

Soil Temperature, Not Aboveground Plant Productivity, Best Predicts Intra-Annual Variations of Soil Respiration in Central Iowa Grasslands

Mathew E. Dornbush,^{1*} and James W. Raich²

¹Department of Natural and Applied Sciences, University of Wisconsin–Green Bay, 2420 Nicolet Drive, Green Bay, Wisconsin 54311, USA; ²Department of Ecology, Evolution, and Organismal Biology, Iowa State University, 253 Bessey Hall, Ames, Iowa 50011, USA

ABSTRACT

Soil respiration (R_{SOIL}) is the second largest carbon flux between terrestrial systems and the atmosphere, with a magnitude 10 times greater than anthropogenic carbon dioxide production. Therefore, it is important that we understand, and be able to predict, how R_{SOIL} responds to climate change. Although a positive, significant temperature effect on R_{SOIL} has long been recognized, recent studies emphasize the overriding importance of current photosynthesis in controlling R_{SOIL} . We tested the hypothesis that model inclusion of intra-annual variations in aboveground net primary productivity (ANPP) significantly improves R_{SOIL} estimates over predictions based on soil temperature alone. We also evaluated the possibility that canopy production is less directly linked to R_{SOIL} , by testing the hypothesis that intersite differences in R_{SOIL} correlate more strongly with root biomass than with ANPP. We tested these hypotheses by measuring R_{SOIL} , ANPP, and root biomass at four Iowa grasslands that differed in aboveground growth phenol-

ogy and productivity. Among all sites, intra-annual variations in R_{SOIL} were most strongly related to soil temperature ($R^2 = 0.89$), not ANPP ($R^2 = 0.53$). All sites responded identically to changes in soil temperature (site-by-temperature $P = 0.53$), but inconsistently to variation in aboveground dynamics (site-by-canopy $P < 0.0001$). Incorporating canopy dynamics into temperature-based predictive models improved model R^2 by a maximum of 0.01. Among-site differences in R_{SOIL} were related to root biomass ($P < 0.001$) but not ANPP ($P = 0.34$). We found no useful linkage between canopy characteristics and intra-annual or site-specific R_{SOIL} predictions, perhaps because shoot and root dynamics were not consistently linked through time or among sites.

Key words: C_3 versus C_4 ; net primary productivity; plant phenology; root biomass; soil carbon dioxide flux; standing live biomass; Iowa grasslands.

INTRODUCTION

Global estimates suggest that 75–80 Pg of carbon dioxide-carbon ($\text{CO}_2\text{-C}$) are produced by soils

annually (Schlesinger 1977; Raich and others 2002), in contrast to approximately 6 Pg from fossil fuel emissions and approximately 2 Pg from land-use change (Houghton and others 2001). Any factors that serve to increase or decrease the magnitude of soil respiration (R_{SOIL}) could significantly alter atmospheric CO_2 concentrations

Received 1 July 2005; accepted 14 November 2005; published online 30 September 2006.

*Corresponding author; e-mail: dornbusm@uwgb.edu

and thus play an important role in future climate change. For this reason, clarifying the relative importance of the environmental factors that control R_{SOIL} would substantially improve our understanding of the terrestrial C cycle and thus our ability to model it.

Soil respiration is a composite measure of total soil activity, driven by respiration from roots, their symbionts, and microbial activity (Raich and Schlesinger 1992). This process has been described historically as a function of soil temperature and moisture (Kucera and Kirkham 1971; Anderson 1973; Knapp and others 1998; Mielenick and Dugas 2000), a relationship justified by the known effects of these variables on microbial and root metabolic activity (Meentemeyer 1978; Boone and others 1998). Recently, however, several studies have suggested that R_{SOIL} is directly dependent on recent plant photosynthesis or growth (Bremer and others 1998; Craine and others 1999; Högberg and others 2001; Bremer and Ham 2002; Franzluebbers and others 2002; Yuste and others 2004). Although these two perspectives are not mutually exclusive, traditional views assume that soils contain excess C substrate, and thus emphasize the importance of factors influencing rates of metabolic C losses, whereas more recent, plant photosynthesis-based views suggest that R_{SOIL} is substrate limited, not climatically limited.

Several studies have emphasized that the physiological linkage between recent plant photosynthesis and R_{SOIL} provides a means to improve R_{SOIL} predictions, if information on aboveground plant growth or canopy characteristics is included in intra-annual R_{SOIL} models (Bremer and others 1998; Fitter and others 1998; Craine and others 1999; Bremer and Ham 2002; Franzluebbers and others 2002; Wan and Luo 2003). For example, Reichstein and others (2003) adopted this approach in a study that used canopy characteristics to improve the site-specific predictive accuracy of a large-scale R_{SOIL} model. The conceptual argument for this position is that a large portion of R_{SOIL} is derived directly from recent plant photosynthesis (Högberg and others 2001; Craine and others 1999; Yuste and others 2004), coupled with the fact that direct quantification of root activity is difficult. In other words, this position suggests that the quantification of aboveground growth or canopy characteristics serves as a useful surrogate for canopy-to-root C flow.

Clearly, relationships between plant photosynthesis or production and R_{SOIL} must exist over the long term, given that soil-derived CO_2 is ultimately based on photosynthetically derived or-

ganic C. In fact, this relationship has been established by a number of large-scale studies (Schlesinger 1977; Raich and Nadelhoffer 1989; Raich and Tufekcioglu 2000; Janssens and others 2001; Litton and others 2004). One key difference, however, is that the more traditional views do not demand the tight linkage between canopy photosynthesis and R_{SOIL} suggested by the recent substrate-limited models. According to the older paradigm, plant production affects R_{SOIL} through less direct or longer-term influences—for example, through effects on root biomass or soil C pool size—yet C release from these pools, via either respiration or decomposition, remains largely temperature controlled.

Despite the logical basis for approaches that use easily quantifiable canopy properties to improve R_{SOIL} predictions, there are many important assumptions that still need to be evaluated. First, the proportion of aboveground to belowground production differs among sites (Coupland 1979; McCulley and others 2005). Second, plant C-allocation strategies vary with site characteristics and nutrient availability (Giardina and others 2003, 2004). Further, above- and belowground activity need not be temporally synchronized, and time lags between the activity of shoots and roots can vary among sites (Fitter and others 1998, 1999). These complications could limit the utility of approaches that use canopy characteristics to improve R_{SOIL} models.

Our objective was to improve the accuracy of intra-annual R_{SOIL} predictions for central Iowa grasslands by investigating the relationship between canopy characteristics and R_{SOIL} . We tested the hypothesis that including intra-annual variations in aboveground net primary productivity (ANPP) or live biomass would significantly improve estimates of R_{SOIL} , in comparison to predictions made from soil climate data alone (for example, Bremer and others 1998; Craine and others 1999; Bremer and Ham 2002; Franzluebbers and others 2002; Wan and Luo 2003). In addition, we tested the hypothesis that intersite differences in R_{SOIL} would be more strongly correlated to among-site differences in root biomass than in annual ANPP. To test these two hypotheses, we investigated four planted grasslands in central Iowa, USA, that were located within 2.7 km of each other, occurred on the same soil series and landscape position, and experienced the same weather conditions. However, the sites differed in terms of history, management, age, and dominant plant species. We selected these diverse sites to capture the landscape variability that exists within a regional vegetation

type, including a variety of phenologies and growth patterns. Because weather conditions were similar among sites, but the sites differed in vegetative characteristics, our site selection provided the greatest potential for observing the effects of canopy dynamics on R_{SOIL} .

MATERIALS AND METHODS

Site Description

This study was conducted from May 2001 to June 2002 at four sites in Story County, Iowa, USA (42°11' N, 93°30' W). All sites were located on Coland soils, a fine-loamy, mixed, mesic Cumic Haplaquoll (DeWitt 1984). General soil properties (0 to 15 cm) for each site are presented in Table 1. Sites varied in planting age and in dominant species. They included a cool-season (C_3) meadow dominated by *Bromus inermis* Leysser (smooth brome), *Dactylis glomerata* L. (orchard grass), and *Phalaris arundinacea* L. (reed canary grass). This site was formerly grazed pasture; grazing was stopped in 1990. The remaining three sites were dominated by warm-season (C_4) species and were all under conventional row crop agriculture prior to being planted. The oldest C_4 site (1994- C_4) was a virtual monoculture of *Panicum virgatum* L. (switchgrass) planted in 1994. A second site (1999- C_4) was planted in 1999 and was dominated by *P. virgatum* L., *Sorghastrum nutans* L. (Indian grass), and *Setaria* spp. (foxtails), but also contained the forbs *Echinacea purpurea* (L.) Moench (Asteraceae), *Solidago canadensis* L. (Asteraceae), *Verbena stricta* Vent. (Verbenaceae), and *Desmanthus illinoensis* (Michx.) MacM. ex B. L. Robinson & Fern (Fabaceae). The fourth site (2001- C_4) was planted in 2001, just before this study began, and contained a mixture of young C_4 grasses and dicotyledonous C_4 annual weeds such as *Amaranthus* spp. (Amaranthaceae) and *Xanthium strumarium* L. (Asteraceae). Both the 1994 and 1999 plantings were burned prior to study initiation in the early spring of 2001. Each site contained three nonadjacent plots that varied in size from 72 to 360 m².

Central Iowa has a continental climate, with a mean annual temperature of 9.2°C; and average monthly temperatures ranging from 23.2°C in July to -7.5°C in January. Approximately 62% of the 86.5 cm of mean annual precipitation falls between April and September, when average monthly temperatures are greater than 15°C (data from the Midwestern Regional Climate Center, available online at <http://mcc.sws.uiuc.edu/>).

Table 1. Mean Annual Soil Respiration, Aboveground Net Primary Production, Root Biomass, Soil Carbon and Nitrogen Content, and Soil Bulk Density in Four Grasslands in Central Iowa, USA

Site	Soil C (%)	Soil N (%)	Soil Bulk Density (g cm ⁻³)	Soil Respiration (g C m ⁻² y ⁻¹)	Scurlock ANPP (g C m ⁻² y ⁻¹)	Gompertz ANPP _G (g C m ⁻² y ⁻¹)	Belowground Biomass (g C m ⁻²)
C_3	3.4 ± 0.2 a	0.29 ± 0.02 a	1.02 ± 0.08 b	1300 ± 100 a	270 ± 70 b	280 ± 70 b	320 ± 50 a
1994- C_4	1.4 ± 0.2 b	0.11 ± 0.02 b	1.27 ± 0.06 a	1260 ± 30 a	820 ± 120 a	850 ± 130 a	190 ± 70 a, b
1999- C_4	3.7 ± 0.4 a	0.30 ± 0.03 a	1.16 ± 0.04 a, b	940 ± 40 b	320 ± 80 b	330 ± 80 b	110 ± 10 b
2001- C_4	1.9 ± 0.2 b	0.16 ± 0.02 b	1.28 ± 0.01 a	730 ± 10 b	380 ± 20 b	400 ± 20 b	20 ± 10 b

C, carbon; N, nitrogen; ANPP, aboveground net primary production; ANPP_G, ANPP determined using the Gompertz growth model.

Mean ± SE is presented for all variables (n = 3).

All sites were on Coland soils, with soil and root biomass values derived from four samples per plot and three plots per site (0 to 15 cm). Soil C and N contents were determined using a Flash EA 1112 Elemental Analyzer (Thermo Finnigan Italia, Rodano, MI, Italy). Bulk density was determined on volumetric cores and is corrected for gravel volume (<5% of total soil volume). The C_3 site was a mixed-species, cool-season meadow; 1994- C_4 was a virtual monoculture of *P. virgatum* planted in 1994; 1999- C_4 was a mixed, warm-season grassland established in 1999; and 2001- C_4 was a mixed, warm-season grassland planted in spring 2001 and was still dominated by annual weeds. ANPP was calculated following Scurlock and others' (2002) method 6, or by fitting a three-parameter Gompertz model to cumulative production data. Different letters (a, b) within a column denote statistically significant differences (Tukey-Kramer HSD, $\alpha = 0.05$).

Soil Respiration

Soil CO₂ efflux rates were measured twice monthly from day-of-year (DOY) 164 through DOY 235 and monthly during the remainder of the study; measurements were taken between 10:00 AM and 3:00 PM. The large number of sites and samples made it impossible to measure R_{SOIL} at all sites on a single day; thus, each sample period took between 2 and 4 days to complete. Subsequent sample dates in this report refer to the median date of each sample period. Soil respiration was measured using a LI-COR 6400 portable photosynthesis system attached to a 6400-09 soil efflux chamber (LI-COR, Lincoln, NE, USA) following standard procedures recommended by LI-COR and used by other authors (Norman and others 1992; Knapp and others 1998; Mielnick and Dugas 2000; Luo and others 2001; Bremer and Ham 2002). Briefly, measurements were taken by setting the soil chamber on 10-cm-diameter PVC collars that were placed randomly throughout each plot. All live aboveground plant tissues within collars were removed, but surface litter was left intact. Soil CO₂ fluxes for each collar were based on an average of two to three measurement cycles. During the growing season, an average of eight collars per plot were installed roughly 1 day prior to R_{SOIL} measurements. From November 2001 to March 2002, six collars were installed per plot and measured throughout the dormant season. Annual R_{SOIL} rates were determined by integration of the area under the intra-annual R_{SOIL} curve from May 2001 to May 2002, as done previously by Bremer and Ham (2002) and Knapp and others (1998).

Soil temperature (°C) at 5-cm depth was recorded whenever R_{SOIL} was measured. Gravimetric soil moisture content (0–5-cm depth) was measured whenever the soil was not frozen. To enhance comparability with other studies, soil gravimetric moisture data were converted to percent water-filled pore space (WFPS) following Linn and Doran (1984).

Plant Biomass and Aboveground Productivity

All living and dead aboveground biomass and surface litter was harvested eight times from four 0.25-m² quadrats per plot. Biomass harvest locations were subsequently excluded from R_{SOIL} measurements. Biomass was sorted into live biomass and detritus. Samples for each date and plot were analyzed for C and nitrogen (N) content using a Flash EA 1112 Elemental Analyzer (Thermo Finnigan Italia, Rodano, MI, Italy). Plant biomass

was converted to a C and N mass basis and corrected to 105°C dry mass. Surface timer values were reported as ash-free (3h at 500°C) dry mass to adjust for possible soil contamination was treated identically, except all values were reported as ash-free (3 h at 500°C) dry mass.

Monthly plot-level live biomass and detritus mass were incorporated into a rule-based procedure to determine ANPP between each successive sample date (method 6 as described by Scurlock and others 2002). Across each time period, ANPP was calculated based on the following rules:

If $\Delta\text{Live} > 0$ and $\Delta\text{Detritus} > 0$, then ANPP =

$$\Delta\text{Live} + \Delta\text{Detritus}$$

If $\Delta\text{Live} > 0$ and $\Delta\text{Detritus} < 0$, then ANPP = ΔLive

If $\Delta\text{Live} < 0$ and $\Delta\text{Detritus} > 0$, then ANPP =

$$\Delta\text{Live} + \Delta\text{Detritus}$$

If $\Delta\text{Live} < 0$ and $\Delta\text{Detritus} < 0$, then ANPP = 0

If ANPP < 0, then ANPP = 0

where ΔLive represents change in live biomass between successive sample dates, and $\Delta\text{Detritus}$ represents change in dead biomass between successive sample dates. This method attempts to account for concurrent biomass production and losses, providing a robust method of estimating grassland ANPP (Scurlock and others 2002). Annual ANPP for each plot was determined by summing ANPP from all periods between DOY 150, 2001, and DOY 154, 2002, then correcting to a 365-day year.

To describe the intra-annual dynamics of aboveground growth, we also used a Gompertz growth model to calculate daily and annual ANPP (ANPP_G). To do so, the field-based estimates of ANPP described above were cumulated through time for each plot, and those cumulative biomass production estimates were fit with a three-parameter Gompertz model using SigmaPlot (SPSS, Chicago, IL, USA).

Root biomass (gC m⁻²) for the 0- to 15-cm depth was sampled using a 5.4-cm-diameter corer in November 2001. Four cores were taken from each plot, roots were carefully removed from soil by hand-washing over a 0.5-mm sieve, organic debris was removed, and all mass values were converted to a 105°C mass basis following the procedure described previously for standing aboveground biomass.

Statistical Analysis

All data were analyzed using JMP version 4.0.4 (SAS Institute, Cary, NC, USA). We applied a two-step process to test the hypothesis that intra-annual

variations in aboveground productivity significantly improve intra-annual estimates of R_{SOIL} . First, stepwise multiple linear regression was used to objectively identify variables useful for predicting intra-annual patterns of R_{SOIL} , including both biotic and abiotic variables. We evaluated multiple measures of plant canopy dynamics, because we had no a priori knowledge of which measure would best correlate with R_{SOIL} and because different studies have suggested different variables (for example, Franzluebbers and others 2002; Bremer and Ham 2002). Second, those variables identified as important by stepwise regression were tested for significance using a general linear model repeated measures analysis of covariance (RM-ANCOVA). Nonsignificant terms ($\alpha > 0.05$) were removed from the final model. All statistics were conducted using plot-level data ($n = 3/\text{site}$). To meet model assumptions of uniform variance, (R_{SOIL}) values were natural-log-transformed prior to analyses, whereas live aboveground biomass and ANPP were square-root-transformed.

Independent abiotic factors considered included soil temperature and soil moisture content. To avoid spurious results due to freeze-thaw events, we excluded the January and February sample dates from our statistical analyses. This resulted in the exclusion of 24 of 168 values, leaving a sample size of 144 in the RM-ANCOVA. Biotic variables examined included live aboveground biomass C, live aboveground biomass N, and ANPP_G. Standing live biomass on R_{SOIL} sampling dates was determined by linear regression between adjacent live biomass harvests. The first derivative of the fitted Gompertz model for each plot was used to determine plot-specific ANPP rates for each R_{SOIL} measurement date. Soil temperature, ANPP_G, live aboveground C, and live aboveground N were also evaluated independently with RM-ANCOVA to define their individual effectiveness for predicting R_{SOIL} .

We used a post hoc analysis that correlated site-specific annual aboveground production (ANPP [$\text{g C m}^{-2} \text{y}^{-1}$] and ANPP_G [$\text{g C m}^{-2} \text{y}^{-1}$]) and root biomass (g C or g N m^{-2}) with site-specific intercepts taken from our soil temperature-based predictive model to address hypothesis two—that canopy production may be less directly linked to R_{SOIL} than suggested by recent substrate-limited models. In addition, we correlated the same intersite R_{SOIL} values with site-specific soil properties (bulk density [g cm^{-3}], soil C [g C m^{-2}], and soil N [g N m^{-2}]) to address potential site-specific effects resulting from the varied site histories.

Among-site differences in soil temperature, WFPS, aboveground biomass C and N, ANPP_G, and

R_{SOIL} were determined using a general linear model repeated-measures analysis of variance. Model parameters included site, sample date, and a site-by-date interaction term. Intra-annual periods of maximum soil temperature, live aboveground biomass, and R_{SOIL} were identified using Tukey-Kramer HSD tests ($\alpha = 0.05$). Intersite differences in annual R_{SOIL} ($\text{g C m}^{-2} \text{y}^{-1}$), ANPP ($\text{g C m}^{-2} \text{y}^{-1}$), end-of-year root biomass (g C m^{-2}), soil C and N (%), and bulk density (g cm^{-3}) were determined using analysis of variance (ANOVA), followed by pairwise comparisons using Tukey-Kramer HSD tests ($\alpha = 0.05$).

RESULTS

Soil Temperature and Moisture

Soil temperature ($^{\circ}\text{C}$) was significantly affected by site ($F_{3,8} = 9.7$, $P < 0.01$), sample date ($F_{11,88} = 906.8$, $P < 0.0001$), and the site-by-date interaction ($F_{33,88} = 8.4$, $P < 0.0001$). Averaged across sample dates, 1999-C₄ and 2001-C₄ had mean soil temperatures of 16.9 ± 1.6 and $17.0 \pm 1.5^{\circ}\text{C}$, respectively, versus $15.0 \pm 1.4^{\circ}\text{C}$ in 1994-C₄ and $14.7 \pm 1.4^{\circ}\text{C}$ in C₃ (Tukey-Kramer HSD, $\alpha = 0.05$). The fact that the sample date effect ($F_{11,88} = 906.8$) was over 100 times greater than the site-by-sample date interaction effect ($F_{33,88} = 8.4$) highlights that intra-annual soil temperature patterns were similar at all sites (Figure 1a). The significant site-by-date interaction resulted at least in part from day-to-day differences in temperature occurring within sample periods (for example, cloudy skies and cool temperatures versus clear skies and warm temperatures). Maximum soil temperatures occurred between DOY 177 and 214 at all sites (Tukey-Kramer HSD, $\alpha = 0.05$).

Soil water-filled pore space (WFPS) was significantly affected by sample date ($F_{11,88} = 40.6$, $P < 0.0001$), due to intra-annual variations in moisture (Figure 1b). The site main effect was not significant ($F_{3,8} = 0.2$, $P = 0.9$), indicating that all sites had similar soil moisture conditions when averaged across the year. The site-by-date interaction was significant ($F_{33,88} = 3.2$, $P < 0.0001$), largely because individual sample periods included rainfall events (for example, DOY 200). Water-filled pore space ranged between 30% and 60% for most of the year (Figure 1b). Lowest recorded WFPS coincided with maximum summer soil temperatures, dropping below 30% from DOY 177 to DOY 214.

Live Aboveground Biomass

Standing live biomass C differed significantly among sites ($F_{3,8} = 58.2$, $P < 0.0001$) and sample

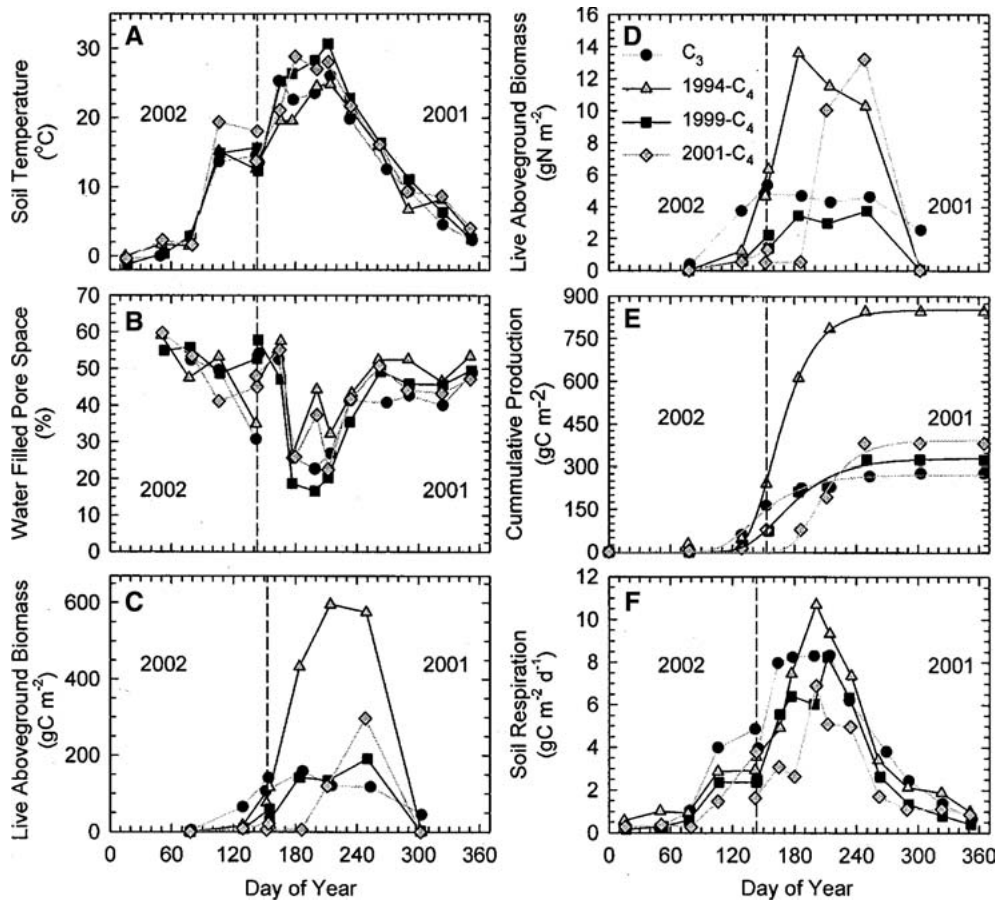


Figure 1. Intra-annual trends in **A** soil temperature, **B** water-filled pore space, **C** live aboveground biomass carbon, **D** live aboveground biomass nitrogen, **E** cumulative aboveground production, and **F** soil respiration at four grasslands in central Iowa, USA. Samples were taken from May 2001 to May 2002. A legend identifying the sites is embedded in part.

periods ($F_{11,88} = 280.7$, $P < 0.0001$), and the site-by-sample period interaction ($F_{33,88} = 30.6$, $P < 0.0001$). Averaged across sample dates, 1994-C₄ had the highest average standing live biomass (246 ± 40 g C m⁻²) (Tukey-Kramer HSD, $\alpha = 0.05$). The C₃ site had the next highest average biomass level (86 ± 8 g C m⁻²), which was statistically greater than levels in both 1999-C₄ (72 ± 12 g C m⁻²) and 2001-C₄ (63 ± 14 g C m⁻²) (Tukey-Kramer HSD, $\alpha = 0.05$). Peak live biomass occurred earliest in the C₃ site, by DOY 164, followed roughly 2 weeks later (DOY 177) in 1999-C₄ (Figure 1c). Maximum live biomass did not occur until DOY 201 at 1994-C₄ and DOY 234 at 2001-C₄. Live biomass at the C₃ site showed low intra-annual changes, with maximum levels maintained for roughly 70 days, starting on DOY 164. This is in contrast to the strong intra-annual variability of C₄ sites, where maximum live biomass was maintained for as little as 28 days at 2001-C₄ and 34 days at 1994-C₄. The 1999-C₄ site maintained a longer period of maximum live aboveground biomass,

from DOY 177 to DOY 263, likely reflecting the mixture of C₃ forbs and C₄ grasses in this planting. In addition to intra-annual biomass differences there was a 3.8-fold difference in maximum live biomass C between the C₃ and 1994-C₄ sites, and a 1.6-fold difference between the 1999-C₄ and 2001-C₄ sites.

Standing live biomass N was significantly affected by site ($F_{3,8} = 19.9$, $P < 0.001$), sample period ($F_{11,88} = 99.6$, $P < 0.0001$), and the site-by-sample period interaction ($F_{33,88} = 11.7$, $P < 0.0001$). Averaged across sample dates, 1994-C₄ (5.8 ± 0.9 g N m⁻²) had statistically higher average live biomass N than 1999-C₄ (1.7 ± 0.3 g N m⁻²) and 2001-C₄ (3.7 ± 0.8 g N m⁻²), but did not differ from C₃ (3.4 ± 0.3 g N m⁻²) (Tukey-Kramer HSD, $\alpha = 0.05$). Average biomass N for C₃ was statistically greater than for 1999-C₄, but 1999-C₄ and 2001-C₄ did not differ statistically. Peak live biomass N was reached by DOY 142 and maintained until DOY 269 at both the C₃ and 1999-C₄ sites (Figure 1d). Maximum live biomass N was reached by DOY 166 at 1994-C₄

and DOY 201 at 2001-C₄ (Figure 1d). These levels were maintained for 95 days, at 1994-C₄ and 61 days at 2001-C₄. As observed with C, biomass N varied considerably among sites: maximum live N at 1994-C₄ and 2001-C₄ were roughly 2.6 times greater than at C₃.

Aboveground Production

The three-parameter Gompertz models fit observed data with an average coefficient of determination (R^2) of 0.98 for each of the 12 plots. At the site level, R^2 ranged from 0.97 for 2001-C₄ to 0.99 for 1994-C₄ and 1999-C₄. ANPP_G was significantly affected by site ($F_{3,8} = 4.4$, $P < 0.05$), sample date ($F_{11,88} = 54.5$, $P < 0.0001$), and the site-by-date interaction ($F_{33,88} = 9.6$, $P < 0.0001$). Average growth rate in 1994-C₄ (3.6 ± 0.8 g C m⁻² d⁻¹) was statistically greater than that in C₃ (0.9 ± 0.2 g C m⁻² d⁻¹) (Tukey-Kramer HSD, $\alpha = 0.05$), but there were no other statistically significant differences among sites (1999-C₄: 1.4 ± 0.3 ; 2001-C₄: 1.7 ± 0.4 g C m⁻² d⁻¹). The C₃ site was the first to begin accumulating new biomass in the spring, followed successively by 1994-C₄, 1999-C₄, and 2001-C₄ (Figure 1e). Maximum ANPP_G at the C₃ site occurred earliest in the growing season, reaching 3.5 ± 0.4 g C m⁻² d⁻¹ on DOY 136 (Figure 2). Aboveground productivity peaked at 13.3 ± 2.5 g C m⁻² d⁻¹ on DOY 159 at 1994-C₄, and at 3.7 ± 0.7 g C m⁻² d⁻¹ from DOY 163 to DOY 165 at 1999-C₄. Maximum ANPP_G was 5.6 ± 1.5 g C m⁻² d⁻¹ at 2001-C₄, but it did not occur until over 1 month later (DOY 205) than at the other two C₄ sites, and more than 2 months later than at the C₃ site. Thus, our sites displayed three distinct intra-annual growth patterns, with maximum aboveground productivity occurring in spring (C₃ site), early summer (1994-C₄ and 1999-C₄), and late summer (2001-C₄). In addition, there was a 3.8-fold difference in maximum productivity between 1994-C₄ and the C₃ sites. The 1994-C₄ and 1999-C₄ sites, which had nearly identical intra-annual growth patterns, differed in maximum productivity by 3.6-fold (Figure 2).

Soil Respiration

Average R_{SOIL} rates (g C m⁻² d⁻¹) differed significantly among sites ($F_{3,8} = 30.5$, $P < 0.0001$) and sample dates ($F_{11,88} = 289.9$, $P < 0.0001$), and the site-by-date interaction was also significant ($F_{33,88} = 7.1$, $P < 0.0001$). Average R_{SOIL} was significantly greater in C₃ (4.8 ± 0.5 g C m⁻² d⁻¹) and 1994-C₄ (4.6 ± 0.5 g C m⁻² d⁻¹) than

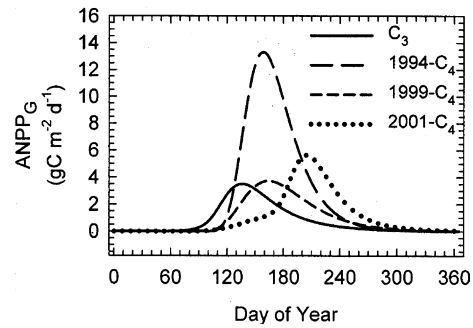


Figure 2. Intra-annual trends in aboveground net primary productivity (ANPP) at four grasslands in central Iowa, USA. Productivity was determined by taking the first derivative of three-parameter Gompertz models fitted to cumulative production at each plot ($n = 3$ per site).

in 1999-C₄ (3.6 ± 0.5 g C m⁻² d⁻¹) and 2001-C₄ (2.8 ± 0.3 g C m⁻² d⁻¹) (Tukey-Kramer HSD, $\alpha = 0.05$). Soil respiration rates at the C₃ site rose rapidly in spring, reaching roughly half of maximum observed rates by DOY 106. Maximum R_{SOIL} rates at the C₃ site were reached as early as DOY 164 (8.3 ± 1.0 g C m⁻² d⁻¹) and remained relatively constant until DOY 214 (Figure 1f). In contrast, R_{SOIL} rates at the three warm-season sites rose steadily through spring and early summer to relatively sharp maximum peaks between DOY 177 and DOY 212, before declining again to winter lows. Maximum observed R_{SOIL} rates were 11 ± 0.5 g C m⁻² d⁻¹ at 1994-C₄. These values are lower than the 16 g C m⁻² d⁻¹ maximum fluxes observed in Texas tallgrass prairie (Mielnick and Dugas 2000), but they are nearly identical to the maximum fluxes (10.6 g C m⁻² d⁻¹) reported for a Kansas tallgrass prairie (Bremer and others 1998).

Predicting Intra-annual Soil Respiration

A soil temperature-based model that included site, date, and soil temperature effects accounted for virtually all differences in observed R_{SOIL} rates among sites and among dates ($R^2 = 0.89$, $R^2_{\text{adj}} = 0.88$, $F_{12, 131} = 85.5$, $P < 0.0001$). Site identity ($F_{3, 8} = 24.3$, $P < 0.001$) and soil temperature ($F_{1, 131} = 935.8$, $P < 0.0001$) main effects were both significant in the model, but the site-by-soil temperature interaction term was not ($P = 0.5$). Thus, all sites, irrespective of the dominant vegetation, past history, or management, responded identically to intra-annual variations in soil temperature, but the sites had significantly different intercepts. In contrast, live aboveground biomass N, which had the highest correlation with R_{SOIL} of all plant variables, was less successful in predict-

ing R_{SOIL} ($R^2 = 0.68$, $R^2_{\text{adj}} = 0.65$, $F_{15, 128} = 18.4$, $P < 0.0001$). As with the temperature-based model, site identity ($F_{3, 8} = 8.8$, $P < 0.0001$) and above-ground biomass N ($F_{1, 128} = 208.1$, $P < 0.0001$) main effects were both significant. However, this model also required the addition of a site-by-aboveground biomass N interaction term ($F_{3, 128} = 18.0$, $P < 0.0001$). In general, R_{SOIL} in the C_3 and 1999- C_4 sites showed a stronger response to increases in aboveground biomass N than did the 1994- C_4 and 2001- C_4 sites. Furthermore, predictions based on soil temperature, live aboveground biomass N, and a significant site-by-aboveground biomass N interaction term, as suggested by stepwise selection, provided only minuscule improvements ($R^2 = 0.90$, $R^2_{\text{adj}} = 0.89$, $F_{16, 127} = 73.8$, $P < 0.0001$) over R_{SOIL} predictions based on soil temperature alone ($R^2 = 0.89$, $R^2_{\text{adj}} = 0.88$).

We also tested the effects of live aboveground biomass C and ANPP_G on intra-annual R_{SOIL} independent of other variables. The predictive accuracy of live aboveground biomass C ($R^2 = 0.65$, $R^2_{\text{adj}} = 0.60$, $F_{15, 128} = 15.5$, $P < 0.0001$) was slightly lower than that of live aboveground biomass N ($R^2 = 0.68$, $R^2_{\text{adj}} = 0.65$). Live aboveground biomass C, as with aboveground biomass N, also required the inclusion of a significant site-by-biomass C interaction term ($P < 0.0001$). ANPP_G was the poorest biotic predictor of R_{SOIL} that we examined ($R^2 = 0.53$, $R^2_{\text{adj}} = 0.47$, $F_{15, 128} = 9.6$, $P < 0.0001$), and also required the inclusion of a significant site-by- ANPP_G interaction term. Irrespective of the model used, soil temperature consistently provided R^2 values of 0.89, did not require the site-specific interaction terms needed for canopy-based models, and the addition of live aboveground biomass N, live aboveground biomass C, or ANPP_G added no more than 0.01 to model R^2 . Reducing our data set to include only the growing season ($n = 107$)—that is, excluding all data from November through March—did not alter any of these trends. The same trends and findings also held true when site-specific analyses were conducted. Thus, our findings were robust across both dominant vegetation types and site histories.

Annual Aboveground Production, Root Biomass, and Soil Respiration

Sites differed significantly in ANPP (ANOVA $F_{3, 11} = 10.2$, $P < 0.01$), ranging from $270 \pm 70 \text{ g C m}^{-2} \text{ y}^{-1}$ at the C_3 site to $820 \pm 120 \text{ g C m}^{-2} \text{ y}^{-1}$ at 1994- C_4 (Table 1). Aboveground production was significantly greater at 1994- C_4 than at all other sites

(Tukey-Kramer HSD, $P \leq 0.05$). Our ANPP values for C_3 , 1999- C_4 , and 2001- C_4 are similar to the $81\text{--}340 \text{ g C m}^{-2} \text{ y}^{-1}$ reported from a Kansas tallgrass prairie (Briggs and Knapp 1995; assuming grass biomass was 45% C). The ANPP values for 1994- C_4 are within the range of production values reported for planted grasslands by Heaton and others (2004) and similar to values reported by Tufekcioglu and others (2003) from a nearby site. Aboveground NPP values (ANPP_G) determined using the Gompertz model were very similar to those determined using Scurlock and others' (2002) method 6, but were in general slightly higher (Table 1).

End-of-season root biomass also differed significantly among sites (ANOVA $F_{3, 11} = 8.1$, $P < 0.01$), ranging from $22 \pm 7 \text{ g C m}^{-2}$ at 2001- C_4 to $320 \pm 51 \text{ g C m}^{-2}$ at the C_3 grassland (Table 1). Root biomass was significantly greater ($P \leq 0.05$) at the C_3 planting than at 1999- C_4 and 2001- C_4 , but it did not differ significantly from that at 1994- C_4 .

Mean annual R_{SOIL} varied nearly twofold among sites, ranging from $730 \pm 10 \text{ g C m}^{-2} \text{ y}^{-1}$ at 2001- C_4 to $1300 \pm 100 \text{ g C m}^{-2} \text{ y}^{-1}$ at the C_3 site (ANOVA $F_{3, 11} = 21.6$, $P < 0.001$) (Table 1). Annual R_{SOIL} at the C_3 and 1994- C_4 sites did not differ significantly, nor was there a significant difference between 1999- C_4 and 2001- C_4 . Annual R_{SOIL} in the two oldest plantings (that is, the C_3 and 1994- C_4 sites) were significantly higher than rates in the two youngest plantings (1999- C_4 and 2001- C_4) (Tukey-Kramer HSD, $P \leq 0.05$). The annual R_{SOIL} values that we report from the C_3 , 1994- C_4 , and 1999- C_4 sites are similar to the 1- to-2.1 $\text{kg C m}^{-2} \text{ y}^{-1}$ range reported by Mielnick and Dugas (2000) for humid Texas tallgrass prairie and the 1.3- to-2.1 $\text{kg C m}^{-2} \text{ y}^{-1}$ range reported for Kansas tallgrass prairie by Knapp and others (1998). The recently planted 2001- C_4 site had slightly lower R_{SOIL} values than these older sites.

Post hoc Test of Hypothesis Two

Despite the fact that all of our sites responded identically to changes in soil temperature (site-by-soil temperature: $P = 0.5$), R_{SOIL} at a given soil temperature still varied significantly among sites (site identity: $F_{3, 8} = 24.3$, $P < 0.001$). We found no significant correlation between site-specific model intercepts and soil bulk density ($r = -0.45$, $n = 12$, $P = 0.14$), soil C ($r = -0.15$, $n = 12$, $P = 0.65$), soil N ($r = -0.14$, $n = 12$, $P = 0.66$), annual ANPP ($r = 0.30$, $n = 12$, $P = 0.34$) (Figure 3a) or annual ANPP_G ($r = 0.30$, $n = 12$, $P = 0.35$). However, site-specific model intercepts were positively and significantly correlated with root biomass C ($r = 0.85$,

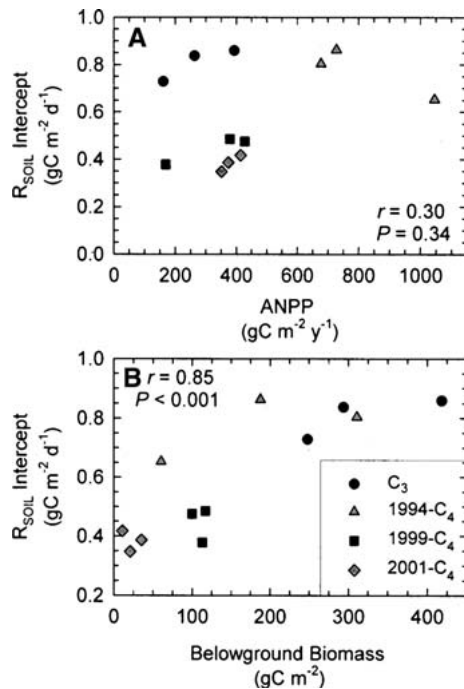


Figure 3. Correlations between plot-specific model soil respiration (R_{SOIL}) intercepts and **A** annual aboveground net primary production (ANPP) and **B** root biomass C (0 to 15-cm deep) at four grasslands in central Iowa, USA.

$n = 12$, $P < 0.001$) (Figure 3b) and root biomass N ($r = 0.84$, $n = 12$, $P < 0.001$).

DISCUSSION

Intra-annual R_{SOIL} was more strongly correlated with soil temperature ($R^2 = 0.89$) than plant ANPP_G ($R^2 = 0.53$). The highest R^2 for any measured plant variable was 0.68 for live standing biomass N. In addition, all three canopy characteristics examined required the addition of a site-by-canopy measure interaction term, complicating the general applicability of these variables for R_{SOIL} models. Omission of interaction terms from canopy-based models significantly reduced their effectiveness; R^2 reductions ranged from 0.08 to 0.13. In contrast, our findings support previous results showing a strong relationship between R_{SOIL} and soil temperature (Knapp and others 1998; Buchmann 2000; Mielnick and Dugas 2000; Tufekcioglu and others 2001). Furthermore, soil temperature-based models were also more parsimonious than canopy-based models: the site-by-soil temperature interaction term was not significant.

Recently, several studies have reported a strong relationship between canopy characteristics and

R_{SOIL} , suggesting a tight coupling between photosynthesis and belowground CO_2 production. Most notably, Högberg and others (2001) girdled *Pinus sylvestris* L. (Scots pine) trees in northern Sweden, and after 1–2 months they noted a 54% reduction in R_{SOIL} . Their result clearly establishes a relationship between R_{SOIL} and recent plant photosynthesis. Our findings do not dispute this conclusion, because prolonged starvation of belowground C supply will result in reduced C availability and subsequent metabolism. In contrast, we addressed the inherent assumption that the inclusion of some measure of canopy activity would significantly improve landscape-level predictive estimates of R_{SOIL} by providing a meaningful surrogate of shoot-to-root C flow. We found no useful linkages between aboveground canopy dynamics and soil respiration rates in our central Iowa grassland sites.

Bremer and others (1998), Bremer and Ham (2002), and Craine and others (1999) reported reductions in R_{SOIL} rates of 19% to 49% after growing-season clippings. Although their results provide evidence that the condition of the canopy can influence C availability and supply belowground, in agreement with root C supply theory (Farrar and Jones 2000), we believe that they may have overestimated the relative importance of this effect. For example, Bremer and others (1998) reported that R_{SOIL} was reduced by up to 49% 2 days after clipping. However, when considered on an annual basis, clipping reduced R_{SOIL} by only roughly 18% (Bremer and others 1998). More significantly, the effects of clipping and grazing may better reflect subsequent changes in root biomass (Knapp and others 1998; Wan and Luo 2003) or plant allocation strategies (Culvenor and others 1989a, 1989b) than intra-annual effects of canopy-to-root C flow on R_{SOIL} . Our results support this conclusion. When data collected during all seasons were evaluated, the addition of live aboveground biomass in our temperature-based intra-annual R_{SOIL} model improved total model R^2_{adj} by only 0.01. This result occurred despite three distinct intra-annual growth patterns (Figures 1e and 2) and a nearly fourfold difference in maximum aboveground live biomass C (Figure 1c) among our sites. Stated another way, the magnitude and importance of seasonal changes in soil temperature far outweighed seasonal changes in, and differences among, aboveground production in affecting R_{SOIL} at our sites.

Despite a threefold range in annual aboveground production (270–820 $\text{g C m}^{-2} \text{y}^{-1}$) and a nearly twofold range in R_{SOIL} (730–1300 $\text{g C m}^{-2} \text{y}^{-1}$) across our sites, there was no significant correlation

between aboveground production and site-specific R_{SOIL} rates (that is, site-specific model intercepts) (Figure 3a). However, site-specific differences in R_{SOIL} were significantly and positively correlated with root biomass (Figure 3b). The dominance of belowground production in total grassland NPP (Dahlman and Kucera and others 1965; Kucera 1992; Gill and Jackson 2000) and the frequent removal of aboveground biomass by fire (Knapp 1985; Knapp and others 1998), mowing, or grazing (McNaughton 1985; Collins and others 1998; Bremer and Ham 2002) may weaken the relationship between grassland ANPP and R_{SOIL} . This conclusion agrees with the results of other grassland studies conducted across similar geographical scales. Kucera and Kirkham (1971) found a strong correlation ($r = 0.72$) between root biomass and soil respiration rates in Missouri tallgrass prairie. Wan and Luo (2003) conducted a clipping and shading experiment in Oklahoma tallgrass prairie. They found that soil respiration reductions of 42%, 46%, and 58%, respectively, for the clipped shaded, and clipped-plus-shaded plots corresponded with decreases in root biomass of 24%, 38%, and 45%, respectively, over the same period. Craine and Wedin (2002) found strong positive relationships between root biomass and soil respiration rates measured in Minnesota experimental grasslands. Knapp and others (1998) attributed observed increases and decreases in soil respiration associated with fire and grazing treatments in Kansas tallgrass prairie to changes in belowground biomass resulting from the same treatments. Our results suggest that intersite differences in R_{SOIL} among grasslands may be better explained by differences in root biomass, root production, or root activity than by differences in aboveground production.

The underlying assumption supporting the use of canopy characteristics for predicting R_{SOIL} is that they can provide a surrogate for a nearly immeasurable flux, short-term C flow from shoots-to-roots. We found no evidence that this is a tenable assumption at our grasslands. In contrast, our results are in direct agreement with numerous studies showing strong positive relationships between temperature and rates of CO_2 loss from incubated soils (Kätterer and others 1998; Lomander and others 1998) and roots (Boone and others 1998; Vose and Ryan 2002). However, our results also underscore the importance of plants, because among-site differences in R_{SOIL} were related to differences in root biomass. Although the total allocation of gross primary production belowground is likely to exert a strong influence over R_{SOIL} (Janssens and others 2001),

canopy characteristics at our sites did not serve as an appropriate surrogate measure for this flux. Our study design included four sites that had unique histories and dominant species. This is exactly what real-world ecosystems are composed of, and any predictive model must be robust to land-cover variability. From this perspective, our study indicates that using canopy characteristics to improve intra-annual predictions of R_{SOIL} has limited value in grasslands. Future investigations need to address the influence of root biomass pools, and root production, decay, and activity on R_{SOIL} directly.

ACKNOWLEDGMENTS

This work was funded by a United States Department of Agriculture Sustainable Agriculture Research and Education grant rewarded to J. W. Raich, C. A. Cambardella, T. M. Isenhardt, R. C. Schultz, and W. W. Simpkins, and a National Science Foundation (DEB 034376 to J.W. Raich and G. Mora). We thank I. Larson, R. and S. Risdal, J. Risdal, and L. Strum for allowing access to their land. E. Arentson, K. C. Dohse, K. Larsen-Ferree, J. McGuire, T. Price, and M. Shimerdla contributed numerous hours of hard work in the field and laboratory. R. Schultz, T. Isenhardt, J. Nelson, and E. Stueffer and the Department of Ecology, Evolution, and Organismal Biology at Iowa State University, and Natural and Applied Sciences at the University of Wisconsin Green Bay provided valuable logistical and technical support during this project. We are also grateful to T. Parkin, B. Wilsey, and several anonymous reviewers for their valuable comments on earlier versions of the manuscript.

REFERENCES

- Anderson JM. 1973. Carbon dioxide evolution from two temperate, deciduous woodland soils. *J Appl Ecol* 10:361–78.
- Boone RD, Nadelhoffer KJ, Canary JD, Kaye JP. 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature* 396:570–72.
- Bremer DJ, Ham JM. 2002. Measurement and modeling of soil CO_2 flux in a temperate grassland under mowed and burned regimes. *Ecol Appl* 12:1318–28.
- Bremer DJ, Ham JM, Owensby CE, Knapp AK. 1998. Responses of soil respiration to clipping and grazing in a tallgrass prairie. *J Environ Qual* 27:1539–48.
- Briggs JM, Knapp AK. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. *Am J Bot* 82:1024–30.
- Buchmann N. 2000. Biotic and abiotic factors controlling soil respiration rates in *Picea abies* stands. *Soil Biol Biochem* 32:1625–35.

- Collins SL, Knapp AK, Briggs JM, Blair JM, Steinauer EM. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science* 280:745–7.
- Coupland RT. 1979. Conclusion. In: Coupland RT, Ed. *Grassland ecosystems of the world: analysis of grasslands and their uses*. New York: Cambridge University Press. p 335–87.
- Craine JM, Wedin DA. 2002. Determinants of growing season soil CO₂ flux in a Minnesota grassland. *Biogeochemistry* 59:303–13.
- Craine JM, Wedin DA, Chapin FS III. 1999. Predominance of ecophysiological controls on soil CO₂ flux in a Minnesota grassland. *Plant Soil* 207:77–86.
- Culvenor RA, Davidson IA, Simpson RJ. 1989a. Regrowth by swards of subterranean clover after defoliation. 1. Growth, non-structural carbohydrate and nitrogen content. *Ann Bot* 64:545–56.
- Culvenor RA, Davidson IA, Simpson RJ. 1989b. Regrowth by swards of subterranean clover after defoliation. 2. Carbon exchange in shoot, root and nodule. *Ann Bot* 64:557–67.
- Dahlman RC, Kucera CL. 1965. Root productivity and turnover in native prairie. *Ecology* 46:84–9.
- Davidson EA, Savage K, Bolstad P, Clark DA, Curtis PS, Ellsworth DS, Hanson PJ, and others. 2002. Belowground carbon allocation in forests estimated from litterfall and IRGA-based soil respiration measurements. *Agric For Meteorol* 113:39–51.
- DeWitt TA. 1984. *Soil survey of Story County, Iowa*. Washington, (DC): USDA Soil Conservation Service, 149 p.
- Farrar JF, Jones DL. 2000. The control of carbon acquisition by roots. *New Phytol* 147:43–53.
- Fitter AH, Graves JD, Self GK, Brown TK, Bogie DS, Taylor K. 1998. Root production, turnover and respiration under two grassland types along an altitudinal gradient: influence of temperature and solar radiation. *Oecologia* 114:20–30.
- Fitter AH, Self GK, Brown TK, Bogie DS, Graves JD, Benham D, Ineson P. 1999. Root production and turnover in an upland grassland subjected to artificial soil warming respond to radiation flux and nutrients, not temperature. *Oecologia* 120:575–81.
- Franzluebbers K, Franzluebbers AJ, Jawson MD. 2002. Environmental controls on soil and whole ecosystem respiration from a tallgrass prairie. *Soil Sci Soc Am J* 66:254–62.
- Giardina CP, Ryan MG, Binkley D, Fownes JH. 2003. Primary production and carbon allocation in relation to nutrient supply in a tropical experimental forest. *Global Change Biol* 9:1438–50.
- Giardina CP, Binkley D, Ryan MG, Fownes JH, Senock RS. 2004. Belowground carbon cycling in a humid tropical forest decreases with fertilization. *Oecologia* 139:545–50.
- Gill RA, Jackson RB. 2000. Global patterns of root turnover for terrestrial ecosystems. *New Phytol* 147:13–31.
- Heaton E, Voigt T, Long SP. 2004. A quantitative review comparing the yields of two candidate C₄ perennial biomass crops in relation to nitrogen, temperature and water. *Biomass Bioenergy* 27:21–30.
- Högberg P, Nordgren A, Buchmann N, Taylor AFS, Ekblad A, Högberg MN, Nyberg G, and others. 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* 411:789–92.
- Houghton JT, Ding Y, Noguier M, van der Linden PJ, Dai X, Maskell K, Johnson CA. 2001. *Climate change 2001: The scientific basis*. Cambridge (UK): Cambridge University Press, 881 p.
- Janssens IA, Lankreijer H, Matteucci G, Kowalski AS, Buchmann N, Epron D, Pilegaard K, and others. 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biol* 7:269–78.
- Kätterer T, Reichstein M, Andrén O, Lomander A. 1998. Temperature dependence of organic matter decomposition: a critical review using literature data analyzed with different models. *Biol Fertil Soils* 27:258–62.
- Knapp AK. 1985. Effect of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie. *Ecology* 66:1309–20.
- Knapp AK, Conrad SL, Blair JM. 1998. Determinants of soil CO₂ flux from a sub-humid grassland: effect of fire and fire history. *Ecol Appl* 8:760–70.
- Kucera CL. 1992. Tall-grass prairie. In: Coupland RT, Ed. *Ecosystems of the world; vol 8A. Natural grasslands: introduction and western hemisphere*. New York: Elsevier. p 227–68.
- Kucera CL, Kirkham DR. 1971. Soil respiration in tallgrass prairie in Missouri. *Ecology* 52:912–5.
- Linn DM, Doran JW. 1984. Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and nontilled soils. *Soil Sci Soc Am J* 48:1267–72.
- Litton CM, Ryan MG, Knight DH. 2004. Effects of tree density and stand age on carbon allocation patterns in postfire lodgepole pine. *Ecol Appl* 14:460–75.
- Lomander A, Kätterer T, Andrén O. 1998. Carbon dioxide evolution from top- and subsoil as affected by moisture and constant and fluctuating temperature. *Soil Biol Biochem* 30:2017–22.
- Luo Y, Wan S, Hui D, Wallace LL. 2001. Acclimatization of soil respiration to warming in a tallgrass prairie. *Nature* 413:622–5.
- McCulley RL, Burke IC, Nelson JA, Lauenroth WK, Knapp AK, Kelly EF. 2005. Regional patterns of carbon cycling across the Great Plains of North America. *Ecosystems* 8:106–21.
- McNaughton SJ. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecol Monogr* 55:259–94.
- Meentemeyer V. 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology* 59:465–72.
- Mielnick PC, Dugas WA. 2000. Soil CO₂ flux in a tallgrass prairie. *Soil Biol Biochem* 32:221–8.
- Norman JM, Garcia R, Verma SB. 1992. Soil surface CO₂ fluxes and the carbon budget of a grassland. *J Geophys Res* 97:18845–53.
- Raich JW, Nadelhoffer KJ. 1989. Belowground carbon allocation in forest ecosystems: global trends. *Ecology* 70:1346–54.
- Raich JW, Schlesinger WH. 1992. The global carbon dioxide flux in soil respiration and its relationship to climate. *Tellus* 44B:81–99.
- Raich JW, Tufekcioglu A. 2000. Vegetation and soil respiration: correlations and controls. *Biogeochemistry* 48:71–90.
- Raich JW, Potter CS, Bhagawati D. 2002. Interannual variability in global soil respiration, 1980–94. *Global Change Biol* 8:800–12.
- Reichstein M, Rey A, Freibauer A, Tenhunen J, Valentini R, Banza J, Casals P, and others. 2003. Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices. *Global Biogeochem Cycles* 17:1104, doi:10.1029/2000Gb002035.

- Schlesinger WH. 1977. Carbon balance in terrestrial detritus. *Ann Rev Ecol System* 8:51–81.
- Scurlock JMO, Johnson K, Olson RJ. 2002. Estimating net primary productivity from grassland biomass dynamics measurements. *Global Change Biol* 8:736–53.
- Tufekcioglu A, Raich JW, Isenhardt TM, Schultz RC. 2001. Soil respiration within riparian buffers and adjacent crop fields. *Plant Soil* 229:117–24.
- Tufekcioglu A, Raich JW, Isenhardt TM, Schultz RC. 2003. Biomass, carbon and nitrogen dynamics of multi-species riparian buffers within an agricultural watershed in Iowa, USA. *Agrofor Syst* 57:187–98.
- Vose JM, Ryan MG. 2002. Intra-annual respiration of foliage, fine roots, and woody tissues in relation to growth, tissue N, and photosynthesis. *Global Change Biol* 8:182–93.
- Wan S, Luo Y. 2003. Substrate regulation of soil respiration in a tallgrass prairie: results of a clipping and shading experiment. *Global Biogeochem Cycles* 17:1–12.
- Yuste JC, Janssens IA, Carrara A, Ceulemans R. 2004. Annual Q_{10} of soil respiration reflects plant phenological patterns as well as temperature sensitivity. *Global Change Biol* 10:161–69.