



Changes in photosynthesis and soil moisture drive the seasonal soil respiration-temperature hysteresis relationship



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ABSTRACT

In nearly all large-scale terrestrial ecosystem models, soil respiration is represented as a function of soil temperature. However, the relationship between soil respiration and soil temperature is highly variable across sites and there is often a pronounced hysteresis in the soil respiration-temperature relationship over the course of the growing season. This phenomenon indicates the importance of biophysical factors beyond just temperature in controlling soil respiration. To identify the potential mechanisms of the seasonal soil respiration-temperature hysteresis, we developed a set of numerical models to demonstrate how photosynthesis, soil moisture, and soil temperature, alone and in combination, affect the hysteresis relationship. Then, we used a variant of the model informed by observations of soil respiration, soil temperature, photosynthesis, and soil moisture from multiple mesic and semi-arid ecosystems to quantify the frequency of hysteresis and identify its potential controls. We show that the hysteresis can result from the seasonal cycle of photosynthesis (which supplies carbon to rhizosphere respiration), and soil moisture (which limits heterotrophic respiration when too low or too high). Using field observations of soil respiration, we found evidence of seasonal hysteresis in 9 out of 15 site-years across 8 diverse biomes. Specifically, clockwise hysteresis occurred when photosynthesis preceded seasonal soil temperature and counterclockwise hysteresis occurred when photosynthesis lagged soil temperature. We found that across all sites, much of the respiration-temperature lag was explained by the decoupling of photosynthesis and temperature, highlighting the importance of recently assimilated carbon to soil respiration. An analysis of observations from 129 FLUXNET sites revealed that time lags between gross primary productivity (a proxy for canopy photosynthesis) and soil temperature were common phenomena, which would tend to drive counterclockwise hysteresis at low-latitude sites and clockwise hysteresis at high-latitude sites. Collectively, our results show that incorporating photosynthesis and soil moisture in the standard exponential soil respiration-temperature model (i.e., Q₁₀ model) improves the explanatory power of models at local scales.

1. Introduction

Soil respiration (R_s ; i.e., the sum of autotrophic and heterotrophic respiration in the soil) is the largest terrestrial carbon (C) source to the atmosphere. Consequently, small changes in the magnitude of R_s can produce considerable fluctuations in atmospheric CO₂ concentration

(Raich and Schlesinger, 1992) and impact global climate. Soil temperature (T_s) is typically the dominant factor controlling the rate of R_s , often explaining most of its variability (Bond-Lamberty and Thomson, 2010a; Davidson et al., 1998; Lloyd and Taylor, 1994), with numerous studies demonstrating that R_s responds exponentially to T_s in ecosystems where water is not limiting (Luo et al., 2001; Zhang et al., 2013).

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Table 1
Observed seasonal soil respiration-temperature hysteresis in previous studies.

Method ^a	Temperature depth (cm) ^b	Hysteresis direction ^c	Suggested factors ^d	Ecosystem type or species ^e	Sources
GC	0 ^f	2	substrate supply	mixed forest	Crill (1991)
DCS	5	1	NA	grassland	Knapp et al. (1998)
DCS	NA	2	NA	Sphagnum moss	Goulden et al. (1998)
DCS	5	2	NA	conifer boreal forest	Morén and Lindroth (2000)
DCS	5	2	temperature profile, root respiration	<i>Pseudotsuga menziesii</i>	Drewitt et al. (2002)
DCS	15	NA	NA	Ponderosa pine	Irvine and Law (2002)
NA	NA	1 ^g	substrate depletion	NA	Kirschbaum (2004)
DCS	7.5	1	NA	grassland	Verburg et al. (2005)
DCS	15	1, 8	seasonal temperature, soil moisture pattern, and phenology	grassland	Harper et al. (2005)
DCS	5	1 ^h	NA	<i>Pseudotsuga menziesii</i>	Jassal et al. (2005)
DCS	2	2	decomposable litter	deciduous forest	Curiel Yuste et al. (2005)
NA	NA	1	substrate depletion	NA	Kirschbaum (2006)
DCS	2	1	soil moisture, fine root production	<i>Populus tremuloides</i>	Gaumont-Guay et al. (2006)
GM222	8	1	root respiration	mixed temperate forest	Vargas and Allen (2008)
DCS	2	2, 8	vegetation type, soil structure	mixed forest	Phillips et al. (2010)
DCS	0, 5, 10	1	root phenology and litterfall	mixed forest	Oe et al. (2011)
DCS	5	1	heterotrophic respiration	mixed temperate forest	Kominami et al. (2012)
DCS	10	2	soil microbial activity, fresh litter	<i>Pinus tabulaeformis</i> plantation	Jia et al. (2013)

a- GMM222: type of probes for CO₂ concentration measurements (soil respiration is calculated based on gas gradient method); GC: gas chromatograph method (air was collected and CO₂ was analyzed by chromatograph); DCS: dynamic closed system containing an Infra-Red Gas Analyzer (IRGA) and a chamber, including the commonly used commercial LI-8100, LI-8100A, LI-6400 systems and other self-made systems; NA: no field measurements were conducted, and numerical methods were used to generate soil respiration.

b- NA: no clear information for depth of temperature measurement, or results are based on model runs.

c- 1: clockwise, 2: counterclockwise, 8: “figure-8”-shaped pattern, NA: no direction was suggested, nor was there sufficient information to derive the direction.

d- All studies suggested factors by speculation.

e- NA: that soil respiration was obtained from numerical methods.

f- Air temperature.

g- Fall has lower respiration rate than spring; the direction is therefore supposed to be clockwise.

h- Greater sensitivity in the latter part of the year; the direction is therefore supposed to be clockwise.

However, in many ecosystems, cycles of R_s are often out of phase with cycles of T_s , leading to hysteresis in the R_s - T_s relationship at both diurnal (see Zhang et al., 2015) and seasonal timescales (see Table 1).

Such hysteresis has been observed most frequently at the diurnal scale, and there is a rich body of literature explaining the mechanisms that control this pattern. First, the dynamics of soil heat flow can cause soil temperature in different soil layers to peak at different times of the day (Phillips et al., 2011; Zhang et al., 2015). Second, the dynamics of gas transport in the soil is affected by soil moisture and soil structure, which determine how efficiently respired CO₂ is transported to the surface where it is measured (Zhang et al., 2015). Finally, the dynamics of photosynthesis and carbon allocation can also affect diurnal hysteresis by regulating the availability of substrate to soil microbes and the rhizosphere (Abramoff and Finzi, 2015; Oikawa et al., 2014; Stoy et al., 2007; Vargas and Allen 2008; Zhang et al., 2015). While reports of hysteresis occurring at seasonal scales have also been widely reported (Table 1), the drivers of these seasonal patterns are poorly understood and no consensus has emerged to explain them.

One challenge to uncovering a single explanation for the hysteresis relationship is that the nature of the hysteresis may differ. In nearly 40% of the previous studies in Table 1, increases in R_s lag increases in T_s , generating a counterclockwise hysteresis (i.e., R_s at a given temperature is lower during the early growing season than during the late growing season). Such a dynamic could occur when photosynthesis is in phase with T_s , but there is a long lag in the delivery of substrate to the roots or microbes (Crill, 1991; Jia et al., 2013, see Table 1) either through allocation processes or through litterfall (Curiel Yuste et al., 2005). In contrast, in ~50% of the studies in Table 1, increases in R_s precede increases in T_s , resulting in a clockwise hysteresis (i.e., R_s at a given temperature is greater during the early growing season than during the late growing season). This sort of pattern could be explained by progressive substrate depletion over the course of the growing season (Kirschbaum, 2006), by greater root productivity early in the

growing season (Oe et al., 2011) or by soil moisture (θ) limitation to soil respiration late in the season (Gaumont-Guay et al., 2006). In addition to these two patterns (i.e., counterclockwise and clockwise), a “figure-8” pattern at the diurnal scale (Zhang et al., 2015) can also characterize seasonal dynamics (e.g., Harper et al., 2005; Phillips et al., 2010, Table 1). This pattern may result from different sensitivities of autotrophic and heterotrophic respiration to their drivers (Song et al., 2015). For example, although both autotrophic and heterotrophic respiration respond positively to T_s (Zhang et al., 2013), a higher temperature sensitivity is commonly assumed for autotrophic respiration (Boone et al., 1998; Savage et al., 2013; Zhang et al., 2013), whereas heterotrophic respiration may be more sensitive to soil moisture (Moyano et al., 2013). Thus, a critical challenge is not merely to understand why hysteresis occurs, but to identify the frequency of environmental conditions conducive to seasonal clockwise, counterclockwise or figure-8 hysteresis.

The primary objective of this work is to present a generalizable framework to elucidate the key mechanisms responsible for generating the various hysteresis patterns at the seasonal timescale. We test the hypotheses that the compound effects of photosynthesis and θ together with T_s are major drivers of the seasonal hysteresis, and the time lag between gross primary productivity (GPP) and T_s is an important factor driving the temporal decoupling of R_s and T_s . We expect that counterclockwise hysteresis will be most common at sites where GPP lags T_s , clockwise hysteresis will be most common at sites where GPP precedes T_s , and the figure-8 pattern will be most common at sites where the dynamics of θ and GPP are out of phase, but both are important in controlling soil respiration. We test these hypotheses by merging field observations with numerical models of R_s that accommodates a variety of mechanisms which may be responsible for seasonal R_s - T_s hysteresis.

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