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Landscape Influences on Potential Soil Respiration Rates in a Forested Watershed of Southeastern Kentucky

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ABSTRACT / Soil respiration measurements conducted in the laboratory have been shown to be related to temperature and moisture, with maximum rates at soil temperatures between 25 and 40°C and soil moisture between −0.01 and −0.10 MPa. A preliminary study using forest soils from eastern Kentucky supported the previous research with soil respiration rates greater at 25°C than at 15°C, with differences in soil respiration rates related to sample site terrain characteristics. To further understand the factors that influence laboratory or potential respiration rates, we conducted a stratified sampling of soils from Robinson Experimental Forest in eastern Kentucky. Sampling was stratified by slope aspect, slope curvature, and landscape position. Potential soil respiration rates varied by slope aspect with NE aspects having greater rates than SW aspects. Rates did not vary by landscape position but did vary by slope curvature on SW aspects with concave curvatures having greater respiration rates than convex curvatures. Predictive soil respiration models based on both terrain attributes and soil chemical properties were created for both slope aspects. The relationships revealed that at this scale soil chemical properties play a more significant role in predicting soil respiration rates than terrain attributes. Models for the NE aspect were stronger than those for the SW aspect. The NE model created from a combination of terrain attributes and chemical properties included extractable Mg, extractable Zn, specific catchment area, and slope aspect (R^2_{adj} = 0.620). The SW model created from a combination of terrain attributes and soil chemical properties included extractable P, extractable Zn, and tangential curvature (R^2_{adj} = 0.413).

Carbon dioxide, an important greenhouse gas, is readily exchanged between the soil and the atmosphere in response to biological activity within the soil ecosystem, including both microbial respiration and root respiration. Microbial metabolism, and the consequent decomposition of soil organic matter and release of CO_2, is controlled by substrate availability, soil temperature, soil matric potential, and other environmental factors (Zak and others 1999). Laboratory studies have shown that aerobic decomposition rates are greatest at soil water tensions ranging from −0.01 to −0.10 MPa and soil temperature ranges of 25–40°C (Zak and others 1999). Although temperature and matric potential differ in their influence, they should not be considered independently. Laboratory incubations by Bowden and others (1998) found that CO_2 emissions from forest floor material increased exponentially with increasing temperature, with emissions reduced at the lowest (20% water-holding capacity) and highest (100% water-holding capacity) soil moisture contents. Their incubations showed an interaction between moisture and temperature, in which the influence of moisture was greater at high temperatures than it was at lower temperatures. Bowden and others (1998) were able to predict forest floor CO_2 emissions with a polynomial regression model of temperature and moisture (R^2 = 0.88). Zak and others (1999) incubated soil from a northern hardwood forest at 15 temperature–matric potential treatment combinations (temperatures: 5, 10,

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or 25°C; matric potentials: −0.01, −0.15, −0.30, −0.90, and −1.85 MPa). They found that temperature had a greater relative influence on respired C pools than did soil matric potential. Mean respired C increased 300% between 5 and 25°C, but only increased 40% between −1.85 and −0.01 MPa (Zak and others 1999). They also observed that the greatest change in respired C pools occurred between −0.01 and −0.30 MPa, and the greatest degree of change was at the warmest soil temperature (25°C).

These local, or proximal, factors—soil temperature and moisture—directly regulate local biological and physical processes. Proximal factors are in turn influenced by distal factors, or characteristics such as soil type, vegetation type, site productivity, climate, topography, and level of disturbance (Matson and Harriss 1995). These distal factors are particularly influential in controlling variability in microbial processes at the landscape scale (Parkin 1993). Topography is a distal factor that can indirectly influence organic matter decomposition and the exchange of greenhouse gases by regulating the proximal factors of soil moisture and soil temperature, as well as influencing soil type, vegetation community, root respiration, and other soil processes. Slope aspect, slope curvature, and landscape position affect soil moisture and soil temperature by determining sunlight exposure and influencing the relative amounts of precipitation, evaporation, infiltration, and the redistribution of water across the landscape (Franzmeier and others 1969, Chamran and others 2002).

These landscape-scale differences produce variation in observed microbial activity in forested ecosystems (Davidson and Swank 1986, Groffman and Tiedje 1989, Groffman and others 1993). These differences may also produce variation in the composition of the microbial community across the landscape. Myers and others (2001) measured microbial community composition and microbial substrate use of microbial communities derived from soils collected from three different forest types. They found that while microbial biomass did not differ, the respective microbial communities did differ in their composition (bacterial versus fungal versus actinomycetal) and their substrate preferences (carbohydrates versus organic acids versus amino acids). Myers and others (2001) suggested that these differences occur as a result of differences in resource availability, which are due to differences in the quantity and quality of organic matter being added to the soil through plant litter.

The variability associated with landscape patterns in soils, vegetation, or microclimate may influence the potential soil respiration rate within these landscapes. In this study, two incubation methods were used to determine potential soil respiration rates under various temperature and moisture content treatments. Maximum potential rates from each method were compared to proximal factors (soil moisture, soil temperature, soil chemical properties) and distal factors (landscape variables) to assess the influence that terrain attributes have on potential soil respiration rates. Our objectives for this study were (1) to relate differences in measured potential respiration rates (PRR) under multiple temperature and moisture content treatments at selected landscape positions in a forested watershed in southeastern Kentucky to measured soil chemical properties and landscape variables; and (2) generate predictive models of PRR based on variability in these measured soil properties and landscape variables.

Materials and Methods

Study Site

This study was conducted in the Little Millseat subwatershed of the Clemons Fork watershed, one of two major watersheds located within the University of Kentucky's Robinson Experimental Forest (37°27'N, 83°08'W), a 6000-ha, mature, mixed mesophytic research forest located on the Cumberland Plateau in southeastern Kentucky. Northeast (NE) and southwest (SW) aspects dominate the Little Millseat subwatershed, with slope gradients ranging from 25% to 60%, with distinct convex (divergent) and concave (convergent) sideslopes (Figure 1). In general, the soils throughout the study site are shallow, with surface soil textures that range from sandy loam to silt loam, and contain 10%–86% coarse fragments (Cremeans 1992). The soils are mapped as mainly Dystrudepts and Hapludults (Hayes 1998). Cremeans (1992) also found that the soils of the NE-facing slopes have slightly thicker sola (110 vs 85 cm) and higher organic matter contents in the surface horizons (63 vs 38 g/kg).

Field Methods

Sampling Design A stratified sampling design was used, with strata defined by differences in slope aspect, slope curvature, and landscape position. Analysis of terrain attributes derived from US Geologic Survey (USGS) digital elevation models (DEM) with a horizontal resolution of 30 m was used to examine the topographic differences within the Little Millseat watershed. We stratified the samples based on topography, in recognition of the influence of topography on soil moisture and soil temperature (Franzmeier and others 1969, Hutchins and others 1972) and soil type (Cremeans 1992, Hayes 1998) in these or similar landscapes.

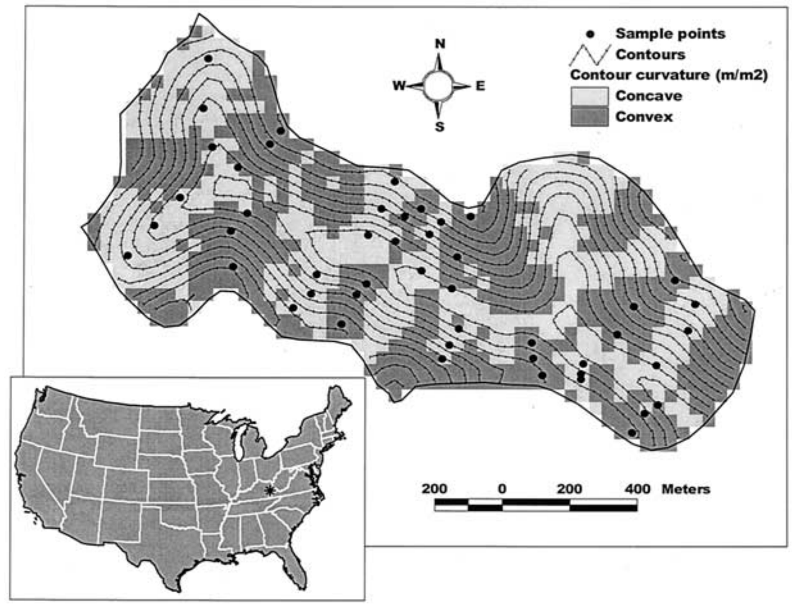

Figure 1. The Little Millseat watershed of Robinson Forest, Kentucky, USA, with the individual sample points displayed on the contour curvature map of the watershed, with 10 m contours included for reference. Inset: The location of Robinson Forest in southeastern Kentucky.

The primary factor for stratification was slope aspect, with two aspect classes: northeast ($A = 0–90°$) and southwest ($A = 180–270°$). Within these aspect classes, two slope curvature classes were defined by contour curvature: concave ($K_c < 0$) and convex ($K_c > 0$). Finally, relative distances from the drainageway defined three landscape positions: lower, middle, and upper backslope. Together these classes produced 12 unique combinations ($2 \times 2 \times 3$) that formed distinct clusters within the watershed. Sample points were randomly selected near the center of selected clusters, with four replicates of each unique combination within the Little Millseat subwatershed, for a total of 48 sampling points (Figure 1).

Field Sampling We collected a composite soil sample, not including the litter layer, from each established sampling point using a 1.7-cm-diameter push probe. The composite sample consisted of three, 15.2 cm deep soil cores taken within 1 m of the established sampling point. Samples were returned to the laboratory and stored at 7°C until beginning the laboratory analysis. Prior to incubation any rock fragments or coarse roots were removed from the moist samples.

Laboratory Methods

We conducted two separate incubation studies, with the first serving as a pilot study to formalize methods and examine gross controls on soil respiration rates, particularly temperature effects. The second incubation study focused on the effects of moisture potential on respiration rates. Samples for the pilot incubation study were collected on 6 September 2000, and samples for formal incubation study were collected on 7 February 2001.

Pilot Study Triplicate 2-g subsamples of soil from each composite sample were placed in 35-ml serum bottles. The bottles were capped with rubber sampling stoppers, and then incubated 14 days at 15° or 25°C. These two temperatures were selected based on data previously collected in Robinson Forest (Hutchins and others 1972). These temperatures, although not necessarily optimum for potential respiration, are representative of conditions that could be found in Robinson Forest. The effect of moisture content was evaluated in a two-phase experiment at each temperature regime. During phase I (0–7 days), respiration was evaluated at the native soil moisture content, which ranged from 0.13 to 0.55 g water/g soil. During phase II (7–14 days), respiration measurements were continued after increasing water content to field capacity (-0.03 MPa) using distilled water. The water required to increase water content to field capacity was calculated from equations by Saxton and others (1986), which relate matric potential to volumetric water content at specified soil texture.

The CO_2 concentration in the headspace gas was measured on days 1, 7, and 14 of incubation. A 100-μl gas sample was removed from each bottle with a syringe and analyzed for carbon dioxide content by using a Shimadzu GC-8A gas chromatograph equipped with a Supelco Custom column maintained at 25°C and injector and detector maintained at 30°C. Helium was used as the carrier gas. The amount of dissolved CO_2 and carbonate species in soil solution was included by using

Table 1. Chemical properties values[a] of soils on NE and SW aspects of Little Millseat subwatershed

Soil property	Aspect: NE	Aspect: SW
pH	5.5 ± 0.7	4.8 ± 0.5
Extractable phosphorus (P, mg/kg)	19.4 ± 7.6	9.5 ± 4.5
Extractable potassium (K, mg/kg)	262.5 ± 106.4	165.3 ± 61.3
Extractable calcium (Ca, mg/kg)	1592 ± 1165	508 ± 490
Extractable magnesium (Mg, mg/kg)	262 ± 150	121 ± 92
Extractable zinc (Zn, mg/kg)	6.8 ± 4.1	4.4 ± 2.6
Carbon (C, %)	3.5 ± 1.6	3.3 ± 1.7
Total nitrogen (TN, mg/kg)	2189 ± 741	1520 ± 583
Cation exchange capacity (CEC, $cmol_c$/kg)	26.0 ± 10.0	18.2 ± 8.9
Base saturation (BS, %)	23.6 ± 17.4	17.5 ± 15.6

[a]Values are mean ± standard deviation.

pH carbonate equilibria calculations (Gale and others 1992).

Formal Study A second incubation was conducted to further examine the influence of moisture potential on soil respiration rates by more closely controlling soil moisture. The effect of moisture was evaluated at two matric potentials: −0.01 and −0.1MPa. Composite soil samples from each sampling point were equilibrated to the desired matric potential on pressure plates in a temperature-controlled environment maintained at 10°C. Triplicate 2-g subsamples of equilibrated soil from each composite sample were placed in 35-ml serum bottles. The bottles were capped with rubber sampling stoppers, and then incubated for 14 days at 25°C.

The CO_2 concentration in the headspace gas was measured on days 1, 7, and 14 of incubation as in the pilot study. These sampling dates were also treated as two phases: phase I (days 0–7) and phase II (days 7–14), although none of the experimental conditions were changed between the two phases.

The remaining soil from the composite samples was analyzed for pH (Thomas 1996), organic carbon content (Nelson and Sommers 1996), total nitrogen (Bremner 1996), extractable P, K, Ca, Mg, and Zn (Mehlich 1984), cation exchange capacity (Sumner and Miller 1996), and base saturation (Table 1).

Terrain Analysis and Statistical Modeling

Terrain data were derived from a USGS 30-m DEM data set and terrain attributes (Table 2) were calculated using Arc/Info (Version 8.0.2, Environmental Systems Research Institute, Inc., Redlands, California, USA). Terrain attributes included elevation, slope gradient, slope aspect, profile curvature (down slope curvature), contour curvature (cross-slope curvature), total curvature (curvature in all directions), tangential curvature, upslope length, specific catchment area (upslope area per unit width of contour), compound topographic index, stream power index, proximity to nearest stream, elevation above nearest stream, and slope to nearest stream. Tangential curvature, a measure of local flow convergence or divergence, is a secondary terrain attribute calculated as the product of contour curvature and slope gradient ($K_t = K_c \times S$). The compound topographic index, a predictor of zones of soil saturation, is the ratio of specific catchment area to slope gradient [$CTI = \ln(A_s/S)$] (Wilson and Gallant 2000). The stream power index, a measure of runoff erosivity, is the product of specific catchment area and slope gradient [$SPI = \ln(A_s \times S)$] (Wilson and Gallant 2000).

Table 2. Terrain attributes calculated from a digital elevation model

Terrain attribute	Symbol (units)
Elevation	Z (m)
Slope aspect	A (degrees)
Slope gradient	S (%)
Total curvature	K (m/m^2)
Profile curvature	K_p (m/m^2)
Contour curvature	K_c (m/m^2)
Tangential curvature	K_t (cm/m^2)
Upslope length	L (m)
Proximity to stream	P_{stream} (m)
Elevation above stream	E_{stream} (m)
Slope to stream	S_{stream} (%)
Specific catchment area	A_s (m^2/m)
Compound topographic index	CTI
Stream power index	SPI

We calculated correlation coefficients to examine the relationships among terrain attributes, soil chemical properties, and PRR. We evaluated the effects of slope aspect, slope curvature, landscape position, incubation temperature, and moisture content on soil respiration using analysis of variance (PC-SAS, Cary, North Carolina, USA). Mean comparisons for main effects of slope aspect, slope curvature, landscape position, incubation temperature, and moisture content were made using least significant differences (LSD). We used stepwise linear regression (Neter and others 1989) and regression trees to identify variables most strongly related to PRR, then used robust linear regression (Rousseeuw and Leroy 1987) to develop predictive models of soil respiration from both soil chemical properties and terrain attributes using the maximum PRR measured for each sample during the second incubation study. Our PRR values from short-term incubations are higher than respiration rates that would be measured during longer incubations (see Winkler and others 1996), such that the absolute magnitude of our modeled PRR may not be significant at the landscape scale. However, these maximum initial PRR values should most readily show differences among the various samples.

Results and Discussion

Pilot Study

In the pilot study, respiration rates at 25°C (native moisture = 29.11 μg C/g soil/day, field capacity moisture = 22.35 μg C/g soil/day) were significantly greater ($P < 0.05$) than respiration rates at 15°C, within respective moisture contents (native moisture = 17.21 μg C/g soil/day, field capacity moisture = 14.57 μg C/g soil/day). This is similar to the trend found by Zak and others (1999), in which mean respiration rates significantly increased from 8.63 μg C/g soil/day at 10°C to 17.74 μg C/g soil/day at 25°C. Respiration rates at native moisture content (phase I, rate = 29.11 μg C/g soil/day) were greater ($P < 0.01$) than respiration rates at field capacity moisture content (phase II, rate = 22.35 μg C/g soil/day) at the 25°C incubation temperature, but not at the 15°C incubation temperature. Winkler and others (1996) found that respiration rates decline rapidly during the first few weeks of a laboratory incubation, and we suspect that the greater respiration rate in phase I versus phase II at the 25°C incubation temperature is most likely a result of labile carbon being consumed during phase I. A difference in respiration rates between phases I and II at the 15°C incubation temperature did not occur.

Analysis of variance indicated that the NE aspect had greater respiration rates ($P < 0.05$) than the SW aspect (NE = 23.34 μg C/g soil/day, SW = 18.28 μg C/g soil/day). The greater NE aspect PRR may be attributed to the higher pH, higher total N, and higher concentrations of extractable plant nutrients of the NE aspect soils (Table 1). There also may be a difference in the quality of the organic matter between the two slopes, although we did not measure this.

Respiration rates from the NE aspect samples were not significantly affected by slope curvature or landscape position ($P > 0.05$) (Table 3). Respiration rates from the SW aspect samples were not significantly affected by slope curvature ($P > 0.05$) but were affected by landscape position. Lower backslope positions had significantly higher ($P < 0.0001$) respiration rates than middle and upper backslope positions on the SW aspect (Table 3) No significant interactions occurred among slope aspect, slope curvature, and landscape position on either aspect.

Formal Study

Phase significantly ($P < 0.05$) influenced respiration rates in the second incubation study on both aspects such that Phase I resulted in greater respiration rates than phase II (Table 3), again suggesting that most labile carbon was consumed during phase I. Respiration rates were greater at the higher moisture content (−0.01 MPa), but this difference was not significant (Table 3).

As before, the NE aspect had greater respiration rates than the SW aspect (NE = 17.11 μg C/g soil/day, SW = 12.05 μg C/g soil/day, $P < 0.05$). As previously discussed, greater NE aspect respiration rates may be due to higher pH, higher total N, and higher concentrations of extractable plant nutrients on the NE aspect versus the SW aspect. Curvature was not a significant factor in predicting respiration on the NE aspect (Table 3). However, respiration rates were significantly ($P < 0.05$) related to curvature on the SW aspect such that concave curvatures had greater respiration rates than convex curvatures (Table 3). It appears that on warmer, drier SW-facing slopes, the concave curvatures contain greater amounts of easily mineralizable soil organic matter than the convex slopes. The influence of slope curvature was not as important on the NE aspect (cooler, moister slopes) where soil organic matter may be more evenly distributed. Landscape position was not a significant factor influencing respiration on either aspect (Table 3).

Correlation coefficients reveal that respiration rates on the NE aspect were significantly correlated ($P < 0.05$) with soil pH, extractable Ca, extractable Mg, and base saturation (Table 4). Respiration rates on the SW aspect were only significantly correlated ($P < 0.05$) with Zn. Overall, the correlation coefficients between PRR and soil properties and terrain attributes are low. We attribute this to the high variability in both PRR and soil

Table 3. Results of analysis of variance comparisons for both incubation methods

Variable	NE Respiration rate (µg C/g soil/day)	NE P	SW Respiration rate (µg C/g soil/day)	SW P
Pilot study				
Curvature				
Concave	21.583	0.2408	20.196	0.1271
Convex	25.099		16.371	
Landscape position				
Upper backslope	20.958		14.617	
Middle backslope	23.925	0.5012	13.937	< 0.0001
Lower backslope	25.140		26.296	
Temperature				
15°C	18.162	0.0008	13.623	0.0003
25°C	28.520		22.944	
Moisture/phase				
Native/phase I	25.862	0.0939	20.464	0.0826
Field capacity/phase II	20.820		16.103	
Formal study				
Curvature				
Concave	17.160	0.9408	14.310	0.0103
Convex	17.060		9.798	
Landscape position				
Upper backslope	16.027		12.985	
Middle backslope	19.188	0.0828	11.146	0.6845
Lower backslope	16.043		12.031	
Phase				
I	19.872	< 0.0001	14.054	0.0224
II	14.348		10.054	
Moisture				
−0.01 MPa	17.759	0.2817	13.170	0.1978
−0.1 MPa	16.403		10.937	

properties. Scatter plots of PRR versus individual soil properties or terrain attributes (not shown) suggests the presence of underlying trends that are clouded by a few influential outliers.

We developed regression models separately for the NE and SW aspects because of the previously identified landscape differences in soil respiration rates (Table 3). Furthermore, simple correlation coefficients between measured soil respiration and individual proximal and distal factors were higher when the data were stratified by slope aspect. We also developed separate models using proximal factors only (Table 1), distal factors only (Table 2), or combinations of both. In all cases, the models that we developed for the NE-facing slopes were better at predicting PRR than models developed for the SW-facing slopes (Table 5). Furthermore, proximal factor models were more explanatory than distal factor models (Table 5). When considering only proximal factors, the model for the NE slope includes Mg and Zn (R^2_{adj} = 0.585) such that as either extractable Mg or Zn increased, PRR also increased (Table 5). The model for the SW slope includes P and Zn (R^2_{adj} = 0.417) such that as either extractable P or Zn increased, so did PRR (Table 5). These three elements (P, Mg and Zn) are important microbial mineral nutrients, and extractable Mg (which is correlated with extractable Ca and pH) may also be a surrogate for a pH response in these models. The model for the NE slope created from distal factors includes Z, A_s and A (R^2_{adj} = 0.487) indicating that PRR increases as elevation or specific catchment area increase or as slope aspect becomes more northerly (Table 5). Higher PRR are associated with higher elevations, likely because organic matter increases with increasing elevation in these landscapes (Thompson and Kolka, unpublished data, 2002). Higher catchment areas are found at the base of slopes, where water and sediments accumulate, creating surface conditions that may promote more microbial activity. The model for the SW slope included A, K_t , and S_{stream} (R^2_{adj} = 0.317) such that as slope aspect becomes more westerly, as tangential curvature decreased, or as the slope to the stream decreases, PRR

Table 4. Correlation coefficients of respiration rates, terrain attributes, and chemical properties[a]

	Aspect	
	NE	SW
Chemical properties		
pH	0.464*[b]	0.166
P	0.031	0.259
K	0.122	0.234
Ca	0.464*	0.215
Mg	0.573	0.351
Zn	0.373	0.392
C	0.104	0.087
TN	0.357	0.284
CEC	0.287	0.042
BS	0.485	0.025
Terrain attributes		
S	0.150	0.017
A	0.146	0.039
K	−0.323	−0.133
K_p	0.354	0.009
K_c	−0.197	−0.263
K_t	−0.105	−0.331
L	0.260	−0.075
P_{stream}	0.274	0.165
E_{stream}	0.099	0.155
S_{stream}	0.007	−0.055
A_s	0.319	−0.092
CTI	0.280	−0.011

See Tables 1 and 2 for variable definitions.
*, ** significant at the 0.05 and 0.01 levels.

Table 5. Predictive soil respiration models using proximal, distal, and a combination of all factors[a]

Aspect	Variable	Intercept	Adjusted R^2
Proximal			
NE	0.0392 Mg	8.79	0.585
	0.314 Zn		
SW	0.178 P	6.49	0.417
	0.992 Zn		
Distal			
NE	0.0335 A_s	−39.1	0.487
	0.160 Z		
	−0.0922 A		
SW	−1.56 K_t	11.2	0.317
	−0.258 S_{stream}		
	0.0483 A		
Combination			
NE	0.0378 Mg	10.6	0.620
	0.336 Zn		
	−0.0575 A		
	0.0155 A_s		
SW	0.203 P	6.05	0.413
	0.977 Zn		
	−8.77 K_t		

[a]See Tables 1 and 2 for variable definitions.

increases (Table 5). Tangential curvature is particularly useful for relating areas of flow convergence (negative K_t) or divergence (positive K_t) (Wilson and Gallant 2000).

When we combined both proximal and distal factors, the regression model for the NE slope could be used to explain more of the variability of PRR. No such improvement is seen in the model for the SW slope. A combination of variables from the previous models are included in the model for the NE slope, with Mg, Zn, A_s , and A being able to explain 62% of the variability in PRR (Table 5). The relationships between PRR and these explanatory variables are the same as in the previous models. Despite the inclusion of the distal factor K_t, there was no improvement in the predictive power of the combined model for the SW slope (R^2_{adj} = 0.413) when compared to the proximal model for the SW slope (Table 5).

Conclusions

For both the pilot study and the formal study, respiration rates were greater during the first phase (days 0–7) of incubation, suggesting that the most of the labile C was consumed during this period. Both studies also revealed soil respiration rates to be greater on the NE-facing slope than on the SW-facing slope. We attribute this difference to a higher pH, higher total N, and higher concentrations of extractable plant nutrients of soils on the NE-facing slope versus the SW-facing slope. Landscape factors (slope curvature, landscape position) did not significantly affect respiration rates on the NW slope. However, slope curvature does appear to affect respiration rates on the SW slope, suggesting that soil variability is controlled, in part, by site differences associated with the topographic variability in these steep, mountainous landscapes.

Of the predictive models of PRR we created for both slope aspects, those from the NE slope were consistently able to explain more of the variability in PRR, whether proximal factors, distal factors, or a combination of the two were used. Furthermore, the variability in soil chemical properties was better able to explain the variability in PRR than were terrain attributes derived from a 30-m DEM. These predictive models contribute to an understanding of system dynamics under ideal conditions for microbial respiration. However, because of the significant microsite variability in soil properties affecting PRR, more research is needed to clarify the relationships among both proximal and distal factors and PRR in these soils and between PRR and actual soil respiration, which includes both microbial and root respiration. Ideally, these models should be tested in other similar landscapes in Robinson Forest or surrounding areas to test their validity in other watersheds.

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