

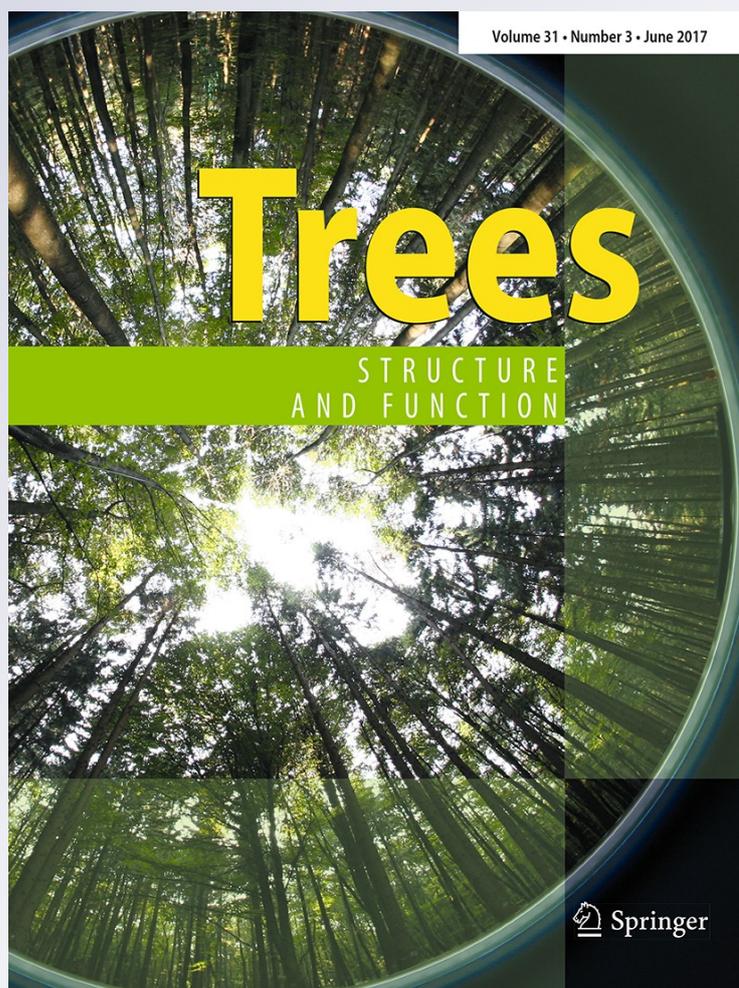
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Sustained carbon uptake in a mixed age southern conifer forest

Cate Macinnis-Ng¹ · Sarah V. Wyse² · Tristan Webb³ · Daniel Taylor¹ · Luitgard Schwendenmann³

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Abstract

Key message Larger trees accumulate more carbon but have lower growth rates per unit biomass. Nevertheless, large trees are a vital part of the carbon cycle of this mixed age forest.

Abstract Globally, there is a strong need for detailed information on carbon (C) budgets of native forests, yet New Zealand forests are underrepresented in C inventories. Stem growth and CO₂ efflux are two of the major components of forest C budgets, especially in forests with long-lived, large trees. In this paper, we present a breakdown of tree-level C accumulation rates for 26 trees [9.7–176 cm diameter at breast height (DBH)] of one of the world's largest tree species: the endemic conifer kauri (*Agathis australis*) over 3 years (2010–2013) in west Auckland. We examined the relationship between C accumulation, tree size, and canopy class (dominant, co-dominant, and intermediate). The total amount of C accumulated was 2.7, 3.5, and 4.2 Mg C ha⁻² year⁻¹ in 2011, 2012, and 2013, respectively. Large trees (>70 cm DBH) had the fastest absolute rates of growth (basal area increment; 30–140 cm² year⁻¹) and C accumulation (0.01–0.048 Mg C year⁻¹), but the lowest rates of relative growth (per unit biomass). Relative growth rates peaked at a diameter at breast height of

25 cm, and consequently, co-dominant trees had the highest annual relative growth rates (1.7–2.2% year⁻¹). The majority of C was accumulated in co-dominant trees (62%), with smaller amounts accumulated in dominant (29%) and intermediate trees (9%). One-third of the stand's C accumulation was accrued by the largest 6% of trees, which made up 46% of the stand's basal area. While maintenance and growth respiration rates were higher for larger trees, C use efficiency (CUE) was consistent across tree-size classes. To extend the size of trees analysed, we included data from tree-ring analysis of 13 additional trees up to 243 cm DBH and found larger trees accumulated proportionally less C per unit biomass than smaller trees.

Keywords Carbon uptake and storage · *Agathis australis* · Carbon-use efficiency · Tree growth · New Zealand kauri · Forest carbon budget

Introduction

Forests play a significant role in the global carbon (C) cycle, with 70–80% of terrestrial C stored in forest ecosystems (Baccini et al. 2012). Globally, forests are a net C sink, currently absorbing more C than they release (Pan et al. 2011, 2013; Houghton et al. 2012). However, it is uncertain if this carbon-sink capacity will persist (Bellassen and Luyssaert 2014). Effects of disturbance events (such as droughts, fire, and insect outbreaks) and changing climatic conditions could result in a net C release across forest biomes (IPCC 2014; Coomes et al. 2014). The question of whether forests are likely to shift from C sinks to C sources is fundamental for forest conservation and management, as well as for greenhouse gas (GHG) mitigation strategies (McKechnie et al. 2014). Consequently, quantifying the C sequestration

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potential of forests is central to predicting changes in the global forest C sink over the coming century.

Quantifying C storage and accumulation of tree stems is crucial to quantifying forest C sequestration. Stems are the major reservoir for C storage, with the largest fraction of total forest C stored in stem biomass (Waring and Schlesinger 1985; Clark et al. 2001). Furthermore, stems store C for longer periods compared to foliage and fine roots (Campioli et al. 2008). The size of a tree's stem has significant consequences for its growth and C accumulation potential, and it is the combination of C accumulation at the tree level, the distribution of tree size, and the mortality patterns within a forest that determine the forest's net productivity (Hicke et al. 2004; Alexandrov 2007). Large dominant trees capture more C less efficiently, but also compete with smaller trees for resources (McDonald et al. 2002) which may result in a decline of small tree C uptake potential (Binkley et al. 2002, 2010) and may enhance small tree mortality (Das et al. 2011; Ruiz-Benito et al. 2013). Moreover, if the tree-size distribution within a forest is skewed towards a greater frequency of dominant trees, then large trees will contribute more to C storage than to forest productivity, given their less efficient C acquisition rates. For example, because of the frequency of dominant trees, the largest trees in old-growth northern conifer forests (Engelmann spruce and subalpine fir) comprise half of the total stand biomass, but contribute only one quarter of the current stem increment (Binkley et al. 2003, 2006). Quantifying these stem growth and frequency patterns is vital for understanding and modelling how future climates will affect forest production.

New Zealand kauri (*Agathis australis* (D. Don) Lindl. ex Loudon, Araucariaceae) forests store large amounts of C by global comparisons and are ranked as one of the most C-dense ecosystems in the world (Silvester and Orchard 1999; Silvester 2000; Keith et al. 2009), with up to 636 Mg C ha⁻² in living woody biomass (Silvester and Orchard 1999). Kauri is a southern conifer endemic to northern New Zealand (north of latitude 38°S) (Ecroyd 1982; Steward and Beveridge 2010), which once covered 1.2 million hectares, but now cover less than 5% of their original area. They are described as a 'foundation species' because of their influence on forest C sequestration, nutrient dynamics, and structuring of species assemblages (Silvester 2000; Silvester and Orchard 1999; Wyse et al. 2013). Kauri trees are long-lived, often in excess of 600 years, and stem diameters wider than 2 m (with heights of up to 30–50 m) are common (Steward and Beveridge 2010). Growth rates of kauri trees are generally slow, but little is known about their growth and productivity, especially with respect to tree size (Steward et al. 2014). Research in other forest ecosystems has shown a variety of patterns among species for rates of

growth and C gain with respect to tree size (Weiner and Thomas 2001; Stephenson et al. 2014). These size patterns are important for understanding C uptake within kauri forests from both a physiological and competitive perspective and may provide insight into mortality and species distribution patterns within kauri forests. Furthermore, in recent years, the fungus-like *Phytophthora agathidicida* (Weir et al. 2015) has been affecting kauri trees, resulting in leaf loss, canopy thinning, and eventual tree death (Beever et al. 2009; Waipara et al. 2013). To understand the impact of this pathogen on forest function, we must first quantify C uptake (accumulation), storage, and sequestration potential of healthy stands.

The efficiency of stem C accumulation (carbon-use-efficiency; CUE) is the fraction of total C accumulated that is incorporated into stem tissue, i.e., the ratio of stem C accumulation to total C accumulation (stem accumulation plus stem CO₂ efflux) (Ryan and Waring 1992; Ryan et al. 1996; Maier 2001). It is informative to measure stem CO₂ efflux, since woody tissue constitutes the largest part of forest biomass and C, and the amount of CO₂ emitted from the stem surface influences the C balance of forest ecosystems (Ryan et al. 2009). The proportion of CO₂ released from woody tissues accounts for 15–30% of forest ecosystem respiration (Ryan et al. 1994; Damesin et al. 2002; Chambers et al. 2004). Stem CO₂ efflux can be partitioned into 'growth respiration', associated with the production of new wood, and 'maintenance respiration', which is related to all plant processes that do not result in a net increase in plant dry matter (Ryan 1990; Maier 2001). The latter can quantify differences in respiration costs between small and large trees (Ryan and Waring 1992) and aid understanding of size-related changes in the efficiency of stem C accumulation.

In this study, we report on the seasonal and tree-size-related patterns of C accumulation (reported as basal area increment (BAI), relative BAI (standardised to basal area), tree and stand total C accumulation), stem C efflux, and C use efficiency of kauri trees in a kauri-dominated forest over for three growing seasons between 2010 and 2013. The aims of this study are the following: first, to examine the effect of tree size on growth rates (BAI per year) and stem C sequestration rates (mass of C per year) of individual kauri trees; second, to assess how the size of individual kauri trees scale to C pool sizes at the stand level; and third, to estimate carbon-use-efficiency and the proportion of growth and maintenance respiration across tree sizes. Finally, we explore the seasonality of growth rates and stem respiration components. We hypothesise that larger trees will have lower growth rates per unit biomass and CUE and will, therefore, contribute proportionally less to stand C uptake than smaller trees.

Methods

Study site and tree selection

The University of Auckland Scientific Reserve at Huapai is a 15 ha remnant of forest surrounded by farmland (Thomas and Ogden 1983). It lies approximately 25 km west of central Auckland on the northern fringe of the Waitakere Ranges (36°47.7'S, 174°29.5'E). Total annual rainfall at the site is approximately 1200 mm and is winter (June–August) dominant. The annual mean temperature is 14 °C. The soil consists of brown granular clay, which is sticky when wet and hard and fragile when dry (Thomas and Ogden 1983). The tree density of the study plot (50×40 m) is 770 stems per ha (Wunder et al. 2010). Kauri contributes 26% of total stem number but accounts for approximately 80% of both total stand basal area (94 m² ha⁻¹, Wunder et al. 2010) and total C in stand stem biomass (280 Mg C ha⁻¹, unpublished data).

Within the study plot, 26 kauri trees (of 154 in the plot) ranging in diameter (at breast height) from 9.7 to 176.0 cm and in age from 80 to 750 years were selected for dendrometer and stem CO₂ efflux measurements (Table 1). These trees had previously been assigned to the canopy classes ‘dominant’, ‘co-dominant’, ‘intermediate’, and ‘suppressed’ by Wunder et al. (2010). Of our 26 sample trees, 8 were classified as dominant, 14 as co-dominant, and 4 as intermediate. The average characteristics of these groups for our sample are given in Table 1. Tree-ring data from a further 13 larger trees (up to 243.0 cm DBH) from a different stand at the same site were added to the analysis of growth response to tree size.

Growth and carbon accumulation

Dendrometer bands with spring tensioning and a resolution of 0.01 cm (D1, UMS GmbH, München Germany) were attached to trees at 1.3 m (breast height) from the ground. Before installation, loose bark was removed from trees. Readings were generally taken fortnightly across the

3 year period (although occasionally readings were taken at monthly intervals when weather made fortnightly measurements difficult). Each measurement was taken mid-morning by the same observer and corrected for the errors outlined by Fowler et al. (2005). The interval used to define annual growth was that between the months in which kauri growth is minimal. Thus, in the present study, annual growth was defined as the gain in basal area or C mass between August in the first year and July of the next year, because kauri growth rates are close to zero in July and August (Fowler et al. 2005; Wunder et al. 2013). For increment cores (from the larger trees), measurements of ring width were used in place of dendrometer readings to calculate annual growth increment.

Tree basal area increment (BAI) was used to provide an indicator of overall tree growth (Biondi and Qeadan 2008) and a measure of the amount of wood added to the stem. Tree BAI was determined by calculating the difference between two basal area measurements, respectively:

$$BAI = \frac{\pi}{4} (DBH_2^2 - DBH_1^2) \tag{1}$$

where DBH₁ and DBH₂ are successive dendrometer readings (or values derived from tree-ring width measurements), respectively. The DBH was measured over the bark. It was assumed that the influence of bark would be consistent across trees and no bark adjustment factor was applied. Linear regression was used to estimate the relationship between DBH and the annual tree BAI. Relative annual tree BAI was calculated by dividing BAI for the year by the basal area of the tree at the start of a given year.

Stem volume per tree was estimated by applying the volume equation developed for mature kauri (Ellis 1979):

$$V = (0.095) \cdot (DBH^{2.05}) \cdot (e^{1.66 \times 10^{-6} DBH^2}) \cdot (H^{0.70}) \tag{2}$$

where V is stem volume (m³), DBH is diameter at breast height (cm), and H is the height of the bole (m). Stem volume was then converted into stem C density using the mean value of kauri stem-wood density (0.473 g cm⁻³, Jager

Table 1 Characteristics of sample trees, including canopy class, diameter at breast height (July 2013), tree height (July 2013), and tree age

Canopy class	Sampling type	Number of sample trees	DBH (cm)	Height (m)	Age (years)
Dominant	Dendrometer	8	98.9 ± 13.3b	20.6 ± 0.4b	350–750
Co-dominant	Dendrometer	14	44.4 ± 3.8c	20.1 ± 1.4b	~100
Intermediate	Dendrometer	4	15.1 ± 2.6d	18*	<100
Dominant	Increment core	13	154.8 ± 12.9a	25.8 ± 0.8a	500–900

Trees were either sampled using fortnightly observations of fitted dendrometer bands or had tree rings counted from increment cores. Canopy class and tree age were taken from Wunder et al. (2010) and Fowler and Boswijk (2001), respectively. Values are means ± standard error. Different letters indicate significant differences at *p* < 0.05

**n* = 1, height measurements of other trees were not possible due to proximity of surrounding trees

et al. 2015) and the mean C concentration of kauri stemwood (47%). Annual stem C accumulation rates were estimated by calculating the difference between stem C density at the start (August) and end of year (July). To upscale the annual stem C accumulation rates (2010–2013) per canopy class to stand level, the mean annual stem C accumulation of each canopy class was calculated as

$$Ca_i = \mu_i \cdot \tau_i \quad (3)$$

where Ca_i ($\text{Mg C ha}^{-2} \text{ yr}^{-1}$) is the annual C accumulation rate of the i th canopy size class, μ_i is the mean annual C accumulation rate of the trees in the i th size class (Mg C yr^{-1}), and τ is the number of trees in the i th size class per hectare of land area (ha^{-2}). For these estimates, the intermediate and suppressed trees were pooled, and our 'intermediate' class, therefore, refers to the combined intermediate and suppressed size cohorts. To extend the size-range of trees studied, our analysis of the relationship between tree size (DBH) and C accumulation also included tree-ring data (from increment cores) on 13 additional kauri trees obtained by Fowler and Boswijk (2001). These trees were on the adjacent ridge, approximately 130 m from the main study stand (as the crow flies). The environmental conditions, including elevation, soil type, and aspect, were similar at the two locations. The C accumulation rates of these extra trees were calculated from Eqs. 1 and 2 using measured tree-ring widths (over a period of 5 years during the 1990s), the measured DBH at the time of sampling, and an assumed C density of 0.22 g cm^{-3} (using wood density and C concentrations as above). While the sampling period for the two methods was different (2010–2013 for dendrometer bands and late 1990s for increment cores), Fowler et al. (2005) and Wunder et al. (2013) found good agreement for the two methods. Furthermore, the radial growth rate based on dendrometer measurements reported by Fowler et al. (2005) for the late 1990s (0.5–3 mm p.a.) was similar to our measured radial growth rates of 0–2.6 mm p.a., so we assume that the growth rates are similar during the two measurement periods. The method of obtaining core samples and measuring tree widths is outlined in detail by Fowler and Boswijk (2001), but is briefly reiterated here. Samples from the same site were obtained in the 1990s (Fowler and Boswijk 2001). Cores were extracted at breast height using a 40 or 80 cm long increment corer. From each tree at least two cores were taken, air dried, glued onto wood mounts, sanded, and then scanned at 1200 dpi. The image was imported into the 'winDendro' program, and rings widths were measured to 0.001 mm. Cross-dating was conducted using the cross-dating program "XMATCH" (Fowler 1998). Tree-ring data from the 13 largest trees (DBH > 100 cm) were used for this study.

Stem CO₂ efflux measurements

To understand the importance of stem CO₂ efflux in this kauri-dominated stand, we measured stem CO₂ efflux on a monthly basis between November 2012 and October 2013 using the dynamic closed-chamber method (Pumpanen et al. 2004). A PVC pipe (8.5–10.5 in length, 10 cm in diameter) was attached to a soil respiration chamber (SRC-1, PP Systems, Amesbury, MA, USA). A 3-cm thick cell foam collar was affixed to the tree trunk (above the bark) at an approximate height of 1.3 m on each tree. The PVC pipe was bevelled on one end to fit the curvature of the tree (with different amounts of bevelling for different sized trees), and a piece of closed cell foam was placed between the tree and the pipe. The chamber was held firmly in place to make a tight seal throughout the 90-s measurement period. The total volume of the system ranged from 2073 to 2238 cm³. The chamber was connected to an infrared gas analyzer (EGM-4, PP Systems, Amesbury, MA, USA) to measure the CO₂ concentration. Kauri lose plates of bark as a strategy to reduce epiphyte coverage (Wyse and Burns 2011), and stem locations for measurements were generally placed within a region with freshly fallen bark to reduce error from measurements of epiphyte CO₂ fluxes. Stem CO₂ efflux measurements were conducted across the day (5 am to 4 pm) on a subset of trees ($n=6$) on 21st December 2012 and 15th January 2013. Stem CO₂ efflux was calculated as

$$\text{Stem CO}_2 \text{ efflux} = \left(\frac{dC}{dt} \right) \left(\frac{PV}{RTA} \right) \quad (4)$$

where dC/dt ($\mu\text{mol C } \mu\text{mol dry air}^{-1} \text{ s}^{-1}$) is the increase of CO₂ concentration in the chamber airspace over time, V (m^3) is the chamber volume, A (m^2) is the enclosed surface area, P (Pa) is atmospheric pressure, T (15 °C, 288 K) is the temperature, and R is the universal gas constant. Flux measurements were conducted under ambient conditions with varying temperatures. We converted the measured values to a common temperature (here 15 °C, annual average air temperature at Huapai) to make comparisons. Stem CO₂ efflux values were estimated only when the coefficient of determination of the linear relationship between time and CO₂ concentration was higher than 0.97.

Whole-stem CO₂ efflux was estimated by multiplying the chamber-based stem CO₂ efflux rate by the stem surface area (Lavigne et al. 1996; Bowman et al. 2005). Stem surface area was calculated using a cone function. Daily stem CO₂ flux values were averaged across the year to obtain mean annual stem CO₂ efflux values. This was a simplified approach, but we found only a weak temperature effect, because the range in temperature at the site is only 5–25 °C across the year. To differentiate total respiration into growth and maintenance components, we used

the subtraction method, also known as the mature tissue method (Amthor 1989; Sprugel 1990; Maier 2001), whereby respiration rates measured, when stem increments were lowest (April–July), are used to represent maintenance respiration. Growth respiration was calculated as the difference between total stem CO₂ efflux and maintenance respiration at a given date. The growth (r_g) and maintenance respiration (r_m) coefficients were estimated as the ratio of annual growth (Rg) and maintenance respiration rate (Rm) to annual stem C accumulation (Lavigne and Ryan 1997).

Stem carbon-use-efficiency (CUE; a dimensionless quantity) for each tree was estimated as the ratio of C contained in new stem growth (i.e., annual stem C accumulation) to total C used for growth plus whole-stem CO₂ efflux (Ryan et al. 1996; Lavigne and Ryan 1997):

$$CUE = \frac{\text{annual stem C accumulation}}{\text{annual stem C accumulation} + \text{annual C arising from stem CO}_2\text{ efflux}}. \quad (5)$$

Statistical analysis

Analysis of variance with size class as a fixed factor was used to test for differences in tree BAI, stem C density, annual stem C accumulation, and stem CO₂ efflux among canopy/size classes and tree age (where applicable). Differences were assumed significant when $p \leq 0.05$ and Tukey's HSD procedure was used for post hoc testing. To describe the relationship between stem C accumulation and tree C mass, we fitted a power function of the form $y = ax^b$, where y is annual stem C accumulation, x is the total C mass of the stem measured at the start of the year, a is a scaling parameter, and b is a shape parameter. The coefficients for this function were obtained via linear regression of $\log_{10}(y)$ on $\log_{10}(x)$ to reduce the influence of an unusually large rate of annual C accumulation of a single tree. Statistical analyses were carried out using IBM SPSS (version 22, IBM-SPSS Inc., Chicago, IL) or R v. 2.13.0 (R Project for Statistical Computing).

Results

Periods of dormancy (July–August) and growth (October–December) were most clearly visible for dominant and co-dominant trees (Fig. 1 a and b). Tree BAI was highest (up to 1.1 cm² day⁻¹) for trees belonging to the dominant canopy class (Fig. 1a). Annual DBH increment ranged between 0 and 5.2 mm year⁻¹, with an average increment of 3 mm year⁻¹ (equivalent to a radial increment of 1.5 mm year⁻¹). Annual tree BAI ranged from 0 to 140 cm² year⁻¹ and increased linearly with DBH when DBH was above 25 cm (Fig. 2a). Relative annual

tree BAI initially peaked (at a DBH of approximately 25–30 cm) but then declined with increasing DBH thereafter (Fig. 2b).

The quickest rates of basal area increment were observed in the dominant kauri trees, with BAIs ranging between 42 and 58 cm² year⁻¹ between 2010 and 2013 (Fig. 3a). Similarly, mean rates of tree C accumulation differed among canopy classes with the highest values measured in the dominant canopy class 12–19 kg C per tree over the 2010–2013 period (Fig. 3b) across the stand. In contrast, total stand C accumulation over each year was greatest for co-dominant trees and smallest for intermediate trees (Fig. 3c).

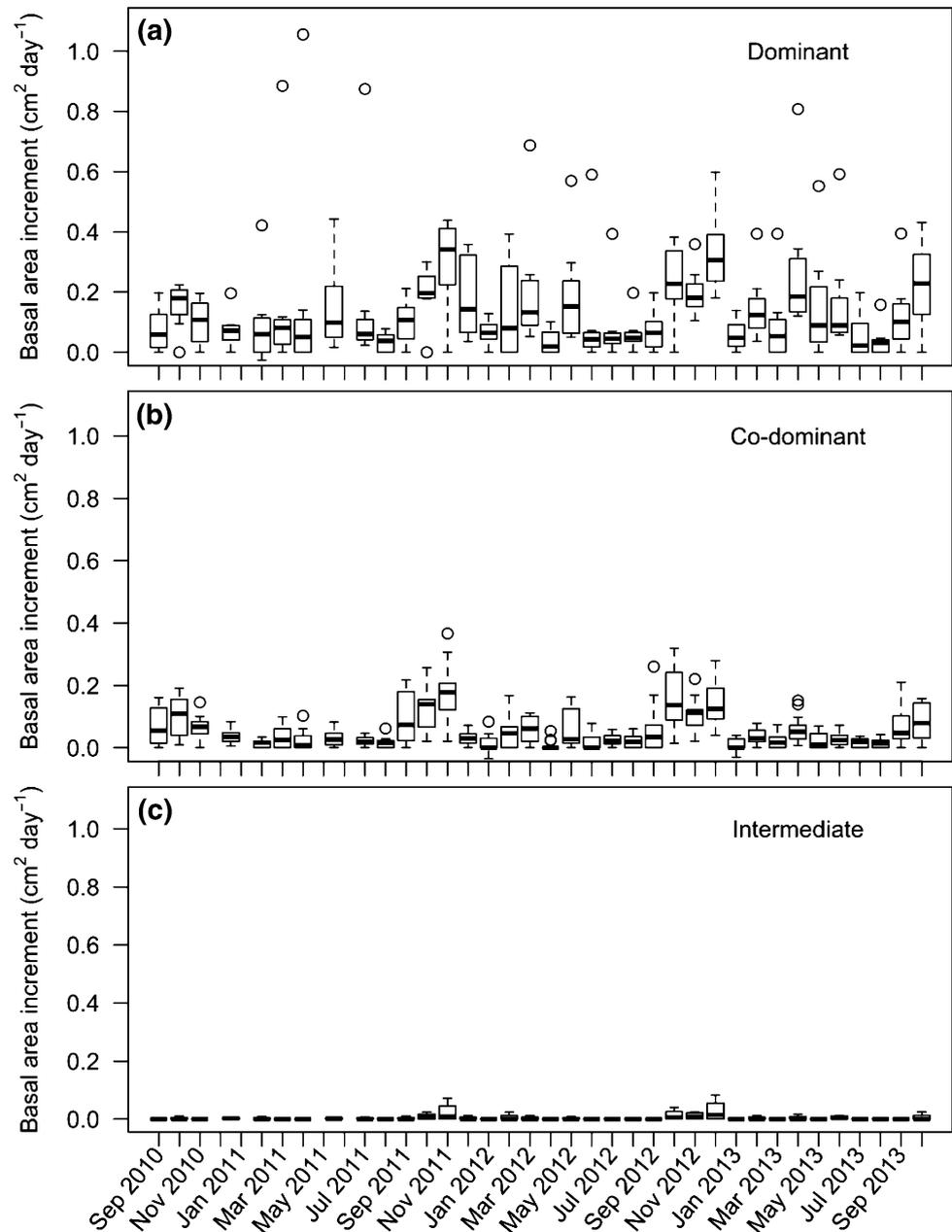
Total stand-level C gain of kauri trees increased for each subsequent year and was 2.69, 3.49, and 4.21 Mg C

ha⁻² yr⁻¹ in each of the three measurement years (Fig. 4). When broken down by canopy class, the majority of C was accumulated by trees classified as co-dominant (62% average between 2010 and 2013) with smaller amounts accumulated in dominant (29%) and intermediate/suppressed trees (9%) (Fig. 4). These proportions were relatively consistent from year to year (Fig. 4). Total stand basal area of dominant and intermediate trees was proportionally larger than their C contributions to the stand, while co-dominant trees contributed proportionally more C (Fig. 4) than the basal area proportion of this canopy class.

Annual C accumulation rates as a function of stem C density showed that C accumulation decelerated ($p < 0.0001$) with increasing stem C density and that C density explained 85.5% of the variation in annual C accumulation (Fig. 5) in a non-linear function.

Mean monthly stem CO₂ efflux per unit stem area varied from 0.7 to 2.8 μmol CO₂ m⁻² s⁻¹ (Fig. 6). For each canopy class, the highest rates of stem CO₂ efflux generally occurred in summer and late spring, and the lowest rates in winter (Fig. 6). In our study, within-day variation (0500–1600 h) in stem CO₂ efflux was small (<10% for four of the six stems measured and around 30% for the other two stems, data not shown). Mean annual stem CO₂ efflux per unit stem area (1.8 ± 0.2 μmol CO₂ m⁻² s⁻¹) and whole-stem efflux (24.6 ± 5.7 kg C per tree) were highest for dominant trees (Table 2). The maintenance respiration coefficient (r_m) differed significantly between the dominant canopy class (0.45) and the intermediate class (1.22) (Table 2). No significant differences among canopy classes were found for r_g and stem CUE (Table 2).

Fig. 1 Box and whisker plots of mean monthly growth presented as tree basal area increment (BAI) for different canopy classes. Data from **a** 8 dominant, **b** 14 co-dominant, and **c** 4 intermediate individuals



Discussion

Kauri growth

Kauri growth rates (annual DBH increment) at Huapai ranged between 0 and 5.2 mm year⁻¹ with an average rate of 3 mm yr⁻¹. Such growth rates are comparable to kauri stands of similar age in the Northland of New Zealand (1.5–4.6 mm year⁻¹, average: 2.3 mm year⁻¹; Ahmed and Odgen 1987), and are typical of large NZ forest trees (*Beilschmiedia tawa*, 2–3 mm year⁻¹; Smale et al. 2014, *Weinmannia racemosa*, 2.2 mm year⁻¹ and *Lophozonia menziesii*, 3.0 mm year⁻¹; Richardson et al. 2009). Globally,

the growth rates (BAI) measured for kauri in this study (35–135 cm² year⁻¹ for trees >70 cm in diameter and aged 350–750 years, Fig. 2a) are comparable to similarly aged conifers in western Oregon (Douglas fir, 60 cm² year⁻¹, 200 years, >100 cm in diameter; Poage and Tappeiner 2002), but substantially higher than that recorded for conifers in the eastern United States (oak, aspen, hemlock and pine, 4–15 cm² year⁻¹, >200 years; Johnson and Abrams 2009).

The fastest rates of growth in kauri basal area were recorded in between October and December (Spring) during 2010 to 2013. Within each year, the BAI of each size class peaked at a common month (October in 2010,

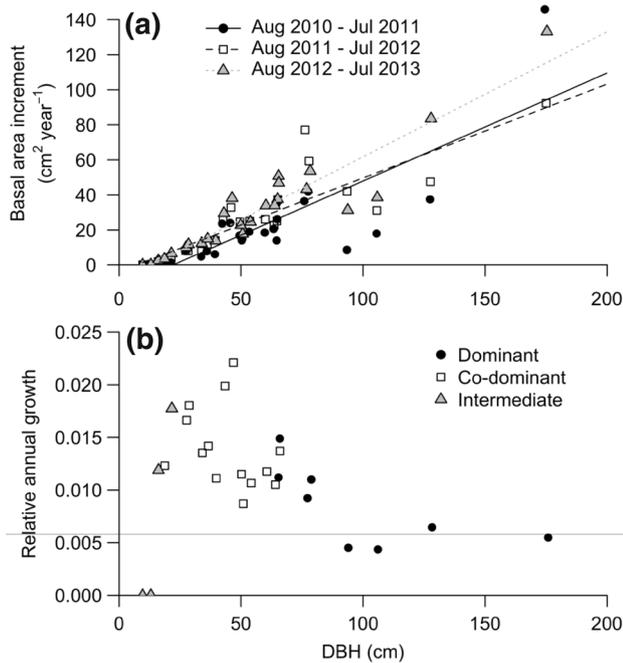


Fig. 2 Growth rates for different tree sizes. **a** Annual tree basal area increment (BAI) versus diameter at breast height. Each point represents one tree in each of the three measurement years. R^2 values are 0.734, 0.806, and 0.884 ($p < 0.001$) for each year chronologically. **b** Relative annual tree basal area increment (BAI) versus diameter at breast height for the 2012–2013 growth year. Relative annual BAI was calculated as BAI for the year divided by the basal area of the tree at the start of the year. Other sampling years had similar relative growth patterns

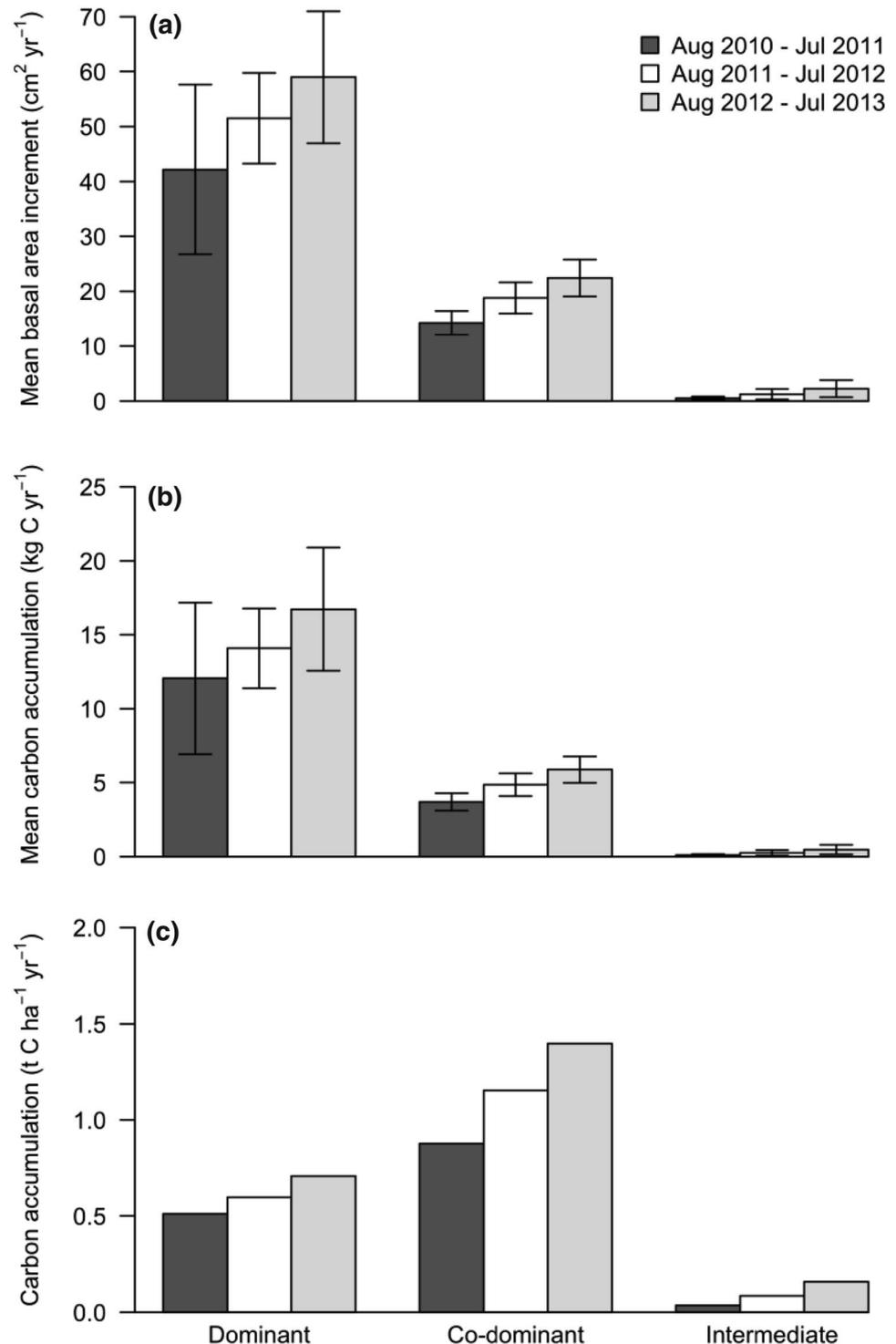
November in 2011, December in 2012, and October in 2013; Fig. 1 a–c). A dominance of spring growth in kauri has been observed previously at Huapai (Fowler et al. 2005, 2010; Wunder et al. 2013); however in contrast to our results, Fowler et al. (2005) observed a difference in the timing of peak growth that was dependent on tree size. Specifically, small- and medium-sized trees experienced peak growth rates in October (0.3–1.1 m in DBH) and larger trees (DBH >1.1 m) in November, a pattern that was consistent over 3 years of observation. These differences were of concern for Fowler et al. (2005), because they represented a potential violation of the assumptions and potentially the validity of climate reconstructions from kauri growth rings. Our data, however, suggest a consistency in peak growth timing among size cohorts. One explanation of the difference in peak growth between our study and that of Fowler et al. (2005) is that our trees are more spatially randomised with respect to tree size, and thus, differences in seasonal growth patterns among size cohorts are less likely to be confounded by any spatial environmental gradients within our study plot, a concern originally raised by Fowler et al. (2005) in their study.

The positive linear relationship between tree BAI (absolute BAI) and DBH, particularly at tree sizes >25 cm in diameter (Fig. 2a), indicates that kauri trees can increase growth and wood production over their natural life span, which can be up to 2000 years. Growth trends like this have been observed for aspen, oak, pine, hemlock, and gum trees >300 years in the eastern United States (Johnson and Abrams 2009), and for *Eucalyptus regnans* and *Sequoia sempervirens* (Sillet et al. 2010). In contrast to absolute BAI, relative BAI initially peaked in 25–30 cm diameter trees, and then declined with further increases in tree size (Fig. 2b), indicating that growth rate per unit tree mass declines in larger kauri. The pattern of change in relative growth with tree size may be due to older trees accumulating less C per unit standing mass, because big trees have such larger mass to begin with, but it may also be explained by differing patterns of biomass allocation in larger compared with smaller kauri. Smaller (and younger) kauri has an architecture and morphology adapted to light capture (apically dominant growth and planar foliage), and much of the C accumulated by small kauri trees is invested in height growth rather than lateral increment (Ecroyd 1982; Wunder et al. 2013). Because of this, relative BAI increment is almost zero in kauri with a DBH <20 cm (Fig. 2b). For larger kauri, relative growth (standardised to basal area) progressively declines due to an accumulation of non-photosynthetic structures, including stems, branches, and roots (Weiner and Thomas 2001; Mencuccini et al. 2005; Bowman et al. 2013). Despite declining relative growth in larger kauri, we still observe increasing overall growth with tree size. The apparently different responses of absolute and relative growth are reconciled by metabolic scaling theory, which predict that leaf mass increases with the square of stem diameter (Enquist et al. 1999). Because an increment in stem diameter results in a more than proportional addition of photosynthetic leaf mass and area, overall tree growth continues to increase with tree size, despite progressive declines in growth per unit tree biomass (Stephenson et al. 2014).

Carbon accumulation (whole stand)

Compared with other kauri stands in New Zealand, C accumulation rates at Huapai (2.7–4.2 Mg C ha⁻² year⁻¹) were considerably faster than that reported for mature, but slightly younger stands. Silvester and Orchard (1999) reported kauri C accumulation rates of 1.5 Mg C ha⁻² year⁻¹ in the Trounson Forest Park in Northland, New Zealand (DBH: 60–216 cm, height: 23–50 m). Young kauri plantations generally accumulate C at a rate that is at the lower end of that recorded at Huapai, with the average accumulation rate of 60–100-year-old plantations being 3 Mg C ha⁻² year⁻¹ across the Northland (Steward 2011).

Fig. 3 **a** Mean tree basal area increment (BAI) in each canopy class in each of the three measurement years. **b** Mean amount of C accumulated each year by each canopy class, **c** Stand-level C accumulated in the stand by each canopy class



This indicates that C uptake in mature kauri stands is similar to younger, fast growing stands. Differences in C uptake between kauri stands can be partially explained by stand age and structure; however, some variation may be caused by the different allometric equations used to calculate stem volume or biomass (Ellis 1979; Steward 2011; Beets et al. 2012). We used a stem volume equation developed by Ellis

(1979), while Silvester and Orchard (1999) multiplied tree basal area by tree height (which is likely to overestimate biomass) and used destructive harvesting for smaller trees. Depending on the method and equations used, our tree-level estimates of kauri biomass varied almost twofold, especially for larger trees (data not shown). This is one of the largest sources of uncertainty in our study.

Fig. 4 Basal area contribution of each of the canopy classes to the stand (*left column*) and stand-scale C accumulated in stems of each of the three canopy classes in the three measurement years

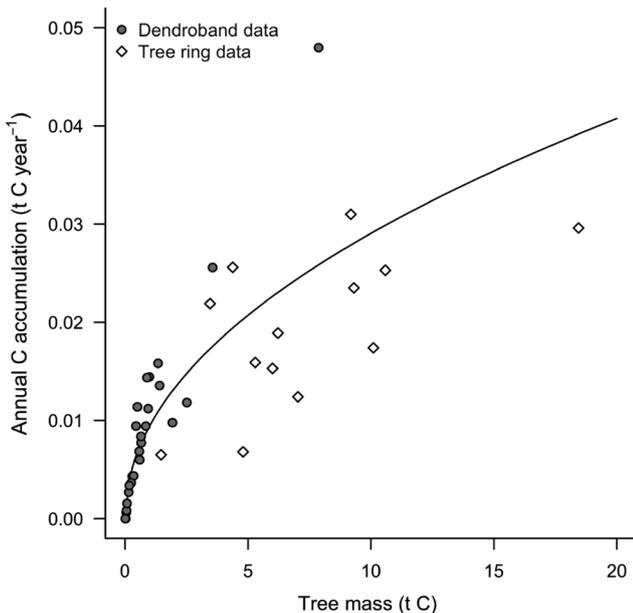
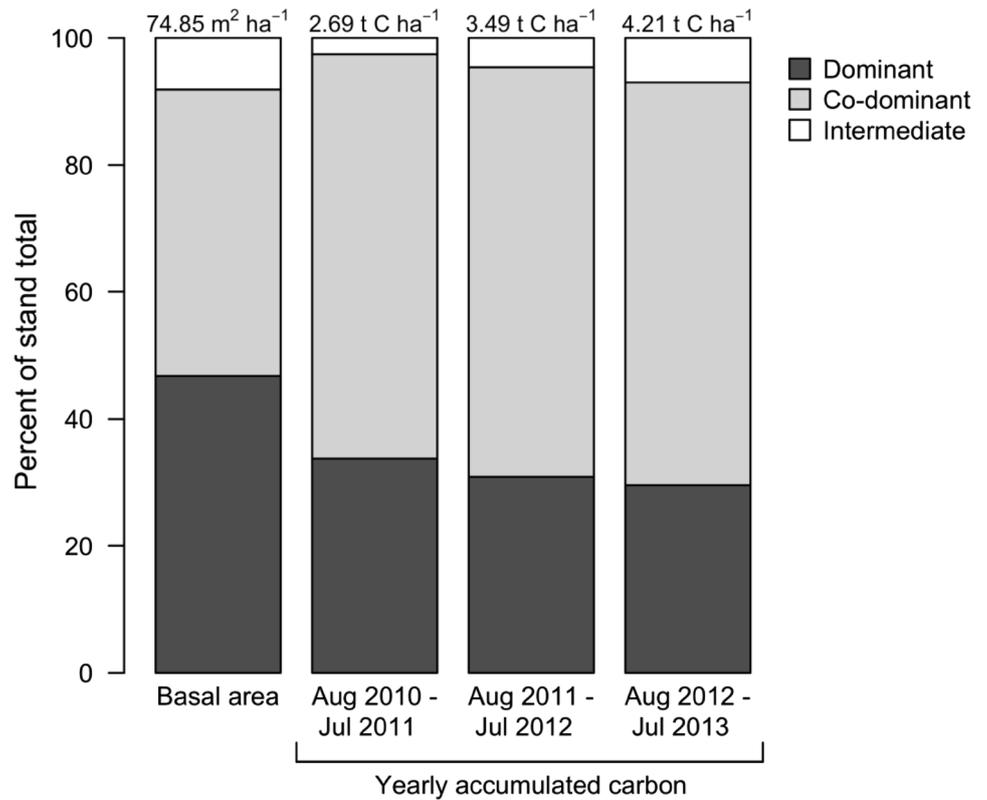


Fig. 5 Annual tree C accumulation rate (t C year⁻¹) as a function of stem C density (t C). Data from dendrobands (2010–2013, east ridge) and tree-ring analysis (Fowler and Boswijk 2001, west ridge). Max DBH: 235 cm

Carbon accumulation (by size cohort)

Basal area increment and mean C accumulation rates were greatest in the dominant size cohort and decreased with size class (Fig. 3a, b). Both measures of growth increased monotonically from 2010 to 2013 and this was consistent among size cohorts (Fig. 3a, b). Despite this, co-dominant trees comprised the bulk of stand C accumulation per year with the dominant cohort contributing around half that of the co-dominant cohort (Fig. 3c). The reasons for this are twofold. First, dominant trees make up only 6% of our stand’s tree density, and therefore, the dominant cohort contributes less to stand C accumulation than co-dominant trees. Second, dominant trees contribute proportionally less C to the stand for a given increment in biomass (or C mass) than do co-dominant or intermediate trees (Fig. 5). This is known as reverse growth dominance (Binkley et al. 2006). As a result, despite comprising the bulk of basal area (46%), dominant trees accumulated only 29% of the stand’s C stock over 3 years (Fig. 4), with the bulk of C taken up by co-dominant trees (62% over 3 years; Fig. 4) with a greater number of stems per hectare and a greater increment in C accumulation for a given increment in biomass (Figs. 2, 5). Overall, this supports our hypothesis that the larger trees have lower growth rates per unit biomass. We did not calculate the growth dominance coefficient of Binkley et al. (2006) for our site, because we do not believe

Fig. 6 Mean monthly growth presented as stem CO₂ efflux for different canopy classes. Data from **a** 8 dominant, **b** 14 co-dominant, and **c** 3 intermediate individuals. Error bars depict the standard error of the mean

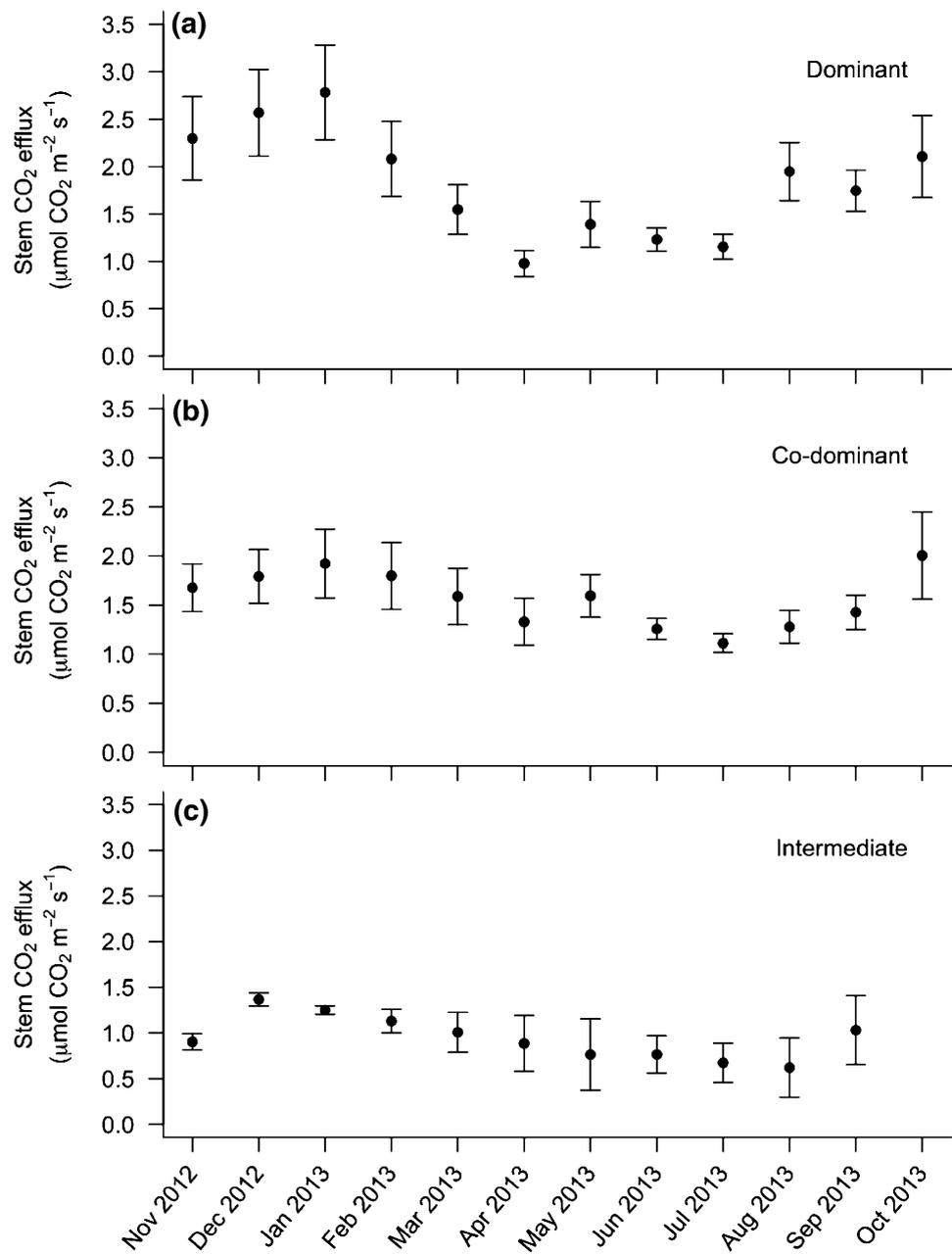


Table 2 Stem CO₂ efflux per unit stem area, whole-stem annual maintenance, and growth respiration rates (R_t, R_m, and R_g in kg C), maintenance respiration coefficient (r_m), growth respiration coefficient (r_g), and stem carbon-use efficiency (CUE)

Canopy class	N	Stem CO ₂ efflux (µmol CO ₂ m ⁻² s ⁻¹)	R _m (kg C)	R _g (kg C)	r _m	r _g	Stem CUE
Dominant	8	1.81 ± 0.20a	7.9 ± 1.8a	6.8 ± 1.8a	0.45 ± 0.06a	0.37 ± 0.07a	0.44 ± 0.04a
Co-dominant	14	1.53 ± 0.16a,b	3.7 ± 0.7a,b	2.3 ± 0.5a,b	0.68 ± 0.11a,b	0.30 ± 0.07a	0.41 ± 0.03a
Intermediate	3	0.94 ± 0.09b	0.9 ± 0.2b	0.4 ± 0.1b	1.22 ± 0.52b	0.39 ± 0.09a	0.34 ± 0.06a

Values are means ± standard error. Different letters indicate significant differences at *p* < 0.05

that it would be meaningful. The stand is recovering from a disturbance event (fire) that occurred in the early 20th century in addition to the fall and removal of five large trees in the 1950s (Thomas and Ogden 1983), and given the longevity of these trees, it may require centuries for the size class distribution to reach an equilibrium.

While we have used two different methods for C accumulation estimates and samples were collected at different times, we believe that the results are comparable, because two papers (Fowler et al. 2005 and; Wunder et al. 2013) reported the approaches produced comparable results. In addition, the radial growth rates measured by Fowler et al. (2005) using dendrometer bands during the 1990s at the same site were within the same range as our measurements, so we assume that any climatic differences had minimal impact on growth rates. Furthermore, the decelerating rate of C accumulation for a given increment in C density is a commonly observed phenomenon in older forests of different types across the globe (Ryan et al. 1997; Binkley et al. 2002, 2006; Rudnicki et al. 2003). Nevertheless, this is the first time that it has been reported in kauri.

Despite a deceleration in relative stem C accumulation rates for larger trees, when we make comparisons with younger kauri stands, our results suggest that basal area and stem C continue to accumulate at the stand level. Stem density and forest composition have remained unchanged for at least the last three decades at Huapai (Fowler pers. comm.) with few new recruits and no large trees dying. This sustained stand C uptake highlights the importance of old (600+ years) kauri-dominated forests for forest C management. Increasingly frequent and widespread disturbance events can compromise the C accumulation capacity of kauri forests. Kauri are particularly vulnerable to the fungus-like plant pathogen *Phytophthora agathidicida* (kauri dieback) which results in leaf loss, canopy thinning, and tree death, and will have major effects on kauri stand C budgets. The future C sequestration potential of kauri may also be modified by changes in temperature (Coomes et al. 2012) and more frequent droughts predicted for the northern part of New Zealand (Salinger and Porteous 2014), especially since drought-induced mortality for large trees can be disproportionately high (Allen et al. 2010; Bennett et al. 2015).

Stem CO₂ efflux, growth and maintenance respiration, stem carbon-use efficiency

Mean instantaneous rates of kauri stem CO₂ efflux rates varied between 0.7 and 2.8 μmol CO₂ m⁻² s⁻¹ per unit surface area (measured at 1.3 m height and 15 °C). Similar variation has been reported previously for northern conifers across a wide range of age classes and environments (Yoda et al. 1965; Ryan 1990; Sprugel 1990; Ryan et al. 1994;

Sprugel et al. 1995; Lavigne and Ryan 1997; Stockfors and Linder 1998; Vose and Ryan 2002). In contrast, the rates of kauri CO₂ efflux measured at Huapai are generally higher than those reported for other New Zealand species (an average of 2.1 μmol CO₂ m⁻² s⁻¹ in kauri during summer versus 0.9 μmol CO₂ m⁻² s⁻¹ in *Dacrydium cupressinum* Lamb during summer; Bowman et al. 2005).

The highest rates of kauri stem CO₂ efflux were measured in December (in the intermediate canopy class) and January (in the dominant and co-dominant canopy class) and did not coincide with peak stem diameter growth in November (Fig. 6 compared to Fig. 1). Time lags of 20–40 days between peak diameter growth and stem CO₂ efflux have been reported for oak and maple trees (Edwards and Hanson 1996). Stem CO₂ efflux and in particular growth respiration trails diameter growth, because cell wall thickening and wood synthesis accrues after cell expansion (Sprugel 1990; Stockfors and Linder 1998). As a result, stem CO₂ efflux is not necessarily correlated with diameter growth and the peak of growth respiration often occurs after the peak of diameter growth (Sprugel 1990). High stem CO₂ efflux in December and January also matched high soil CO₂ efflux rates (Schwendenmann and Macinnis-Ng 2016). This suggests that CO₂ from root respiration transported in the xylem may also contribute to the seasonality in kauri stem CO₂ efflux as has been shown in other conifers (Etzold et al. 2013) and deciduous tree species (Teskey and McGuire 2007; Bloemen et al. 2013).

Our whole-tree stem CO₂ efflux rates are likely an underestimation as we measured at breast height only. Previous studies have shown that stem CO₂ efflux tends to be greater in upper stem sections located inside the crown and branches (Sprugel 1990; Ryan et al. 1996; Damesin et al. 2002; Bowman et al. 2008; Araki et al. 2010; Katayama et al. 2014).

The growth respiration coefficients (r_g) measured for kauri in this study ranged between 0.30 and 0.39. This is at the lower end of values (0.24–0.76) reported for conifers in temperate and boreal regions (Sprugel et al. 1995; Lavigne and Ryan 1997; Maier 2001). Higher r_g values suggest that kauri stem growth is less efficient than in many other species, with large costs for biosynthesis, ion uptake, N assimilation, and translocation of substrates used in growth (Roy et al. 2001). Kauri stem CUE values (0.33–0.44) are similar to estimates reported for old black spruce trees (0.37–0.42, >90 years) in the southern and northern boreal zones (Lavigne and Ryan 1997). Higher stem CUE was estimated for young (10-years) *Pinus taeda* plantations in North Carolina (0.63; Maier 2001). Carbon-use efficiency values, estimated as the ratio of net primary production (NPP) to gross primary production (GPP), from evergreen and deciduous forests and pine plantations in the USA, Australia, and

New Zealand ranged from 0.40 to 0.53. A comparative analysis of conifer, evergreen, and temperate deciduous forests and plantations resulted in an overall CUE value of 0.43 (Litton et al. 2007). Comparing 60 mainly temperate North American monoculture forests and plantations showed that CUE differs among forest type with lower CUE in west coast maritime Douglas fir, Western hemlock, and lodgepole pine forests (0.32–0.48) compared to temperate deciduous forests (0.45–0.75). Some studies and theoretical approaches show evidence that CUE declines as trees grow taller or age (Mäkelä and Valentine 2001; DeLucia et al. 2007; Ogawa 2009). This is explained by an increase in maintenance respiration resulting in a decrease in NPP. We speculate that intermediate canopy class trees were likely suppressed and outcompeted by the dominant and co-dominant trees. Growth rates of these trees were consistently low or even zero (Fig. 2b). As growth, cellular activity, and respiration are tightly linked (Amthor 1989, 2003), we expected to see a decline in stem CO₂ efflux with tree size. Stem CO₂ efflux in the smaller kauri trees was lower compared to the other canopy classes. However, stem CO₂ efflux and in particular maintenance respiration did not decline to the same extent as growth, thus resulting in a slightly lower CUE.

Conclusions

The death of century-old trees will significantly reduce C uptake and storage in this forest. Our results highlight the importance of protecting and conserving large old trees, especially during pathogen attacks, disease events, or extreme climatic conditions. Disturbance events such as these will have ongoing legacy effects on C accumulation rates and the size of C storage pools. Recovery from such events will take decades to centuries as these large trees take centuries to regrow.

Authors contribution statement CM and LS designed the study, CM and TW collected the data, SW, TW and DT analysed the data and produced the figures and tables and all authors contributed to the writing and revision of the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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