

# Seasonal and Spatial Controls over Nutrient Cycling in a Pacific Northwest Prairie

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## ABSTRACT

West Coast prairies in the US are an endangered ecosystem, and effective conservation will require an understanding of how changing climate will impact nutrient cycling and availability. We examined how seasonal patterns and micro-heterogeneity in edaphic conditions (% moisture, total organic carbon, % clay, pH, and inorganic nitrogen and phosphorus) control carbon, nitrogen, and phosphorus cycling in an upland prairie in western Oregon, USA. Across the prairie, we collected soils seasonally and measured microbial respiration, net nitrogen mineralization, net nitrification, and phosphorus availability under field conditions and under experimentally varied temperature and moisture treatments. The response variables differed in the degree of temperature and moisture limitation within seasons and how these factors varied across sampling sites. In general, we found that microbial respiration was limited by low soil moisture year-round and by low temperatures in

the winter. Net nitrogen mineralization and net nitrification were never limited by temperature, but both were limited by excessive soil moisture in winter, and net nitrification was also inhibited by low soil moisture in the summer. Factors that enhanced microbial respiration tended to decrease soil phosphorus availability. Edaphic factors explained 76% of the seasonal and spatial variation in microbial respiration, 35% of the variation in phosphorus availability, and 29% of the variation in net nitrification. Much of the variation in net nitrogen mineralization remained unexplained ( $R^2 = 0.19$ ). This study, for the first time, demonstrates the complex seasonal controls over nutrient cycling in a Pacific Northwest prairie.

**Key words:** microbial respiration; moisture availability; net nitrification; net nitrogen mineralization; Oregon; phosphorus availability; temperature.

## INTRODUCTION

Numerous studies have shown the importance of temperature, moisture, and edaphic factors such as pH, soil texture, and organic matter in controlling carbon, nitrogen, and phosphorus cycling, but results conflict regarding the relative importance of these factors seasonally and spatially in different prairie ecosystems (for example, Schimel and Par-

ton 1986; Pastor and others 1987; Franzluebbers and others 2002; Wan and Luo 2003; Booth and others 2005). Most of these studies have been conducted in grasslands with a mid-continental climate. Far fewer studies have investigated grasslands with a Mediterranean climate, and, to our knowledge, no study has examined perennial-dominated prairies with a Mediterranean climate, such as occur in the Pacific Northwest, USA. These different types of prairies may not respond similarly to future climatic forcing. Therefore knowledge of the full spectrum of responses of prairie habitats to

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variable moisture and temperature will require a better understanding of grasslands with a Mediterranean climate, particularly those dominated by perennials.

Within the US, prairies with a Mediterranean climate occur only in California and the Pacific Northwest. These West Coast prairies are quite different from those in mid-continental areas of the US in terms of climate, nutrient inputs, and species composition. In general, Midwest prairies have deeper soils, are dominated by warm season ( $C_4$ ) grasses, and most of the precipitation falls in the spring and summer months (Porazinska and others 2003; Fitzpatrick 2004). In contrast, West Coast prairies have cool season ( $C_3$ ) grasses, a rainy season that begins in the fall and ends in the spring, and often shallow soils. As a result of the climatic differences, the primary growing season of West Coast prairies is during the winter and spring months in contrast to the summer growing season in the Midwest (Xu and Baldocchi 2004). Inorganic nitrogen (N) deposition from nitrate and ammonium is also much higher in Midwest prairies (2–7 kg N/ha) than West Coast prairies (0–2 kg N/ha) (National Atmospheric Deposition Program 2005). Among West Coast prairies, the climate of Oregon upland prairies is wetter and cooler than California prairies (National Climatic Data Center 2005). Furthermore, although all West Coast prairies were historically dominated by perennial bunchgrasses, invasion by exotic annual grasses in California has resulted in predominantly annual grasslands (Buisson and others 2006), whereas western Oregon prairies continue to be dominated by perennial grasses.

Over the past century, the Pacific Northwest has seen an increase in temperature of 0.5–1.5°C and a 10% increase in precipitation (Parson 2001). In the next 50 years, climate change models predict an increase in mean annual temperature of 3°C in this region, with most of the warming expected to occur in winter months. Predicted changes in precipitation vary more among models, but most agree that precipitation will increase in the winter, and summers will experience little change or a slight decrease in the Pacific Northwest (Parson 2001). These changes in climate will likely have complex effects, both direct and indirect, on nutrient cycling and will vary among ecosystems and spatially within ecosystems.

Therefore, our objective was to understand the degree to which seasonal patterns of carbon, nitrogen, and phosphorous cycling depend on temperature and soil moisture availability, and how these seasonal controls vary due to micro-heterogeneity in edaphic conditions, within an

upland prairie in Oregon, USA. We collected soils seasonally across an upland prairie hillslope and measured microbial respiration, net nitrogen mineralization, net nitrification, and phosphorus availability under field conditions and under varied temperature and soil moisture conditions in the laboratory. The treatments were designed to tease apart the effects of soil moisture and temperature as seasonal controls over nutrient cycling.

## METHODS

### Study Site

Field sampling was conducted in a remnant upland prairie at Mt. Pisgah, located within the 930-ha Howard Buford Recreation area, approximately 11 km southeast of Eugene, Oregon. The summit of Mt. Pisgah is at 467-m elevation, whereas the study site is located at the base of the south facing slope at 190-m elevation. The slope and aspect of the site are 7% and 154°, respectively. The climate is Mediterranean with a mean annual temperature of 12°C, and a mean annual precipitation of 117 cm, falling primarily between October and May (National Climatic Data Center 2005). Plots were located randomly across a 6-ha hillslope dominated by grasses and forbs with occasional *Quercus garryana* (white oak). Areas with *Q. garryana* were excluded to restrict sampling to prairie. Dominant species include exotic grasses *Bromus japonicus* and *Schedonorus arundinaceus*, the native grass *Danthonia californica*, and native forbs *Lomatium nudicaule*, and *Wyethia angustifolia*; however, more than 550 plant species have been identified within this recreational area (Friends of Buford Park 2000). Across the hillslope, many of the native species appeared to be restricted to areas characterized by shallow, rocky, or heavy clay soils, whereas exotics appeared to be abundant in more mesic areas. The soil is classified as Philomath series, clayey, smectitic, mesic, shallow, vertic haploxerolls and the average soil depth is 43 cm, but ranges between 7 and 100 cm. Additional edaphic site characteristics are given in Table 1.

### Experimental Design

We conducted a 1-year study to determine seasonal controls over carbon and nutrient cycling in this upland prairie. Sixteen 9 by 5-m plots were randomly established. Within each of these plots, four 1 by 1-m subplots were randomly chosen to seasonally measure (28 August 2003; 25 January 2004, and 6 May 2004) microbial respiration, net nitrogen mineralization, net nitrification, and

**Table 1.** Seasonal Means ( $\pm$  Standard Error) of Site Characteristics at Mt. Pisgah (Lane County, Oregon)

	Gravimetric % moisture	% Field capacity	Temperature (°C)	Initial NH <sub>4</sub> <sup>+</sup> ( $\mu$ g N/g soil)	Initial NO <sub>3</sub> <sup>-</sup> ( $\mu$ g N/g soil)	pH	% Clay	% Sand	% Silt	Total % carbon	Total % nitrogen
August 2003	9.2 $\pm$ 0.4c	12.1 $\pm$ 0.4c	19	9.1 $\pm$ 0.3a	0.7 $\pm$ 0.1b	6.5 $\pm$ 0.02	56.5 $\pm$ 0.5	16.7 $\pm$ 0.3	26.7 $\pm$ 0.8	3.4 $\pm$ 0.05	0.27 $\pm$ 0.004
January 2004	50.8 $\pm$ 0.7a	66.9 $\pm$ 0.7a	5	2.3 $\pm$ 0.2b	2.4 $\pm$ 0.2a	-	-	-	-	-	-
May 2004	21.9 $\pm$ 0.5b	28.9 $\pm$ 0.5b	13	1.8 $\pm$ 0.2b	0.8 $\pm$ 0.1b	-	-	-	-	-	-

Lower case letter differences indicate significant effects ( $P < 0.05$ ) of site characteristics among seasons. pH, % clay, % sand, % silt, total % carbon, and total % nitrogen were measured once in August 2003.

phosphorous availability. In the fall of 2002, half of the plots were burned as part of an earlier experiment (Johnson and Roy, unpublished data), but in no case did the burn create significant differences in the response variables measured in this paper ( $P$  range: 0.11–0.44,  $n = 64$ ).

On each sampling date, we collected soils from the 64 1-m<sup>2</sup> subplots, brought them back to the laboratory, and separated them into three treatments: (1) field temperature and field moisture, (2) field temperature and 60% field capacity moisture, and (3) 19°C and field moisture. The treatments were designed to sort out the relative importance of soil moisture and temperature as seasonal controls over microbial respiration, net nitrogen mineralization, net nitrification, and phosphorus availability. Field temperature was considered to be the average monthly temperature in which soils were collected from the 16 plots, and field moisture was the gravimetric moisture content of soils when collected. Field capacity was determined on soil from each subplot in the summer of 2003 prior to implementation of the experiment by saturating soils with deionized water twice, covering, allowing them to drain for 2 h, and drying at 105°C for 48 h. Gravimetric field moisture, field capacity, and temperature on each sampling date are given in Table 1. As field temperature in August was 19°C, treatments 1 and 3 were the same.

### Field Sampling and Incubation Set-up

On each sampling date, two cores were taken per 1-m<sup>2</sup> subplot to a depth of 15 cm with a soil auger (5-cm width). These cores were homogenized into one sealed plastic bag and brought back to the laboratory. Once large roots and small rocks were removed from the soil cores by hand, the soils were weighed into wide-mouth Mason jars and incubated for 2 weeks in a dark incubator at the appropriate temperature. The lids of the Mason jars were drilled with 1.25-cm diameter holes, and glass wool was stuffed into these holes to allow air exchange while minimizing moisture loss. In the summer and spring, soils were wetted to achieve the 60% field capacity in treatment 2, but in winter the soils were air-dried to achieve 60% field capacity. While waiting for soils to dry (under winter conditions), all soils were kept at field temperature. In all cases, the incubations began no more than 5 days after soils were originally collected. To maintain appropriate moisture levels throughout the duration of the experiment, deionized water was added every 2 days to the

Mason jars. The evaporation of water never exceeded more than 1% of total soil moisture.

## Soil Analyses

On the first and last day (day 14) of the lab incubations, separate sub-samples of soil were removed and extracted for  $\text{NO}_2^- + \text{NO}_3^-$  and  $\text{NH}_4^+$  using 2 M KCl (Maynard and Kalra 1993). The KCl extracts were filtered through Whatman No. 5 acid-washed filter paper and frozen until analysis. Net nitrification is the difference in  $\text{NO}_2^- + \text{NO}_3^-$  over the 2 week incubation, whereas net nitrogen mineralization is the difference over the 2 weeks in  $\text{NO}_2^- + \text{NO}_3^- + \text{NH}_4^+$ . On the last day of the incubation, soils were extracted with 0.5 M  $\text{NaHCO}_3$  to determine phosphorus availability (Kuo 1996). Similarly, these extracts were filtered through acid-washed Whatman No. 42 filter paper and frozen until analysis.  $\text{NH}_4^+$ ,  $\text{NO}_2^- + \text{NO}_3^-$ , and  $\text{PO}_4^{3-}$  were measured with an Astoria II autoanalyzer (Astoria Pacific International, Clackamas, OR, USA) using the phenate (Solorzano 1969), cadmium reduction (Wood and others 1967), and ascorbic acid methods (Murphy and Riley 1962), respectively.

To determine microbial respiration, the Mason jars were closed with septa for 24 h on days 1, 7, and 14 of the incubation. A 10-cc gas sample was taken from the headspace initially and 24 h later; the initial headspace sample was replaced with 10-cc of  $\text{N}_2$  gas. Gas samples were immediately run on a Li-COR 6400 infrared gas analyzer set-up to measure discrete injections of  $\text{CO}_2$ . Headspace  $\text{CO}_2$  concentrations were corrected for dissolution into soil water based upon soil moisture content and soil pH (Stumm and Morgan 1981). The difference in  $\text{CO}_2\text{-C}$  over the course of 24 h was considered microbial respiration. Over the course of the incubation, respiration rates decreased. However, to simplify the many complex interactions between time and treatments, cumulative  $\mu\text{g C/g soil/day}$  for the entire 2-week incubation was calculated for final statistical analyses.

Soil texture, pH, total carbon, and total nitrogen were determined once on soils collected in each of the subplots on 28 August 2003. pH was determined immediately after collection using a 1:1 soil-deionized water slurry. For soil texture analysis, dried soils ( $105^\circ\text{C}$  for 48 h) were sieved to less than 2-mm (10 mesh) diameter. To calculate percent clay, we used the hydrometer method (Gee and Bauder 1986). Percent sand was calculated by weight using a 53- $\mu\text{m}$  sieve (270 mesh). Percent silt was calculated by difference. We determined total carbon and nitrogen on dried, ground soil using a

Costech Analytical Technologies 4010 elemental combustion analyzer (Valencia, CA, USA).

## Statistical Analyses

To determine the controls over microbial respiration, net nitrogen mineralization, net nitrification, and phosphorus availability, a repeated-measures ANOVA was run for each response variable using SPSS 11.0 for Windows. The between-subject factors included treatment and plot, and the within-subject factor was season. To meet the normality assumption of ANOVA, microbial respiration and phosphorus availability were square-root transformed for analysis and back-transformed for presentation. All other residuals were normally distributed and the assumption of sphericity was not violated.

To deconvolve the many significant interactions with plot and season, a multiple regression approach was used on the field-condition data set (treatment 1). This allowed us to explore how seasonal and edaphic factors affected nutrient cycling across the hillslope. Akaike Information Criterion (AIC) was employed to select the best models. AIC is derived from Kullback–Leibler information and maximum likelihood theories, and does not use traditional hypothesis testing (Anderson and others 2000; Burnham and Anderson 2002). Instead, the most probable model has the lowest AIC score. Based on this model, one can calculate the differences in AIC scores ( $\delta\text{AIC}$ ) to determine the likelihood of each model being the best correlative relationship, allowing comparison between multiple models simultaneously, as opposed to traditional stepwise regression where only a single model is presented, even if it is only marginally better than other candidate models. The corrected AIC score ( $\text{AIC}_c$ ) accounts for any bias from the large number of parameters relative to sample size. Additionally, Akaike's weights ( $\omega$ ) can be used to standardize the AIC scores between 0 and 1, and determine the probability of any given model being the best model (for example, a  $\omega$  of 0.7 indicates that 70% of the time that particular model would be selected). Following convention, we used a criterion of a  $\omega \geq 0.1$  to determine the most probable models in our data set (Burnham and Anderson 2002). AIC values were calculated using SAS 9.1 (SAS Institute). All  $\text{AIC}_c$ ,  $\delta\text{AIC}_c$ , and  $\omega$  values were then calculated using equations from Burnham and Anderson (2002) in a Microsoft Excel spreadsheet. To avoid multicollinearity, predictors that were highly autocorrelated ( $r > 0.7$ ) were not included in the models; autocorrelated vari-

ables included % clay, % sand, and % silt ( $r > 0.85$ ), total C and total N ( $r = 0.91$ ), and % moisture and temperature ( $r = -0.93$ ). Parameters included in all models were % moisture, total C, pH, and % clay. In addition to these parameters, inorganic nitrogen and phosphorus were included for microbial respiration, inorganic phosphorus was included for net nitrogen mineralization and net nitrification, and inorganic nitrogen was included for phosphorus availability.

## RESULTS

Season significantly affected all variables measured (Table 2). The experimental treatments had a direct effect on microbial respiration, nitrification, and phosphorous availability, but not nitrogen mineralization. However in all cases, treatment effects depended upon season (Table 2, Figure 1). The effect of season on all response variables depended on plot, and was thus site specific (Table 2). The initial inorganic nitrogen also differed among seasons (Table 1). In the summer, ammonium was the dominant form of inorganic nitrogen, and nitrate levels were low. In the winter, nitrate and ammonium were available in approximately equal concentrations, and in the spring both ammonium and nitrate concentrations were low, but ammonium was the dominant form.

### Microbial Respiration

Under field conditions (treatment 1), microbial respiration was lower during the summer than during the winter or spring (Figure 1). In the summer, increasing moisture content to 60% field capacity increased microbial respiration. In the winter, highest respiration rates were achieved through increasing the temperature from 5 to 19°C. The soils were at 67% field capacity in the winter, and drying the soils to 60% field capacity decreased microbial respiration. In the spring, increasing moisture from 29 to 60% field capacity or increasing temperature to 19°C led to an equivalent increase in respiration.

To disentangle the significant interaction between season and plot (Table 2), AIC was employed. Using our criterion, there were two probable models, which explained between 75 and 76% of the variation (Table 3). The most likely model included % moisture, % clay, total carbon, and inorganic nitrogen and phosphorus. The alternative model also included pH. Percent moisture explained the largest proportion of the total variance, with an average partial  $R^2$  of 65% (Figure 2). Total carbon, inorganic nitrogen, % clay,

inorganic phosphorus, and pH only explained a small amount of the variance, with average partial  $R^2$ 's of 4, 2.5, 2, 1, and 0.5%, respectively.

### Net Nitrogen Mineralization

Similar to microbial respiration, under field conditions net nitrogen mineralization was lowest during the summer (with net immobilization of nitrogen), with no detectable difference in the winter and spring (Figure 1). In the summer and spring, the moisture and temperature treatments had no effect. However, in the winter, drying the soils to 60% field capacity increased net nitrogen mineralization.

The results from the AIC led to four probable models (Table 3, Figure 2). Soil moisture (average partial  $R^2 = 16.5\%$ ) and total carbon (average partial  $R^2 = 2\%$ ) were always important predictors of net nitrogen mineralization. Some models also included %clay and pH, but they explained less than 1% of additional variance. However, no model had high explanatory power, with the best model explaining 19% of the variance (Table 3).

### Net Nitrification

Under field conditions, net nitrification followed the same trends as both microbial respiration and nitrogen mineralization with the lowest nitrification rates in the summer (Figure 1). In contrast to net nitrogen mineralization, increasing moisture content in the summer caused a 30-fold increase in net nitrification. Additionally, drying the soils in the winter increased net nitrification, suggesting that nitrification is limited by both too little and too much water in different seasons. Increasing the temperature never significantly affected nitrification rates, nor were there any treatment effects on nitrification rates in the spring.

The three probable models for net nitrification all explained 29% of the variation (Table 3, Figure 2). The best model included % moisture and % clay. Alternative models included inorganic phosphorus and total carbon. As was the case for microbial respiration and net nitrogen mineralization, % moisture explained the largest portion of the variance (average partial  $R^2 = 21\%$ ), with clay only explaining 7% of the variance, and inorganic phosphorus and total carbon explaining an even smaller amount (average partial  $R^2 < 1\%$ ).

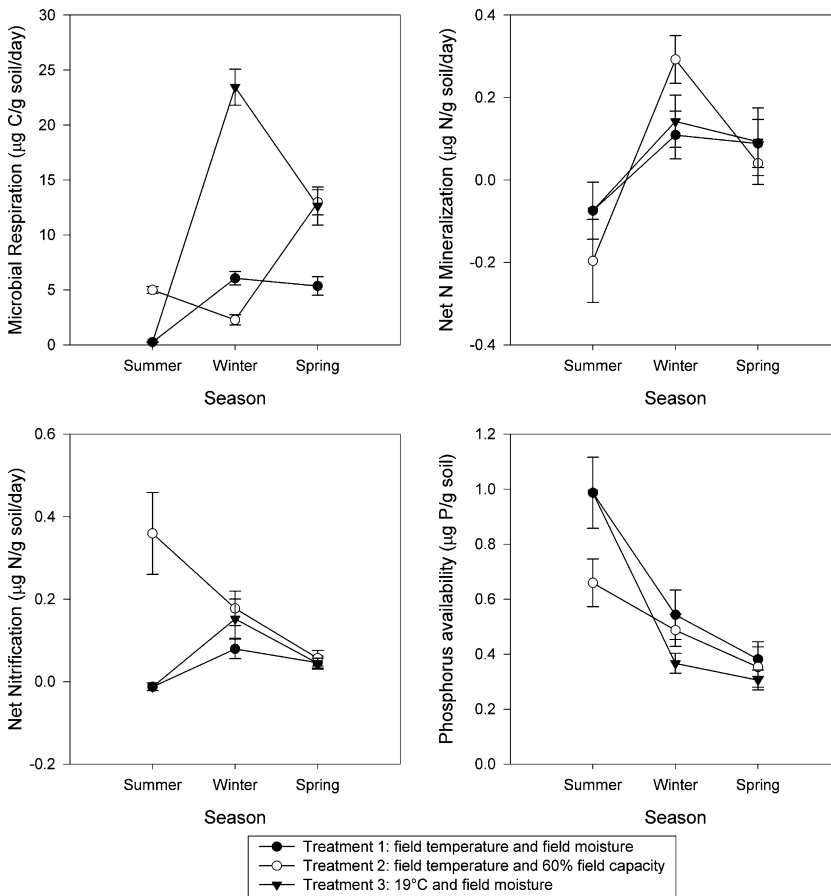
### Phosphorus Availability

Unlike the other response variables, phosphorus availability was higher in the summer than in the

**Table 2.** P-values from Repeated-Measures ANOVAs for the Effect of Season, Treatment, and Plot on Microbial Respiration, Net Nitrogen Mineralization, Net Nitrification, and Phosphorus Availability

	Microbial respiration ( $\mu\text{g C/g soil/day}$ )	Net nitrogen mineralization ( $\mu\text{g N/g soil/day}$ )	Net nitrification ( $\mu\text{g N/g soil/day}$ )	Phosphorus availability ( $\mu\text{g P/g soil}$ )
Between				
Treatment	<b>&lt;0.001</b>	0.842	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Plot	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Treatment*plot	<b>0.004</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.310
Within				
Season	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Season*treatment	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Season*plot	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>0.002</b>
Season*treatment*plot	<b>&lt;0.001</b>	<b>0.004</b>	<b>&lt;0.001</b>	<b>0.002</b>

Values in bold are significant at an alpha <0.05.



**Figure 1.** Significant interactions between season and treatments for microbial respiration, net nitrogen (N) mineralization, net nitrification, and phosphorus availability. Error bars represent 95% confidence intervals. Treatments 1 and 3 were the same in the summer, as field temperature was 19°C. Negative numbers for net nitrogen mineralization and net nitrification indicate a net immobilization of nitrogen and positive numbers indicate a net mineralization of nitrogen.

winter or spring when incubated under field conditions. In the summer, wetting the soils decreased phosphorus availability. In the winter, increasing the temperature decreased phosphorus availability. In the spring, the moisture and temperature treatments had no effect.

From the AIC results, the five best models explained between 33 and 35% of the variance (Table 3, Figure 2). All models included % moisture (average partial  $R^2 = 19.5\%$ ) and inorganic nitrogen (average partial  $R^2 = 10\%$ ). The most probable model also included total carbon (average partial

**Table 3.** Candidate Models Describing Patterns of Microbial Respiration, Net Nitrogen Mineralization, Net Nitrification, and Phosphorus Availability where  $K$  is the Number of Parameters,  $\delta AIC_c$  is the Change in the Akaike's Corrected Information Criterion, and  $\omega$  is the Akaike's Weight (See Methods for Statistical Description)

Model	$K$	$\delta AIC_c$	$\omega$	$R^2$
Microbial respiration ( $\mu\text{g C/g soil/day}$ )				
Moisture + total C + clay –inorganic N –inorganic P	5	0	0.54	0.75
Moisture + total C + clay –inorganic N –inorganic P + pH	6	0.58	0.41	0.76
Net nitrogen mineralization ( $\mu\text{g N/g soil/day}$ )				
Moisture–total C	2	0	0.23	0.18
Moisture–total C–clay	3	1.18	0.13	0.19
Moisture–total C–clay–pH	4	1.20	0.13	0.19
Moisture–total C–pH	3	1.62	0.10	0.18
Net nitrification ( $\mu\text{g N/g soil/day}$ )				
Moisture + clay–inorganic P	3	0	0.27	0.29
Moisture + clay	2	0.03	0.26	0.29
Moisture + clay–inorganic P + total C	4	1.95	0.10	0.29
Phosphorus availability ( $\mu\text{g P/g soil}$ )				
–Moisture + total C + pH + inorganic N	4	0	0.27	0.35
–Moisture + pH + inorganic N + clay	4	0.41	0.22	0.34
–Moisture + pH + inorganic N	3	1.10	0.16	0.33
–Moisture + inorganic N + clay	3	1.30	0.14	0.33
–Moisture + total C + pH + inorganic N + clay	5	1.34	0.14	0.35

A criterion of  $\omega \geq 0.1$  was used to determine candidate models. Positive and negative signs denote the direction of individual correlations.

$R^2 = 1.5\%$ ) and pH (average partial  $R^2 = 2.5\%$ ). Three of the alternative models also included % clay (average partial  $R^2 = 1\%$ ).

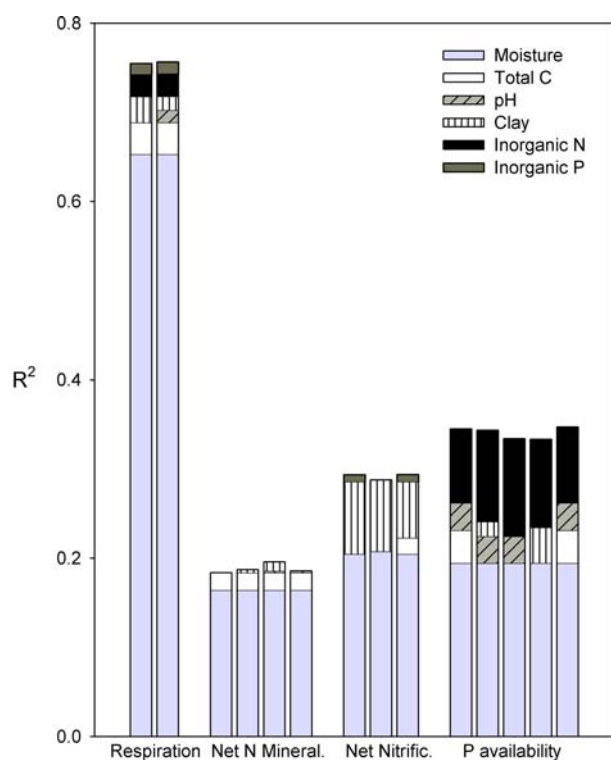
## DISCUSSION

To our knowledge, this is the first study to examine nutrient dynamics in a perennial-dominated prairie with a Mediterranean climate. The availability of nutrients is clearly important in structuring plant communities in this prairie as they have been shown to affect the competitive hierarchies between native and exotic grass species (Pfeifer-Meister and others 2007). We found the expected seasonal variation in microbial respiration, net nitrogen mineralization, net nitrification, and phosphorus availability, but the underlying causes of this seasonal variation were complex. The relative importance of the soil moisture and temperature treatments varied among response variables, plot, and season. The degree to which abiotic factors explained the plot effect also differed among response variables ( $R^2$  range: 0.18–0.76, Table 2). In all cases, soil moisture was the best predictor (Figure 2), but it was highly correlated with temperature (which we did not use in the AICs), so soil moisture probably

acted as an overall indicator of seasonal environmental effects.

## Microbial Respiration

Overall, respiration rates under field conditions ( $\sim 0.5 \mu\text{mol C/m}^2/\text{s}$ ) were lower than prairies throughout the country ( $1.4\text{--}8 \mu\text{mol C/m}^2/\text{s}$ ) (Luo and others 1996; Raich and Tufekcioglu 2000; Franzluebbers and others 2002; Wan and Luo 2003). Seasonally, respiration rates were lower in the summer than winter or spring. This result is similar to California prairies (Luo and others 1996), but differs from Midwest prairies where respiration rates are lowest in the winter months and highest in summer months (Raich and Tufekcioglu 2000; Wan and Luo 2003). The most likely explanation is that the rainy season occurs during the winter and spring on the West Coast as opposed to the summer rainy season in the Midwest. Depending on season, soil moisture and/or temperature limited respiration rates. Not surprisingly, in the summer moisture was limiting; a 25% increase in soil moisture led to a 20-fold increase in respiration rates. In the winter, a decrease in soil moisture led to a decrease in respiration suggesting that microbial activity was not inhibited by excessive soil moisture, even at 67% water holding capacity, and an increase in



**Figure 2.** Candidate models describing patterns of microbial respiration, net nitrogen (N) mineralization, net nitrification, and phosphorus availability under field temperature and moisture conditions. The total bar height represents the total  $R^2$  for each response variable, which are further partitioned into the partial  $R^2$  for the individual predictors.

temperature led to the highest respiration rates in this study ( $24 \mu\text{g C/g soil/day}$ ). As winters are expected to get warmer and wetter in the Pacific Northwest (Parson 2001), these (and similar Mediterranean grasslands) may end up becoming a net source of atmospheric  $\text{CO}_2$ . In the spring, both a small increase in soil moisture and a  $6^\circ\text{C}$  increase in temperature led to an increase in respiration rates. A meta-analysis of ecosystem warming experiments also showed that increased temperature significantly increased soil respiration (Rustad and others 2001). However, in a tallgrass prairie, Luo and others (2001) demonstrated that over time the soil respiration response to warming decreased as the soil community acclimated.

To understand how seasonal controls and microheterogeneity in edaphic conditions explained differences in respiration rates, we used a multiple regression approach. However, we were limited in interpreting the seasonal controls as only soil moisture could be included in the models due to the high correlation ( $r = -0.93$ ) between soil

moisture and temperature. Overall, the most probable models explained a high proportion of the variance (75–76%), with soil moisture explaining most of this (partial  $R^2 = 65\%$ ). Other studies have observed this high correlation with soil moisture. For example, in a tallgrass prairie in Oklahoma, soil moisture explained 59% of the variation in soil  $\text{CO}_2$  efflux (Liu and others 2002) and in a California grassland, belowground respiration was positively correlated with moisture ( $R^2 = 0.66$ ) (Luo and others 1996). In addition to soil moisture and temperature, organic matter is also considered a major control and has been shown to influence respiration rates (Bridgman and Richardson 1992; Raich and Tufekcioglu 2000; Flanagan and others 2002; Franzluebbers and others 2002; Wan and Luo 2003). In our study, total carbon was positively correlated with soil respiration, but, on average, explained only 4% of the variation. Other edaphic factors, including soil texture, inorganic nitrogen and phosphorus, and pH, explained even less of the variation in respiration rates (0.5–2.5%).

### Net Nitrogen Mineralization

In general, net nitrogen mineralization was low in this prairie (average:  $0.0041 \text{ g/m}^2/\text{day}$ ; range:  $-0.008$ – $0.012 \text{ g/m}^2/\text{day}$ ), perhaps due to the high clay content and low organic matter of these soils. As with soil respiration, mineralization rates under field conditions were lower in the summer than the spring and winter. This same pattern has been seen in other Mediterranean prairies (Taylor and others 1982; Davidson and others 1990; Jamieson and others 1998, 1999), but in Midwest grasslands the seasonal effect is often reversed (Wedin and Tilman 1990). Surprisingly, increasing temperature never affected net nitrogen mineralization. Many studies have seen a positive correlation with soil temperature and mineralization rates (MacDonald and others 1995; Updegraff and others 1995; Burke and others 1997), and in a meta-analysis of soil warming experiments, an increase in soil temperature led to a 46% average increase in net nitrogen mineralization (Rustad and others 2001). However, as warming experiments typically occur over a much longer time-frame, this increase could be explained by the indirect effects of warming on other factors (that is, changes in soil moisture or litter quality and quantity). In our study, a decrease in soil moisture in the winter led to a threefold increase in net nitrogen mineralization rates. This is likely due to the decrease in microbial activity (seen in respiration rates) resulting in a decrease in nitrogen immobilization.

Moisture and total carbon were always significant in explaining the seasonal variation in net nitrogen mineralization rates across the hillslope, with pH and clay sometimes explaining less than 1% of the variation. However, no model explained more than 19% of the variation. Other studies with similar sets of variables have shown similarly low correlations. For example, in a transect of grasslands from Colorado to Kansas, temperature, site, and moisture explained 24% of the variation in net nitrogen mineralization (Barrett and others 2002). The predictability of nitrogen mineralization may be improved by separating net nitrogen mineralization into its component parts of gross mineralization and gross immobilization. However, soil moisture explained only 18% of the variation in gross nitrogen mineralization rates in a California annual grassland (Hungate and others 1997). Other studies have shown a higher correlation with net nitrogen mineralization and climatic variables ( $r^2 = 0.69\text{--}0.91$ ), but the soils were collected from plant monocultures (Cassman and Munns 1980; Taylor and others 1982). Indeed, Wedin and Tilman (1990) demonstrated that by including plant species differences along with environmental factors in their regression model, they could explain 88% of the variation in net nitrogen mineralization.

### Net Nitrification

Net nitrification followed the same seasonal trends as net nitrogen mineralization, and nitrification rates were also never affected by an increase in temperature. This lack of response to an increase in temperature has been demonstrated in soil warming experiments (Peterjohn and others 1994; Shaw and Harte 2001). Despite the fact that mineralization rates did not respond to an increase in soil moisture during the summer, there was a 30-fold increase in net nitrification, suggesting that the large initial pool of ammonium was quickly nitrified in the presence of adequate soil moisture (Table 1). The opposite effect was seen in the winter, where a decrease in moisture availability increased net nitrification, indicating that excessive soil moisture in winter may inhibit nitrification in these prairies. At low summer moisture levels, gross nitrification is likely the limiting step, and at high moisture levels, either a decrease in nitrification or an increase in denitrification due to anaerobic micro-sites could lead to the decrease in net nitrification observed. However, as respiration rates did not decrease at the high moisture availability, denitrification is the most probable explanation.

Schimel and Parton (1986) also demonstrated that nitrification is inhibited at higher water potentials more than ammonification. In the spring, when plants are most actively growing and competing for nutrients, the treatments had no effect on nitrification rates which may reflect the low overall nitrogen availability (Table 1).

Soil moisture and % clay content explained the most variation in net nitrification, and both were positively correlated with nitrification rates. Potential nitrification is often limited by moisture availability (Robertson 1982; Davidson and others 1990), and a positive correlation with soil moisture is common (for example, Shaw and Harte 2001). Clay, with its high water tension (Hillel 1998), could also increase moisture availability to microbes under dry conditions. The high cation exchange capacity of clays (Chapin and others 2002) could also explain the correlation found. Despite the positive relationships with moisture and clay, 70% of the variance remained unexplained. As there is a large biotic gradient across this hillslope (unpublished data), species effects on litter quality and belowground competition for nutrients could explain this missing variance (Wedin and Tilman 1990). It may also be explained by the opposing environmental effects on gross nitrification versus microbial immobilization and denitrification.

### Phosphorus Availability

Due to the strong geochemical sorption of phosphorus, net mineralization rates are difficult to interpret (Bridgham and others 1998; Kellogg and others 2006). However, changes in phosphorus availability over time are important for understanding how phosphorus may limit productivity and structure plant communities. When incubated under field conditions, phosphorus availability was higher in the summer than the winter or spring, as opposed to microbial respiration, net nitrification, and net nitrogen mineralization. This same seasonal pattern has been reported in a California annual grassland (Hooper and Vitousek 1998). In the summer, increasing moisture decreased phosphorus availability, and in the winter, increasing temperature decreased phosphorus availability. As microbial activity increased under these conditions (evidenced in respiration rates), it follows that phosphate would be incorporated into microbial biomass and become unavailable.

The results of the AIC analyses suggest that moisture availability and inorganic nitrogen are major controls of phosphorus availability across this hillslope, and to a lesser extent pH, total carbon, and

clay content. In a study that manipulated moisture and organic matter, Braschi and others (2003) demonstrated that increases in moisture could decrease phosphate availability and that increases in organic matter could increase phosphate availability. Similarly, in our study phosphorus availability was negatively correlated with moisture and positively correlated with total carbon. The positive correlation between phosphorus availability and inorganic nitrogen may suggest that microbial communities are co-limited by these nutrients. As the soils across this hillslope range from slightly acidic to neutral (pH range: 5.5–6.8), it is not surprising that a positive correlation was found between phosphorus availability and pH. The availability of phosphorus decreases at low pH because of sorption onto the surface of clays and iron and aluminum oxides (Chapin and others 2002).

## CONCLUSIONS

We have demonstrated complex seasonal controls over microbial respiration, nitrogen cycling, and phosphorus availability in an upland Oregon prairie. The few related studies from California grasslands suggest similar sets of seasonal controls over these processes in Mediterranean grasslands. In our study, the relative importance of temperature and moisture varied among response variables, season, and sampling site. Overall, our results suggest that in Pacific Northwest prairies microbial respiration is limited by low temperatures in the winter and spring and by low soil moisture year-round. Net nitrogen mineralization and net nitrification are never limited by soil temperature, but both are limited by excessive soil moisture in winter, and net nitrification is also limited by low soil moisture in the summer. Factors that enhance microbial respiration tended to decrease soil phosphorus availability. It is likely that these seasonal dynamics have strong effects on plant community structure and the competitive dynamics of native and exotic plant species in these prairies (Pfeifer-Meister and others 2007).

Considering current climate models for the Pacific Northwest, we would expect climate change to have the largest direct effects on carbon, nitrogen, and phosphorus cycling in the winter as all response variables measured responded to a change in moisture and/or temperature in this season. Under warmer, wetter winter conditions, we would expect soil respiration to increase and plant-available nitrogen and phosphorus to decrease. As plants are actively growing during the winter in the Pacific Northwest, these changes will have large effects on community structure, which in turn

could feedback to nutrient cycling processes. To effectively restore and conserve the remaining prairies of the Pacific Northwest, it is essential to understand how major ecosystem processes will respond to changes in climatic factors and how they may interact with other edaphic factors to structure plant communities.

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