



The influence of stocking levels, clone, fertilization, and weed control on surface CO₂ efflux in a mid-rotation *Pinus radiata* D. Don plantation in Canterbury, New Zealand

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Abstract Silvicultural practices applied in managed forest plantations may help counteract the effects of climate change by influencing soil surface CO₂ efflux (F_s). Understanding the effects of silvicultural practices on F_s will provide unbiased estimates of carbon fluxes and allow better silvicultural decisions for carbon sequestration. Therefore, we assessed how F_s differed seasonally across silvicultural practices (i.e., stocking levels, clone, fertilization and weed control treatments) and evaluated the effects of soil temperature (T_s) and soil volumetric water content (θ_v) on F_s across these practices for a mid-rotation (14 year-old) *Pinus radiata* plantation in the Canterbury region of New Zealand. There were significant differences in F_s ($p < 0.05$) over the four seasons, three levels of stocking, and five clones. The effects of fertilization and weed control applied 12 years previously on F_s were insignificant. Annual estimate of F_s (mean \pm 1 standard deviation) from the study site was 22.7 ± 7.1 t ha⁻¹

a⁻¹ in the form of CO₂ (6.2 ± 2.1 t ha⁻¹ a⁻¹ in the form of C). F_s values were consistently higher in plots with 1250 stems ha⁻¹ compared to 2500 stems ha⁻¹, which may be related to a strong soil resource limitation because of the close spacing in the latter plantation. Significant differences in F_s across clones suggest that variations in carbon partitioning might explain their growth performance. Silvicultural treatments influenced F_s response to soil temperature ($p < 0.05$), resulting in models explaining 28–49% of the total variance in F_s . These findings provide insights into how silvicultural management decisions may impact F_s in mid-rotation radiata pine plantations, contributing towards developing more precise and unbiased plantation carbon budgets.

Keywords Clone · Silvicultural practices · Soil CO₂ efflux · Stocking · Weed control

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Introduction

Forests store some 75% of all carbon in terrestrial ecosystems accounting for up to 40% of carbon exchange between the biosphere and the atmosphere (Raich and Schlesinger 1992). Soil CO₂ efflux is the second largest flux in the global carbon cycle, which is a magnitude greater than emissions from the burning of fossil fuel (Raich and Schlesinger 1992). Soil CO₂ efflux changes due to anthropogenic factors may therefore accelerate global warming by speeding up global carbon cycling (Raich and Potter 1995; Schlesinger and Andrews 2000). For example, land clearing and utilization, and deforestation increases soil CO₂ efflux as a result of increased rates of decomposition (Rapp 2014). Given the extent of global forest cover, minor changes in disturbance regimes and forest management practices may considerably affect soil carbon fluxes (Maier and Kress 2000).

Radiata pine (*Pinus radiata* D. Don) plantations occupy more than four million hectares worldwide (Mead 2013), exhibiting greater productivity and plasticity than many other tree species. In New Zealand, radiata pine is the predominantly planted species, accounting for about 90% of 1.73 million ha (NZFOA 2019). Intensively managed plantations represent an important pool in the global carbon cycle (Templeton et al. 2015). The productivity of radiata pine plantations can be greatly altered by silvicultural management practices (Hollinger et al. 1993). In intensively managed plantations, these practices may contribute to counteract the effects of climate change. Total soil surface CO₂ efflux (F_s) consists of two parts (Tyree et al. 2014): (1) autotrophic respiration, which is root respiration resulting from maintenance, growth and ion uptake; and, (2) heterotrophic respiration from the decomposition of soil organic matter by micro and macro fauna. Environmental factors significantly influence forest productivity and decomposition of soil organic matter, explaining seasonal variation in F_s (Schlesinger and Andrews 2000). For example, F_s was higher in summer and lower in winter in North Florida's slash pine (*Pinus elliottii* Engelm) plantation, corresponding to changes in ambient temperatures and soil moisture (Ewel et al. 1987).

Fertilization, weed control, planting at different stocking levels and with different genotypes are common silvicultural practices for radiata pine plantations throughout New Zealand (Mason and Milne 1999). The purpose of these practices is to produce healthy and vigorous trees by enhancing growth and productivity (Mason 1992). A previous study indicated that silvicultural practices have long term impacts on F_s in intensively managed plantations (Tyree et al. 2006). These practices can significantly influence F_s by altering the microclimate of the site, including light, soil moisture (θ_v), soil temperature (T_s), and the soil microbial community. For example, fertilization has been shown to decrease (Samuelson et al. 2004), be independent of (Tyree et al. 2006; Templeton et al. 2015), and increase (Bracho et al. 2018) F_s in loblolly pine (*Pinus taeda* L.) plantations. Moreover, two contrasting loblolly pine clones differed in their F_s responses to nutrient manipulations in terms of both partitioning and physiology (Tyree et al. 2009). Furthermore, stocking levels significantly affected both heterotrophic and autotrophic soil CO₂ efflux in lodgepole pine (*Pinus contorta* Dougl.) (Litton et al. 2003a).

The main research topics for radiata pine plantations in New Zealand are silviculture practices, genetics (Mason and Kirongo 1999; Lasserre et al. 2005; Mason 2008), growth and yield modelling, fertilization, and weed control practices (Mason et al. 1996; Mason and Milne 1999), and carbon cycling and partitioning (KC et al. 2020). However, understanding how these practices affect the dynamics of F_s in radiata pine plantations is limited. Therefore, the objectives

of this study were: (a) to assess the influence of stocking, fertilization, weed control, and clone selection on F_s ; and, (b) to determine the influence of soil temperature and soil volumetric water on F_s across silvicultural treatments in a young radiata pine plantation. It was hypothesized that: (1) F_s would increase with stocking; (2) faster growing clones would exhibit greater F_s ; (3) F_s would be independent of fertilization carried out 12 years before; (4) F_s would be independent of weed control carried out 12 years before; and, (5) both T_s and θ_v would explain most of the variations in F_s across the silvicultural treatments. This study will contribute to better understanding of differences among silvicultural management decisions on F_s when developing stand-level carbon budget models in forest plantations.

Materials and methods

Study site and experiment

The experiment was located in Rolleston, Canterbury, New Zealand (43° 37.2' S and 172° 20.4' E) (Fig. 1a). It was established by the School of Forestry, University of Canterbury on land owned by the Selwyn District Council, comprising 7.5 ha of radiata pine planted in 2005. The site is approximately 45 m a.s.l. on a plain (Fig. 1a). Typical summer daytime maximum temperatures range from 18 to 26 °C (Fig. 1b), but may rise above 30 °C. Winters have daytime maximum temperatures from 7 to 14 °C (Salekin et al. 2019; NIWA 2020) (Fig. 1b). Mean annual rainfall is approximately 618 mm with a monthly range of 38 to 68 mm (NIWA 2020) (Fig. 1b). Northeasterly winds occur most frequently in coastal sites throughout the year while southwesterly winds are more frequent during winter (NIWA 2020). The site had formerly been livestock pasture. The soil is a Lismore stony silt loam with aggradation gravel as a parent material and also includes partial glacial gravel (Rennie and Bennett 1981; Hewitt 2010).

The experimental design consisted of 48 permanent plots with a randomized complete block factorial split plot with four complete blocks (Mason 2008), with an arrangement of factors within each block. Plots 1–12, 13–24, 25–36, and 37–48 corresponded to blocks one, two, three, and four respectively (Fig. 1c). The main plots consisted of three levels of stocking (625, 1250 and 2500 stems ha⁻¹). A first split consisted of four levels of follow-up weed control and fertilization treatments (fertilization, F; herbicide, H; both, FH; and no chemicals). Fertilization was carried out once in year 1 and once in year 3 (Nitrogen, Phosphorus, Potassium, Sulphur, and trace elements at a rate of 80 g per tree). Strip weed control was applied in years 1 and 2, and a follow-up herbicide treatment with complete clearance in year 3 and in subsequent years when required. A second split consisted of

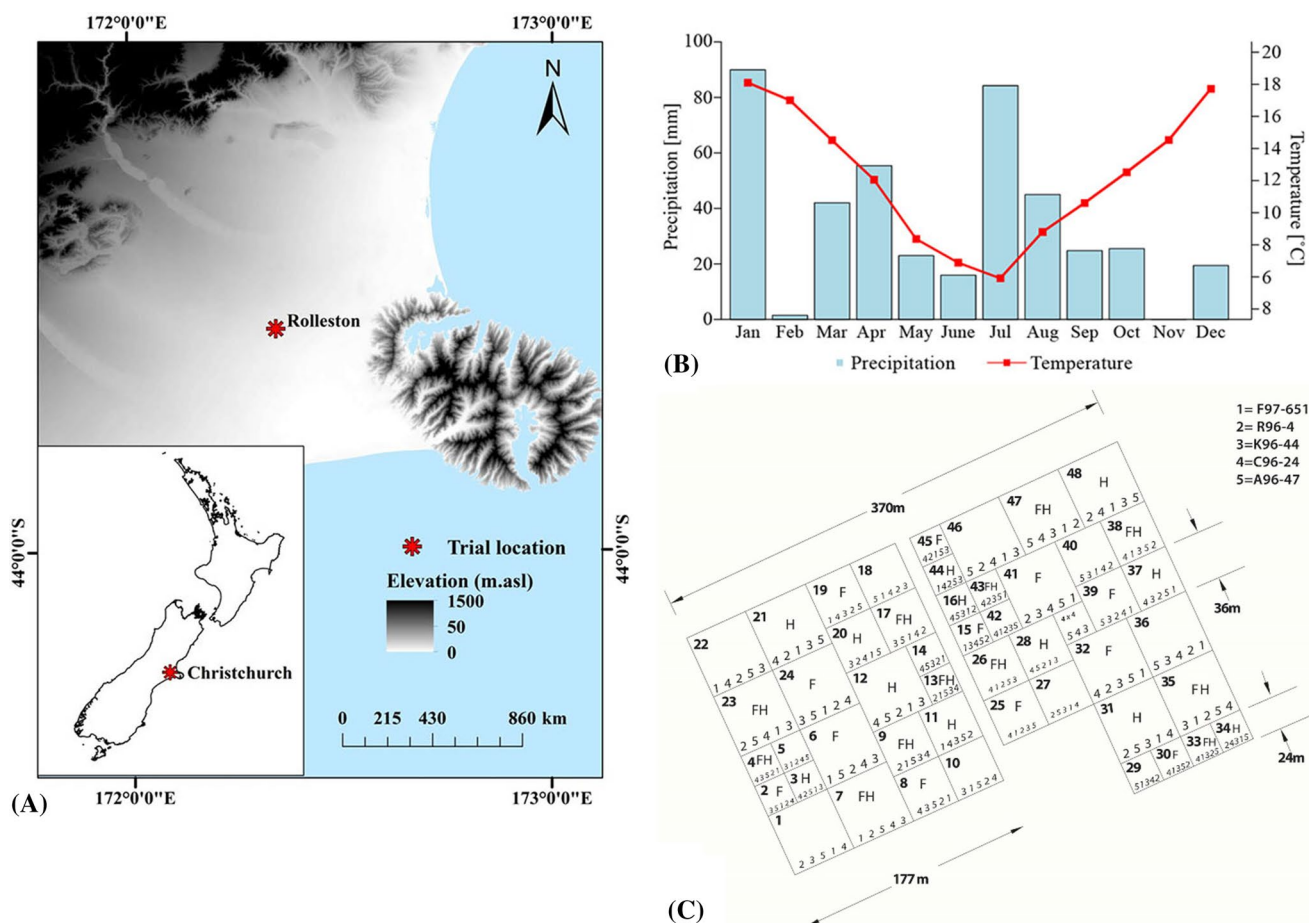


Fig. 1 Location (a), ombrothermic diagram–January–December 2017 (b) and layout of the experimental trial (c)

five different clones randomly allocated to all plots, with 1, 2, 3, 4 and 5 indicating different clonal genotypes (Mason 2008). Measurements of soil surface CO₂ efflux rates (F_s) were carried out when the plantation was 14 years-old, 12 years after the last fertilization and herbicide applications were performed.

Measurement of soil surface CO₂ efflux

Efflux rates (F_s) were measured using an infrared gas analyzer (EGM-4, PP Systems, Hitchin, Hertfordshire, UK) equipped with a soil respiration chamber (SRC-1) with a 10-cm inner diameter. Two hundred and forty PVC collars (10 cm wide × 6 cm high) were placed into the soil and left undisturbed for one year before F_s measurements were made. F_s was measured at the centre within the two rows for each clone in each plot. Nine hundred and sixty measurements were made (48 plots × 5 clones × 4 seasons). Measurements were carried out between 9:00 AM and 4:00 PM during autumn (13–16 April 2017), winter (7–10 July 2017), spring (3–6 October 2017), and summer (13–16 January 2018).

Measurement of soil temperature and soil water content

Soil temperature (T_s) and soil volumetric water (θ_v) were measured simultaneously to F_s , within 10 cm of the PVC collar. T_s values were determined using a built-in temperature probe (STP-1) of the EGM-4 at a 10-cm soil depth. The θ_v was measured with a portable moisture meter SM150T (Delta-T Devices Ltd., Burwell, Cambridge, UK), at 10 cm. Measurements of the SM150T were calibrated using samples analyzed by a gravimetric method consisting of oven drying soil samples of a known volume (Walker et al. 2004).

Scaling to annual soil surface CO₂ efflux

F_s values were scaled into t ha⁻¹ a⁻¹ in the form of CO₂ using the exponential equations of F_s vs T_s and θ_v developed for this experiment (Eq. 4) and continuous measurements of T_s and θ_v recorded by in-site micrometeorological stations.

Statistical analysis

The influence of stocking, specific clone, fertilization, weed control, and season on F_s , T_s , and θ_v were examined using linear mixed effects models of the *nlme* package in R statistical software (R Core Team 2018), considering blocks as random effects. Fixed effects consisted of stocking, clone, fertilization, and weed control and their two-way interactions. A mathematical representation of the linear mixed-effects model in matrix form is given in Eq. (1) (Zuur et al. 2009).

$$Y_i = X_i \times \beta + Z_i \times b_i + \varepsilon_i \quad (1)$$

where Y_i is the response variable (F_s , T_s , and θ_v) for different treatment levels i (i.e., three levels of stocking, two levels of fertilization, two levels of weed control, and five levels of type of clone), $X_i \times \beta$ is the fixed term, $Z_i \times b_i$ is the random term, and ε_i is error term.

To determine the influence of T_s and θ_v on F_s across silvicultural treatments, the following commonly used exponential functions were tested: T_s -based model [Eq. (2)] (Lloyd and Taylor 1994), and the combined T_s and θ_v -based model [Eq. (4)] (Lavigne et al. 2004). Temperature sensitivity (Q_{10}), i.e., the response of F_s to a 10 °C change in T_s values, was estimated across all silvicultural treatments using Eq. (3) based on the model of Lloyd and Taylor (1994). Fitted models were evaluated using two of the most commonly used goodness-of-fit statistics (Huber-Carol et al. 2012): the root mean square error (RMSE), and the coefficient of determination (R^2). Regression models were fitted in the R statistical software (R Core Team 2018).

$$F_s = ae^{bT_s} \quad (2)$$

$$Q_{10} = e^{10b} \quad (3)$$

$$F_s = ae^{bT_s} e^{c\theta_v} \quad (4)$$

where F_s is the measured soil surface CO₂ efflux rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), T_s is the measured soil temperature at 10 cm soil depth (°C), Q_{10} is the temperature sensitivity response of F_s , θ_v is the measured volumetric water content (%) at 10 cm soil depth; and a , b , and c are fitted parameters of the regression.

Results

Influence of T_s and θ_v on F_s across silvicultural treatments

For the period of the experiment, T_s was strongly controlled by the season ($F_{3,889} = 9677$, $p < 0.001$), and specific clone ($F_{4,889} = 9.37$, $p < 0.001$) (Table 1). Stocking, fertilization, and follow-up herbicide treatments had no significant effects on T_s ($p > 0.05$). When examined by season, T_s was significantly influenced by the main clonal effect in all seasons ($F_{4,172} > 3.27$, $p < 0.05$) (Table 2). Volumetric water content (θ_v) followed an opposite trend to T_s (soil temperature), being lower in summer ($7.3\% \pm 1\%$) compared to spring ($14.6\% \pm 1.6\%$), winter ($17.1\% \pm 1\%$), and autumn ($17.7\% \pm 1\%$) (Table 3). For the period of the experiment, θ_v was strongly affected by the interacting effects of stocking \times herbicide ($F_{2,29} = 8.06$, $p < 0.01$) (Table 1). Significant interactions of stocking \times fertilization ($F_{2,29} = 5$, $p < 0.05$) and herbicide \times clone ($F_{4,172} = 2.54$, $p < 0.05$) were observed in autumn and spring, respectively (Table 2). No significant ($p > 0.05$) effects of silvicultural treatments on θ_v were observed in summer (Table 2).

The combined T_s and θ_v -based model [Eq. (4)] was selected as best to predict F_s as it yielded highest R^2 values

Table 1 ANOVA statistics for the fixed components of the linear mixed effect model for soil surface CO₂ efflux (F_s), soil temperature (T_s), and soil volumetric water content (θ_v) fitted for the period of the experiment. Fixed effects included stocking, clone, fertilization, and follow-up herbicide, and their two-way interactions and season. Degrees of freedom (df) for treatments and error used in the calculation of the F-statistic are presented

| Factors | df treatments | df error | F_s | | T_s | | θ_v | |
|--------------|---------------|----------|-----------|---------|-----------|---------|------------|---------|
| | | | F-value | p-value | F-value | p-value | F-value | p-value |
| (Intercept) | 1 | 889 | 22,873.63 | <0.0001 | 21,515.07 | <0.0001 | 2708.53 | <0.0001 |
| Stock (S) | 2 | 6 | 9.92 | 0.0125 | 1.41 | 0.3155 | 10.29 | 0.0115 |
| Fert (F) | 1 | 29 | 0.94 | 0.3414 | 0 | 0.9871 | 0.01 | 0.9253 |
| Herb (H) | 1 | 29 | 2.52 | 0.1231 | 0.78 | 0.3836 | 11.07 | 0.0024 |
| Clone (C) | 4 | 889 | 4.32 | 0.0018 | 9.37 | <0.0001 | 0.57 | 0.6865 |
| Season (Se) | 3 | 889 | 319.68 | <0.0001 | 9676.54 | <0.0001 | 2001.12 | <0.0001 |
| S \times F | 2 | 29 | 0.05 | 0.9536 | 1.39 | 0.2631 | 3.16 | 0.0572 |
| S \times H | 2 | 29 | 0.60 | 0.5548 | 1.24 | 0.3053 | 8.06 | 0.0016 |
| F \times C | 4 | 889 | 1.64 | 0.1632 | 1.13 | 0.3426 | 0.46 | 0.7662 |
| H \times C | 4 | 889 | 1.86 | 0.1172 | 1.38 | 0.2405 | 0.39 | 0.8108 |
| F \times H | 1 | 29 | 2.05 | 0.1632 | 1.37 | 0.2509 | 2.29 | 0.1407 |
| S \times C | 8 | 889 | 0.55 | 0.8194 | 1.50 | 0.1519 | 0.29 | 0.9701 |

Table 2 ANOVA statistics for the fixed components of linear mixed effect model for soil surface CO₂ efflux (F_s), soil temperature (T_s), and soil volumetric water content (θ_v) fitted with the data separately for each season. Fixed effects included stocking (S), clone (C), fertilization (F), and follow-up herbicide (H) treatment, and their two-way interaction. Degrees of freedom (df) for treatments and error used in the calculation of the F-statistic are presented. Only significant results ($p < 0.05$) are reported

| Season | Factor | df treatments | df error | F_s | | T_s | | θ_v | |
|--------|--------|---------------|----------|---------|---------|---------|---------|------------|---------|
| | | | | F-value | p-value | F-value | p-value | F-value | p-value |
| Autumn | H | 1 | 29 | | | | | 10 | 0.0031 |
| | C | 4 | 172 | 7.74 | <0.0001 | 7.43 | <0.0001 | | |
| | S×F | 2 | 29 | | | | | 5 | 0.011 |
| Winter | S×H | 2 | 29 | | | | | 11 | 0.0004 |
| | H | 1 | 29 | | | | | 7 | 0.0137 |
| | C | 4 | 172 | | | 4 | 0.0043 | 6 | 0.0001 |
| Spring | S×H | 2 | 29 | | | | | 5 | 0.0172 |
| | S | 2 | 6 | 17.69 | 0.003 | | | 5.99 | 0.0371 |
| | H | 1 | 29 | | | | | 4.95 | 0.034 |
| Summer | C | 4 | 172 | | | 7 | <0.0001 | | |
| | H×C | 4 | 172 | | | | | 2.54 | 0.0419 |
| | S | 2 | 6 | 7.75 | 0.0218 | | | | |
| | C | 4 | 172 | 2.68 | 0.0336 | 3.27 | 0.0129 | | |

and lowest RMSE compared to T_s -based models across all levels of treatments (Table 4). The Q_{10} values from the combined model ranged from 2.91 to 5.23 and were marginally higher than the ones estimated from the T_s -based model, with the highest Q_{10} observed with clone 3 and the lowest in clone 2. Comparing across silvicultural treatments, Q_{10} values were higher with clone 3, a stocking level of 1250 stems ha⁻¹, and in unfertilized plots without weed control than in other treatments (Table 4). The slope between T_s and F_s increased exponentially and was higher in fertilized plots (Fig. S1-A), and in plots without weed control (Fig. S1-B) than in unfertilized plots and in plots with weed control. The slope of the relationship between T_s and F_s tended to be higher for the 1250 stems ha⁻¹ stocking than for stocking levels of 625 and 2500 stems ha⁻¹ (Fig. S1-C). For the model with clones, the slope of T_s with F_s was significantly higher in clone 3 than in the other four clones (Fig. S1-D). The slope of the F_s - T_s was positive but that of the F_s - θ_v was negative across all levels of treatments (Table 4). There was a strongly negative correlation between the T_s and θ_v ($r = -0.89$) (Fig. S2), indicating that soil temperatures were high when soil volumetric water was low, and vice versa. Therefore, in the regression models for the relationship between F_s against T_s , and θ_v , the estimated values of parameters a and b were always positive, and values of c always negative (Table 4).

Influence of season and silvicultural treatments on surface CO₂ efflux

Values of F_s were strongly controlled by the effects of season ($F_{3,889} = 319.68$, $p < 0.001$), stocking ($F_{2,6} = 9.92$, $p < 0.05$), and clone ($F_{4,889} = 4.32$, $p < 0.01$) (Table 1). No significant

effects of fertilization or follow-up weed control, or two-way interaction between stocking levels, clone, fertilization, and weed control treatments on F_s were observed ($p > 0.05$) (Table 1). Annual F_s estimated from the study site was on average 22.7 ± 7.1 t ha⁻¹ a⁻¹ for CO₂ (range 15.6–27.8). The rate of F_s was highest in autumn (27.7 ± 7.1 t ha⁻¹ a⁻¹ for CO₂, range 25.2–32.5) and lowest in winter (15.6 ± 7.0 t ha⁻¹ a⁻¹ for CO₂, range 14.4–17.4) (Table 3).

When seasonal data were examined separately, the clone significantly affected F_s for summer ($F_{4,172} = 2.68$, $p < 0.05$), and autumn ($F_{4,172} = 7.74$, $p < 0.001$) (Table 2). There were no significant differences between mean soil efflux rates for any clones during winter and spring. Clone 3 exhibited a consistently higher F_s compared to other clones (Table 3). For all clones, values of F_s were at their highest in autumn and lowest in winter, while spring and summer showed intermediate rates between these two extremes (Fig. 2a). Stocking levels significantly influenced F_s in spring ($F_{2,6} = 17.69$, $p < 0.01$) and summer ($F_{2,6} = 7.75$, $p < 0.05$) (Table 2). In spring, F_s was highest (29.5 t ha⁻¹ a⁻¹ for CO₂) for the 1250 stems ha⁻¹ stocking level and lowest (20.9 t ha⁻¹ a⁻¹ for CO₂) for the 2500 stems ha⁻¹ stocking level (Fig. 2b, Table 3). F_s values were consistently higher at a stocking level of 1250 stems ha⁻¹ compared to 625 (by 22%) and 2500 (by 18%) stems ha⁻¹ over all seasons (Table 3). There were no significant main or interactive effects of fertilization and herbicide treatments on F_s ($p > 0.05$) (Table 2).

Discussion

The first hypothesis that F_s would increase with stocking because of greater root and microbial biomass and

Table 3 Soil surface CO₂ efflux rates (mean ± SE), soil temperature (mean ± SE), and soil volumetric water content (mean ± SE) values observed by stockings (stems ha⁻¹), clones (1–5), fertilization (Yes, No), and follow-up herbicide (Yes, No) treatments in *P. radiata* plantations during four seasons. Treatment means within a season followed by the same letter do not differ significantly at $\alpha=0.05$ level using Tukey's HSD test

| Factor | Levels | Soil surface CO ₂ efflux (t ha ⁻¹ a ⁻¹) | | | | | Soil temperature (°C) | | | | | Soil moisture (%) | | | | |
|---------------|--------|---|-------------|-------------|--------------|--------------|-----------------------|-------------|--------------|--------------|--------------|-------------------|--------------|--------------|------------|--------------|
| | | Autumn | Winter | Spring | Summer | Overall mean | Autumn | Winter | Spring | Summer | Overall mean | Autumn | Winter | Spring | Summer | Overall mean |
| Stocking | 625 | 25.2 ± 1.0a | 14.3 ± 1.0a | 22.7 ± 1.0a | 20.0 ± 1.0a | 20.6 ± 1.0 | 11.4 ± 7.0a | 6.7 ± 1.0a | 10.0 ± 1.0a | 17.2 ± 1.0a | 11.3 ± 2.5 | 17.9 ± 1.0a | 17.2 ± 1.0ab | 15.1 ± 1.7b | 7.3 ± 1.0a | 14.4 ± 1.2 |
| | 1250 | 31.4 ± 1.0a | 17.4 ± 1.0a | 29.5 ± 1.0b | 26.9 ± 1.0b | 26.3 ± 1.0 | 11.4 ± 7.0a | 7.1 ± 1.0a | 10.2 ± 1.0a | 17.1 ± 1.0a | 11.4 ± 2.5 | 17.7 ± 1.0a | 17.0 ± 1.0a | 14.7 ± 1.7ab | 7.4 ± 1.0a | 14.2 ± 1.2 |
| | 2500 | 26.8 ± 1.0a | 15.3 ± 1.0a | 20.9 ± 1.0a | 23.4 ± 1.0ab | 21.6 ± 1.0 | 11.4 ± 7.0a | 6.8 ± 1.0a | 10.0 ± 1.0a | 16.7 ± 1.0a | 11.2 ± 2.5 | 17.4 ± 1.0a | 17.2 ± 1.0b | 14.1 ± 1.7a | 7.3 ± 1.0a | 14.0 ± 1.2 |
| Clone | 1 | 25.3 ± 1.0a | 15.1 ± 1.0a | 23.2 ± 1.0a | 23.5 ± 1.0ab | 21.8 ± 1.0 | 11.3 ± 6.7a | 6.8 ± 1.0ab | 10.1 ± 1.0b | 17.0 ± 1.0ab | 11.3 ± 2.4 | 17.8 ± 1.0a | 17.1 ± 1.0ab | 14.5 ± 1.6a | 7.4 ± 1.0a | 14.2 ± 1.2 |
| | 2 | 26.1 ± 1.0a | 15.4 ± 1.0a | 23.9 ± 1.0a | 22.2 ± 1.0a | 21.9 ± 1.0 | 11.3 ± 6.7a | 6.8 ± 1.0a | 10.0 ± 1.0ab | 16.9 ± 1.0ab | 11.3 ± 2.4 | 17.7 ± 1.0a | 17.1 ± 1.0ab | 14.8 ± 1.6a | 7.3 ± 1.0a | 14.2 ± 1.2 |
| | 3 | 32.6 ± 1.0b | 16.5 ± 1.0a | 25.1 ± 1.0a | 22.9 ± 1.0ab | 24.3 ± 1.0 | 11.6 ± 6.7b | 6.9 ± 1.0b | 10.2 ± 1.0b | 16.9 ± 1.0ab | 11.4 ± 2.4 | 17.4 ± 1.0a | 17.3 ± 1.0c | 14.6 ± 1.6a | 7.3 ± 1.0a | 14.1 ± 1.2 |
| | 4 | 26.2 ± 1.0a | 15.7 ± 1.0a | 23.7 ± 1.0a | 22.4 ± 1.0ab | 22.0 ± 1.0 | 11.4 ± 6.7a | 6.8 ± 1.0ab | 9.9 ± 1.0a | 16.8 ± 1.0a | 11.2 ± 2.4 | 17.8 ± 1.0a | 17.2 ± 1.0bc | 14.6 ± 1.6a | 7.3 ± 1.0a | 14.2 ± 1.2 |
| | 5 | 28.8 ± 1.0ab | 15.3 ± 1.0a | 24.4 ± 1.0 | 25.0 ± 1.0 | 23.4 ± 1.0 | 11.4 ± 6.7a | 6.8 ± 1.0ab | 10.1 ± 1.0b | 17.1 ± 1.0b | 11.4 ± 2.4 | 17.8 ± 1.0a | 17.1 ± 1.0a | 14.7 ± 1.6a | 7.3 ± 1.0a | 14.2 ± 1.2 |
| Fertilization | Yes | 28.5 ± 1.0a | 16.1 ± 1.0a | 24.6 ± 1.0a | 23.3 ± 1.0a | 23.1 ± 1.0 | 11.4 ± 6.7a | 6.8 ± 1.0a | 10.1 ± 1.0a | 16.9 ± 1.0a | 11.3 ± 2.4 | 17.6 ± 1.0a | 17.2 ± 1.0a | 14.6 ± 1.6a | 7.3 ± 1.0a | 14.2 ± 1.2 |
| | No | 26.8 ± 1.0a | 15.1 ± 1.0a | 23.6 ± 1.0 | 23.1 ± 1.0a | 22.2 ± 1.0 | 11.4 ± 6.7a | 6.9 ± 1.0a | 10.0 ± 1.0a | 17.1 ± 1.0a | 11.3 ± 2.4 | 17.8 ± 1.0a | 17.1 ± 1.0a | 14.6 ± 1.6a | 7.3 ± 1.0a | 14.2 ± 1.2 |
| Herbicide | Yes | 26.5 ± 1.0a | 15.1 ± 1.0a | 23.8 ± 1.0a | 22.4 ± 1.0a | 21.9 ± 1.0 | 11.4 ± 6.7a | 6.8 ± 1.0a | 10.1 ± 1.0a | 17.1 ± 1.0a | 11.4 ± 2.4 | 17.9 ± 1.0b | 17.1 ± 1.0a | 14.9 ± 1.6b | 7.4 ± 1.0a | 14.3 ± 1.2 |
| | No | 28.9 ± 1.0a | 16.2 ± 1.0a | 24.3 ± 1.0a | 24.1 ± 1.0a | 23.3 ± 1.0 | 11.4 ± 6.7a | 6.8 ± 1.0a | 10.0 ± 1.0a | 16.8 ± 1.0a | 11.3 ± 2.4 | 17.5 ± 1.0a | 17.2 ± 1.0b | 14.4 ± 1.6a | 7.3 ± 1.0a | 14.1 ± 1.2 |
| Overall mean | | 27.7 ± 1.0 | 15.6 ± 1.0 | 24.1 ± 1.0 | 23.3 ± 1.0 | 22.7 ± 1.0 | 11.5 ± 6.7 | 6.8 ± 1.0 | 10.1 ± 1.0 | 16.9 ± 1 | 11.3 ± 2.4 | 17.7 ± 1.0 | 17.2 ± 1.0 | 14.6 ± 1.6 | 7.3 ± 1.0 | 14.2 ± 1.2 |

competition, was only partially supported by the results of this study. F_s values were higher at a medium (1250 stems ha⁻¹) stocking level compared to low (625 stems ha⁻¹) and high (2500 stems ha⁻¹) stocking level across all silvicultural treatments. Observed values of F_s (20.6–26.3 t ha⁻¹ a⁻¹ for CO₂) were within the range reported by Noh et al. (2010) for a Korean red pine (*Pinus densifolia* Siebold & Zucc.) forest in Korea (22.8–27.3 t ha⁻¹ a⁻¹ for CO₂) with the highest value at a medium stocking level, similar to this study. Other studies, however, have found that surface CO₂ efflux increased with stand density (Litton et al. 2003b, 2004) which might be explained by greater root and microbial biomass and higher litter production and decomposition (Litton et al. 2001) at higher densities. There are several possible causes why F_s was greatest at a medium (1250 stems ha⁻¹) level of stocking. First, surface CO₂ efflux may increase from a low to medium stocking level brought about by increases in root and microbial biomass. In addition, F_s may decrease from a medium to a high level of stocking associated with (1) lower soil temperatures and less available water at high stocking levels or, (2) light becoming the most limiting growth factor triggering greater carbon allocation aboveground at the expense of belowground processes. The former may be more likely as our results showed that soil volumetric water content was significantly lower at 2500 stems ha⁻¹ by 2.6 and 1.6% compared to 625 and 1250 stems ha⁻¹, respectively (Table 3).

The second hypothesis was that faster growing clones would show higher surface CO₂ efflux levels, which is fully supported by this study. Clone 3, the fastest growing, had the highest F_s average values (3–10%) compared with the other clones. This indicates that clone 3, having overall greater carbon assimilation, also allocated a greater proportion of fixed carbon belowground compared to the other clones (Bown et al. 2009).

The third hypothesis for this study was that fertilization would not influence surface CO₂ efflux as it was carried out 12 years before the measurements. There were no significant effects of fertilization on surface CO₂ emissions in any season during the year which is consistent with research on radiata pine in Chile (Bown and Watt 2016), slash pine in Florida, USA (Shan et al. 2001), and loblolly pine in Virginia (Tyree et al. 2006) and North Carolina, USA (Maier and Kress 2000). Our study, however, contains only one-year data and the absence of inter-annual variability may prevent finding F_s responses to fertilization (Tyree et al. 2006). However, the insignificant effects of fertilization on surface CO₂ efflux in this study may be because the last fertilization was applied three years after planting and its effects after nine years might have ceased. It may also be because the fertilization level was too small to trigger a growth response (Tyree et al. 2006). At the same time, our temperate study site experiences strong

Table 4 Regression models for the relationship between F_s , T_s , and θ_v across the clones (1–5), stocking levels (625, 1250, and 2500 stems ha⁻¹), fertilization (Yes, No), and follow-up herbicide (Yes, No) treatments. Given a, b, and c are parameter estimates of the regression,

RMSE is the root mean square error, R^2 is the coefficient of determination, Q_{10} is the temperature sensitivity index for F_s (at 10 °C increase in T_s)

| Factors | Levels | T_s -based: $F_s = ae^{bT_s}$ | | | | | T_s and θ_v -based: $F_s = ae^{bT_s}e^{c\theta_v}$ | | | | | |
|---------------|--------|---------------------------------|---------|-------|----------|------|---|---------|----------|-------|----------|------|
| | | a | b | R^2 | Q_{10} | RMSE | a | b | c | R^2 | Q_{10} | RMSE |
| Clone | 1 | 0.54*** | 0.12*** | 0.27 | 3.26 | 0.66 | 0.98* | 0.12*** | -0.04ns | 0.28 | 3.41 | 0.65 |
| | 2 | 0.59*** | 0.11*** | 0.29 | 2.98 | 0.57 | 0.41* | 0.11*** | 0.02ns | 0.30 | 2.91 | 0.56 |
| | 3 | 0.39*** | 0.16*** | 0.47 | 5.03 | 0.63 | 0.79* | 0.17*** | -0.04ns | 0.48 | 5.23 | 0.62 |
| | 4 | 0.55*** | 0.11*** | 0.41 | 3.13 | 0.44 | 0.86* | 0.12*** | -0.03ns | 0.42 | 3.24 | 0.44 |
| | 5 | 0.44*** | 0.14*** | 0.43 | 4.17 | 0.54 | 0.69** | 0.15*** | -0.03ns | 0.44 | 4.42 | 0.54 |
| Stock | 625 | 0.50*** | 0.12*** | 0.33 | 3.34 | 0.54 | 1.01** | 0.13*** | -0.04* | 0.35 | 3.54 | 0.54 |
| | 1250 | 0.49*** | 0.14*** | 0.48 | 4.14 | 0.54 | 0.78*** | 0.15*** | -0.03* | 0.49 | 4.37 | 0.53 |
| | 2500 | 0.49*** | 0.13*** | 0.31 | 3.49 | 0.62 | 0.49* | 0.13*** | 0.03ns | 0.31 | 3.49 | 0.62 |
| Fertilization | Yes | 0.51*** | 0.13*** | 0.36 | 3.68 | 0.61 | 0.74*** | 0.13*** | -0.02ns | 0.36 | 3.76 | 0.61 |
| | No | 0.47*** | 0.13*** | 0.38 | 3.76 | 0.56 | 0.83*** | 0.14*** | -0.0374* | 0.39 | 3.99 | 0.55 |
| Herbicide | Yes | 0.50*** | 0.12*** | 0.39 | 3.47 | 0.52 | 0.92*** | 0.13*** | -0.04** | 0.41 | 3.68 | 0.50 |
| | No | 0.47*** | 0.14*** | 0.36 | 4.01 | 0.64 | 0.61** | 0.14*** | -0.02ns | 0.36 | 4.08 | 0.65 |

Significance values denoted as * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, ns Not significant

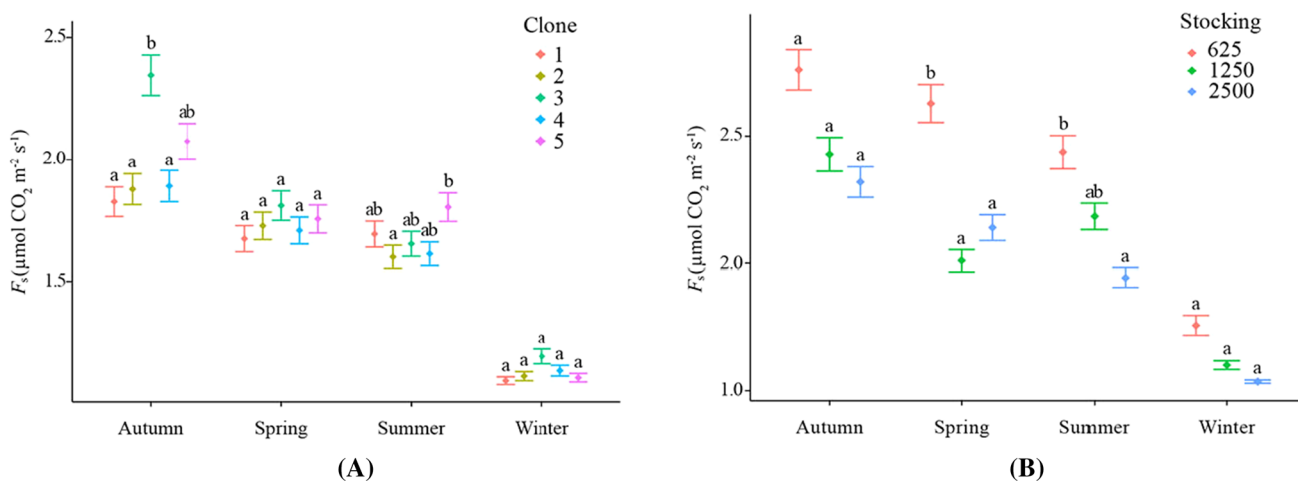


Fig. 2 Seasonal dynamics of F_s ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) across silvicultural treatments across five clones (a), and three stockings (b). Values are presented as least square mean (± 1 SE) of F_s , by season. Treat-

ment means within a season followed by the same letter do not differ significantly at $\alpha=0.05$ level using Tukey’s HSD test

water limitations, particularly during summer, and therefore water rather than nutrients might be the major limiting factor affecting plant growth (Davidson et al. 1998; Lavigne et al. 2004).

The fourth hypothesis that there would be no effects of weed control on soil surface CO₂ efflux was supported by this study. In contrast, research by Shan et al. (2001) in slash pine plantations in Florida, USA, indicated that the elimination of the understory significantly affected surface CO₂ effluxes. This suggests that weed control reduced F_s by decreasing below-ground biomass. However, we believe the insignificant effects of weed control on F_s in this study

is the result of the time elapsed. Weed control was applied to all plots during the first two years, while total weed control was carried out prior to canopy closure in weed control plots only (Mason 2008). However, surface CO₂ efflux measurements in this study were carried out at age 12, eight years after the follow up weed control when the effects of weeds were likely to have ceased.

The fifth hypothesis that both soil temperature and soil water would control CO₂ effluxes across all silvicultural treatments is supported by this study. Collectively, both explain 27.9–48.9% of the efflux variance as being significantly better to the model that considered only soil

temperature (Table 4). Other studies have also reported that the combination of soil temperature and water can explain most of the variations in CO₂ efflux as being the most important controlling factors (Gough and Seiler 2004; Liu et al. 2011). Soil temperatures contributed positively to F_s , while soil water contributed negatively (Table 4). However, there was a strong, negative correlation between soil temperature and soil water (Fig. S2), indicating that soil temperatures were high when soil water was low and vice versa, which may confound the interpretation of the model. The temperature sensitivity of surface CO₂ efflux (Q_{10}) values in this study (2.9 to 5.2) across all silvicultural treatments were in the 1–10 range of other reports (Raich and Schlesinger 1992; Davidson et al. 1998; Gulledge and Schimel 2000; Xu and Qi 2001a, b) depending on the type of ecosystem and climatic conditions. The Q_{10} value in this study was highest for the fast-growing clone 3 at a stocking level of 1250 stems ha⁻¹.

This study provides insight into how silvicultural management decisions may impact soil surface CO₂ effluxes and may contribute towards better estimates of carbon budgets in plantations. Surface CO₂ emissions varied with plantation density and clone, and with soil temperatures and water content, both contributing to the differences in fluxes across seasons. Higher efflux rates at a medium (1250 stems ha⁻¹) stocking level compared to low (625 stems ha⁻¹) and high (2500 stems ha⁻¹) stocking levels were observed. There were no effects of fertilization and weed control after 12 years, indicating that the effects of these treatments might have ceased. Efflux levels varied with clones, being higher in faster growing clones. In conclusion, surface CO₂ effluxes changed with silvicultural practices which might have implications for carbon accounting.

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