the Bt1 and Bt2 horizons beneath the oak canopy compared to the open grasslands (Table 3). The pH beneath the oak canopy was 0.7 and 0.3 units higher in the A and AB horizons, respectively. This increase in pH appears to be primarily due to greater cycling of base cations by the oak. This is supported by the higher base saturation values in A horizons beneath the oak canopy (72%) compared

Table 3. Mean (±SD) pH and statistical analysis comparing the effects of vegetation (Ok-oak versus Gs-grass) and management practices (Gz-grazed versus Ng-nongrazed) on soil pH.

Treatment	Horizon A	AB	Bt1	Bt2	BC
Ok/Ng	7.16 (0.15)a[†]	6.82 (0.09)a	6.60 (0.23)a	6.59 (0.24)a	6.77 (0.07)a
Ok/Gz	6.86 (0.19)b	6.62 (0.35)ab	6.56 (0.46)a	6.57 (0.10)a	6.73 (0.12)a
Gs/Ng	6.44 (0.15)c	6.52 (0.19)b	6.88 (0.11)a	6.89 (0.06)b	6.72 (0.11)a
Gs/Gz	6.19 (0.09)d	6.38 (0.14)b	6.81 (0.07)a	6.95 (0.09)b	6.87 (0.25)a
Vegetation	Ok>Gs[‡]	Ok>Gs	Gs>Ok	Gs>Ok	Gs=Ok
Management	Ng>Gz	Ng=Gz	Ng=Gz	Ng=Gz	Ng=Gz

[†] Means in each column with the same letter are not statistically different at $p < 0.05$.
[‡] Statistical differences determined at a significance level of $p = 0.05$.

to the open grasslands (51%). A second factor that may contribute to the greater pH is the buffering of the rainfall acidity by canopy processes. The pH of the canopy throughfall was generally 0.5 to 1 unit greater than that of the precipitation (Dahlgren & Singer 1994).

The pH decrease of 0.3 units in the Bt1 and Bt2 horizons beneath the oak canopy (Dahlgren & Singer 1994) may result from acidification processes related to the oak roots. A portion of root uptake to replenish nutrients lost in litterfall and canopy throughfall will originate from the B horizons and will result in proton production within these horizons when cation uptake exceeds anion uptake. Carbonic acid originating from root respiration may further contribute to greater proton production and acidification in the B horizons beneath oak trees.

The pH was approximately 0.2–0.3 units lower in the A horizons of grazed soils compared to those in the natural area. We can only speculate as to the reasons for this pH decrease. Studies of nitrification rates (Firestone et al. 1995) and soil solution nitrate concentrations (Dahlgren & Singer 1991) showed that nitrification and nitrate leaching were greater in A horizons of grazed soils. This creates the potential for soil acidification due to proton production and base cation leaching (van Breemen et al. 1983). Additionally, the export of base cations from the grazed area by cattle may have an acidifying effect. Because 85% of the grass roots occur in the upper 10 cm of the soil, acidification due to export of base cations by grazing would have its greatest impact in the A horizon. No consistent trend was observed for the effects of grazing on soil pH in a worldwide grazing comparison (Milchunas & Lauenroth 1993).

Carbon, nitrogen, and phosphorus

Concentrations of organic carbon, nitrogen, and total phosphorus responded identically with respect to management and vegetation (Table 4). No differences were observed between grazed and non-grazed treatments. In contrast, concentrations of carbon, nitrogen, and phosphorus were higher in all soil horizons beneath the oak canopy compared to the open grasslands. It is remarkable that oak trees are capable of affecting these components throughout the entire profile rather than just in the surface horizons. Since carbon, nitrogen, and phosphorus are major components of organic matter, it is assumed that the strong relationship between these components is associated with organic matter concentrations. The higher concentrations in the upper soil horizons can be explained by greater detrital inputs associated with litterfall beneath the oak canopy. Detrital inputs of grass litter over a three year period averaged 1758 and 2911 kg/ha/yr for the oak understory and open grasslands, respectively (Dahlgren & Singer 1994). In addition, oak litterfall contributed 9064 kg/ha/yr of organic matter over the same period. Thus, there was nearly a four-fold increase in organic matter returned to the soil surface beneath the oak canopy compared to the open grasslands. While nitrogen fixing legumes were present in the open grasslands, there were no legumes found beneath the oak canopy. Thus, differences in soil nitrogen concentrations are not due to the distribution of nitrogen fixing legumes.

Carbon, nitrogen, and phosphorus concentrations in the B horizons were approximately twice those measured in the open grasslands. Root turnover is the most likely source of these nutrients because oak roots are common throughout the B horizons beneath oak trees (Table 1). Oak root biomass >2 mm diameter for six trees ranging from 7.6 to 33.3 cm DBH was 16 to 193 kg per tree in a nearby blue oak woodland (Millikin et al. 1997); however, little in known about root turnover rates in California oak woodlands. A secondary source of organic matter in B horizons is from retention of dissolved organic matter leaching from the litter decomposing at the soil surface. Soil solutions from A horizons contained approximately 2000 μmol/L of dissolved organic carbon (DOC) beneath the oak canopy compared to 500 μmol DOC/L in the open grasslands (Dahlgren & Singer 1994). The dissolved organic matter decreased with depth in the profile; however, greater than 1000 μmol DOC/L entered into the B horizons where it may be adsorbed by silicate clays and iron oxides.

The C:N molar ratios of soil organic matter showed a narrow range of 11 to 18 for all combinations of vegetation and management (Table 4). The only significant difference ($p < 0.05$) between treatments was a greater C:N ratio in A horizons for non-grazed versus the grazed sites; however, this difference was very small. The processing of forage by cattle may contribute to this

Table 4. Mean (±SD) concentrations of organic carbon (g/kg), nitrogen (g/kg), C/N molar ratio, total phosphorus (mg/kg), and available P (mg/kg), and statistical analysis comparing the effects of vegetation (Ok-oak versus Gs-grass) and management practices (Gz-grazed versus Ng-nongrazed) on these parameters.

	Horizon				
Treatment	A	AB	Bt1	Bt2	BC
Organic C					
Ok/Ng	66.0 (8.3)a†	19.0 (8.0)a	7.3 (1.3)a	3.9 (0.8)a	2.4 (0.5)a
Ok/Gz	63.8 (7.4)a	21.5 (11.1)a	7.2 (1.2)a	3.8 (1.1)a	2.2 (0.7)a
Gs/Ng	40.9 (4.1)b	10.9 (1.1)b	3.3 (0.6)b	2.2 (0.5)b	0.8 (0.2)b
Gs/Gz	42.3 (5.3)b	10.0 (3.0)b	4.1 (1.3)b	2.2 (0.4)b	1.0 (0.3)b
Vegetation	Ok>Gs‡	Ok>Gs	Ok>Gs	Ok>Gs	Ok>Gs
Management	Ng=Gz	Ng=Gz	Ng=Gz	Ng=Gz	Ng=Gz
Nitrogen					
Ok/Ng	4.44 (0.88)a	1.64 (0.95)a	0.65 (0.18)a	0.40 (0.09)a	0.23 (0.10)a
Ok/Gz	4.86 (0.91)a	1.89 (1.16)a	0.74 (0.14)a	0.37 (0.07)a	0.24 (0.07)a
Gs/Ng	2.98 (0.45)b	0.83 (0.11)b	0.30 (0.09)b	0.21 (0.06)b	0.08 (0.02)b
Gs/Gz	3.34 (0.56)b	0.76 (0.27)b	0.35 (0.11)b	0.22 (0.05)b	0.12 (0.07)b
Vegetation	Ok>Gs	Ok>Gs	Ok>Gs	Ok>Gs	Ok>Gs
Management	Ng=Gz	Ng=Gz	Ng=Gz	Ng=Gz	Ng=Gz
C/N ratio					
Ok/Ng	17.5 (1.3)a	14.5 (3.4)a	13.4 (1.5)a	11.2 (0.7)a	13.8 (5.5)a
Ok/Gz	15.5 (1.9)ab	13.8 (1.9)a	11.4 (0.4)a	11.9 (2.3)a	10.7 (1.3)a
Gs/Ng	16.2 (1.6)ab	15.5 (2.2)a	13.1 (1.8)a	12.9 (1.6)a	11.6 (2.5)a
Gs/Gz	14.9 (1.4)b	16.3 (6.4)a	13.8 (2.7)a	12.2 (2.5)a	11.2 (3.0)a
Vegetation	Gs=Ok	Gs=Ok	Gs=Ok	Gs=Ok	Gs=Ok
Management	Ng>Gz	Ng=Gz	Ng=Gz	Ng=Gz	Ng=Gz
Total P					
Ok/Ng	718 (204)a	492 (117)a	374 (52)a	290 (46)a	176 (38)a
Ok/Gz	790 (90)a	534 (93)a	384 (50)a	314 (74)a	162 (37)a
Gs/Ng	406 (71)b	292 (44)b	240 (46)b	114 (27)b	76 (25)b
Gs/Gz	414 (101)b	360 (50)b	264 (76)b	116 (34)b	68 (40)b
Vegetation	Ok>Gs	Ok>Gs	Ok>Gs	Ok>Gs	Ok>Gs
Management	Ng=Gz	Ng=Gz	Ng=Gz	Ng=Gz	Ng=Gz
Available P					
Ok/Ng	39.6 (14.1)a	8.7 (3.6)a	2.1 (0.8)a	1.9 (0.8)a	1.1 (0.1)a
Ok/Gz	130.7 (41)b	60.6 (27.5)b	15.4 (4.8)b	4.2 (0.8)b	3.8 (1.0)b
Gs/Ng	11.8 (3.0)a	3.9 (1.6)a	0.6 (0.3)a	0.3 (0.2)c	0.7 (0.8)a
Gs/Gz	29.2 (8.4)a	10.0 (3.6)a	1.5 (0.8)a	1.7 (0.5)a	1.0 (0.3)a
Vegetation	Ok>Gs	Ok>Gs	Ok>Gs	Ok>Gs	Ok>Gs
Management	Gz>Ng	Gz>Ng	Gz>Ng	Gz>Ng	Gz>Ng

† Means in each column with the same letter are not statistically different at $p < 0.05$.
‡ Statistical differences determined at a significance level of $p = 0.05$.

difference by enhancing the decomposition process through predigesting the organic matter.

Plant-available phosphorus, as measured by Bray extraction, was increased throughout the entire soil profile by both oak trees and grazing (Table 4). Cycling of phosphorus with oak litterfall is the most probable explanation for the increased available P concentrations beneath the oak canopy. Litterfall returns 8 kg/ha/yr of P to the soil surface (Dahlgren & Singer 1994). Leaching of appreciable concentrations of ortho-PO_4 ($\sim$15 μmol/L) from A horizons to lower horizons was apparent from soil solution studies (Dahlgren & Singer 1991). Leaching of ortho-PO_4 to the lower soil horizons would be expected to increase levels of available P in the subsoil horizons. The effects of grazing on available P concentrations are especially pronounced in the oak/grazed (Ok/Gz) combination. Cattle tend to seek shade during the hot midday period, and may transport P from the surrounding areas to the soils beneath the oak canopy where dung and urine are preferentially deposited. With a readily mineralizeable P source in dung and urine, it can be reasoned that cattle excrement enhances P mineralization and leaching. Leaching of ortho-PO_4 is exceptionally high in A horizon soil solutions ($>$20 μmol/L) within the oak/grazed (Ok/Gz) treatment resulting in leaching of phosphorus to the deeper soil horizons (Dahlgren & Singer 1991).

Cation exchange capacity and exchangeable cations

Cation exchange capacity was increased in the A and AB horizons beneath the oak canopy, but showed no difference between the grazed and non-grazed sites (Table 5). Organic matter contributes appreciably to the CEC in the A and AB horizons due to its high concentrations (10 to 70 g C/kg) and high CEC per unit mass (200–400 $cmol_c$/kg organic matter). It follows that the 1.5 to 2-fold greater organic matter concentrations in A and AB horizons beneath the oak canopy are responsible for the greater CEC. Because the high clay concentrations in the B horizons provide the dominant source of CEC, the small absolute increase in organic matter concentrations in these horizons does not appreciably affect the total CEC.

With the exception of sodium, exchangeable cation concentrations were greater in the upper soil horizons beneath the oak canopy (Table 5). The greater concentration of exchangeable cations is a direct consequence of the greater CEC resulting from higher soil organic matter concentrations. Nutrient cycling by oak selectively replenishes the Ca, Mg, and K concentrations while Na, a non-essential plant nutrient, is not accumulated beneath the oak canopy. Litterfall and canopy throughfall return 173, 27, and 75 kg/ha/yr of Ca, Mg, and K, respectively, to the soils beneath the oak canopy (Dahlgren & Singer 1994). Since many of the oak roots are located in the B horizons,

Table 5. Mean (±SD) cation exchange capacity ($cmol_c$/kg), exchangeable cation concentrations ($cmol_c$/kg), and base saturation (%) along with statistical analysis comparing the effects of vegetation (Ok-oak versus Gs-grass) and management practices (Gz-grazed versus Ng-nongrazed) on these parameters.

	Horizon				
Treatment	A	AB	Bt1	Bt2	BC
CEC					
Ok/Ng	29.4 (3.4)a[†]	17.8 (2.3)ac	17.0 (1.2)a	20.0 (2.5)a	22.8 (3.4)a
Ok/Gz	28.5 (5.1)a	20.1 (3.5)a	17.0 (1.1)a	20.9 (2.4)a	23.5 (3.6)a
Gs/Ng	21.1 (1.8)b	14.0 (1.5)b	16.2 (1.9)a	19.4 (1.8)a	23.1 (3.0)a
Gs/Gz	20.1 (2.6)b	15.8 (1.2)bc	18.1 (3.5)a	22.7 (3.8)a	24.0 (2.3)a
Vegetation	Ok>Gs[‡]	Ok>Gs	Gs=Ok	Gs=Ok	Gs=Ok
Management	Ng=Gz	Ng=Gz	Ng=Gz	Ng=Gz	Ng=Gz
Exch-Ca					
Ok/Ng	16.8 (1.9)a	7.9 (1.4)a	9.2 (0.7)a	11.9 (2.0)a	13.3 (1.4)a
Ok/Gz	16.1 (2.3)a	10.5 (2.8)b	9.2 (1.0)a	12.6 (1.4)a	13.8 (2.2)a
Gs/Ng	7.9 (1.0)b	6.7 (1.2)a	8.6 (0.9)a	11.3 (1.7)a	12.9 (1.9)a
Gs/Gz	7.7 (1.4)b	7.5 (1.5)a	8.9 (1.0)a	11.6 (1.8)a	12.2 (1.5)a
Vegetation	Ok>Gs	Ok>Gs	Gs=Ok	Gs=Ok	Gs=Ok
Management	Ng=Gz	Ng=Gz	Ng=Gz	Ng=Gz	Ng=Gz
Exch-Mg					
Ok/Ng	3.0 (0.3)a	3.0 (0.4)a	4.2 (0.8)a	5.4 (0.8)a	6.9 (1.4)a
Ok/Gz	2.7 (0.4)a	2.6 (0.4)a	4.0 (0.8)a	6.0 (0.9)ab	7.2 (0.8)a
Gs/Ng	2.1 (0.5)b	2.9 (0.4)a	4.4 (0.7)a	5.5 (0.7)ab	6.7 (1.1)a
Gs/Gz	2.0 (0.4)b	3.0 (0.4)a	5.3 (1.2)a	6.9 (1.0)b	7.3 (0.9)a
Vegetation	Ok>Gs	Gs=Ok	Gs=Ok	Gs=Ok	Gs=Ok
Management	Ng=Gz	Ng=Gz	Ng=Gz	Gz>Ng	Ng=Gz
Exch-K					
Ok/Ng	0.91 (0.39)a	0.37 (0.15)ac	0.18 (0.05)ab	0.17 (0.07)a	0.10 (0.01)a
Ok/Gz	1.09 (0.14)a	0.45 (0.07)a	0.23 (0.06)a	0.12 (0.02)a	0.11 (0.02)a
Gs/Ng	0.44 (0.07)b	0.25 (0.05)b	0.14 (0.03)b	0.12 (0.01)a	0.11 (0.01)a
Gs/Gz	0.54 (0.15)b	0.26 (0.03)bc	0.15 (0.03)b	0.11 (0.01)a	0.11 (0.02)a
Vegetation	Ok>Gs	Ok>Gs	Ok>Gs	Gs=Ok	Gs=Ok
Management	Ng=Gz	Ng=Gz	Ng=Gz	Ng=Gz	Ng=Gz
Exch-Na					
Ok/Ng	0.27 (0.11)a	0.21 (0.09)ab	0.26 (0.09)a	0.44 (0.07)a	0.49 (0.14)a
Ok/Gz	0.27 (0.08)a	0.27 (0.08)ab	0.30 (0.07)a	0.47 (0.21)a	0.59 (0.14)a
Gs/Ng	0.18 (0.01)a	0.20 (0.03)a	0.29 (0.09)a	0.49 (0.11)a	0.56 (0.15)a
Gs/Gz	0.26 (0.06)a	0.29 (0.07)b	0.30 (0.11)a	0.56 (0.15)a	0.55 (0.16)a
Vegetation	Gs=Ok	Gs=Ok	Gs=Ok	Gs=Ok	Gs=Ok
Management	Ng=Gz	Gz>Ng	Ng=Gz	Ng=Gz	Ng=Gz

Table 5. Continued.

Treatment	Horizon A	AB	Bt1	Bt2	BC
Base Sat.%					
Ok/Ng	71.8 (8.4)a	64.8 (7.7)a	81.6 (7.4)a	89.8 (3.4)a	91.5 (4.9)ab
Ok/Gz	71.6 (8.7)a	68.3 (5.2)a	80.3 (4.3)a	92.0 (1.8)a	92.3 (3.6)a
Gs/Ng	50.9 (9.2)b	71.1 (4.5)a	83.5 (3.3)a	89.7 (3.8)a	88.5 (4.6)b
Gs/Gz	52.0 (3.1)b	69.9 (6.0)a	81.7 (7.5)a	85.1 (10.8)a	84.5 (6.8)b
Vegetation	Ok>Gs	Gs=Ok	Gs=Ok	Gs=Ok	Ok>Gs
Management	Ng=Gz	Ng=Gz	Ng=Gz	Ng=Gz	Ng=Gz

† Means in each column with the same letter are not statistically different at $p < 0.05$.
‡ Statistical differences determined at a significance level of p=0.05.

much of this flux represents nutrients that would have been lost from the soil profile in the absence of oak trees. In addition, canopy interception and greater transpiration by the oak reduce the leaching potential by 23% and 7%, respectively, beneath the blue oak canopy (Dahlgren & Singer 1994). It is also possible that extension of oak roots beyond the canopy leads to translocation of nutrients from the open grasslands to the soils beneath the oak canopy. Jackson et al. (1990) found that oak roots extending into the open grasslands were 10% of that found beneath the canopy, in the upper 30 cm of the soil profile.

Base saturation showed an increase in the A horizon beneath the oak canopy (72%) compared to the open grasslands (51%) (Table 5). This is consistent with the litterfall return of appreciable quantities of base cations to the soil surface, reduced leaching potential beneath the canopy, and pH buffering of precipitation acidity by canopy processes. The higher pH observed in the upper soil horizons appears to be a direct consequence of this higher base status.

Soil nutrient pools

The pools of organic carbon and nitrogen in the solum were 55–60% greater beneath the oak canopy as compared to the open grassland (Figure 2). These values are somewhat larger than values of 27–42% previously reported for the upper 10 cm of the soil profile at this study site (Jackson et al. 1990). The majority of this increase was due to accumulation of organic matter in the A and AB horizons. The large increases in organic carbon (40 Mg/ha) and nitrogen (3.4 Mg/ha) pools are higher than can be accounted for by litterfall additions alone over the life of a 100 year old oak tree. The amount of below-ground detrital material incorporated into the soil organic matter pools is not known; however, it may contribute substantially to the soil organic matter pool. Another possible explanation is that oak seedlings preferentially establish in soils influenced by a previous oak canopy. Blue oaks are relatively shade tolerant and show greater survival in shaded habitats than in the open (Muick & Bartolome 1987; Muick 1991). The nutrient and soil water relations beneath the oak canopy may favor blue oak regeneration preferentially beneath the canopy. Thus, the organic matter and nutrients accumulated under the existing oak canopy may reflect the cumulative effects of several generations of blue oak.

In contrast to the effect of the oak canopy on organic carbon and nitrogen pools, there appears to be little effect by low to moderate intensity grazing. This is consistent with the results of the worldwide grazing comparison which found no difference in soil organic matter and nitrogen pools between grazed and non-grazed sites (Milchunas & Lauenroth 1993). They found responses nearly equally divided between negative and positive suggesting that site factors and grazing practices (e.g., grazing intensity) determine the grazing response.

Similar to organic carbon and nitrogen pools, the total phosphorus pool was 1.5-fold greater beneath the oak canopy (Figure 2). Nutrient pools were increased in all horizons, but most strongly in the A and AB horizons. This further suggests that the primary source of the total P pool is from the soil organic matter pool. However, the relatively high total P concentrations in the B horizons suggest that a portion of the inorganic P, as well as organic P, is extracted by the modified Kjeldahl digest. Available P pools were higher beneath the oak canopy and were also higher in the grazed sites. The amount of available P is very high at this site and greatly exceeds the plant uptake requirement of approximately 12 and 6 kg/ha/yr for the oak/understory and open grasslands, respectively (Dahlgren & Singer 1994). The high available P concentrations result in appreciable leaching of ortho-PO_4 (15–20 μmol/L) from the A horizons beneath the oak canopy. Most of the soluble ortho-PO_4 is retained by plant uptake and adsorption resulting in little loss of P from the ecosystem in streamwater.

Among the pools of exchangeable cations, potassium (57% increase) showed a large increase and calcium (17% increase) a small increase beneath the oak canopy (Figure 2). As indicated previously, calcium and potassium are the two cations cycled in the greatest quantities by blue oak. The increased pools of calcium and potassium are found largely in the A horizons where increased organic matter concentrations provide greater CEC to retain nutrient cations. Grazing had no apparent affect on the pools of exchangeable cations.

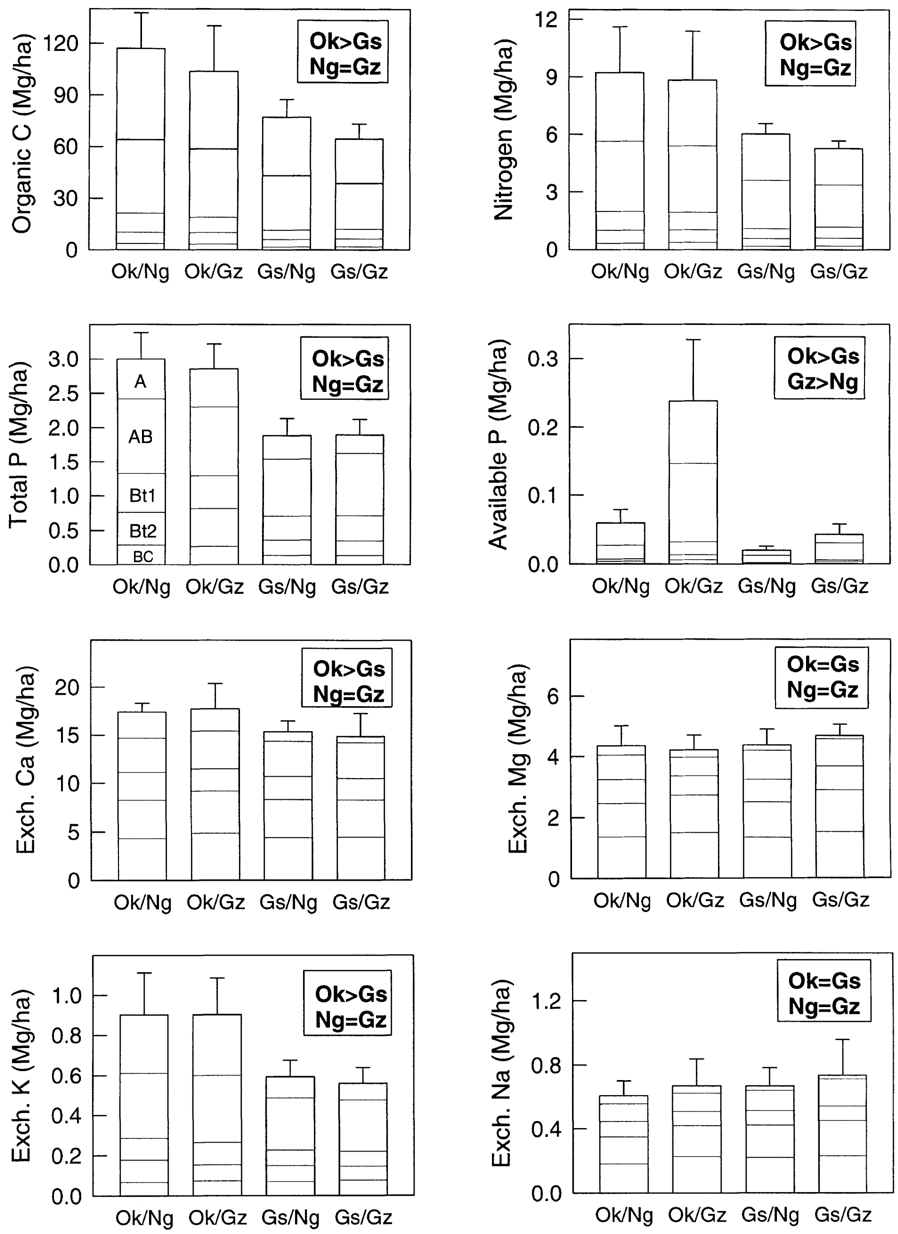

Figure 2. Nutrient pools in the soil solum as related to grazing and oak canopy effects. Treatment designations are oak (Ok), open grasslands (Gs), grazed (Gz), and non-grazed (Ng). Each component of the stacked bar indicates the contribution of an individual soil horizon in relation to its position in the soil profile (see total phosphorus graph for horizon designations). The data in the inner box indicate whether soil nutrient pools are different between treatments at the $p = 0.05$ significance level.

Implications for nutrient cycling and ecosystem sustainability

The ability of plants to alter their edaphic environment occurs primarily through addition of organic matter and nutrient cycling. Blue oaks at our study site display a striking ability to enhance soil organic matter concentrations and nutrient pools beneath their canopies. These approximately 100 year old oaks returned an average 9100 kg/ha/yr of litterfall to the soil surface with its associated nutrients. The added organic matter stores nutrients within its structure (e.g., N, P, S) and also provides nutrient storage capacity in the form of cation exchange capacity. Additionally, canopy throughfall contributed appreciable fluxes of calcium, magnesium, potassium, sulfur, and ammonium to the soil surface. Nutrient fluxes in canopy throughfall originate from root uptake and capture of atmospheric aerosols and particulate matter. Because oak roots are found at greater depths compared to the shallow rooted annual grasses, nutrient uptake by oak roots attenuates leaching losses of nutrients from the soil. The extension of oak roots beyond the edge of the canopy may also contribute to nutrient differences between soils beneath the oak canopy and open grasslands. Selective uptake of nutrients by oak roots will deplete the open grasslands of nutrients while concentrating these nutrients beneath the oak canopy. Shading up by cattle may also result in some transport of nutrients from open grasslands to soils beneath the oak canopy as they seek shade and preferentially defecate beneath the oak canopy. Similar mechanisms of nutrient enrichment beneath tree canopies in savanna have been previously proposed (e.g., Kellman 1979; Belsky et al. 1989; Weltzin & Coughenour 1990; Vetass 1992).

A further effect of the oak canopy on nutrient cycling occurs through canopy processes reducing the leaching and erosion potentials (Dahlgren & Singer 1994). Transpiration at our study site was approximately 7% greater in the oak/understory compared to the open grasslands and canopy interception reduced the amount of water reaching the soil surface by 23%. The combined effect is 30% less water available for leaching in the soils beneath the oak canopy. In addition to the positive effect of organic matter on the soil nutrient status, higher organic matter concentrations lead to lower soil bulk density and greater porosity. This in turn provides increased infiltration rates which reduces surface runoff, water erosion, and stream water sediment with its associated nutrients. Preferential transport of litter and sediments from open grasslands to soils beneath the canopy by surface runoff may further enhance the accumulation of organic matter and nutrients beneath the canopy. Thus, there are several biogeochemical processes by which oak trees concentrate nutrients and create islands of enhanced fertility beneath their canopy.

The effects of grazing were minimal compared to the non-grazed area which had not been grazed in 20 years. A small increase in the bulk density of the A horizons and enhanced available P concentrations throughout the entire soil profile were the primary effects observed due to grazing. In conjunction with this study, Firestone et al. (1995) measured increased microbial N and C, inorganic N, nitrification, nitrification potential, and populations of nitrifying bacteria. This suggests that grazing by cattle leads to predigestion of organic matter which results in greater fluxes of nutrients in the grazed area. Our study showed no evidence of detrimental effects to the long-term sustainability of the nutrient status by low to moderate intensity grazing; however, larger impacts would be expected under the more intensive grazing practices utilized on many oak woodland rangelands. It must also be stressed that 20 years with no grazing may not be sufficient time for some soil properties to recovery from previous grazing effects; therefore, these results should be interpreted with due care.

The practice of removing oak trees to enhance forage production is predicted to lead to considerable organic carbon and nutrient losses from the ecosystem. Rangeland management practices in California oak woodlands have been based on the premise that oaks reduce forage productivity by competing for nutrient, light, and water resources. The increased forage production found in areas beneath oak canopies following tree removal are short-term, often lasting less than 15 years (Kay 1987). Our soil solution studies also show a rapid decline in soil solution nutrient concentrations following oak tree removal (Dahlgren & Singer 1994). Thus, all evidence suggests that oak trees are an important component of the ecosystem that serve a valuable role in retention of nutrients which in turn contributes to long-term ecosystem sustainability.

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