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Response of soil respiration and its components to experimental warming and water addition in a temperate Sitka spruce forest ecosystem

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ABSTRACT

Future climate change is expected to alter the terrestrial carbon cycle through its impact on soil respiration. In this study, we determined the responses of soil respiration and its components to experimental warming with or without water addition. A replicated *in situ* heating (~2 °C above ambient soil temperatures) and water addition (170 mm in total each year) experiment was carried out for the first time in a temperate plantation forest of Sitka spruce over the period 2014–2016. R_h was measured inside deep collars (35 cm deep) that excluded root growth, while R_s was measured using the static chamber approach and near-surface collars (5 cm deep) and R_a calculated by subtracting R_h from total soil respiration (R_s). Experimental warming significantly increased R_s, R_h and R_h/R_s, but had no effect on R_a. In contrast, none of the respiration components were affected by water addition. Warming increased annual R_h by 62% but had no effect on R_a. Overall, warming did not significantly increase annual R_s. Warming showed a stronger impact on R_s in the non-growing season but had a smaller impact in the growing season. Warming increased R_a in the non-growing season but decreased it in the growing season. The effects of warming on R_h were similar for the two periods. Our results highlight the differential response of R_a and R_h to warming, which was mediated by water addition or season. For this and other similar forest sites that don't experience water limitation, global warming may have a positive feedback on atmospheric CO_2 concentrations through enhanced soil respiration.

1. Introduction

Tropospheric concentrations of carbon dioxide (CO_2) and other trace gases have been increasing since the beginning of the Industrial Revolution, with an even more rapid increase over the last 50 years (IPCC, 2013) and this has been closely linked to climate warming (Crowley, 2000). It has been predicted that this increase in greenhouse gases will raise the mean global air temperature by 1.1–6.4 °C by the end of this century, with an increased warming rate occurring in Europe (IPCC, 2013). Soil respiration (soil surface CO_2 flux, R_s) is the second largest carbon flux (60–80 Pg C yr^{-1}) in the terrestrial carbon cycle (Davidson et al., 2002) and comprises 20–40% of the carbon (C) exchange to the atmosphere. Previous global warming manipulation experiments, conducted during the last two decades, have reported a stimulation of R_s and an increase in the flux of C from the soil to the atmosphere (Rustad et al., 2001; Wu et al., 2011). For example, an increase of 1 °C in air temperature could cause a 10–28% greater C release (11–34 Pg C yr^{-1}) due to increased soil respiration (Schimel et al., 1994). An increase in R_s could weaken the C sink strength of terrestrial ecosystems and even turn them into C sources (Canadell et al., 2007; Cox et al., 2000; Jones and Huntingford, 2003). Forest soils in the northern hemisphere in particular, constitute an important terrestrial C sink (Goodale et al., 2002; Janssens et al., 2003). Therefore, even small increases in C emissions induced by climate change for these forest soils could lead to large global increases in atmospheric CO_2 concentrations.

As one of the main environmental factors driving R_s, soil temperature controls and regulates a range of biogeochemical processes that determine the cycling of C (Flanagan et al., 2013). R_s is also affected by water availability and generally increases with an increase in SWC at the lower range of values for SWC, but can decrease at higher values (Davidson et al., 1998; Deng et al., 2012; Hui and Luo, 2004; Linn and

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Doran, 1984). Nevertheless, the nature of the impact of soil temperature in combination with other environmental factors, such as water availability, on R_s can be highly variable (Fernandez et al., 2006; Jenkinson et al., 1991). Reductions in R_s have been reported in drier ecosystems where moisture deficits were increased by warming, whilst increases have been reported in ecosystems with higher water availability. Therefore, the response of R_s to elevated temperature in individual studies may vary from an increase in emissions (Lin et al., 2011; Melillo et al., 2017; Noh et al., 2016; Schindlbacher et al., 2009; Wan et al., 2007; Zhou et al., 2006), no effect (De Boeck et al., 2007; Li et al., 2013) or even reduced emissions (Liu et al., 2009; Pajari, 1995; Saleska et al., 1999; Verburg et al., 2005). Generally, fewer warming studies on soil respiration have been carried out in temperate forest ecosystems where water availability is less constrained, with the nature of the impact of elevated temperature remaining uncertain.

As the primary pathway for the return of soil C to the atmosphere, a better understanding of R_s, and its components, as well as their response to a changing climate is important to assess the future ecosystem C balance. Total soil respiration comprises two major source components: an autotrophic component (R_a), originating from the respiratory activity of roots and the associated rhizosphere, and a heterotrophic component (R_h), arising from microbe-associated soil organic matter (SOM) decomposition (Hanson et al., 2000; Kuzyakov, 2006; Subke et al., 2006). The important distinction between R_a and R_h is that the former largely represents the respiration of C recently assimilated by plants, whereas the latter releases C that may have had up to millennial residence times in the soil (Trumbore, 2000). In studies conducted in temperate coniferous forests, R_h and R_a responded similarly to increasing temperatures (Schindlbacher et al., 2009; Vogel et al., 2014. In contrast, Zhou et al. (2010) reported a negative effect of warming on both R_h and R_a. In a recent report of a long-term warming study on a mixed hardwood forest stand, most of the warming-induced increase (66%) in R_s was due to an increase in R_h, with a smaller effect (33%) on R_a (Melillo et al., 2017). As the experimental conditions may have a large impact on the responses of the soil C cycle to warming, as well as ongoing uncertainties about how warming affects R_h and R_a in different ecosystems, more information is required to obtain a better understanding of how increased temperatures affect the soil C balance.

Terrestrial C cycle feedbacks to climate warming can vary strongly with precipitation, which is projected to increase at high latitudes and decrease in most subtropical regions (IPCC, 2013). The combined effects of warming and altered precipitation are expected to have strong influences on the C balance. For example, a combination of warming and decreased precipitation can cause large C losses (Angert et al., 2005; Breshears et al., 2005; Ciais et al., 2005; Loik et al., 2004). In contrast, decreased water availability could also diminish or even inhibit any warming-induced stimulation of R_s (Liu et al., 2009; Schindlbacher et al., 2009; Suseela and Dukes, 2013; Wang et al., 2014). Divergent results have also been reported from experimental manipulations of the effect of precipitation/water addition on R_s (Jia et al., 2014; Liu et al., 2015; Wan et al., 2007; Wei et al., 2016), and few studies have quantified the responses of R_h and R_a in response to warming in combination with differences in soil moisture (Suseela et al., 2012). Therefore, it remains unclear whether or not R_s and its components respond in a similar manner to simultaneous warming and altered precipitation.

In this study, we investigated the impacts of soil warming and water addition, as well as their interaction, on R_s and its components, R_a and R_h. Such multifactor experiments are important to improve the predictive ability of multifactor climate models, as single factor experiments may fail to account for the interactive effects of different climate change drivers (Leuzinger et al., 2011; Norby and Luo, 2004). Likewise, partitioning the autotrophic and heterotrophic components of R_s can lead to a greater mechanistic understanding of the response of R_s to environmental factors (Chen et al., 2011). This study reports on measurements made in a Sitka spruce (*Picea sitchensis* (Bong.) Carr.) forest stand in central Ireland. These plantations are of significant commercial benefit and are considered a critical store of C in Ireland and elsewhere, a role that could be developed more extensively to further offset national greenhouse gas emissions (DAFM, 2012). Soil respiration and R_h were measured in forest plots over a period of 24 months, where the major objective was to compare seasonal variations in R_s and its components in response to atmospheric warming and how this is further impacted by alterations in water availability.

2. Materials and methods

2.1. Experimental site

The field study area was located in Dooary Forest, Co. Laois, central Ireland (52°57′N, 7°15′W; altitude of 260 m). The 30-year (1978–2007) mean annual temperature and precipitation at this site were 9.9 °C and 857 mm, with a climate typical of the northern temperate zone. Mean monthly air temperatures range from 13 to 16 °C during summer, 4–6 °C during winter, and 7–12 °C during spring and autumn. Precipitation is quite evenly distributed over the year with slightly higher rainfall during winter. The commercial management of the forest is under the control of Coillte, a semi-state forestry company and the measurement plots were located in a Sitka spruce first rotation stand planted in 1988 on previously unmanaged grassland without fertilization, at a planting density of 2300 stems ha^{-1}. The size of the forest stand covers a total area of 42 ha. The measurements for this investigation were conducted in close proximity to an eddy covariance tower used for long-term (2002-present) measurements of C fluxes, with available biomass and climatic data, which have been used as part of a long-term forest C sequestration and greenhouse gas emissions monitoring site. Shallow drains were created to improve soil drainage prior to forest establishment in 1988 and trees planted on a 2 m by 2 m grid. The dominant soil type in the area is a wet mineral soil classified as low humic surface-water gley. The main soil properties for this site are detailed in Table 1. The forest stand has been thinned four times, in 2006, 2008, 2012 and 2015 resulting in a more open canopy. Little understory vegetation was present except some moss and fungi. However, some herbaceous vegetation was present in the thinning lines where trees were removed and the forest floor was open to receive radiation and rainfall directly. Other biometric and micrometeorological information can be found in Saunders et al. (2012, 2014).

2.2. Experimental design

The experiment used a paired nested design with warming as the main factor and watering as a secondary factor. Infra-red (IR) heaters were used in this study in order to simulate warming in a comparable way to the way that GHGs warm the earth surface through their influence on the downward infra-red flux (Aronson and McNulty, 2009). Whilst the disadvantage of this approach is that the air underneath the heaters is drier compared to the control, reducing the relative humidity

Table 1
Soil properties at the forest site. Values are mean (SE). BD, bulk density; STC, soil total carbon; STN, soil total nitrogen; NH_4^+, ammonium; NO_3^-, nitrate.

Variables	Unit	Mean	SE
BD	$g\ cm^{-3}$	0.83	(0.04)
STC	%	4.22	(0.58)
STN	%	0.27	(0.01)
NH_4^+	$mg\ kg^{-1}$ soil	6.51	(0.83)
NO_3^-	$mg\ kg^{-1}$ soil	2.51	(1.06)
pH	–	3.90	(0.12)
Sand	%	9	(2.0)
Silt	%	38	(0.9)
Clay	%	53	(1.8)