Forest thinning and soil respiration in a Sitka spruce forest in Ireland

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A R T I C L E   I N F O

A B S T R A C T

Forest thinning influences soil processes by altering key microclimatic conditions, root density, microbial communities, organic matter turnover and nutrient budgets. It introduces a large pulse of harvest residues (brash) to the soil surface and can alter the balance between autotrophic and heterotrophic respiration. This study determined the influence of thinning, microclimatic factors and plant productivity on carbon (C) losses through the emission of carbon dioxide (CO_2) respired from thinning lines (brash lanes or BL) and the forest floor (FF: without brash) in a first rotation Sitka spruce (*Picea sitchensis* (Bong.) Carr.) forest in Ireland. Weekly measurements of CO_2 efflux were carried out using an Infra-Red Gas Analyser connected to static chambers; while soil moisture content and soil surface temperature were measured, using theta probes and data loggers, respectively. The soil respiration measurements were also correlated with the gross primary productivity (GPP) determined by eddy covariance techniques. The highest CO_2 efflux were observed at the peak of summer in July/2010 (FF = 699.20 mg CO_2 m^{-2} h^{-1} and BL = 374.22 mg CO_2 m^{-2} h^{-1}) and were associated with maximum soil surface temperatures and higher rates of GPP. Soil temperature had a strong positive influence on the variation of CO_2 from the forest (FF = 75% and BL = 59%), and the temperature sensitivity (Q_{10}) of soil respiration from the FF (5.47) was higher than from the BL (2.72). Soil moisture was inversely correlated with soil respiration from both FF ($R = -0.73$, $p < 0.0001$) and BL ($R = -0.53$, $p = 0.003$). The combined effect of temperature and moisture gave a better description of the variability in CO_2 respired from both the FF ($R^2 = 0.85$, $p < 0.0001$) and BL ($R^2 = 0.67$, $p < 0.0001$) than temperature and/or moisture alone. GPP was positively correlated with soil respiration with a stronger relationship observed in the FF ($R^2 = 0.73$, $p < 0.0001$) than the BL ($R^2 = 0.45$, $p < 0.0001$). The total C loss due to soil respiration from the FF (448.93 g C m^{-2} year^{-1}) was significantly higher than BL (351.77 g C m^{-2} year^{-1}). The annual soil respiratory C loss was 435.32 g C m^{-2} year^{-1} (calculated based on the contribution of the BL (14%) and FF (86%) to the total forest area).

1. Introduction

Forest ecosystems store and exchange significant amounts of carbon (C) with the atmosphere (Kasischke and Stocks, 2000). Soil respiration, the efflux of carbon-dioxide (CO_2), contributes between 30 and 80% of the total forest ecosystem respiration depending on the localized site and climatic conditions (Davidson and Janssens, 2006; Janssens et al., 2001). The production of CO_2 in the soil is primarily due to autotrophic respiration by live roots and their associated mycorrhizae, and heterotrophic respiration by microbes oxidizing plant detritus (decomposition), root exudates and humified organic matter (Boone et al., 1998; Buchmann, 2000; Han et al., 2007). A better understanding of the impacts of thinning and changing climatic factors such as temperature and moisture

on C assimilation, emission and subsequent sequestration in intensively managed forest, is required in order to improve projections about the impacts of future climate change on soil CO_2 emissions from managed forest ecosystems (Cox et al., 2000; Drewitt et al., 2002; Raich and Tufekcioglu, 2000; Valentini et al., 2000).

The decomposition of organic matter and root respiration have been found to be highly variable in space and time, as many factors such as, soil temperature, moisture, site productivity, soil physical and chemical characteristics and soil microbial communities influence the rates of CO_2 loss (Billings et al., 1998; Longdoz et al., 2000; Peng et al., 2008; Qi et al., 2010; Rochette et al., 1991). In forest ecosystems, high spatio-temporal variation of soil CO_2 efflux is directly linked to the spatial distribution of fine roots, the accumulation of forest floor litter and the quantity and quality of soil organic matter (Klopatek, 2002; Pregitzer et al., 2000; Saiz et al., 2006a).

The isotopic composition of CO_2 respired in forest ecosystem has shown that plant productivity stimulates soil respiration over short time intervals (Andrews et al., 1999, 2000; Ekblad et al., 2005;

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Flanagan et al., 1996) and the C used during canopy photosynthesis could be available for root respiration after 1–4 days (Ekblad and Högberg, 2001). For example, Sampson et al. (2007) confirmed that a direct correlation exists between plant photosynthetic activity and soil respiration in a mixed coniferous/deciduous forest in Northern Belgium and suggested that changes in the rate of photosynthesis are likely to affect soil respiration via alterations in belowground substrate supply.

The influence of plant productivity on soil respiration is confounded by the local microclimatic conditions, soil microbial communities, litter input and management decisions such as thinning. At longer time scales and over broader spatial scales, seasonal and spatial differences in soil respiration have been linked to variation in leaf area index, suggesting that annual and seasonal variations in photosynthetic activity could result in similar fluctuations in soil respiration (Curiel Yuste et al., 2003, 2007; Raich and Tufekcioglu, 2000; Reichstein et al., 2003).

Many studies have shown that soil temperature is a key factor when estimating the CO_2 respired from forest soils (Londo et al., 1999; Parkin and Kaspar, 2003). The temperature sensitivity coefficient of soil respiration, commonly referred to as Q_{10}, has been extensively used to describe the difference in rates of soil respiration over 10 °C temperature intervals (Lloyd and Taylor, 1994; Rayment and Jarvis, 2000; Wen et al., 2006). Soil temperature can also be used to reliably predict rates of soil respiration where there are no other limiting factors such as variations in soil moisture content, quantity of root biomass, inputs from litter decomposition and microbial activity which may all influence annual or seasonal variations in soil respiration (Bekku et al., 2003; Chen et al., 2010; Zheng et al., 2009).

Soil moisture content is another important variable for validating process-based models predicting soil respiration. Low soil moisture content inhibits the physiological performance of microbes and reduces the availability of nutrients in soils (Reichstein et al., 2003; Riveros-Iregui et al., 2007; Tang et al., 2005a,b). In general, soil metabolic activity decreases as soils dry out below or become saturated above a certain threshold, and changes in soil moisture availability potentially modulate temperature-driven changes in soil respiration.

Over annual and inter-annual timeframes in particular forest ecosystems, it has been shown that the temperature sensitivity (Q_{10}) of total soil respiration is negatively correlated with temperature and positively correlated with soil moisture content (Drewitt et al., 2002; Janssens and Pilegaard, 2003; Xu and Qi, 2001). The interaction between temperature and moisture significantly drives the rate of organic matter decomposition and root respiration in forest ecosystems (Curiel Yuste et al., 2003; Howard and Howard, 1993).

Forest management practices (such as pruning, prescribed burning, thinning and clear cutting) influence both autotrophic and heterotrophic soil respiration through biomass removal and the opening of the forest canopy which alters the microclimatic properties of the soil, as well as influence the quantity and quality of substrate inputs into the soil (Masyagina et al., 2010; Maassen and Wirth, 2006; Tang et al., 2005a). These silvicultural activities affect the soil C dynamics by changing the forest floor energy balance, soil moisture content, nutrient availability and biomass production (Jassal et al., 2007; Johnson and Curtis, 2001; Qiu et al., 2011).

Thinning, which partially removes trees from a forest in order to redistribute tree growth onto fewer and consequently more valuable stems, is an important and common silvicultural practice (Weiskittel et al., 2011). It decreases stand density and leaf area, improves tree productivity, reduces wildfire risk and maintains the forest's health. Thinning affects the forest soil by influencing root density, microbial communities, organic matter turnover and nutrient budgets (Ma et al., 2004; Tian et al., 2010; Qiu et al., 2011) and

may lead to an increase in the quantity of organic matter stored in soils (Janssens et al., 2001; Peng et al., 2008). Thinning will result in the death of root systems of harvested trees, which should reduce the contribution of root respiration to CO_2 released from soils. However, C released from the decay of litter, fine and coarse woody debris (including roots) is also expected to contribute to a short-term increase in soil respiration (Misson et al., 2005; Ohashi et al., 2000; Son et al., 2004; Sullivan et al., 2008). For instance, Ohashi et al. (1999) found that soil respiration from the thinned sections of a Japanese cedar (Cryptomeria japonica D. Don) forest was higher than from the unthinned sections for the first four years after thinning.

This study was conducted in a Sitka spruce (Picea sitchensis (Bong.) Carr.) forest, which had been thinned twice. In Ireland, first thinnings are almost entirely systematic, where every seventh row of trees in the stand is removed. The mechanical harvesters use these harvested rows (brash lanes) for access to the forest, and the brash (lop and top) from the harvested trees are utilized to produce a brash mat over which the harvester and forwarder travels (to minimize damage to frequently wet forest soils). Brash is defined as the aboveground parts of the tree not normally removed from site by thinning or clear felling (which remove timber lengths from tree stems to a top diameter of 7 cm). Subsequent thinnings are purely selective, where individual trees are removed from the remaining stand. Thinning residues including brash serve various functions, such as increasing habitat diversity, enhancing tree seedling survival, and providing a significant reservoir of nutrients for trees (Forestry Commission, 2006; Titus and Malcolm, 1991).

The aims of this study were to: (1) determine the effect of thinning on the CO_2 respired from the forest floor (FF) as compared to the thinning lines (or brash lanes (BL)); (2) determine the influence of soil surface temperature, soil moisture and their combined effect, as well as, forest gross primary productivity (GPP) on soil respiration from the FF and BL; and (3) provide an estimate of annual C loss due to soil respiration.

2. Materials and methods

2.1. Site description

The study site is a 23-year-old Sitka spruce forest (Dooary forest) growing on wet mineral gley soil located in Co. Laois in the Irish midlands (52°57′N, 7°15′W; altitude of 260 m). The 30-year mean annual temperature and precipitation were 9.3 °C and 850 mm, respectively. The forest covers a total area of 42 ha and is made up of two management compartments which are 25.8 ha and 16.2 ha in size, respectively. The soil respiration measurements were conducted in the 25.8 ha stand in close proximity to an eddy covariance tower used for long-term measurements of C flux, biomass and climatic data, as part of a forest C sequestration project (CARBiFOR; (Black and Farrell, 2006)).

The Dooary forest was previously an unmanaged grassland, and was afforested in 1988 at a stocking density of 2300 stems ha^{-1}. The forest was thinned in 2006 and 2008 where tree density was reduced to 1768 and 1345 stems ha^{-1}, respectively. Every seventh row of trees, which was removed during the first thinning, became a BL and represented ~14% of the total forest area per ha. The total brash input from the two thinning events was 23.10 t C ha^{-1}, while coarse woody debris input was 6.98 t C ha^{-1} (Olajuyigbe et al., 2011). The GPP determined from eddy covariance techniques were 24.75 and 19.04 t C ha^{-1} year^{-1} while, total ecosystem respiration were 14.42 and 10.90 t C ha^{-1} year^{-1} in 2007, and 2009, respectively (further information on the site's biometric and micrometeorological data is available in Saunders et al. (2012).

Table 1
Model parameters derived for the regression equations relating soil surface temperature and moisture content to soil respiration from the FF and BL.

Soil surface temperature					Soil moisture content			
Treatment[a]	Parameter	Value	S.E.	R^2	Parameter	Value	S.E.	R^2
Forest floor (FF)	β_0	39.46	13.85	0.75	β_2	505.72	251.26	0.55
	β_1	0.17	0.03		β_3	66.55	1225.19	
					β_4	−1183.14	1369.87	
Brash lane (BL)	β_0	61.49	14.87	0.59	β_2	507.19	3091.42	0.28
	β_1	0.10	0.02		β_3	250.95	9055.02	
					B_4	−1083.58	6611.74	

[a] $p < 0.05$ for all equations.

2.2. Experimental design and measurement of environmental variables

Ten stainless steel collars (60 cm × 60 cm) were inserted into the soil to a depth of 5 cm within the forest stand (FF: 5 collars) and in the brash lanes (BL: 5 collars). In the BL, the collars were carefully inserted through the brash layer. The distance between each of the collars was 20 m as a mains power supply was required by the gas analyser. A closed static chamber (stainless steel, 59.5 cm × 59.5 cm × 24 cm) was used to measure CO_2 efflux by connecting it to a portable Infra-Red Gas Analyser (IRGA) (ADC 2250, ADC BioScientific Ltd., United Kingdom). Air was continuously drawn from the chamber and passed through the IRGA (operated in differential mode) and returned to the chamber. An internal fan was used to ensure the homogeneous mixing of the chamber's air. The tubing and mixing volume were flushed and allowed to equilibrate during the first 2 min of each sample run before each measurement was taken over a 5 min period. Using this approach, the rate of increase in gas concentration within the chamber's headspace was measured and the CO_2 emitted was assumed to be proportional to the rate of increase (Drewitt et al., 2002).

The experiment commenced in October 2008 before the second thinning operation took place. Weekly measurements were undertaken in the BL, 3 weeks before the second thinning, and measurements resumed intensively after the thinning in both the BL and FF and were maintained for 3 months to capture the initial pulse of CO_2 associated with the decomposition of the thinning residues. However, measurements were suspended in February 2009 due to equipment failure and required repairs. The soil CO_2 efflux data collection resumed in June 2010 and continued until February 2011. Measurements were taken between 12 and 5 p.m. on each of the sampling dates. The diel variation in soil respiration has been suggested to be of little importance in some shaded forested areas (Davidson et al., 2000; Epron et al., 1999; Saiz et al., 2006a). Furthermore, Saiz et al. (2006a) confirmed that there was no significant diurnal variation from 24 h measurements of soil respiration carried out on this and similar sites.

Soil surface temperature was continuously monitored, and recorded at 30 min intervals using Tiny Tag data loggers (Gemini data loggers (UK) Ltd.). The soil moisture content was measured using a moisture probe (ThetaProbe ML2x, Delta-T Devices, Cambridge, U.K.) inserted to a depth of 6 cm in 3 randomly selected spots around each collar during each CO_2 measurement. Daily precipitation was obtained from the long-term measurements of climatic data associated with the eddy covariance tower.

2.3. Respiration rate determination

The FF and BL respiration rates, F_s (mg CO_2 m^{-2} h^{-1}) were calculated using Eq. (1)

$$F_s = \left(\frac{\Delta CO_2 \times 10^{-6}}{t} \times \frac{PVM}{RTA} \times 10^3 \right) 60^2 \tag{1}$$

where ΔCO_2 is the rate of change of CO_2 concentration (ppm) in the chamber headspace during the measurement, P is the atmospheric pressure (Pa), V is the volume of the chamber (m^3), M is the molecular weight of CO_2 (g), A is the area (m^2) of soil surface covered by the chamber, T is the soil surface temperature (K) and R is the universal gas constant (8.314 J mol^{-1} K^{-1}).

2.4. Relationship between soil respiration, temperature and moisture content

A two parameter exponential function was used to describe the relationship between soil respiration and soil surface temperature (Eq. (2)), while, temperature sensitivity (Q_{10}) was estimated using Eq. (3) (based on Lloyd and Taylor (1994)).

$$F_s = \beta_o e^{\beta_1 T} \tag{2}$$

$$Q_{10} = e^{10\beta_1} \tag{3}$$

where F_s is the measured soil respiration rate, T is the measured soil surface temperature (°C), β_o and β_1 are fitted parameters obtained using a least square non-linear regression; Q_{10} is the temperature sensitivity of F_s and was estimated from the exponential relationship between β_1 and 10 °C.

The standard error ((S.E. (Q_{10})) of Q_{10} was calculated using Eq. (4):

$$S.E.(Q_{10}) = Q_{10} \times 10 \times S.E.(\beta_1) \tag{4}$$

The relationship between soil respiration rate and moisture content was described using a quadratic regression, as shown in Eq. (5):

$$F_s = \beta_2 + \beta_3 M + \beta_4 M^2 \tag{5}$$

where M is the volumetric soil moisture content (m^3 m^{-3}), β_2, β_3, and β_4 are regression parameters.

A bivariate equation was used to describe the combined effect of temperature and moisture on soil respiration rate following the method of Tang et al. (2005a), as shown in Eq. (6):

$$F_s = (\beta_5 e^{\beta_6 T})(e^{\beta_7 M + \beta_3 M^2}) \tag{6}$$

where β_5, β_6, β_7, β_8, are regression parameters of the model.

2.5. Gross primary productivity, soil respiration and annual C loss

The daily GPP values for the days on which soil respiration measurements were conducted were obtained from eddy covariance data (Saunders et al., 2012). The daily efflux from FF and BL was estimated by substituting T in Eq. (2) with the daily mean soil surface temperature to simulate the daily soil respiration rate. The modeled daily values were then summed to obtain the annual estimates from the BL and FF. The annual soil respiratory C loss from the forest was then determined. The contribution of autotrophic and heterotrophic respiration to annual CO_2 respired from the FF was partitioned based on the proportions described in Saiz et al. (2006a).
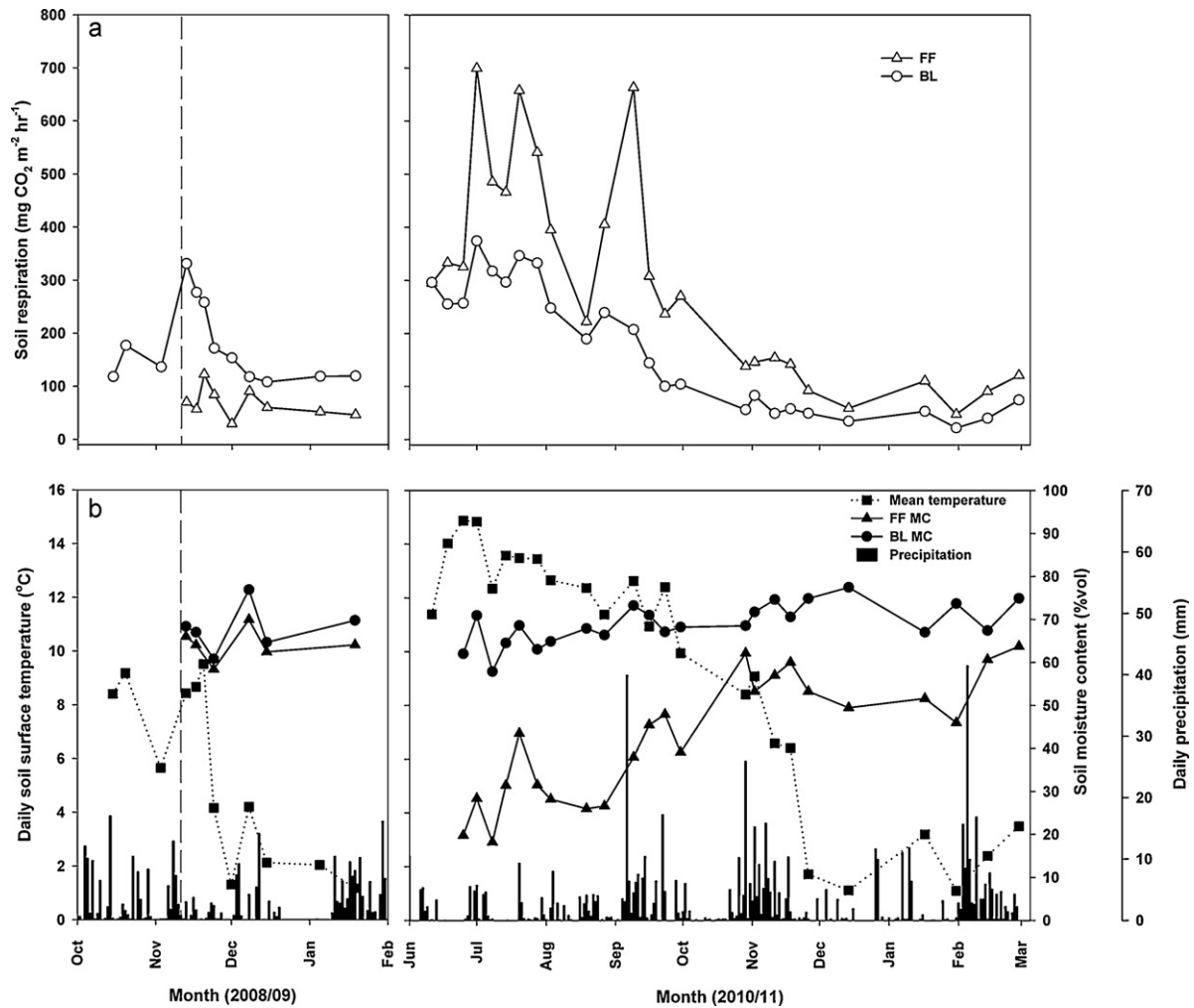
Fig. 1. Temporal variation of: (a) soil respiration, (b) soil surface temperature (no significant differences between the forest floor (FF) and brash lanes (BL) and the mean was used); moisture content in the FF and BL; and mean daily precipitation (data points before dashed line were measured before the thinning in the winter of 2008/2009).

2.6. Statistical analysis

Statistical tests to determine the significant differences and interactions between soil respiration rate, temperature and moisture content of the FF and BL were performed using a repeated measure ANOVA, with significant differences determined at $p < 0.05$. Regression and correlation analyses were used to compare the relationship between variables. The CO_2 efflux from the FF and BL were also correlated with the GPP (on sampling days). Statistical analyses were conducted using SigmaStat 11 for Windows (Systat Software Inc. UK).

3. Results

3.1. Variation of soil respiration

Before the thinning event in 2008, an increase and decrease in daily average soil temperature corresponded to a rise and fall in the BL soil respiration, but this association changed following the thinning. A spike in CO_2 efflux was observed, representing a 100% increase in the relative rate of CO_2 efflux from the BL when measurements taken three weeks prior to (mean = 143.86 ± 17.41 mg CO_2 m^{-2} h^{-1}) and three weeks after (mean = 288.64 ± 21.81 mg CO_2 m^{-2} h^{-1}) the thinning event were compared. Immediately after thinning, the BL soil respiration did

not continue to respond as directly to average daily soil surface temperature. Indeed, when temperature increased after the thinning, respiration dropped sharply. However, the initial pulse of CO_2 returned to pre-thin levels (171.57 mg CO_2 m^{-2} h^{-1}) after 3–4 weeks (Fig. 1a and b).

During the first sampling period (winter 2008/09), the soil respiration measured from the BL (mean = 183.83 ± 27.75 mg CO_2 m^{-2} h^{-1}) was significantly higher ($p = 0.001$) than from the FF (mean = 67.93 ± 9.25 mg CO_2 m^{-2} h^{-1}). In contrast, during the second sampling period (summer to winter 2010/11), soil respiration from the BL (mean = 169.05 ± 23.54 mg CO_2 m^{-2} h^{-1}) was significantly lower ($p < 0.001$) than the FF (mean: 296.11 ± 39.69 mg CO_2 m^{-2} h^{-1}) (Fig. 1a). Consequently, there was a significant difference in the overall CO_2 respired from the FF and BL ($p = 0.019$), when all the data from the two sampling periods were pooled.

The soil respiration showed a distinct variation that matched the change in soil surface temperature between seasons. The lowest efflux was recorded at the end of winter (January/2011; FF: 47.40 mg CO_2 m^{-2} h^{-1} and BL: 21.98 mg CO_2 m^{-2} h^{-1}), when mean daily soil surface temperature was low ($1.1\,^{\circ}C$). Soil moisture in the BL did not vary with time, but that of FF did vary during the study period. The change in soil moisture influenced the amount of CO_2 respired from the FF during the summer months (Fig. 1a and b). The highest efflux was observed at the peak of summer in July/2010
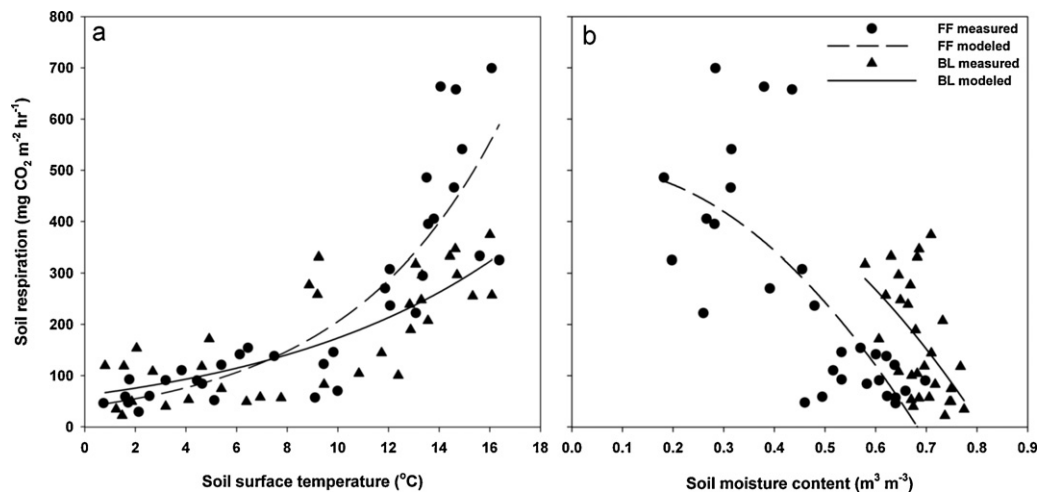
Fig. 2. The relationship between soil respiration and soil (a) surface temperature, (b) moisture content, of the forest floor and brash lanes (pooled data for measurements made in 2008/09 and 2010/11).

(FF = 699.20 mg CO_2 m^{-2} h^{-1} and BL = 374.22 mg CO_2 m^{-2} h^{-1}) and were associated with maximum soil temperatures and an increase in the soil moisture content.

There was no significant difference between the mean daily soil surface temperature recorded in the FF and BL ($p = 0.29$). The soil surface temperature ranged from 0.74–16.37 °C in the FF and 0.80–16.08 °C in the BL during the experiment. However, there was a significant difference in the soil moisture content ($p < 0.001$), with higher moisture contents measured in the BL (mean: 68.72 ± 0.01%) in comparison to the FF (mean: 47.08 ± 0.03%) across the experimental period. The lowest soil moisture (18.18%) was recorded in the FF during the summer 2010 (Fig. 1b). Generally, the variation of CO_2 efflux from the BL and FF followed similar trends, with the highest respiration rates in the summer before gradually dropping as winter progressed. Similar patterns of soil respiration were observed in the winters of 2008/09 and 2010/11.

3.2. Soil surface temperature and CO_2 efflux

The soil respiration rate was directly correlated with temperature in both the FF and BL; an increase in temperature resulted in an increase in CO_2 efflux from the soil (Fig. 2a). There was a better fit for the relationship between soil respiration and temperature from the FF ($R^2 = 0.75$, $p < 0.001$) than from the BL ($R^2 = 0.59$, $p < 0.001$) (Table 1). The Q_{10} value for the BL (2.72 ± 0.54) was lower than for the FF (5.47 ± 1.64).

3.3. Soil moisture and CO_2 efflux

The soil moisture was inversely correlated with the soil respiration from both FF ($R = -0.73$, $p < 0.0001$) and BL ($R = -0.53$, $p = 0.003$). High moisture in the BL limited CO_2 efflux from this area throughout the experiment (Fig. 2b). However, fluctuations in moisture played a significant role in the CO_2 respired from FF.

The quadratic regression (Table 1) showed a stronger relationship between moisture and soil respiration for the FF ($R^2 = 0.55$, $p < 0.0001$) than the BL ($R^2 = 0.28$, $p = 0.014$). The BL was mostly water logged and moisture content barely dropped below 60% (ranging from 57 to 77%) throughout the period of measurement, while a significant reduction, from 70 to 18% was observed in FF.

3.4. Combined effect of temperature and moisture on soil respiration

The combined effect of temperature and moisture gave a better description of the variability in soil respiration from FF ($R^2 = 0.85$, $p < 0.0001$) than from BL ($R^2 = 0.67$, $p < 0.0001$) (Table 2). During the winter period, low CO_2 efflux was observed, corresponding with low soil temperatures and high soil moisture contents in FF but an opposite response was observed in the BL (Fig. 3a and b). During high temperature periods an increase in soil moisture content due to precipitation increased soil respiration in FF.

3.5. GPP and soil respiration

Gross primary productivity was positively correlated with soil respiration from both the FF ($R^2 = 0.73$, $p < 0.0001$) and BL ($R^2 = 0.45$, $p = 0.0001$). The daily GPP accounted for 73% of the variation in the CO_2 efflux from FF as compared to 45% of the efflux variation from BL (Fig. 4a and b). Low GPP corresponded with low soil respiration during the sampling period.

3.6. Total soil respiration and annual C loss

Fig. 5a and b shows the modeled and measured soil respiration rates for the forest in 2010/11 (the measured data collected on days: 17, 31, 45 and 59; were measured in 2011). The modeled total C loss was 448.93 g C m^{-2} year^{-1} from FF and

Table 2
Bivariate model parameters derived for the combined influence of soil surface temperature and moisture content on the soil respiration from the FF and BL.

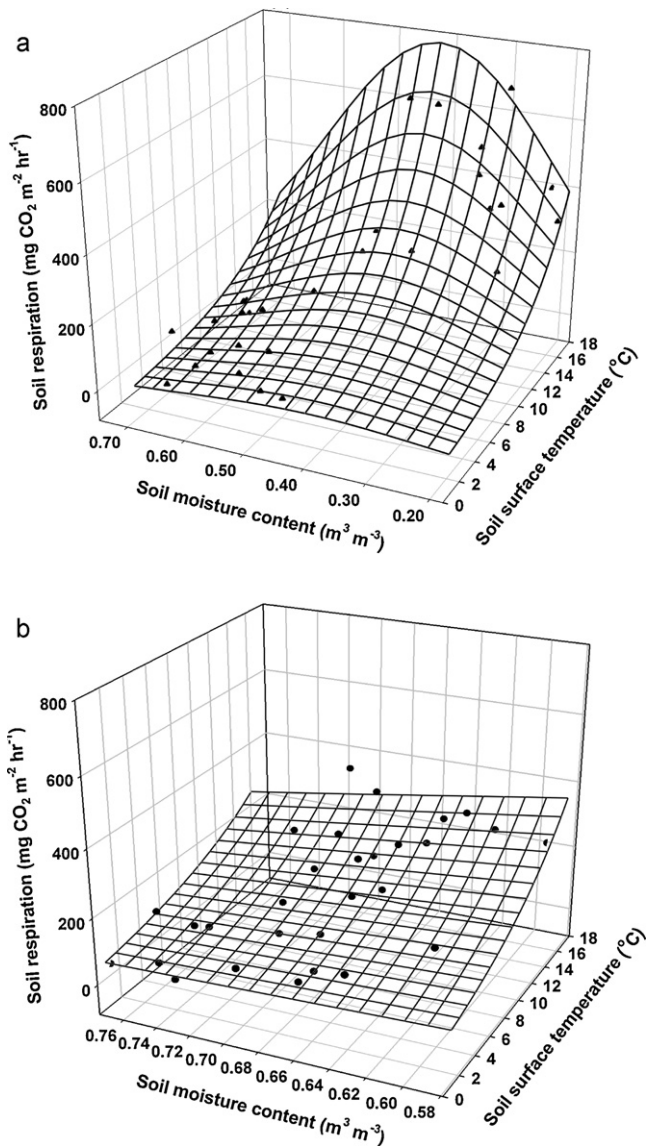| Parameter[a]	Forest floor (FF)			Brash lane (BL)		
	Coefficient	S.E.	R^2	Coefficient	S.E.	R^2
β_5	5.50	3.98	0.85	92.71	1261.97	0.65
β_6	0.18	0.04		0.11	0.02	
β_7	10.34	3.14		1.00	41.50	
β_8	−12.73	4.37		−2.50	31.44	

[a] $p < 0.0001$ for both equations.

Fig. 3. The combined effect of soil surface temperature and moisture content on the soil respiration, from (a) the forest floor and (b) the brash lanes.

351.77 g C m^{-2} year^{-1} from BL. The estimated annual C loss from the total forest area (total area comprising 14% BL and 86% FF) was 435.32 g C m^{-2} year^{-1}. Assuming that autotrophic respiration contributes approximately 57% of the total annual soil respiration in first rotation, thinned Sitka spruce forest (Saiz et al., 2006a), we estimate the annual C loss, calculated for 2010/11, from the FF due to autotrophic and heterotrophic respiration was 200.51 g C m^{-2} year^{-1} and 151.26 g C m^{-2} year^{-1}, respectively.

4. Discussion

4.1. Effects of thinning on soil respiration and microclimatic conditions

Thinning management affects the interaction between the biotic (roots, invertebrates and microorganisms) and abiotic (temperature and moisture) components of a forest ecosystem, resulting in a change in the CO_2 respired from the forest soil (Masyagina et al., 2010; Tang et al., 2008). The higher CO_2 respired from the BL after the thinning in 2008 over a 3–4-week period was attributed to the management event. This sudden increase in the CO_2 efflux from

the BL collars was caused by the addition of fresh detrital material to this section of the forest. As the spike did not follow the general pattern where changes in winter soil temperature resulted in consequent changes in respiration, we conclude that climatic variability was not responsible.

Previous studies that focused on soil-derived CO_2 efflux in forest ecosystems have shown conflicting responses to thinning, where both increases and decreases in soil respiration have been observed (Londo et al., 1999; Ma et al., 2004; Ohashi et al., 1999; Sullivan et al., 2008; Tang et al., 2005a). An important factor contributing to the variation of this response is likely to be the differences in the timing and duration of the measurement campaigns undertaken following thinning in the different studies. In this study, the CO_2 respiration rate from the BL was higher than the rate from the FF in winter 2008/09 after the thinning event, but the respiration rate from the BL was consistently lower than the FF rate throughout the 2010/11 measurements, 1.5 years after the management activity. Tang et al. (2005a) found that soil respiration in a Ponderosa pine (*Pinus ponderosa* (Doug.)) plantation decreased during 1–2 years after thinning in Sierra Nevada, while Sullivan et al. (2008) reported a decrease in soil respiration in a similar forest type in Southwestern USA within a year of the management activity. The decrease in soil respiration in thinned forests has been attributed to a greater reduction in autotrophic (root) respiration than the increase in heterotrophic respiration from the above- and below-ground debris (Sullivan et al., 2008). Hence, the lower respiration observed in the BL in 2010/11 is probably due to the reduction in the number of live roots as well as the brash substrate quality in this part of the forest (Curiel Yuste et al., 2003; Ohashi et al., 2000; Tang et al., 2005a). Respiration from live roots is largely driven by current or recent assimilates from photosynthesis, which would eventually decline after thinning (Koster et al., 2011; Sampson et al., 2007). However; a weakness of the current study was the inability to obtain sufficient data prior to the thinning event to examine fully the extent of the thinning influence on soil CO_2 efflux from the study site.

Thinning can also influence site specific microclimatic conditions. For example, the removal of aboveground vegetation is known to increase soil temperature, and a strong positive correlation exists between soil respiration and temperature in thinned forests (Koster et al., 2011; Masyagina et al., 2006). On the contrary, no significant difference was observed between the soil surface temperature of BL and FF (overall mean of BL was 0.1 °C lower than FF). This is most likely due to the higher average soil moisture content observed in the BL (68%), in comparison to FF (47%), as a result of the poor percolation of water through the soil and the retention of moisture by brash in the BL. Furthermore, soil moisture was lower in FF because of increased GPP, and consequently higher transpiration.

4.2. Spatio-temporal variation and environmental factors

High spatial variation in soil CO_2 efflux is a common phenomenon in forests (Curiel Yuste et al., 2007; Saiz et al., 2006b). The higher spatial variation observed in FF measurements compared to BL measurements (Fig. 5a and b), was attributed largely to the growth of fungal mycelia (indicated by the emergence of fruiting bodies in some of the FF collars); the effects of high photosynthetic activity on root respiration (i.e. from increased incidence and quality of root exudates); as well as rapid organic matter decomposition during the summer/autumn months, as highlighted by Pumpanen et al. (2004).

Seasonal variation in soil respiration is related to climatic factors, stand openness, plant physiology, microbial populations and the quantity and quality of dead organic matter. These site-specific characteristics are important when quantifying and evaluating soil
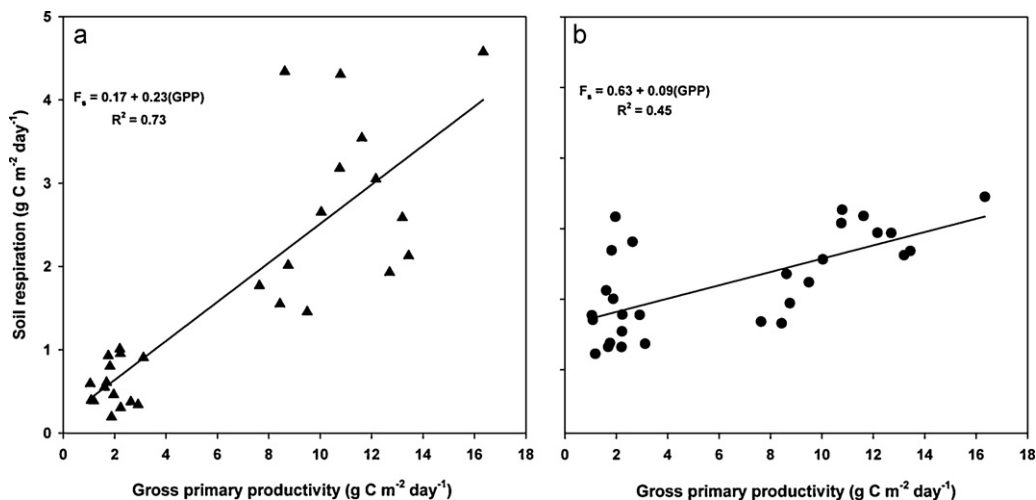
Fig. 4. The relationship between gross primary productivity (GPP) and soil respiration, from (a) the forest floor and (b) the brash lanes.

respiration at local and regional scales (Hanpattanakit et al., 2009; Raich and Tufekcioglu, 2000).

In several studies, higher rates of soil CO_2 efflux have generally been observed during summer months, and are associated with periods of high temperature (Högberg et al., 2001; Saiz et al., 2006b). In this study, soil respiration rates peaked in the summer (699.20 mg CO_2 m^{-2} h^{-1}) and were lowest during winter (29.16 mg CO_2 m^{-2} h^{-1}) and this trend was similar to the findings of Saiz et al. (2006a). This seasonal trend agrees with other studies that have observed the temperature sensitivity of soil respiration in forest ecosystems (Borken et al., 2002; Chen et al., 2010; Davidson et al., 1998).

Soil surface temperature accounted for 75% and 59% of the variation in FF and BL CO_2 efflux, respectively. It has been suggested that temperature has a greater limiting effect on microbial populations at lower temperatures than at higher temperatures (Andrews et al., 2000). Lower temperatures might cause active microbes to become dormant, hence decreasing the richness of active microbial species, potentially resulting in a lower soil respiration rate (Chen et al., 2010; Janssens and Pilegaard, 2003).

The annual Q_{10} of soil respiration is a measure of temperature sensitivity that may mask a combination of several factors such as plant phenological patterns, moisture conditions, and perhaps other unknown variables (Curiel Yuste et al., 2003). However, seasonal changes in the above factors do not significantly alter the

accuracy of the annual Q_{10} value (Janssens and Pilegaard, 2003). The Q_{10} values in this study ranged from 2.72 (BL) to 5.47 (FF), and were similar to values (2.0–6.3) published by Saiz et al. (2006a) obtained from similar sites, as well as, those reported for other temperate forest ecosystems (Buchmann, 2000; Davidson et al., 2000; Kirschbaum, 2000). The difference between the Q_{10} of BL and FF reflects both a direct sensitivity of the involved processes as well as the change in quantity and quality of the respiring components (i.e. stumps, roots and associated microbes) (Epron et al., 2004). The lower Q_{10} value observed in BL may be due to the lower sensitivity of microbial respiration to temperature, i.e. lower proportion of autotrophic respiration (Boone et al., 1998; Kirschbaum, 1995; Saiz et al., 2006a); as there was a greater proportion of decaying material (available for heterotrophic respiration) present in BL in comparison to FF, which had a greater density of live roots and continuous input of litter. Root respiration accounts for a large fraction of soil respiration and exerts a strong influence on the temperature sensitivity of soil respiration (Boone et al., 1998, Wen et al., 2006). For instance, Saiz et al. (2006a) attributed a high Q_{10} (5.7) in a 10-year-old Sitka spruce forest to high levels of fine root biomass and root exudation.

Davidson et al. (2000) suggested that seasonal patterns of soil respiration follow dynamics of soil moisture as were observed in FF data. Soil moisture directly affects microbial activity and several physical processes, such as water movement, and gas or solute
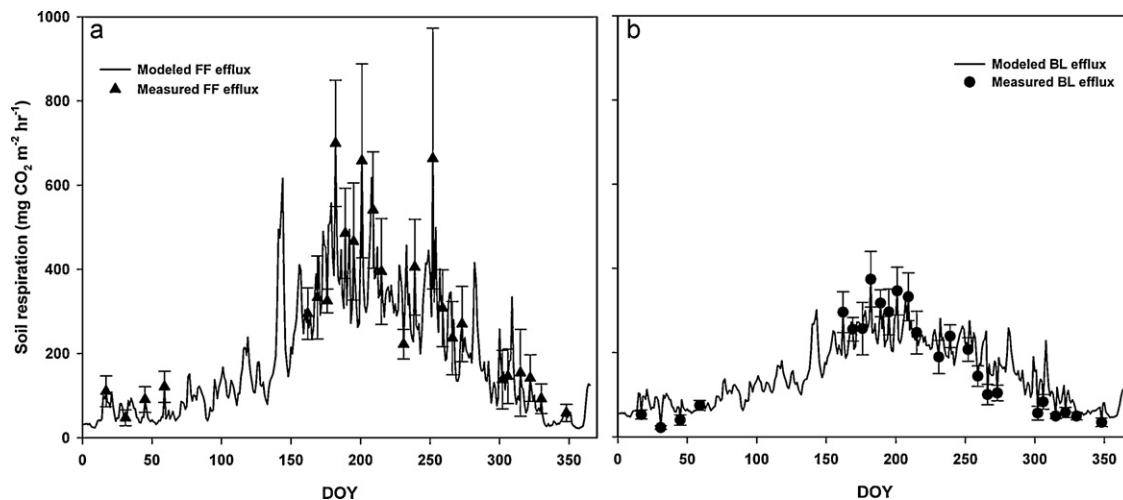

Fig. 5. Modeled and measured (mean with S.E. bars) soil respiration rates from (a) forest floor and (b) brash lanes, for each day of the year (DOY) during 2010/11.

diffusion (Curiel Yuste et al., 2007; Goncalves and Carlyle, 1994; Leiros et al., 1999). The soil in BL was mostly saturated during this study, potentially inhibiting CO_2 production and emission; as too much or too little water can inhibit respiration in soil microorganisms (Drewitt et al., 2002).

A sharp rise in soil respiration was observed following rainfall events (Fig. 1a and b) during the summer period (June and July/2010), and this phenomenon has been reported in earlier studies where sporadic rainfall in summer stimulated microbial activity thus shifting the C balance of the ecosystem (Curiel Yuste et al., 2003; Davidson et al., 2000; Rey et al., 2002; Xu et al., 2004).

Over short timeframes, soil respiration is mainly driven by the combined effects of temperature and moisture (Peng et al., 2008; Risk et al., 2002; Riveros-Iregui et al., 2007; Stoyan et al., 2000). In this study, a stronger, combined influence of temperature and moisture was exerted on CO_2 efflux from the FF when compared to the BL, partly due to the waterlogged condition of the BL. Reichstein et al. (2002) mentioned that an indirect effect of moisture on soil temperature sensitivity would reduce the enhancing effect of higher temperatures on CO_2 efflux. The thinning changed the moisture dynamics in the BL soil, thus, making the response of soil respiration to changes in soil moisture at higher temperatures more evident in the FF (Fig. 3a and b).

A drop in soil respiration (June/2010), at a time of high soil surface temperature, may be due to the extended dry period experienced at this time. Some authors have suggested that this decrease is linked to drought stress on the metabolic activity associated with soil microbial communities and tree roots (Epron et al., 1999, 2004; Rey et al., 2002; Wen et al., 2006). In addition, the seasonal change in growth patterns of trees also significantly alters the combined influence of temperature and moisture on soil respiration (DeForest et al., 2009)

4.3. Plant productivity and soil respiration

Plant productivity (GPP) had a greater influence on soil respiration from the FF than from the BL (Fig. 4a and b) confirming that microbial activity and soil respiration were higher under active trees than in dead organic material. Curiel Yuste et al. (2007) showed that active trees exerted a strong influence on autotrophic and heterotrophic respiration, indicating the important contribution of photosynthesis to short-term spatio-temporal variation in soil respiration. Active plants are continuously translocating organic material to the soil in the form of easily decomposable substrates such as simple sugars, amino- and organic acids (Curiel Yuste et al., 2007; Saiz et al., 2006b; Scherer-Lorenzen et al., 2005).

It has been suggested that GPP and site disturbances (such as thinning) have a larger influence on soil respiration than the mean annual temperature, and that the effect of temperature on root respiration is constrained by GPP in some European forest ecosystems (Janssens et al., 2001). The positive correlation between photosynthetic activity (GPP) and soil respiration, as found in this study supports the assertion that soil respiration may be a useful indicator of the total belowground allocation of C and ecosystem productivity and vice versa (Raich and Nadelhoffer, 1989; Raich and Tufekcioglu, 2000). Tang and Baldocchi (2005) showed how photosynthesis strongly controlled soil respiration in an oak-savanna system, while Högberg et al. (2001) demonstrated that the flux of current assimilates from photosynthesis to roots was a key driver of soil respiration in a large scale forest tree girdling experiment.

4.4. Annual C loss

The estimated total annual respiratory C loss from soil in 2010/11 ($435.332\,g\,C\,m^{-2}\,year^{-1}$) falls within the lower range of published values for temperate forest, which range from 250 to $1255\,g\,C\,m^{-2}\,year^{-1}$ (Raich and Schlesinger, 1992) and is similar to values published by Saiz et al. (2006a), who estimated C loss from soil respiration in the region of $556\,g\,C\,m^{-2}\,year^{-1}$ from a 31-year-old first rotation Sitka spruce forest in the Irish midlands. Similarly, Zerva et al. (2005) found the C loss due to soil respiration in a 30-year-old second rotation Sitka spruce forest growing on peaty gley soil in England to be $540\,g\,C\,m^{-2}$. Soil respiration was estimated to contribute approximately 31% of the total forest ecosystem respiration in 2010/11, based on eddy covariance methods (Saunders, personal communication).

The distribution of the brash material solely over the BL partition of the forest, as a result of thinning, did not lead to an increase in soil respiration as might have been expected. A combination of the wet Irish climate, the absence of an overhead canopy and the reduction in the amount of live root activity allowed a greater moisture content to prevail, and this counteracted the stimulation of heterotrophic efflux from the input of high concentrations of decomposing material; therefore, when both the BL and FF respiration rates were taken into account, the total annual forest soil respiration was reduced by 3%.

In Ireland, projected climate change scenarios suggest a general increase in mean monthly temperature (1.2–1.4 °C) with the greatest warming in July; while precipitation is predicted to decrease in the summer months (10–18%) and increase in the autumn and winter (15–20%) in the next 50 years (McGrath et al., 2008). Increases in temperature with corresponding decreases in precipitation, especially during the summer months (Black et al., 2010), may result in a decrease in GPP corresponding to a similar drop in forest soil respiration.

5. Conclusions

The impact of thinning on soil respiration is often confounded by the complex and heterogeneous changes that occur to the canopy structure and forest floor microclimatic conditions. In this study, an increase in the soil moisture content of the BL when compared to the FF was attributed to the thinning management. Our results showed that thinning resulted in a short-term increase in CO_2 efflux from BL, which eventually stabilized and became lower than the efflux from the FF. Thinning improves the site quality by reducing competition and enhancing tree growth thus increasing root and microbial activity under live trees and eventually improving the net productivity of the forest. The photosynthetic activity of trees appeared to drive the soil respiration, as GPP was positively correlated with soil respiration. Temperature and moisture contributed significantly to the seasonal variability of soil respiration directly and indirectly through their influence on annual productivity.

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