Biology Faculty Research   Department of Biological Sciences

12-7-2014

Soil respiration patterns and controls in limestone cedar glades

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Recommended Citation

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Abstract

Aims Drivers of soil respiration (R_s) in rock outcrop ecosystems remain poorly understood. We investigated these drivers in limestone cedar glades, known for their concentrations of endemic plant species and for seasonal hydrologic extremes (xeric and saturated conditions), and compared our findings to those in temperate grasslands and semi-arid ecosystems.

Methods We measured R_s, soil temperature (T_s), volumetric soil water content (SWC), soil organic matter (SOM), soil depth, and vegetation cover monthly over 16 mo and analyzed effects of these variables on R_s.

Results Seasonally, R_s primarily tracked T_s ($r^2 = 0.77$; $P < 0.01$), however R_s was depressed during a summer drought. SOM was highly variable spatially, and incorporating SOM effects into the R_s model dramatically improved model performance. Both shallow soil and sparse vegetation cover were also associated with lower R_s.

Conclusions Soil depth, SOM, and vegetation cover were important drivers of R_s in limestone cedar glades.

Seasonal R_s patterns reflected those for mesic temperate grasslands more than for semi-arid ecosystems, in that R_s primarily tracked temperature for most of the year.

Keywords Limestone cedar glades · Rock outcrop ecosystems · Soil depth · Soil organic matter · Soil moisture · Soil respiration

Abbreviations

R_s	Soil respiration
T_s	Soil temperature
AIC	Akaike Information Criterion
NPS	National Park Service
SOM	Soil Organic Matter
SWC	Volumetric Soil Water Content
TDR	Time Domain Reflectometry

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Introduction

Soil respiration (R_s) in terrestrial ecosystems is the primary means of carbon transfer to the atmosphere and is the most important carbon flux other than gross primary productivity (Dixon et al. 1994; Schimel 1995). Rates and controls of R_s are highly variable across ecosystems and across a range of spatial and temporal scales (Luo et al. 2001; Hui and Luo 2004; Bond-Lamberty and Thomson 2010). Although the biotic and abiotic controls on R_s have been extensively investigated across many of Earth's major ecosystems (Liu et al. 2002; Luo and Zhou 2006; Subke et al. 2006; Deng et al. 2012),

these controls remain unstudied in certain rock outcrop ecosystems, such as limestone cedar glades (Quarterman 1950a; Baskin and Baskin 1999). The abiotic stress regime in limestone cedar glades is characterized by very thin soils (Baskin and Baskin 2003; Baskin et al. 2007a), widely fluctuating hydrologic conditions (Quarterman 1950b; Norton 2010), and ground surface temperatures as high as 50 °C during the growing season in zones lacking canopy coverage (Freeman 1933; Baskin and Baskin 1999). Although the roles of these stressors in maintaining high densities of rare, endemic, and biogeographically disjunct plant taxa have been explored (Baskin and Baskin 1985; 1988; 1989), no studies have been conducted on their effects on R_s.

Limestone cedar glades share some aspects of abiotic stress regime, landscape physiognomy, and vegetation composition with temperate mesic grasslands and semi-arid ecosystems (Quarterman 1989; Quarterman et al. 1993; Jarvis et al. 2007). In temperate mesic grasslands, R_s is controlled primarily by soil temperature (T_s) and soil water content (SWC) (Kucera and Kirkham 1971; Mielnick and Dugas 2000), and is also influenced by vegetation cover, soil thickness, topographic position on the landscape, soil organic matter content (SOM), and soil carbon content (Bremer et al. 1998; Craine and Wedin 2002; Flanagan and Johnson 2005; Risch and Frank 2006; Thomson et al. 2010; Craine and Gelderman 2011). Cedar glades fit standard definitions as grasslands (Noss 2013), since their vegetation is predominantly herbaceous with sparse shrub and tree cover (Baskin and Baskin 1999; Baskin et al. 2007b). However, they have shallower soils, more exposed bedrock, and different plant community composition than do prairies or savannas (Anderson et al. 1999; Lawless et al. 2006; Baskin et al. 2007a).

Cedar glade vegetation has constituents adapted to seasonally xeric soil conditions—e.g. succulents, crassulacean acid metabolism (CAM) species—suggesting a similarity to arid or semi-arid ecosystems (Quarterman 1950a; Baskin et al. 1995; Norton 2010). In ecosystems such as deserts, semi-arid steppes, and Mediterranean ecosystems, soil moisture limitations are especially important controls on R_s (Amundson et al. 1989; Reichstein et al. 2002; Jia et al. 2006; Zhang et al. 2009; Talmon et al. 2011). Precipitation-triggered CO_2 efflux pulses often contribute substantially to seasonal and annual efflux totals (Xu et al. 2004; Tang and Baldocchi 2005; Jarvis et al. 2007; Vargas and Allen 2008; Munson et al. 2009), highlighting the importance

of precipitation timing and antecedent soil moisture conditions (Schwinning et al. 2004; Rey et al. 2005; Jarvis et al. 2007; Sponseller 2007; Cable et al. 2008, 2013; Shen et al. 2008; Munson et al. 2009). In contrast to mesic ecosystems, xeric soil conditions commonly suppress R_s on a seasonal basis despite favorable temperatures, such that the R_s response to T_s varies based on soil moisture conditions (Rey et al. 2002; Joffre et al. 2003; Xu et al. 2004; Almagro et al. 2009; Liu et al. 2009; Carbone et al. 2011; Rey et al. 2011). R_s in arid and semi-arid ecosystems is also influenced by vegetation cover (Maestre and Cortina 2003; Tang and Baldocchi 2005; Vargas and Allen 2008; Cable et al. 2008; Almagro et al. 2009) and soil organic carbon pools (Conant et al. 2000; Sponseller 2007; Talmon et al. 2011; Balogh et al. 2011), and by their interactive effects with temperature and moisture (Wildung et al. 1975).

In contrast to many arid and semi-arid ecosystems, cedar glades commonly contain microhabitats that are seasonally saturated or inundated as well as seasonally xeric (Quarterman 1950b; Nordman 2004; Norton 2010). Also, seasonally xeric soil conditions in cedar glades are produced primarily by edaphic rather than climatic factors: although the timing and magnitude of precipitation are comparable to those of surrounding mesic forests, cedar glade soils experience more intense summer drying due to their shallowness and insolation (Quarterman 1950b; Martin and Sharp 1983; Baskin and Baskin 1999).

In this study, we investigated relationships between R_s and known elements of the abiotic stress regime of limestone cedar glades (e.g. shallow soil, seasonal extremes in SWC, and seasonally high T_s). We also analyzed the effects of SOM and vegetation cover, biotic factors known to influence R_s in temperate grasslands and in arid and semi-arid ecosystems. Our primary objectives were to: (1) determine whether temperature- and moisture-based R_s models could be improved by incorporating SOM effects, and (2) assess differences in R_s based on spatial variability in soil depth and vegetation cover.

Materials and methods

Study site

Field investigations were conducted at Stones River National Battlefield near Murfreesboro, Tennessee

(35°52'35" N, 86°25'58" W), USA, a 120-acre federal-ly-managed park that consists mostly of red cedar (*Juniperus virginiana*) and oak (*Quercus* spp.) forest in which several dozen limestone cedar glades are inter-spersed, on outcrops of thin-bedded, fine-grained Ordovician limestone (Mahr and Mathis 1981; Morris et al. 2002; Adams et al. 2012). Limestone cedar glades are a calcareous rock outcrop ecosystem present in the Interior Low Plateau, Appalachian Plateau, and Ridge and Valley physiographic provinces of the Southeastern United States (Fenneman 1938; Baskin and Baskin 1999). They contain edaphic climax communities in which succession is constrained by shallow soil (Quarterman 1950b; Baskin and Baskin 2003; Baskin et al. 2007b). Vascular plant density exhibits high spatial variability, ranging from sparsely vegetated areas of exposed bedrock to thickly vegetated glade-shrub com-munities in areas with deeper soil (see Figs. 2–8 in Quarterman 1950a; Nordman 2004).

Dominant vegetation includes C_4 summer annual grasses, C_3 forbs, mosses, cyanobacteria, and lichens, with generally sparse woody cover (Quarterman 1950a; Baskin and Baskin 1999; Baskin et al. 2007b). Characteristic plant taxa at this site include (graminoids) *Andropogon gyrans*, *A. ternarius*, *A. virginicus*, *Sorghastrum nutans*, and *Sporobolus vaginiflorus*; (forbs) *Croton monanthogynus*, *Dalea gattingeri*, *Erigeron strigosus*, *Leavenworthia* spp., *Ruellia humilis*, *Sedum pulchellum*, and *Talinum calcaricum*; and (shrubs) *J. virginiana*, *Forestiera ligustrina*, and *Frangula caroliniana* (Baskin and Baskin 1999; 2003; Nordman 2004). Cedar glades at this site also support the globally rare *Astragalus bibullatus*, *A. tennesseensis*, and *Echinacea tennesseensis* (Nordman 2004). The macroclimate of the region is humid and mesothermal (Baskin and Baskin 1999). The mean annual temperature is 12.2 °C, with monthly mean temperatures ranging from −3.2 to 32.6 °C. Monthly precipitation averages 12.4 cm and ranges from 4.0 cm to 17.1 cm (National Climatic Data Center 2014).

Sampling design

We established 36 quadrats, each measuring 0.5- m × 0.5-m, in 12 cedar glades. Roughly 80 % (28 quadrats) were located within the glades, generally within zones of gravel pavement and graminoids, forbs, and moss. Roughly 20 % (8 quadrats) were situated within a 3-m buffer of *J. virginiana* shrubland / forest immediately surrounding the glades. Quadrat locations within glades and within *J. virginiana* buffers were randomly assigned using ArcGIS version 9.3 (Esri, Redlands, CA, USA). Sampling was conducted monthly for 16 months (February 2012 through May 2013) following a rota-tional schedule, such that each quadrat was sampled four times at roughly four month intervals.

Environmental measurements

Soil depth (depth to bedrock; mean of four measure-ments per quadrat) was measured using a 1-cm diameter metal probe inserted as far down into the soil as possible. T_s (mean of three measurements per quadrat) was mea-sured at 4-cm soil depth using a Taylor 9842 N water-proof digital thermometer (Taylor Inc., Oak Brook, IL, USA). Ground surface temperature (one measurement per quadrat) was measured using a Lloyd and Taylor 1994 indoor/outdoor digital thermometer and hygrome-ter (Taylor Inc., Oak Brook, IL, USA). SOM was esti-mated according to the loss-on-ignition method (Davies 1973) using soil samples obtained at 4-cm depth. For quadrats in which soil depth was less than 4 cm, T_s measurements and SOM estimations (at 4-cm depth) were performed as close to the quadrat as possible.

SWC was measured using time-domain reflectome-try (TDR) probes (FieldScout TDR 300, Spectrum Technologies, Inc., Plainfield, IL, USA), fitted with 3.8 cm rods, where soil was sufficiently deep (at least two soil depth measurements within the quadrat were greater than 4 cm), or otherwise by oven-drying per-formed according to Topp and Ferre (2002). Six TDR measurements or three oven-drying samples were taken per quadrat. Gravimetric soil water content was convert-ed to volumetric equivalents using soil bulk density based on measured soil-core volume.

To establish a relationship between TDR and oven-drying measurement methods, an independent sample of 48 measurements, each conducted by both methods, was collected in November 2011, January 2013 and May 2013, within the same cedar glades used for monthly SWC observations. These paired measure-ments ranged from less than 8 % to greater than 50 % SWC, and were used to establish a natural log regression relationship (r^2=0.95, P<0.01):

$$\ln(SWC_{OD}) = 1.6881(\ln(SWC_{TDR}))-2.7187 \qquad (1)$$

where SWC_{OD} is the volumetric soil water content calculated from bulk density and gravimetric soil water content as measured by oven drying (expressed as percent dry weight) and SWC_{TDR} is the volumetric soil water content measured by TDR (expressed as volumetric percent).

The quadrat percentage of graminoids, forbs, vines and shrubs—a rough classification of vascular plants following Cofer et al. (2008)—was estimated at each point based on visual examination, and categorized as "none," "less than 30 %," "30 to 70 %," or "greater than 70 %" with scores assigned from 0 to 3, respectively. The sum of these individual scores by vegetation type was calculated as an overall vegetation score for each quadrat.

Field measurements of in situ R_s were obtained using a Li-Cor Infrared Gas Analyzer, LI-6400 XT Portable Photosynthesis System (Li-Cor Inc., Lincoln, NE, USA), fitted with a soil chamber attachment. At least 48 hours prior to the first R_s measurement, three soil collars were inserted into the soil surface at each quadrat and the height of each collar above the soil surface was measured. Two measurement cycles were completed at each collar, yielding six R_s measurements per quadrat.

Evaluation of soil respiration models

To explore the relationships between R_s (CO_2 efflux in μmol m^{-2} s^{-1}) and T_s (soil temperature in °C), SWC (% volumetric soil water content), and SOM (% loss on ignition), scatter plots were constructed of R_s with these variables (Fig. 1). Based on these potential relationships, four models were tested:

$$\text{Model 1}: R_s = ae^{bT_s} \tag{2}$$

$$\text{Model 2}: R_s = ae^{bT_s}\left(c^{SWC}\right) \tag{3}$$

$$\text{Model 3}: R_s = ae^{bTs}(SWC - 0.03)(0.6 - SWC)^c \tag{4}$$

$$\text{Model 4}: R_s = ae^{bT_s}\left(C^{SWC}\right)\left(SOM^d\right) \tag{5}$$

In Model 1, R_s was exponentially related to T_s (Kucera and Kirkham 1971; Luo et al. 2001; Rey et al. 2002; Fig. 1a). Model 2 incorporated SWC as an

exponential function (Fig. 1b). Model 3 used observed upper and lower bounds on SWC and predicted highest R_s at intermediate SWC values (Davidson et al. 1998; Moyano et al. 2013; Fig. 1c). Model 4 was based on Model 2, and incorporated SOM as a power function (Fig. 1d). For all models, SWC was expressed as a decimal and a, b, c, and d were fitted model parameters, with a representing the basal respiration rate at a temperature of 0 °C, and b, c, and d representing the effects on R_s of T_s, SWC, and SOM, respectively. The increase in R_s for a 10 °C temperature increase (Q_{10}, temperature sensitivity) was calculated as:

$$Q_{10} = e^{10b} \tag{6}$$

The criteria for model selection were: (1) Akaike Information Criterion (AIC), (2) comparison of r^2 values, and (3) evaluation of model residuals. AIC was used as a penalized likelihood criterion:

$$AIC = -2 \ln(L) + 2p \tag{7}$$

where L is the likelihood of the fitted model and p is the number of parameters in the model (Burnham and Anderson 2002). Following model evaluation based on minimized AIC value, model selection was confirmed based on maximized r^2 value, lack of correlation between model residuals and explanatory variables, and a Wald-Wolfowitz runs test for randomness of the model residuals (Motulsky and Ransnas 1987).

Statistical analysis

All analyses were performed using SAS 9.3 (SAS Institute, Cary, NC, USA). Comparison of R_s across soil moisture categories (SWC below 15 %, between 15 and 40 %, and above 40 %) was performed using ANOVA and a Tukey's *post hoc* test. To detect whether these differences existed independently from temperature effects, the same analysis was performed using residuals from Models 1 and 4. Parameter estimates for Model 4 were compared across soil moisture categories using a Student's *t*-test.

Relationships between R_s and soil depth and between R_s and vegetation cover were evaluated using ANOVA and a Tukey's *post hoc* test across three soil depth classes: shallow (soil depth less than 5 cm, $n=33$), moderate (5 to 10 cm, $n=58$) and deep (greater than 10 cm, n =31); and across three vegetation cover classes:
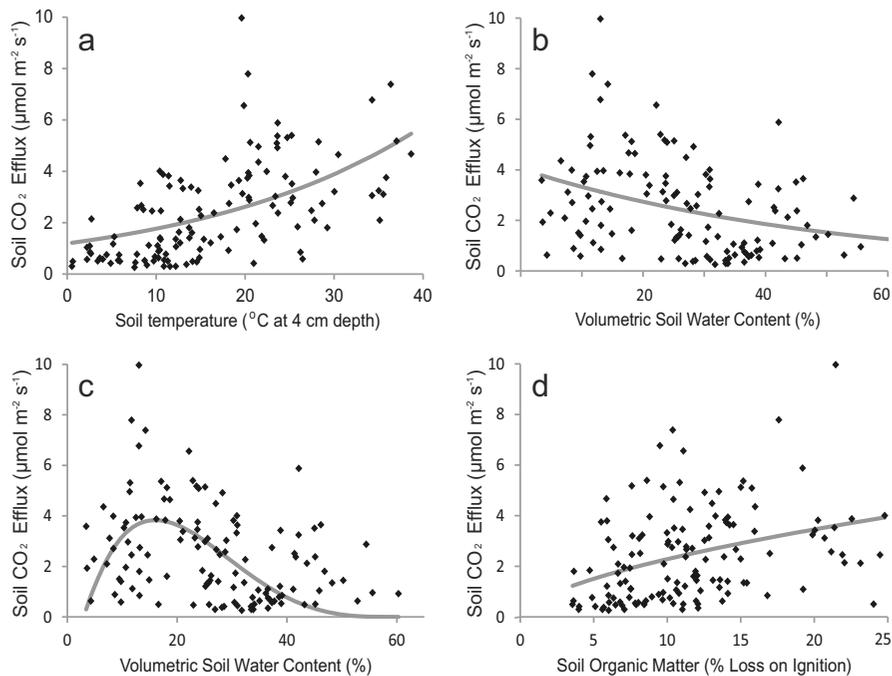
Fig. 1 Modelled relationships between soil respiration rates and model variables: (**a**) soil temperature (Model 1); (**b**) the soil water content relationship in Model 2; (**c**) the soil water content relationship in Model 3; and (**d**) the soil organic matter relationship in Model 4

sparse (vegetation score of 1 or 2, n=63), moderate (3 to 4, n=40), and dense (score above 4, n=19). To detect differences in R_s related to soil depth and vegetation cover after having accounted for T_s, SWC, and SOM, the same analysis was conducted using Model 4 residuals.

Results

Seasonal patterns of soil temperature, moisture, and respiration

Over the 16 months of the study period, ground surface temperatures (means across sampling locations) ranged from 3.7 °C in January 2013 to 41.9 °C in June 2012 (Fig. 2a), and mean T_s at 4-cm soil depth ranged from 2.6 °C in January 2013 to 30.6 °C in July 2012. The annual mean (February 2012 through January 2013) was 25.3 °C for ground surface temperature and 17.6 °C for T_s at 4-cm soil depth. Consistent with previous observations in limestone cedar glades (e.g. Quarterman 1950b; Norton 2010), hydrologic conditions seasonally ranged from xeric (the minimum SWC measured at a particular sampling location was less than 3.5 % in June 2012)

to visibly saturated (individual observations of SWC greater than 50 % in December 2012, March 2013 and May 2013). Mean SWC across sampling locations ranged from 6.1 % in June 2012 to 43.5 % in March 2013, with an annual mean of 23.0 % (Fig. 2b). Soil moisture was generally lowest in the summer and autumn (with the exception of July), and higher in the winter and early spring. Reflecting these seasonal patterns, SWC was inversely correlated with ground surface temperature (r^2=0.47; P<0.05) and with T_s (r^2=0.35; P<0.05).

Mean R_s rates across sampling locations ranged from 0.7 µmol m^{-2} s^{-1} in December 2012 to 5.3 µmol m^{-2} s^{-1} in August 2012, with an annual mean of 2.7 µmol m^{-2} s^{-1} (Fig. 2c). We estimated an overall Q_{10} value of 2.01. Seasonally, R_s was strongly positively correlated with ground surface temperature (r^2=0.81; P<0.01) and T_s (r^2=0.77; P<0.01) and was inversely correlated with SWC (r^2=0.50; P<0.01). Both R_s and ground surface temperature were relatively high during the summer, declined throughout the autumn, remained low over the winter and began to rise again during the spring (Figs. 2a and c). From May through September 2012, mean ground surface temperatures above 30 °C were observed along with mean R_s rates above 3.0 µmol m^{-2} s^{-1}, except for the field visit in late June

Fig. 2 Seasonal patterns of (**a**) ground surface temperature, (**b**) volumetric soil water content, and (**c**) soil CO_2 efflux from February 2012 to May 2013 (squares indicate means across all sampling locations; error bars indicate one standard error)
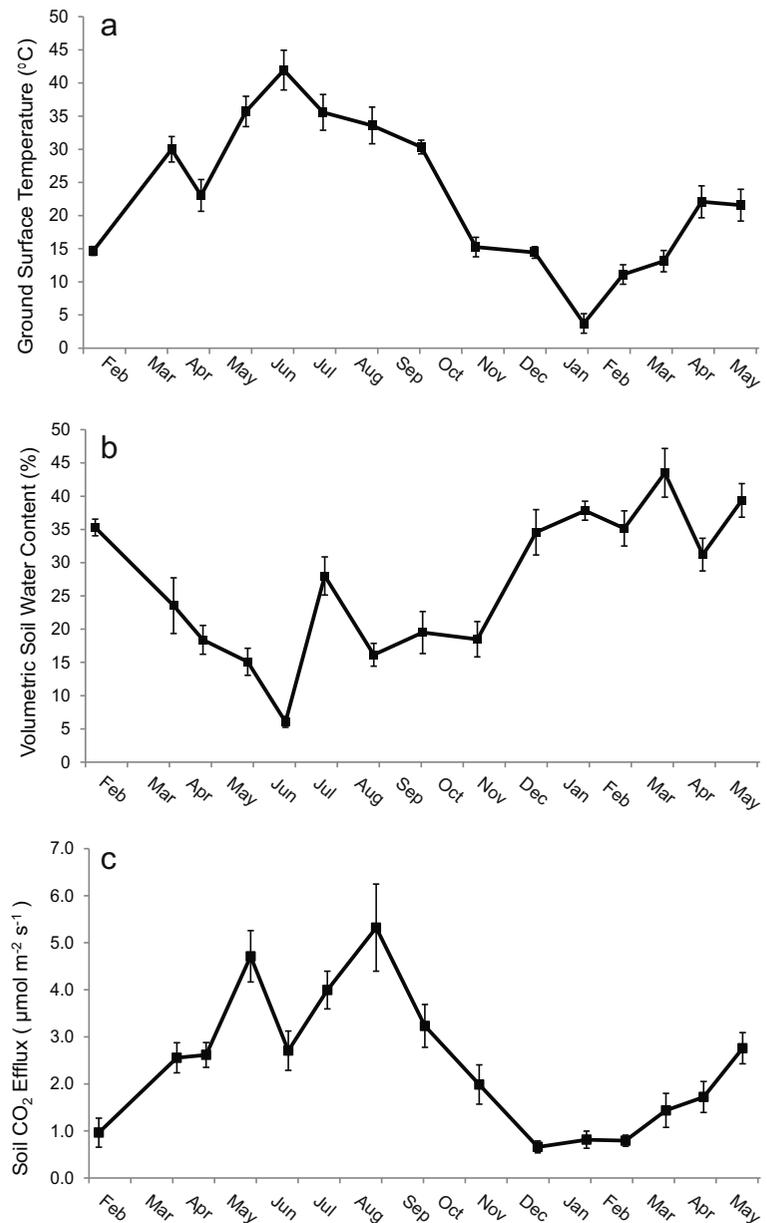
for which a dip in mean R_s rate (to 2.7 μmol m^{-2} s^{-1}) coincided with extremely dry soil conditions (mean SWC of 6.1 %) toward the end of a drought lasting several weeks. Under relatively dry soil conditions for this site (SWC less than 15 %), the temperature effect on R_s was significantly greater (b=0.09) than when SWC was greater than 15 % (b=0.06); t(113)=2.25, P<0.05. Rates of R_s were significantly higher (P<0.05) when SWC was less than 15 % (mean 3.50 μmol m^{-2} s^{-1}) as compared to SWC ranging between 15 % and 40 % (mean 2.25 μmol m^{-2} s^{-1}) or when SWC was greater

than 40 % (mean 2.04 μmol m^{-2} s^{-1}). After accounting for temperature effects using Model 1 and Model 4 residuals, however, these differences were not significant (P>0.05), indicating that differences in R_s across these soil moisture categories did not exist independently from temperature effects.

Evaluation of soil respiration models

Model 4 was selected as the best model based on minimized AIC value (Table 1). Additionally, Model 4 had

Table 1 Parameter estimates and model evaluation data for the four soil respiration models; * indicates significant correlation ($P<0.05$) of model residuals with explanatory variables; ** indicates significance ($P<0.05$) of the Wald-Wolfowitz Z statistic

Soil respiration model	Parameter estimates (standard error)				AIC	r^2	P-value	Correlation of model residuals with			Wald-Wolfowitz Z
	a	b	c	d				T_s	SWC	SOM	
Model 1: $R_s = ae^{bT_s}$	1.19 (0.17)	0.04(0.01)	–	–	477.3	0.30	<0.01	0.11	–	–	−6.02**
Model 2: $R_s=ae^{bT_s}(c^{SWC})$	1.87 (0.44)	0.03(0.01)	0.31(0.17)	–	435.5	0.33	<0.01	0.19*	−0.09	–	−5.37**
Model 3: $R_s = ae^{bT_s}(SWC-0.03)(0.6-SWC)^c$	154.7 (61.11)	0.03(0.01)	2.78 (0.32)	–	451.5	0.23	<0.01	−0.03	0.22*	–	−3.92**
Model 4: $R_s=ae^{bT_s}(c^{SWC})(SOM^d)$	0.04 (0.02)	0.07 (0.01)	0.38 (0.12)	1.27 (0.12)	342.3	0.71	<0.01	−0.09	0.06	−0.05	−1.52

the highest r^2 value and was the only model that did not deviate systematically from the data based on a Wald-Wolfowitz runs test for randomness of the model residuals (Motulsky and Ransnas 1987). Of the models that incorporated SWC (Models 2 through 4), only Model 4 had model residuals that were uncorrelated with all explanatory variables. Based on AIC value, r^2 value, and residuals analysis, incorporating SWC (Models 2 and 3) improved model performance only marginally as compared to the temperature-only model (Model 1). Based on the same criteria, however, incorporation of SOM effects (Model 4) dramatically improved model performance. Several other models incorporating T_s, SOM, and/or SWC were also tested (data not shown), but they did not fit the data as well as did Model 4 based on the stated model selection criteria. Some studies have reported optimal temperatures above which R_s rates decline (Parker et al. 1983; O'Connell 1990; Fernandez et al. 2006), however analysis of Model 4 residuals indicated that the exponential relationship between R_s and T_s was valid even when T_s exceeded 35 °C.

Relationships between soil respiration, soil depth, soil organic matter, and vegetation cover

Soil depth (depth to bedrock) ranged from 2.4 cm to 22.6 cm. Mean R_s rates were 2.01 μmol m^{-2} s^{-1} for quadrats located in shallow soil areas, 2.33 μmol m^{-2} s^{-1} for moderate soil depth, and 3.07 μmol m^{-2} s^{-1} for deep soil. Rates of R_s differed significantly across soil depth classes, F(2,132)=3.29, $P<0.05$, and were significantly lower for shallow soil quadrats than for those at deep soil locations ($P<0.05$), but were not different between shallow and moderate soil depths or between moderate and deep soil depths (both $P>0.05$). Rates of R_s —after having accounted for the effects of T_s, SWC, and SOM (Model 4 residuals)— were significantly lower for the shallow soil depth class ($P<0.05$) but were not different between the moderate and deep classes ($P>0.05$; Fig. 3a).

Vegetation cover ranged from one to eight and was positively correlated with soil depth (r^2=0.46, $P<0.01$). Mean R_s rates were 1.88 μmol m^{-2} s^{-1} for quadrats in areas of sparse vegetation, 3.00 μmol m^{-2} s^{-1} for moderate vegetation, and 2.99 μmol m^{-2} s^{-1} for thick vegetation. Rates of R_s differed significantly across vegetation cover classes, F(2,132)=6.95, $P<0.05$, as did Model 4 residuals, F(2,112)=11.22, $P<0.05$. Areas of sparse vegetation had lower R_s rates and lower Model 4
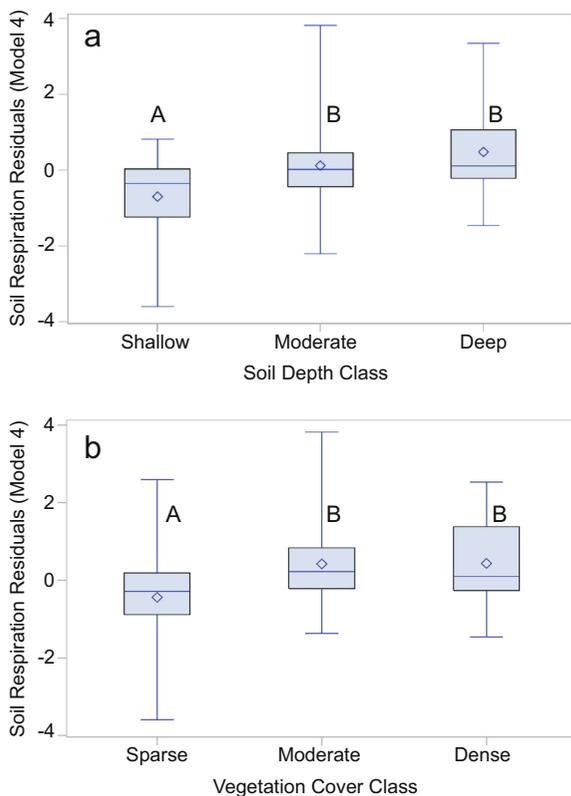
Fig. 3 Soil respiration residuals from Model 4, by (a) soil depth class and (b) vegetation cover class; box and whiskers indicate four quartiles; diamonds indicate group means; letters accompanying each bar represent significant differences ($P<0.05$) based on ANOVA and a Tukey's post hoc test

residuals than did those in areas of moderate or dense vegetation (both $P<0.05$), but neither R_s rates nor Model 4 residuals were significantly different between moderately and densely vegetated areas (both $P>0.05$; Fig. 3b). SOM (an explanatory variable in Model 4) ranged from 3.6 % to 24.8 %, and was positively correlated with both soil depth ($r^2=0.24$, $P<0.01$) and with vegetation cover score ($r^2=0.15$, $P<0.01$). Under relatively dry conditions for this site (SWC below 15 %), the SOM effect on R_s was increased: $d=2.01$ compared to $d=1.02$; t (113)=3.30, $P<0.05$.

Discussion

Seasonal patterns of soil respiration, soil temperature, and soil moisture

In this study of limestone cedar glades, mean monthly R_s rates across sampling locations (0.7 – 5.3 μmol m^{-2} s^{-1})

were somewhat lower than ranges reported for deep-soil temperate grasslands such as tallgrass prairies (Bremer et al. 1998; Mielnick and Dugas 2000; Liu et al. 2002), where mean R_s rates greater than 7.5 μmol m^{-2} s^{-1} have been observed (Craine and Wedin 2002). This difference may be attributable to edaphic and vegetation characteristics in this ecosystem (i.e. much thinner soils, patchy vegetation distribution, and high spatial variability in SOM). The Q_{10} value for this study (2.01) was within the range of values (1.3 to 3.3) commonly reported for in situ R_s globally (Raich and Schlesinger 1992), and within ranges reported for mesic grasslands and semi-arid ecosystems (Xu and Qi 2001; Rey et al. 2002; Craine and Gelderman 2011).

Over the course of this study, T_s and SWC were inversely related on a seasonal basis, reflecting regional patterns of higher precipitation and reduced evapotranspiration in winter and early spring (Baskin and Baskin 1999), a relationship that has been observed in a number of semi-arid ecosystems (Xu et al. 2004; Baldocchi et al. 2006; Almagro et al. 2009; Carbone et al. 2011; Talmon et al. 2011). While isolating the individual effects of T_s and SWC on R_s is problematic under such conditions (Davidson et al. 1998), our findings suggest that R_s was largely controlled by T_s over the course of this study. Rates of R_s showed clear seasonal patterns, generally tracking seasonal temperature trends. The addition of SWC as an explanatory variable (Models 2 and 3) failed to substantially improve explanatory power over a temperature-only model (Model 1). The close association between R_s and T_s on a seasonal basis that we observed in limestone cedar glades has been widely observed in mesic ecosystems, including temperate mesic grasslands (Kucera and Kirkham 1971; Singh and Gupta 1977; Raich and Schlesinger 1992; Lloyd and Taylor 1994; Mielnick and Dugas 2000; Subke et al. 2006).

In this study, one clear exception occurred to the general seasonal pattern in which R_s tracked T_s: a reduction in R_s under very dry conditions in late June 2012 despite high temperatures (Fig. 2). Several studies in arid and semi-arid ecosystems have also reported relatively low R_s rates during periods of high temperature and low rainfall (Maestre and Cortina 2003; Xu et al. 2004; Baldocchi et al. 2006; Fernandez et al. 2006; Talmon et al. 2011; Cable et al. 2013). In these ecosystems, R_s commonly tracks SWC on a seasonal basis and may be asynchronous with T_s, since for much of the year R_s rates are constrained by moisture limitation (Shen

et al. 2008; Almagro et al. 2009; Carbone et al. 2011; Rey et al. 2011). With the exception of the June 2012 sampling visit, we did not observe this type of seasonal pattern in limestone cedar glades. Across the 16 months of this study, we did not find evidence of reduced temperature effects on R_s under relatively dry conditions (below 15 % SWC).

In sharp contrast to many arid and semi-arid ecosystems, limestone cedar glade soils are also seasonally subjected to wet conditions, up to and including soil saturation (Quarterman 1950b; Norton 2010), conditions we observed most often during the winter and spring (Fig. 2b). Depending on soil porosity, very high soil moisture levels have the potential to interfere with R_s by inhibiting the diffusion of CO_2 and O_2 (Linn and Doran 1984; Hui and Luo 2004; Davidson and Janssens 2006; Almagro et al. 2009; Butler et al. 2011). We observed lower R_s rates under relatively wet conditions (SWC above 40 %) in limestone cedar glades, however, residuals analysis indicated that these wet soil conditions did not suppress R_s independently from co-occurring low temperatures.

Influences of soil organic matter, soil depth, and vegetation on soil respiration

In this study of limestone cedar glades, SOM exhibited considerable spatial variability and was an important control on R_s. We observed a roughly seven-fold difference between maximum and minimum SOM values, and found that the incorporation of SOM (Model 4) dramatically improved model performance relative to a model based only on T_s and SWC (Model 2). Our findings in limestone cedar glades are consistent with studies showing SOM and the soil carbon pool size to be important controls on R_s in grasslands (Thomson et al., 2010; Balogh et al., 2011) and in arid and semi-arid ecosystems (Conant et al. 2000; Sponseller 2007; Talmon et al. 2011). Although we did not measure soil organic carbon or the labile carbon fraction directly, the strong positive relationship we observed between R_s rates and SOM was not surprising, given that R_s can often be predicted effectively using first-order kinetic models (Parton et al. 1988; Zak et al. 1999). This finding supports assertions that Q_{10} estimates can be improved by incorporating substrate-limitation effects on the temperature sensitivity of decomposition (Davidson and Janssens 2006), as our Q_{10} estimate would have been

33 % lower had we failed to incorporate SOM as a model variable.

We observed an increased effect of SOM on R_s under relatively dry conditions for this site (SWC below 15 %). Although we did not partition R_s into autotrophic versus heterotrophic components, this finding is consistent with a hypothesis of increased heterotrophic relative to autotrophic respiration during senescence periods when root-growth respiration is restricted by moisture limitation (Baldocchi et al. 2006; Butler et al. 2011). Under such a scenario, heterotrophic respiration sustained by existing carbon substrate pools might assume greater relative importance to soil CO_2 efflux totals, resulting in R_s patterns that correspond more closely to spatial variability in SOM. To evaluate this hypothesis, future research efforts in limestone cedar glades would need to partition the components of soil CO_2 efflux and compare the relative contributions of these components—as well as their individual relationships to soil carbon pool size—to measurements of root proliferation under various soil moisture conditions.

Results from this study indicate that spatial heterogeneity in soil depth and vegetation cover influenced R_s in limestone cedar glades. Shallow soil and sparse vegetation were both associated with reduced R_s levels, and residuals analysis showed these relationships existed even after accounting for the effects of T_s, SWC, and SOM (Fig. 3). We did not attempt to isolate the effects of soil depth from those of vegetation cover since, as noted by Risch and Frank (2006), effects on R_s of topographic gradients (e.g. soil depth and landscape position) may be difficult to separate from those of the biotic gradients they influence (e.g., vegetation cover). Indeed, vegetation patterns are strongly related to soil depth in limestone cedar glades (Freeman 1933; Quarterman 1950a; Norton 2010). It is noteworthy that our finding of depressed R_s occurred at soil depths below 5 cm, since analysis of botanical data from this ecosystem previously identified the same soil depth threshold to delineate ecological zones (Quarterman 1973; 1989; Quarterman et al. 1993) and primary plant community types (Somers et al. 1986). It should also be noted that our inability to measure R_s in zones of extremely thin soil (below 2 cm soil depth) suggests that the true range of R_s rates in limestone cedar glades—including zones of exposed bedrock and their peripheries—likely includes lower R_s rates than were observed in this study.

The significant positive relationship between vegetation cover and R_s in this study is consistent with

observations from temperate grasslands (Craine and Wedin 2002; Flanagan and Johnson 2005; Risch and Frank 2006; Thomson et al. 2010) and arid and semi-arid ecosystems (Maestre and Cortina 2003; Sponseller 2007; Cable et al. 2008; Talmon et al. 2011). In addition to direct contributions through autotrophic respiration, plants can facilitate heterotrophic respiration by providing carbon substrates in the form of litter and root exudates, thus concentrating resources and associated microbes in rhizosphere soil (Sponseller 2007; Thomson et al. 2010). Plants also affect R_s by influencing the microclimates of their surroundings through effects such as transpiration, rainfall interception, and shading (Raich and Tufekciogul 2000; Almagro et al. 2009). Future research could seek to quantify and partition these effects, as certain zones and ecotones in cedar glades may be vulnerable to vegetation changes such as woody encroachment (Sutter et al. 2011), which can alter R_s dynamics in grasslands (Eler et al. 2013). Future research could also examine R_s across vascular plant associations, e.g. grass-dominated versus forb-dominated communities, and unique assemblages of xerophytic and hydrophytic vegetation (Quarterman 1950a; Norton 2010).

Conclusions

This was the first reported study of R_s in limestone cedar glades. In this rock outcrop ecosystem, Q_{10} was within ranges reported for temperate mesic grasslands, however, R_s rates were somewhat lower than in several studies of tallgrass prairies. Cedar glades are distinguishable from such deep-soil grasslands by having zones of exposed bedrock, extremely thin soils, patchy vegetation distribution, and seasonal fluctuation between both hydrologic extremes. In several respects, the seasonal controls on R_s in limestone cedar glades resembled those in temperate mesic grasslands more than those in arid and semi-arid ecosystems. At a seasonal level, R_s generally tracked T_s for most of the year, and although extreme soil moisture conditions (both xeric and saturated) were occasionally observed, apparent differences in R_s under relatively dry or wet conditions did not exist independently from temperature effects. Although we observed depressed R_s during one sampling visit under summer drought conditions, we did not detect a shift in the temperature sensitivity of R_s when SWC was less than 15 %. SOM was highly variable spatially and an

important control on R_s, such that incorporating its effects dramatically improved model performance over models based only on T_s and SWC. Shallow soils and sparse vegetation cover—defining features of certain ecological zones within this ecosystem—were associated with reduced rates of R_s. Further investigations of soil respiration patterns in limestone cedar glades could employ intensive sampling under xeric conditions, partition heterotrophic versus autotrophic respiration, and examine R_s relationships to vegetation dynamics (e.g. woody encroachment).

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