



Soil respiration negatively correlated with volume gains by a young *Pinus radiata* clone over five months

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ABSTRACT

It is assumed that greater plant productivity enhances autotrophic respiration (R_a). In a glasshouse trial using a one year old *Pinus radiata* D. Don clone selected for rapid growth, we examined the relationship between soil respiration, its components and tree growth rates over approximately five months. Soil respiration and R_a were significantly influenced by temperature; the response of heterotrophic respiration (R_h) approached significance. Soil moisture content had no effect on respiration. The productivity of individual clones, measured as volume increment, was not consistently positively correlated with soil respiration across the measurement intervals. Indeed, over the life of the trial it was found that individual tree volume increments were significantly negatively correlated with soil respiration. These results indicate that the most productive trees were associated with lower rates of autotrophic respiration, contradicting past studies. Further work is recommended to determine if this relationship holds true for these, and other, *P. radiata* clones in forest settings.

Soil respiration contributes substantially to net ecosystem carbon (C) exchange and is the second largest flux of C in terrestrial ecosystems ($\sim 75 \times 10^{15} \text{ g C yr}^{-1}$) (Schlesinger and Andrews 2000). Given the global interest in forest establishment to increase the capture of atmospheric carbon dioxide (CO_2) (Rudel et al. 2005), studies have identified the influence of temperature, soil moisture (e.g. Buchmann 2000) and management practices on respiration in forest ecosystems (e.g. Jandl et al. 2007). Research has also indicated that more productive systems are associated with increased soil respiration (Hopkins et al., 2013), due to increased root associated autotrophic respiration (R_a), which is supported by field data suggesting tree size can account for 10–19% of the variation in soil respiration (e.g. Sørensen and Buchmann, 2005; Bréchet et al., 2011). Therefore, while increased tree growth rates will result in greater aboveground C storage (Rudel et al. 2005), it appears likely that this may be offset to some extent by enhanced soil CO_2 release.

The dominant plantation tree species in New Zealand is *Pinus radiata* D. Don. Significant efforts have been made in New Zealand to enhance the growth of this species through breeding programmes and the deployment of clonal material (Burdon et al., 2008). To explore the linkage between tree productivity and soil respiration for this species we established a glasshouse study using a high-productivity one year old *P. radiata* clone. Based on past findings, we hypothesized that soil

respiration would be positively correlated with tree productivity across the individual trees used in the study.

The glasshouse experiment was conducted at the University of Canterbury, Christchurch, New Zealand. The experiment consisted of 42 plastic pots (height 100 cm, diameter 30 cm, drainage holes in the bottom covered with cloth) filled with soil collected from the nearby Bottle Lake *P. radiata* plantation in September 2012, taken to a depth of 10 cm. The soil was prepared by passing through a 2 mm sieve to remove stones and plant debris, and then mixed thoroughly on a large tarpaulin. Following this process approximately 50 kg of soil was added to every pot, creating a column approximately 80 cm high within each cylinder. This process was completed two days after soil collection. Analysis determined the soil was 18% sand, 60% silt, 22% clay, with a pH of (1:5) 5.0, total organic C of 44.7 g kg^{-1} and total N of 2.59 g kg^{-1} . Thirty seven pots were randomly selected for planting with a one year old *Pinus radiata* clone, grown in the nursery as bareroot stock from cuttings collected from clonal mother plants. The specimens used in the trial were selected for uniformity based on diameter at the root/shoot interface, branching structure and foliage properties. The remaining five pots acted as unplanted ambient controls. The pots were randomly placed in seven rows within the glasshouse and watered every third or fourth day on an alternating basis, following a previously established protocol. During a watering event all pots were given the

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same volume of water via an automated drip-feeding system. To equalize the solar radiation and account for any microclimate effects within the glasshouse, pots were repositioned within the glasshouse on a weekly basis so that all pots spent an equal amount of time in each row.

Three weeks after planting, open topped polyvinyl chloride cylinders (height 5 cm, diameter 8 cm) were placed into the soil to a depth of 3 cm within every pot, taking care to avoid disrupting the *P. radiata* clones (c.f. Slesak et al., 2010). Measurements of soil respiration ($\text{mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) began one week after the cylinders were placed to allow any effects of this disturbance to subside. Soil respiration was measured approximately every two weeks using a Servomex 1450 infra-red gas analyser (Servomex Group, Crowborough, UK); a total of 11 measurements were taken per pot. Respiration measurements occurred immediately before a watering event to reduce this potential source of variation, and always took place between 5 pm and 7 pm under natural light. Soil respiration from the five unplanted pots was averaged to provide a mean heterotrophic respiration (R_h) value for each measurement window, enabling soil R_a to be calculated by subtracting R_h from the soil respiration values determined for each planted pot. Throughout the experiment an EL-USB data logger (Lascar Electronics, Erie, PA) recorded air temperature every five minutes. Mean daily air temperature was 20.9 °C; the maximum and minimum temperatures were 22.5 °C and 16.2 °C, respectively. Pot soil moisture content (0–15 cm depth) was recorded using a TDR 300 soil moisture probe (Spectrum Technologies Aurora, IL) every 2–3 days, producing an average value of 18.7% across the study period. Measurements of clone ground level diameter (GLD) and height occurred with each measurement of soil respiration to assess productivity. The experiment commenced in September 2012 (spring); soil respiration measurements began in October 2012 and concluded in early April 2013 (autumn). Tree volume was calculated following Lu et al. (2018). Briefly, tree GLD and height was used to calculate the volume of a cylinder representing each tree at each measurement, which was then multiplied by a correction factor of 0.35 to account for stem tapering. While this correction factor is an approximation of the tapering effect, it was applied consistently and therefore had no impact on the significance of any relationship between tree volume and measurement of respiration. All statistical analysis (Pearson's product moment correlation coefficient and calculation of coefficient of variation (CV) values) was carried out in R Version 3.3.3. A single tree died between the first and second measurement period and was excluded from all analysis; therefore, for statistical purposes, 36 planted and five unplanted pots were assessed.

Temporal trends in mean respiration are shown in Fig. 1. As anticipated, soil respiration and R_a were positively correlated with air

temperature at time of sampling ($P < 0.05$); R_h also tended to follow temperature ($P = 0.07$). Mean pot soil moisture content was not correlated with mean respiration through time and was also not correlated with air temperature; this was likely due to the combination of frequent watering and good drainage within the pots.

The daily volume increment of the clones and the relationship between the growth individual clones and soil respiration for each measurement interval and across the life of the experiment are shown in Table 1. Differences in the mean growth rate between measurement intervals were observed, but the growth rate of individual clones within any given measurement interval also varied considerably, evidenced by values for CV approaching and surpassing 1 (Table 1). By the end of the trial, mean tree volume was 53.2 cm^3 , but for individual trees this value ranged from 27.2 to 98.2 cm^3 , indicating the extent of variation in tree growth rate. Examination of the changes in soil respiration in relation to the growth of each tree determined that these two metrics were positively correlated for only a single measurement interval; conversely, across the full length of the experiment the productivity of individual trees was significantly negatively correlated with the change in soil respiration associated with that tree.

The positive effect of temperature on soil respiration agrees well with past research (e.g. Hopkins et al., 2013). The soil respiration values reported here are somewhat greater than those generated by studies of *P. radiata* in field conditions (e.g. Carlyle and Than 1988; Arnett et al., 1998) but given the relatively high temperature maintained in the glasshouse relative to field conditions this is not surprising. As expected, R_a contributed considerably more than R_h to variations in soil respiration, implying that the presence of the clone caused a significant increase in soil respiration – but due to the overall negative correlation with individual plant productivity, it appears that this effect is predominantly qualitative, as the hypothesized positive, quantitative effect of tree productivity did not manifest. If this effect occurs in plantation settings, this has potential implications for the management of C in forests (Canadell and Raupach 2008).

As this finding disagrees with conventional wisdom, various factors such as soil properties and plant behaviour that influence soil respiration and plant productivity need to be considered. However, the design of the trial reduced or otherwise minimised many of these influences. For example, differences in plant physiology can lead to variations in root exudation (Ryan et al. 1996); here this effect was minimised by using a clone and managing the environmental conditions. In addition, the soil preparation process was designed specifically to reduce heterogeneity, while the management of the clones within the glasshouse reduced variation in the environment the trees were exposed to. Despite this, the authors freely accept that much supporting information, such

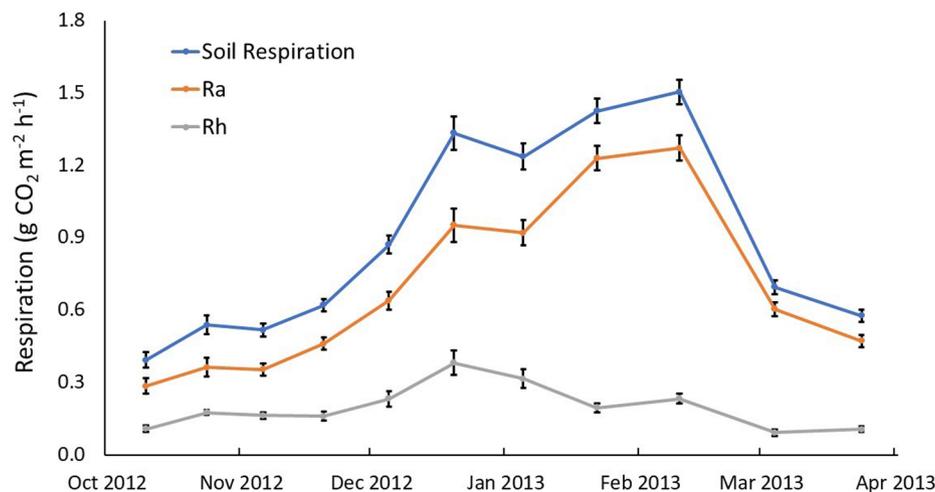


Fig. 1. Variation in mean soil respiration, autotrophic respiration (R_a) and heterotrophic respiration (R_h) through time.

Table 1

Daily volume increments, coefficient of variation (CV) in volume increment and assessments of the correlation between the volume increment and change in soil respiration in each individual planted pot across the measurement intervals.

Measurement interval		Mean volume increment		Correlation with change in soil respiration	
Start	End	cm ³ day ⁻¹	CV	r	P
19/10/2012	2/11/2012	0.46	0.61	0.26	0.13
2/11/2012	15/11/2012	0.21	1.14	-0.21	0.23
15/11/2012	29/11/2012	0.33	0.81	0.05	0.77
29/11/2012	14/12/2012	0.21	1.33	0.38	0.02
14/12/2012	29/12/2012	0.06	1.71	0.05	0.76
29/12/2012	14/01/2013	0.16	0.66	-0.02	0.93
14/01/2013	31/01/2013	0.08	1.75	0.06	0.73
31/01/2013	19/02/2013	0.16	1.05	-0.10	0.59
19/02/2013	13/03/2013	0.18	0.98	0.10	0.58
13/03/2013	2/04/2013	0.12	1.02	0.10	0.58
19/10/2012	2/04/2013	0.19	0.28	-0.38	0.02

n = 36 for all correlations.

Bolded correlations indicate significance at $\alpha = 0.05$.

as root biomass, root/shoot ratio and incremental measures of soil C and soil microbial biomass C could shed considerably more light on whatever process is driving the observed reduction in soil respiration with increased plant productivity (Chen et al., 2006). We recommend that further research examining soil respiration under existing forest stands be undertaken to test the generality of the relationship with productivity observed here and to identify the potential drivers.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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