

Net ecosystem productivity, net primary productivity and ecosystem carbon sequestration in a *Pinus radiata* plantation subject to soil water deficit

A. ARNETH,^{1,3} F. M. KELLIHER,^{1,2} T. M. MCSEVENY² and J. N. BYERS²

¹ Lincoln University, Soil Science Department, P.O. Box 84, Lincoln, New Zealand

² Manaaki Whenua-Landcare Research, P.O. Box 69, Lincoln, New Zealand

³ Present address: Almut Arneth, Landcare Research, P.O. Box 69, Lincoln, New Zealand

Received March 2, 1998

Summary Tree carbon (C) uptake (net primary productivity excluding fine root turnover, NPP') in a New Zealand *Pinus radiata* D. Don plantation (42°52' S, 172°45' E) growing in a region subject to summer soil water deficit was investigated jointly with canopy assimilation (A_c) and ecosystem-atmosphere C exchange rate (net ecosystem productivity, NEP). Net primary productivity was derived from biweekly stem diameter growth measurements using allometric relations, established after selective tree harvesting, and a litterfall model. Estimates of A_c and NEP were used to drive a biochemically based and environmentally constrained model validated by seasonal eddy covariance measurements. Over three years with variable rainfall, NPP' varied between 8.8 and 10.6 Mg C ha⁻¹ year⁻¹, whereas A_c and NEP were 16.9 to 18.4 Mg C ha⁻¹ year⁻¹ and 5.0–7.2 Mg C ha⁻¹ year⁻¹, respectively. At the end of the growing season, C was mostly allocated to wood, with nearly half (47%) to stems and 27% to coarse roots. On an annual basis, the ratio of NEP to stand stem volume growth rate was 0.24 ± 0.02 Mg C m⁻³. The conservative nature of this ratio suggests that annual NEP can be estimated from forest yield tables.

On a biweekly basis, NPP' repeatedly lagged A_c , suggesting the occurrence of intermediate C storage. Seasonal NPP'/ A_c thus varied between nearly zero and one. On an annual basis, however, NPP'/ A_c was 0.54 ± 0.03 , indicating a conservative allocation of C to autotrophic respiration. In the water-limited environment, variation in C sequestration rate was largely accounted for by a parameter integrative for changes in soil water content. The combination of mensurational data with canopy and ecosystem C fluxes yielded an estimate of heterotrophic respiration (NPP' – NEP) approximately 30% of NPP' and approximately 50% of NEP. The estimation of fine-root turnover rate is discussed.

Keywords: canopy assimilation, eddy covariance, interannual variability, model, respiration, water stress.

Introduction

The pivotal contribution of forests to the terrestrial carbon (C) cycle is undisputed. Forests store an estimated 360 Pg C in

living biomass (plus 790 Pg in forest soils, Dixon et al. 1994), and forest C sequestration is believed to account substantially for the “missing carbon sink” (Tans et al. 1990, Schimel 1995). Further, strategies to “offset” net C emissions by the promotion of C uptake in additional plantations have been proposed (Vitousek 1991, Kürsten and Burschel 1993). These strategies take advantage of the relatively long life span of trees and the amount of C that can be stored in wood products.

Forest growth is usually measured in terms of annual stem volume increment or aboveground biomass increase (e.g., Hollinger et al. 1993, Kauppi and Tomppo 1993, Shvidenko and Nilsson 1994). However, these measurements ignore C allocated to root turnover. Because the understanding of C cycles in forest soils and the regulation of heterotrophic respiration loss is incomplete, assessments of total forest C cycles based solely on growth measurements are severely limited.

During the last ten years, seasonal and continuous eddy covariance measurements of ecosystem-atmosphere C exchange rates have become technically feasible (e.g., Wofsy et al. 1993, Hollinger et al. 1994, Grace et al. 1995, Black et al. 1996). In forests these rates range from, for example, –0.3 Mg C ha⁻¹ year⁻¹ in a boreal (Goulden et al. 1998) to 5.3 Mg C ha⁻¹ year⁻¹ in a temperate deciduous forest (Greco and Baldocchi 1996). Significant interannual variability within the same forest ecosystem has been related to changes in the weather (Goulden et al. 1996). The micrometeorological flux data are also increasingly utilized to analyze the processes underlying the observed spatial and temporal variability in C exchange rates (e.g., Amthor et al. 1994, Hollinger et al. 1994, Lloyd et al. 1995, Arneth et al. 1998c). However, we are aware of no studies combining seasonal micrometeorological C flux and tree growth measurements. This combination facilitates assessment of autotrophic and heterotrophic respiration at the ecosystem scale. It also provides means to independently test parts of ecosystem C flux models (Williams et al. 1997).

This study combines regular tree-growth measurements and modeled forest-atmosphere ecosystem C exchange rates to determine how they are related and to estimate the allocation of C to autotrophic and heterotrophic respiration. The model

combines a mechanistic understanding of canopy photosynthesis with empirical functions for canopy stomatal conductance and ground evaporation and respiration. The model has been validated with eddy covariance data (Arneth et al. 1998c). The repeated tree growth and eddy flux measurements were made over 3 years that differed markedly in rainfall in a New Zealand *Pinus radiata* D. Don plantation growing in a water-limited environment.

Methods

Site description

All measurements were made within a 20 km² *Pinus radiata* plantation, located 100 km northwest of Christchurch, New Zealand (42°52' S, 172°45' E, 198 m asl). In October 1994, when tree-growth measurements commenced, the selected stand was 8 years old. Trees were planted at a density of 1250 ha⁻¹ year⁻¹ in east–west rows at a spacing of 4 m between rows and 2 m within rows. There was no understory vegetation. Mean annual precipitation is 658 mm and the monthly distribution is even (55 ± 5 mm month⁻¹). Mean monthly air temperatures range from 4.5 °C in the coldest month (July) to 16 °C in the warmest month (February), with an annual mean of 10.8 °C. Frost occurs frequently during winter, mostly at night or early morning, but air temperatures are only a few degrees below zero (N.Z. Met. Service 1983).

The soil is a stony sandy loam, an Inceptisol classified as Ustrochrept (T. Webb, Landcare Research, Lincoln, New Zealand, personal communication 1996), containing more than 30% stone by volume (Arneth et al. 1998a, 1998b). Water content in the upper 0.3 m of soil (θ , m³ water m⁻³ soil) was measured by excavation and by time domain reflectometry. This depth was equivalent to the main rooting zone observed in soil pits. From autumn through spring, soil water was generally plentiful with maximum $\theta = 0.24$ (≈ 10 kPa suction, field capacity; J. Claydon, Landcare Research, Lincoln, New Zealand, personal communication 1995). During summer, a frequently severe soil water deficit develops with minimum measured $\theta = 0.08$ (Arneth et al. 1998c). Available soil water storage capacity thus is limited to 48 mm, equivalent to approximately 16 days of forest evaporation during fine summer weather (Arneth et al. 1998b, 1998c).

Flux measurements and model

Half-hourly eddy covariance measurements of whole-forest sensible and latent heat, and CO₂ fluxes were made regularly during seven campaigns. The campaigns were conducted between November 1994 and March 1996 and each lasted 6 to 8 days. The instrumentation and flux corrections applied were described by Hollinger et al. (1994) and Arneth et al. (1998a, 1998b). During the campaigns, forest floor evaporation was measured from the weight loss of small lysimeters and respiration with a portable infrared gas analyzer–soil chamber system. Half-hourly measurements of associated climatic variables included air and soil temperatures (T and T_s , respectively), air saturation deficit (D), rainfall, wind speed and direction, and quantum irradiance absorbed by the canopy

(Q_{abs}) (Arneth et al. 1998a, 1998b). Climatic data from the forest's fire station about 5 km southeast of the study site were also used.

Eddy covariance and ground flux data were used to define parameter values of a biochemically based model that calculates forest–atmosphere CO₂ exchange and evaporation rates from climatic data. The model treats the entire canopy as a single entity (“big-leaf”) with the forest floor fluxes calculated separately. Model calculations and validation at this site have been described by Arneth et al. (1998c). Calculations are made in five steps. (1) Tree canopy conductance for water vapor transfer (G_c) is determined from a multiplicative, environmental-constraint submodel. A maximum G_c ($G_{c\text{max}}$) is defined from the data, and it is accordingly reduced when either θ , D , Q_{abs} , or all, are limiting. (2) The G_c submodel is coupled to a canopy assimilation (A_c) submodel, based on leaf biochemistry (Farquhar et al. 1980), using the analytical solution of Lloyd et al. (1995). The calculation of A_c includes the contribution of leaf respiration which was reduced in sunlight compared to its “dark” rate (Lloyd et al. 1995). (3) Forest floor evaporation (E_g) is proportional to the available energy, but with a proportionality coefficient depending on θ . Ground and ecosystem respiration (R_g and R_{eco} , respectively) are modeled from an Arrhenius-type relationship and thus increase exponentially with temperature. (4) The G_c , A_c , E_g , R_{eco} and R_g submodels are coupled to soil water balance and soil temperature subroutines. (5) The model, including the summary calculation of annual forest carbon uptake (net ecosystem productivity, $\text{NEP} = A_c - R_{\text{eco}}$), is driven by half-hourly weather data from the forest fire station.

Tree growth, biomass and net primary productivity

In October 1994, a 100-tree (20 m by 40 m) mensurational plot was established about 50 m west of the eddy covariance tower. Dendrometer bands, fabricated from 10 mm wide by 0.5 mm thick stainless steel sheeting held tightly on tree stems with a stainless steel spring, were placed below the lowest living branch of 16 trees. The selected trees represented the forest's stem diameter distribution. In 1994, the living crowns reached to the lowest clusters of branches, and the dendrometer bands were located about 0.2 m above the stem base. With continuing tree growth, height and leaf area increased and needles at the lowest branches subsequently died, so that in August 1995 nine of the 16 diameter bands were shifted about 0.4 m up the stem.

Until March 1996, vernier scales on the bands were read regularly, usually bi-weekly, but monthly during winter (June–August) when the rate of diameter growth was low. Four further readings were taken in September and October 1996, and in August 1997. Tree height growth was recorded monthly until March 1996, and again in September 1996 and August 1997.

Allometric relationships between stem cross-sectional area below the living crown (A_s) and tree growth ($dM dt^{-1}$, where t = time and M = biomass) were established from six trees harvested in July 1995 and five trees harvested in August 1996 (Table 1). Choosing A_s as the independent variable reflected the functional interdependence between sapwood area and leaf

Table 1. Allometric relationships derived from the carbon (C) and nitrogen (N) in tree biomass measurements in a *Pinus radiata* stand. The relationships were based on aboveground tree harvesting in July 1995 (6 trees) and August 1996 (5 trees), and additional harvesting of coarse root systems in a nearby clear-cut in November 1995. Abbreviations are: A_s = stem cross-sectional area below the living (green) crown (m^2), SBA = stump basal area, and P_n = current-year leaf production. Tree needle area is given as one half of the measured total surface area. The data may be converted to a ground area basis using the stem density of 1250 ha^{-1} and stem volume may be calculated from the mean wood density of 330 kg m^{-3} (A. Walcroft, Hort. Research, Palmerston North, New Zealand, personal communication 1997).

Quantity	Function
Total tree (kg C tree^{-1})	$1568 A_s, r^2 = 0.86$
Stem (kg C tree^{-1})	$765 A_s, r^2 = 0.69$
Needle (kg C tree^{-1})	$194 A_s, r^2 = 0.83$
Branch (kg C tree^{-1})	$220 A_s, r^2 = 0.66$
Coarse root (kg C tree^{-1})	$443 \text{ SBA}, r^2 = 0.96$
P_n ($\text{kg C tree}^{-1} \text{ year}^{-1}$)	$60 A_s, r^2 = 0.65$
Tree needle area ($\text{m}^2 \text{ tree}^{-1}$)	$1155 A_s, r^2 = 0.84$
N in canopy, per ground area (g m^{-2})	$618 A_s, r^2 = 0.90$

area (e.g., Waring et al. 1982, Cannell and Dewar 1994). For each tree, dry weights of stem, branches and needles were determined and branch cluster height was measured. The needles and branches from each cluster were separated into current-year and older age classes. From five to six positions within the tree crown, all-surfaces area of about 10 fresh fascicles was calculated from measurements of volume and length following Beets (1977). All-surface area was converted to a hemispherical projected area by dividing by two (Chen and Black 1992). Current-year branch and foliage subsamples for carbon and nitrogen analyses (CN analyser, Carlo Erba Instruments, Rodano, Italy) were collected along a vertical profile. Stemwood subsamples for C-N analyses were taken from the base, and at 25, 50 and 75% of tree height.

In July 1995, the root system of one of the harvested trees was excavated with a small digger. In November 1995, four more root systems were excavated from similar soil in a recently logged stand of 22-year-old trees about 2 km away (Arneith et al. 1998a). The lack of a living crown for the logged trees meant that the resultant coarse root biomass (> approximately 5 mm diameter) allometric relationship used stump cross-sectional area rather than A_s .

Annual litterfall was calculated as the difference between current-year needle production (P_n) and changes in the total needle biomass (Table 1). The seasonality of P_n was assumed to be similar to that of *P. radiata* growing in a comparable, dry summer climate near Canberra, Australia (Raison et al. 1992a). There, 85% of annual P_n was completed at a nearly constant rate between mid-October and late January. The remaining 15% of P_n occurred during September–mid-October and in February. The seasonality of annual litterfall (L) was estimated after Raison et al. (1992b) assuming 80% of L occurred in late summer–autumn (mid-February–May) and the remaining 20% evenly throughout the rest of the year.

We calculated forest C exchange for three years: November 1, 1994 to October 31, 1995, November 1, 1995 to October 31, 1996 and August 1, 1996 to July 31, 1997. This allowed alignment with the tree-diameter growth measurements and the comparison of three years with considerable variations in rainfall, particularly during summer. Annual net primary productivity was calculated from $dM \text{ dr}^{-1} + L$ (Lloyd and Farquhar 1996). This calculation excludes the contribution of fine root turnover; thus, net primary productivity is denoted afterwards by a prime as NPP' . The seasonal course of NPP' was estimated by combining the calculated growth of the woody parts of the trees (Table 1) with the seasonal course of P_n and L (see above). The calculation of NPP' does not include tree mortality. During the three-year study, only one tree out of 100 died in this young, managed measurement plot.

Results and discussion

Annual mean air temperatures during the study period (November 1994 to June 1997) were normal and varied between 9.5 and 10 °C (Table 2). By contrast, annual rainfall varied 1.3-fold between the wettest (1996–97, 715 mm) and the driest year (1995–96, 532 mm). For the dry year, annual rainfall was only 80% of the long-term mean, and summer (December 1 to March 31) rainfall (64 mm) was only one-third of the seasonal norm (203 mm, N.Z. Met. Service 1983). Rainfall during 1994–95 (696 mm) was near-normal, despite an unusually wet June with more than three times the monthly mean (173 versus 54 mm). Because both winter atmospheric evaporative demand and soil water storage capacity are low, most of this water was lost by soil drainage. Rainfall in the summer months 1994–95 (150 mm) was more than twice that in 1995–96, but was still

Table 2. Modeled annual carbon flux densities ($\text{Mg C ha}^{-1} \text{ year}^{-1}$), and evaporation rates (E), in the *Pinus radiata* stand during the three-year study. Rates of tree canopy assimilation (A_c), ecosystem respiration (R_{eco}) and net carbon exchange (NEP) were estimated using a biophysical model described by Arneith et al. (1998c). Tree net carbon uptake (NPP') and stem volume growth rates were determined from measured stem cross-sectional area below the living tree crown (A_s), height and the allometric relationships in Table 1. The annual climatic data are quantum irradiance absorbed by the tree canopy (Q_{abs}), mean air temperature (T), rainfall and the mean daily maximum air saturation deficit (D_{max}).

	Q_{abs} (mol m^{-2})	T (°C)	Rain (mm)	D_{max} (kPa)	A_s ($\text{m}^2 \text{ 10}^{-3}$)	A_c (Mg C ha^{-1})	NEP (Mg C ha^{-1})	R_{eco} (Mg C ha^{-1})	NPP' (Mg C ha^{-1})	Volume growth ($\text{m}^3 \text{ ha}^{-1}$)	E (mm)
11/94–10/95	7916	10.0	696	1.24	4.56	18.1	5.9	12.2	9.4	25.4	463
11/95–10/96	7503	9.9	532	1.21	4.01	16.9	5.0	11.9	8.8	22.4	399
08/96–07/97	7746	9.5	715	1.12	4.88	18.4	7.2	11.2	10.6	27.2	488

below average. Summer rainfall during the wettest year was 277 mm greater than normal.

In November 1994, the 8-year-old trees were 8.5 m tall (± 0.6 m, standard deviation, $n = 100$), stem diameters were 133 ± 18 mm at breast height (DBH) and 172 ± 24 mm below the living crown. The corresponding basal areas were calculated as 17 and 27 $\text{m}^2 \text{ha}^{-1}$, respectively. Tree height and diameter at Balmoral Forest closely resembled young *P. radiata* stands growing in a comparable drought-prone climate near Canberra (annual rainfall = 790 mm) before the onset of the Biology of Forest Growth Experiment (BFG; Linder et al. 1987, Benson et al. 1992) and at Woodhill Forest in the North Island of New Zealand (McMurtrie et al. 1990).

Annual tree growth

At the beginning of the measurements, nearly half of the C in tree biomass (44 Mg C ha^{-1} , Figure 1) was fixed in stems and a further 25% was nearly equally divided between branches and needles. More than 25% of tree C was in the form of coarse roots. The data exclude the contribution of roots with diameter < 5 mm (defined here as fine roots) to the total tree root biomass. Although fine root production can be a significant sink for tree C allocation (see later discussion), the life span of fine roots is also generally short. At any given time, their omission thus introduces only a small error in the assessment of tree biomass (e.g., Vogt et al. 1996). In four soil pits excavated during July 1995, the biomass of fine roots was $2.9 \pm 0.9 \text{ Mg C ha}^{-1}$ in our stand (N. Scott, Landcare Research, Palmerston North, New Zealand, personal communication 1997). This included live and dead, but not decomposed, roots. In a *P. radiata* plantation in the North Island of New Zealand, only one-third of excavated fine roots (< 5 mm diameter) were alive (Santantonio and Santantonio 1987). Assuming a similar ratio of live to dead roots for Balmoral Forest suggests a value of 0.96 Mg C ha^{-1} for living fine roots in July 1995, equal to 7% of coarse root biomass and 2% of the total tree biomass (14 and 52 Mg C ha^{-1} , respectively, in July 1995).

Allocation of C to roots reflects the tree's need for nutrient and water uptake and structural integrity. Jackson and Chitten-

den (1981) measured coarse root growth in New Zealand *P. radiata* growing in containers or trenches filled with nutrient rich, deep pumiceous sandy loam soil under non-water limiting conditions. Applying their biomass relationship ($\ln(M) = 2.73 \ln(\text{DBH}) - 5.009$; DBH = 13.3 cm in November 1994) led to a calculated mean root C of 3.9 kg tree^{-1} and grossly underestimated root C at Balmoral Forest (10 kg tree^{-1}). By contrast, a relationship derived by Watson and O'Loughlin (1990) for *P. radiata* roots excavated from field-grown trees in the East Coast of New Zealand's North Island ($\ln(M) = 2.24 \ln(\text{DBH}) - 2.68$) resulted in a calculated root C of 11 kg tree^{-1} and could thus also be successfully applied to our stand. The coarse root to aboveground (shoot) weight ratio at Balmoral Forest was relatively large (0.37), twice the average for temperate coniferous forests (Jackson et al. 1996). Heavy and expansive root systems reflect a site subject to recurring soil water deficit (Cannell and Dewar 1994). Furthermore, a large amount of structural root biomass may be needed in a windy climate like that at Balmoral Forest, where 3-s gusts regularly exceed 25 m s^{-1} .

Seasonal tree growth and net ecosystem productivity

A distinct seasonality was evident in A_s growth with maximum rates in spring (September–November; Figure 2C) and a period of near-zero gain during winter (June–August). In the two dry years 1994–95 and 1995–96, nearly half (38% and 49%, respectively) of annual stem diameter growth was completed in spring. During summer, growth rates varied with soil water supply and were close to zero when the soil was driest (e.g., January 1995, January–March 1996). Stem shrinkage during drought was observed during one bi-weekly summer measurement period as has been reported elsewhere (Benson et al. 1992). Annual A_s growth during nearly three years of measurements varied by about 20% from $4.0 \times 10^{-3} \text{ m}^2$ in the driest year (11/95–10/96) to $4.9 \times 10^{-3} \text{ m}^2$ in the wettest year (7/96–6/97, Table 2).

The mean leaf area to weight ratio at Balmoral Forest was $5.9 \text{ m}^2 \text{ kg}^{-1}$, similar to values reported for the nonirrigated BFG *P. radiata* site ($4.5\text{--}6 \text{ m}^2 \text{ kg}^{-1}$, Raison et al. 1992a), but only 60% of values reported for well-watered sites ($8 \text{ m}^2 \text{ kg}^{-1}$, Beets and Lane 1987). Current-year leaf production averaged $2.2 \pm 0.3 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ (Tables 1 and 2), total leaf C increased by $1.04 \pm 0.08 \text{ Mg ha}^{-1} \text{ year}^{-1}$, and dead leaf C remaining on the trees was about 7% of the total. The difference between these rates suggests a litter fall of about 50% of production ($1.08 \pm 0.3 \text{ Mg C ha}^{-1}$). In November 1994, the leaf area index was 6.5 and it increased by 16% per year (Table 1). The N content of needles (mean = 13 mg g^{-1}) at Balmoral Forest is high compared to other unfertilized *P. radiata* forests (McMurtrie et al. 1990, Raison and Myers 1992), and reflects adequate N supply from the soil (C:N ratio of 19 in 0 to 0.3 m depth; N. Scott, personal communication 1996). More than 40% of total tree N was located in needle biomass (140 kg N ha^{-1} , Table 1, Figure 1).

Figure 2 also summarizes modeled weekly mean canopy evaporation (Figure 2A), assimilation (A_c), ecosystem respiration (R_{eco}) and net ecosystem C uptake (NEP, Figure 2D).

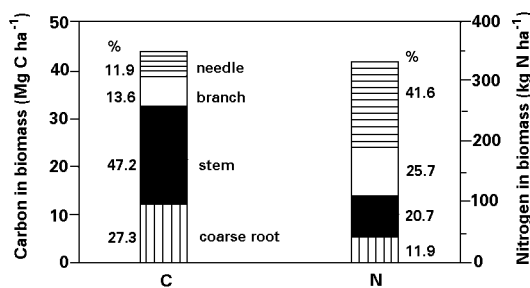


Figure 1. *Pinus radiata* C (left bar, Mg C ha^{-1}) and nitrogen (N) (right bar, kg N ha^{-1}) content in biomass, and allocation to coarse roots, stems, branches and needles on November 2, 1994. The biomass fractions were determined from measurements of stem cross-sectional area below the living crown and the allometric relationships in Table 1, as described in the text. Stem wood and coarse root, and branch N contents were 0.16 (SD = 0.03) and 0.69% (SD = 0.22), respectively.

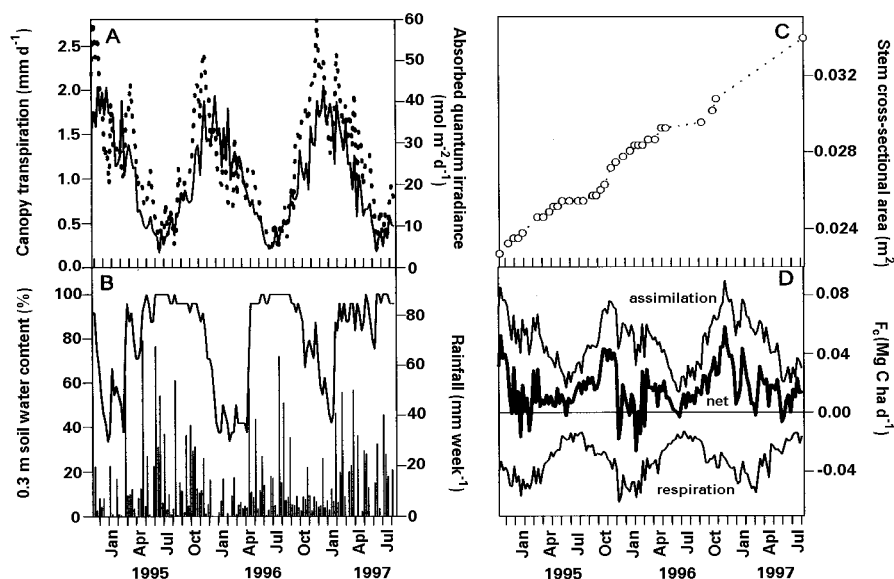


Figure 2. Tree stem diameter growth rate, modeled weekly means of net forest–atmosphere carbon exchange rate, the component fluxes, transpiration and environmental variables between November 1, 1994 and July 31, 1997. (A) Canopy transpiration (dotted line) and quantum irradiance absorbed by the tree canopy (solid line). (B) Measured rainfall (bars) and modeled volumetric soil water content in the main rooting zone (0–0.3 m depth, line) expressed as a percentage of the maximum value. (C) Cumulative measured tree stem growth. Data between 11/94 and 5/96 were obtained bi-weekly or monthly. Between 6/97 and 7/97 four additional measurements were obtained. (D) Modeled tree canopy assimilation rate (positive values), ecosystem respiration rate (negative values) and net forest–atmosphere C exchange rate (thick line). Positive values indicate a net uptake of C. Variable F_c is the C flux.

These flux densities were calculated with the forest C and water flux model briefly described before and were discussed in detail in Arneeth et al. (1998c). In short, during autumn, winter and spring R_{eco} , A_c and E followed the seasonality in irradiance (Figure 2A), temperature and air saturation deficit. During summer, the significant decline of soil water and the hot, dry atmosphere caused stomatal closure and considerable declines in A_c and E , whereas R_{eco} reached annual maximum (most negative) rates. The ecosystem was thus a carbon source during drought periods, which was particularly evident in the very dry summer of 1995–96.

Between 1995 and 1997, NPP' varied between 8.8 and 10.6 $Mg\ C\ ha^{-1}$ whereas annual A_c varied from 16.9 to 18.4 $Mg\ C\ ha^{-1}$ (Table 2). At Balmoral Forest, A_c is close to the values modeled by McMurtrie et al. (1992) in the comparable unfertilized and fertilized, but not irrigated, *P. radiata* plantations at the BFG site (17 to 20 $Mg\ C\ ha^{-1}\ year^{-1}$), which had corresponding measured annual aboveground C uptake rates of 8 and 10 $Mg\ C\ ha^{-1}$, respectively (Snowdon and Benson 1992). Combining irrigation and fertilization increased modeled A_c and aboveground C uptake to 45 and 20 $Mg\ C\ ha^{-1}\ year^{-1}$, respectively. In Woodhill Forest, with twice the rainfall, A_c was about 25 $Mg\ C\ ha^{-1}\ year^{-1}$ in the unfertilized stand and up to 33 $Mg\ C\ ha^{-1}\ year^{-1}$ at fertilized sites (McMurtrie et al. 1990). These results indicate that, on drought-prone sites, the growth rate of *P. radiata* may be limited by water supply, irrespective of soil fertility.

Based on data for three years, a linear relationship between A_c and NPP' accounted for 76% of the variation (Figure 3, $NPP' = 1.01A_c - 8.2$, $r^2 = 0.76$). For the shorter intervals between diameter growth measurements, the relationship between NPP' and A_c was also linear (Figure 4A, $NPP' = 0.71A_c - 0.07$, $r^2 = 0.68$),

however, there was a tendency during winter for A_c to continue when tree growth was negligible (Figure 4). This lag between A_c and tree growth response can be understood from allocation theory. Low temperatures decrease sink activity more than assimilation, which in turn results in increased intermediate storage of assimilates (Cannell and Dewar 1994). The utilization of these storage carbohydrates results in the relatively greater acceleration of tree growth observed in early spring (Figure 4B).

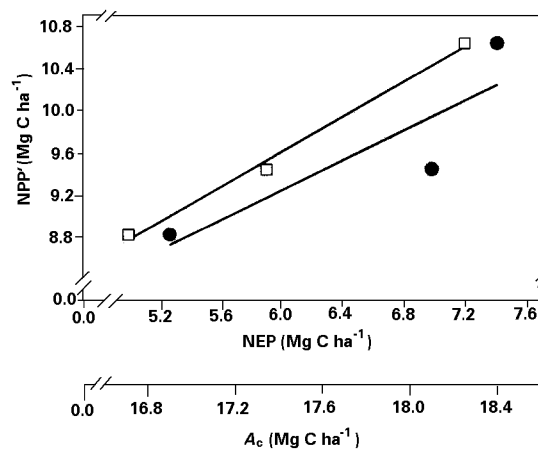


Figure 3. Relationships between modeled annual net primary productivity (NPP') and tree canopy assimilation rate (A_c , closed circles and regression line of $NPP' = 1.01A_c - 8.2$, $r^2 = 0.76$) and net ecosystem carbon uptake rate (NEP , open squares and regression line of $NPP' = 0.83NEP + 4.6$, $r^2 = 0.99$). The three years varied significantly in rainfall (Table 2).

The ratio of annual NPP'/A_c was nearly constant (0.54 ± 0.02), slightly greater than the value of 0.45 reported by Landsberg and Waring (1997). By contrast, seasonal NPP'/A_c varied between nearly 0 in winter and 1 in spring, and in summer after rain (Figure 4B). Concluding that respiration loss is a constant fraction of NPP' may thus only be valid over long integration periods and some caution is needed (e.g., Malet et al. 1997). More work is also required to validate whether such a simplification is appropriate outside the temperate zone.

Combining A_c and autotrophic as well as heterotrophic respiration rates (R_{eco}), modeled NEP accumulated notably only during spring (Figure 5) when A_c was at its maximum and R_{eco} below its annual peak (Figure 2D; Arneth et al. 1998c). In dry summer conditions, when water stress reduced canopy conductance and A_c but the high temperatures increased R_{eco} , mean daily NEP was close to zero. Refilled soil water storage in autumn (Figure 2B) corresponded with an increase in NEP. Photosynthesis was then constrained by lower irradiance and temperature which also decreased R_{eco} . From autumn until early spring, the forest constantly accumulated C at a slow rate.

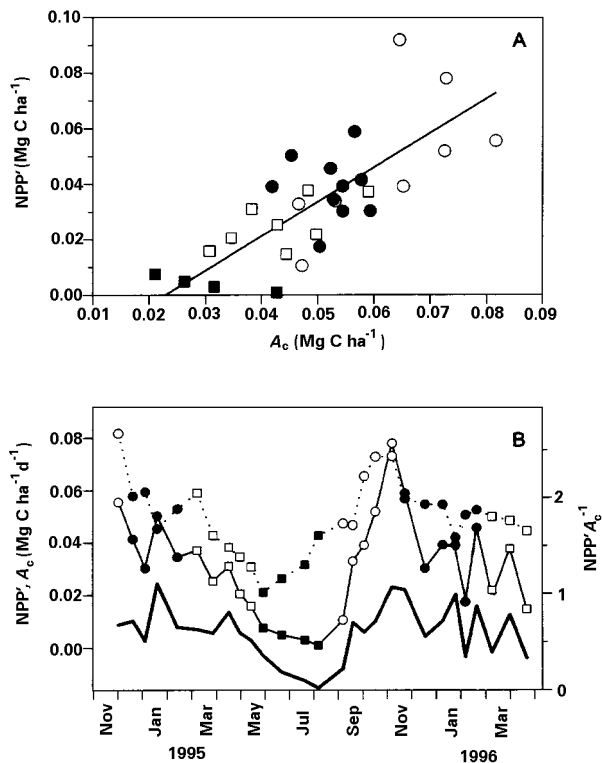


Figure 4. (A) Relationship between modeled tree canopy assimilation rate (A_c) and net primary productivity (NPP') in a *Pinus radiata* stand. Tree stem diameter growth rate was measured using dendrometer bands, and NPP' was determined from it and the allometric relationships in Table 1. The regression line is $NPP' = 0.71A_c - 0.07$ ($r^2 = 0.68$). Symbols: spring = \circ ; summer = \bullet ; autumn = \square ; winter = \blacksquare . (B) Seasonal courses of modeled tree canopy assimilation rate (A_c , dotted line), net primary productivity (NPP' , thin line) and NPP'/A_c (thick line) between November 1994 and May 1995. Symbols are as in A.

Interannual variation of NEP was tightly linearly related to NPP' ($r^2 = 0.99$, Figure 3). Stem biomass and volume growth rates were a near-constant proportion of NPP' (Table 1, Table 2) and, correspondingly, the ratio of annual NEP and stand stem volume growth rate was also conservative for the three years at 0.24 ± 0.02 . Because of its commercial value, most countries possess extensive collections of forest yield data that relate stem volume growth and tree age. A conservative ratio of NEP/volume growth can facilitate the estimation of NEP from stand volume growth. However, the ratio may vary across environments and further studies are required to identify how site conditions and forest management affect it.

Interactive forest carbon and water exchange

Measured tree growth and modeled C sequestration rates showed a strong constraint by soil water deficit. Consequently, the soil water stress integral $S_w = \sum [(\theta_{max} - \theta)t]$ ($t = 1$ for a daily time step) was modified from Myers (1988), where θ_{max} is maximum θ . A large value of S_w indicates a high number of days when θ was low. Reflecting the generally strong coupling of available soil water, forest evaporation rate (E), and T via the forest energy balance, S_w integrates also over D and E as factors reducing canopy conductance, A_c and growth. All three C uptake processes were inversely proportional to S_w with linear regressions accounting for 86%, 98% and 91% of the variation in NPP' , A_c and NEP, respectively (Figure 6). Because interannual climatic variability was dominated by summer weather patterns, especially rainfall, low annual S_w represents wet, cool summer weather. The strong decline in all three C fluxes with increasing S_w reflects a primary role of summer soil water availability in governing interannual fluctuations of C uptake. The increased sensitivity displayed in the S_w versus NEP relationship (slope of the regression = -0.28) illustrates the synergistic effect of increased soil water deficit and temperature on NEP. Because the drier years were also the warmest, decreasing NEP was the result of decreased A_c and increased R_{eco} .

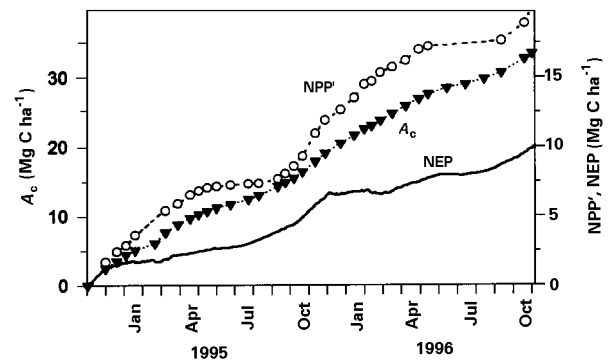


Figure 5. Seasonal courses of cumulative modeled tree canopy assimilation rate (A_c , \blacktriangle), net ecosystem carbon uptake rate (NEP, solid line) and net primary productivity (NPP' , \circ) based on the stem dendrometer band measurements and the allometric relationships in Table 1. The model was run and the measurements made in a *Pinus radiata* stand over two years from November 1, 1994.

Annual ground evaporation contributed about 30% of E , varying from 158, 127 and 167 mm during the three years. For a leaf, control theory postulates that stomatal opening evolved to maximize C assimilation per unit water transpired. Accordingly, for the tree canopy the ratio of $\text{NPP}'/E_{\text{tree}}$ ($E_{\text{tree}} = E - E_{\text{ground}}$) was conservative at $3.22 \pm 0.09 \text{ g C kg H}_2\text{O}^{-1}$. For an ecosystem, however, non-stomatal processes like ground evaporation and respiration from soil heterotrophic organisms also contribute to the corresponding ratio NEP/E . The annual ratio was constant at 1.27 and 1.25 $\text{g C kg H}_2\text{O}^{-1}$ in the two dry years, but it increased to 1.48 in the wettest year. This increase reflected the 277 mm summer rainfall and associated decreased temperature and increased humidity in the wetter year. This favored higher stomatal conductance and A_c , but E did not increase accordingly because of lower D . Moreover, because of the exponential relationship between temperature and respiration, R_{eco} decreased during the wet year.

Combining modeled annual C sequestration and evaporation rates for *P. radiata* stands at the BFG site yielded mixed results. The ratio of aboveground production/ E_{tree} in the control, fertilized and irrigated + liquid fertilizer stands was constant (about 1.5; aboveground production from Snowdon and Benson 1992; E_{tree} from McMurtrie et al. 1992). However, in the irrigated and irrigated + solid fertilizer BFG stands, the ratio was considerably smaller at about 1 to 1.2 $\text{g C kg H}_2\text{O}^{-1}$.

Belowground processes

The contribution of heterotrophic respiration (R_{het}) was estimated from the difference between NPP' and NEP (Figure 7). For the three years, mean R_{het} was $3.1 \pm 0.9 \text{ Mg C ha}^{-1}$, about 30% of NPP' and 26% of R_{eco} (Table 2). Based on soil chamber and nighttime eddy flux measurements, ground respiration (R_g) contributed 80% of R_{eco} (Armeth et al. 1998c). These values suggest about one-third of R_g originated from heterotrophic activity, somewhat lower than estimates of R_{het} in other pine forests. Chamber measurements in trenched and untrenched, unfertilized plots of *Pinus resinosa* Ait. in Wisconsin suggested R_{het} (excluding mycorrhiza) contributed 51 to 62%

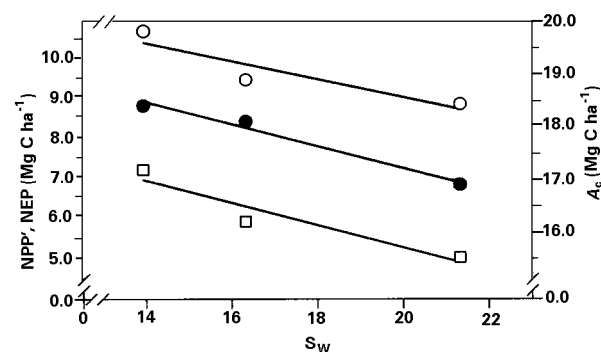


Figure 6. Relationships between an annual soil water stress integral (S_w) and annual rates of net primary productivity (NPP' , \circ ; $\text{NPP}' = -0.22S_w + 13.5$, $r^2 = 0.86$), ecosystem net carbon uptake (NEP , \square ; $\text{NEP} = -0.28S_w + 10.8$, $r^2 = 0.91$) and tree canopy assimilation (A_c , \bullet ; $A_c = -0.21S_w + 21.4$, $r^2 = 0.98$). The three years varied significantly in rainfall (Table 2).

of R_g (Haynes and Gower 1995), whereas soil chamber measurements for a Florida *Pinus eleottii* Engelm. plantation indicated R_{het} was 38 to 42% of R_g (Ewel et al. 1987).

At a clear-cut, located about 2 km southeast of the study site, where all the tree roots had died, Armeth et al. (1998a) estimated annual R_{het} to be 3.7 and 4.4 $\text{Mg C ha}^{-1} \text{ year}^{-1}$ depending on rainfall. Soil type and physical properties are similar at the two sites (Armeth et al. 1998a, 1998b), as is potential soil microbial activity determined from controlled laboratory incubations (D.J. Ross, Landcare Research, Palmerston North, New Zealand, personal communication 1996). However, a significant number of additional factors prevent the conclusion that clear-cutting might increase R_{het} . At the clear-cut, a "pumping effect" induced by air turbulence enhanced soil CO_2 efflux significantly when the surface was wet. This turbulence effect was greatly reduced in the forest, where momentum was mostly absorbed by the canopy. Further, daily and annual soil temperature (T_s) fluctuations in the forest were dampened compared to the clear-cut because both radiation input and loss were reduced beneath the canopy. For example, during 1994–95, modeled mean T_s (0 to 0.3 m depth) in the forest was 0.6 °C cooler than in the clear-cut. Soil water content also differed between the sites. In the forest, root water uptake contributes to the depletion of soil water storage, whereas small rainfall events will be mostly intercepted by the canopy. Finally, differences in R_{het} might be attributable to root exudates, mycorrhiza activity and constant fine root turnover. These processes suggest a more constant C supply for soil microbes in the forest that was probably absent in the clear-cut where the roots had died.

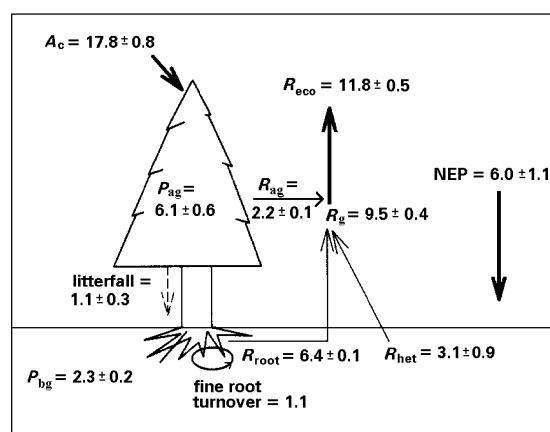


Figure 7. Summary of annual carbon flux densities in the *Pinus radiata* stand during the three-year study ($\text{Mg C ha}^{-1} \text{ year}^{-1}$, mean \pm SD). Tree canopy assimilation (A_c), ecosystem respiration (R_{eco}), net ecosystem carbon uptake (NEP) and ground respiration (R_g) rates were calculated from the biophysical model. Above- and belowground net carbon uptake for the trees (P_{ag} and P_{bg}) and litterfall rates were determined from stem diameter growth measurements and the allometric relationships in Table 2, and tree harvesting, respectively. Derived respiration rates included those attributable to aboveground autotrophic ($R_{\text{ag}} = R_{\text{eco}} - R_g$), heterotrophic ($R_{\text{het}} = \text{NPP}' - \text{NEP}$), and root ($R_{\text{root}} = R_{\text{eco}} - R_{\text{ag}} - R_{\text{het}}$) sources. The estimation of fine root turnover rate is described in the text.

The annual values of NEP and NPP' can also be utilized to derive a "best-guess" estimate of the annual belowground C turnover rate, assuming annual changes in the soil C content are negligible (Figure 7). In a closed canopy forest without major disturbances, an increase in ecosystem C results mainly from an increase in the storage of biomass (aboveground and coarse roots). Assuming no net accumulation of litter on the ground, R_{het} must equal the rate of C input to the soil by root exudates, fine root turnover and litter fall. From $L = 1.1 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ and $R_{\text{het}} = 3.1 \text{ Mg C ha}^{-1} \text{ year}^{-1}$, the annual fine root turnover and root exudation rate was estimated to be $2.0 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ or 20% of mean annual NPP'. This may be compared to estimates of fine root NPP' from regressions, using annual minimum temperature and precipitation rates as independent variables, based on a review of pine forest data (Vogt et al. 1996). Using annual minimum temperature = $-7.8 \text{ }^\circ\text{C}$ and precipitation rate = 660 mm year^{-1} at Balmoral Forest (N.Z. Met. Service 1983), fine root NPP' was 1.3 and $1.9 \text{ Mg C ha}^{-1} \text{ year}^{-1}$, respectively. Considering the crude nature of our calculation and inclusion of many assumptions, these two values from the literature are remarkably corroborative.

Acknowledgments

A. Arneth acknowledges financial support from AGMARDT and Lincoln University Doctoral scholarships. Funding for this research and the Manaaki Whenua-Landcare Research team was provided by a long-term grant for atmospheric research to F.M. Kelliher from the New Zealand Foundation for Research, Science and Technology. We are grateful to Drs. N. Scott, J. Claydon and T. Webb who supplied the data on fine roots and soil physical properties. The C/N analyses were completed by G. Rogers who also skillfully excavated the root systems. Constructive critiques of the manuscript were provided by Dr. G. Buchan of Lincoln University. Finally, we thank Carter Holt Harvey Ltd. for giving us permission to work in Balmoral Forest.

References

- Amthor, J.S., M.L. Goulden, J.W. Munger and S.C. Wofsy. 1994. Testing a mechanistic model of forest-canopy mass and energy exchange using eddy correlation: Carbon dioxide and ozone uptake by a mixed oak-maple stand. *Aust. J. Plant Physiol.* 21:623–651.
- Arneth, A., F.M. Kelliher, S.T. Gower, N.A. Scott, T.M. McSeveny and J.N. Byers. 1998a. Environmental variables regulating soil CO₂ efflux following clear-cutting of a *Pinus radiata* D. Don plantation. *J. Geophys. Res.* 103:5695–5705.
- Arneth, A., F.M. Kelliher, T.M. McSeveny and J.N. Byers. 1998b. Carbon and water fluxes in a *Pinus radiata* forest subject to soil water deficit. *Aust. J. Plant Physiol.* 25:557–570.
- Arneth, A., F.M. Kelliher, T.M. McSeveny and J.N. Byers. 1998c. Assessment of annual carbon exchange in a water-stressed *Pinus radiata* plantation using a big leaf model. *Global Change Biol.* In press.
- Beets, P.N. 1977. Determination of the fascicle surface area for *Pinus radiata*. *N.Z. J. For. Sci.* 7:397–407.
- Beets, P.N. and P.M. Lane. 1987. Specific leaf area of *Pinus radiata* as influenced by stand age, leaf age, and thinning. *N.Z. J. For. Sci.* 17:283–291.
- Benson, M.L., B.J. Myers and R.J. Raison. 1992. Dynamics of stem growth of *Pinus radiata* as affected by water and nitrogen supply. *For. Ecol. Manag.* 52:117–137.
- Black, T.A., G. den Hartog, H.H. Neumann, P.D. Blanken, P.C. Yang, C. Russel, Z. Nestic, X. Lee, S.G. Chen, R. Staebler and M.D. Novak. 1996. Annual cycles of water vapour and carbon dioxide fluxes in and above a boreal aspen forest. *Global Change Biol.* 2:219–229.
- Cannell, M.G.R. and R.C. Dewar. 1994. Carbon allocation in trees: A review of concepts for modelling. *In Adv. Ecol. Res.*, Vol. 25. Eds. M. Begon and A.H. Fitter. Academic Press, New York, pp 60–104.
- Chen, J.M. and T.A. Black. 1992. Defining leaf area index for non-flat leaves. *Plant Cell Environ.* 15:421–429.
- Dixon, R.K., S. Brown, R.A. Houghton, A.M. Solomon, M.C. Trexler and J. Wisniewski. 1994. Carbon pools and flux of global forest ecosystems. *Science* 263:185–190.
- Ewel, K.C., W.C. Cropper and H.L. Gholz. 1987. Soil CO₂ evolution in Florida slash pine plantations. II. Importance of root respiration. *Can. J. For. Res.* 17:330–333.
- Farquhar, G.D., S. von Caemmerer and J.A. Berry. 1980. A biochemical model of photosynthetic CO₂ assimilation. *Planta* 149:78–90.
- Goulden, M.L., J.W. Munger, S.-M. Fan, B.C. Daube and S.C. Wofsy. 1996. Exchange of carbon dioxide by a deciduous forest: Response to interannual climate variability. *Science* 271:1576–1578.
- Goulden, M.L., S.C. Wofsy, J.W. Harden, S.E. Trumbore, P.M. Crill, S.T. Gower, T. Fries, B.C. Daube, S.-M. Fan, D.J. Sutton, A. Bazzaz and J.W. Munger. 1998. Sensitivity of boreal forest carbon balance to soil thaw. *Science* 279:214–217.
- Grace, J., J. Lloyd, J. McIntyre, A.C. Miranda, P. Meir, H.S. Miranda, C. Nobre, J. Moncrieff, J. Massheder, Y. Mahli, I. Wright and J. Gash. 1995. Carbon dioxide uptake by an undisturbed tropical rain forest in southwest Amazonia, 1992 to 1993. *Science* 270:778–780.
- Greco, S. and D.D. Baldocchi. 1996. Seasonal variations of CO₂ and water vapour exchange rates over a temperate deciduous forest. *Global Change Biol.* 2:183–198.
- Haynes, B.E. and S.T. Gower. 1995. Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. *Tree Physiol.* 15:317–325.
- Hollinger, D.Y., J.P. MacLaren, P.N. Beets and J. Turland. 1993. Carbon sequestration by New Zealand's plantation forests. *N.Z. J. For. Sci.* 23:194–208.
- Hollinger, D.Y., F.M. Kelliher, J.N. Byers, J.E. Hunt, T.M. McSeveny and P.L. Weir. 1994. Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. *Ecology* 75:134–150.
- Jackson, D.S. and J. Chittenden. 1981. Estimation of dry matter in *Pinus radiata* root system. I. Individual tree. *N.Z. J. For. Sci.* 11:164–182.
- Jackson, R.B., J. Canadell, J.R. Ehleringer, H.A. Mooney, O.E. Sala and E.-D. Schulze. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* 108:389–411.
- Kauppi, P.E. and E. Tomppo. 1993. Impact of forests on net national emissions of carbon dioxide in West Europe. *Water Air Soil Pollut.* 70:187–196.
- Kürsten, E. and P. Burschel. 1993. CO₂-mitigation by agroforestry. *Water Air Soil Pollut.* 70:533–544.
- Landsberg, J.J. and R.H. Waring. 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *For. Ecol. Manag.* 95:209–228.
- Linder, S., M.L. Benson, B.J. Myers and R.J. Raison. 1987. Canopy dynamics and growth of *Pinus radiata*. I. Effects of irrigation and fertilization during a drought. *Can. J. For. Res.* 17:1157–1165.
- Lloyd, J. and G.D. Farquhar. 1996. The CO₂ dependence of photosynthesis, plant growth responses to elevated atmospheric CO₂ concentrations and their interaction with soil nutrient status. I. General principles and forest ecosystems. *Funct. Ecol.* 10:4–32.

- Lloyd, J., J. Grace, A.C. Miranda, P. Meir, S.C. Wong, H.S. Miranda, I.R. Wright, J.H.C. Gash and J. McIntyre. 1995. A simple calibrated model of Amazon rainforest productivity based on leaf biochemical properties. *Plant Cell Environ.* 18:1129–1145.
- Malet, P., F. Pécaut and C. Bruchon. 1997. Beware of using cumulated variables in growth and development models. *Agric. For. Meteorol.* 88:137–144.
- McMurtrie, R.E., D.A. Rook and F.M. Kelliher. 1990. Modelling the yield of *Pinus radiata* on a site limited by water and nitrogen. *For. Ecol. Manag.* 30:381–413.
- McMurtrie, R.E., R. Leuning, W.A. Thompson and A.M. Wheeler. 1992. A model of canopy photosynthesis and water use incorporating a mechanistic formulation of leaf CO₂ exchange. *For. Ecol. Manag.* 52:261–278.
- Myers, B.J. 1988. Water stress integral—a link between short-term stress and long-term growth. *Tree Physiol.* 4:315–323
- N.Z. Met. Service. 1983. Summaries of climatological observations to 1980, New Zealand Meteorological Service Misc. Pub. 177, Wellington, New Zealand, 172 p.
- Raison, R.J. and B.J. Myers. 1992. The biology of forest growth experiment: Linking water and nitrogen availability to the growth of *Pinus radiata*. *For. Ecol. Manag.* 52:279–308.
- Raison, R.J., B.J. Myers and M.L. Benson. 1992a. Dynamics for *Pinus radiata* foliage in relation to water and nitrogen stress: I. Needle production and properties. *For. Ecol. Manag.* 52:139–158.
- Raison, R.J., P.K. Khanna, B.J. Myers, R.E. McMurtrie and A.R.G. Lang. 1992b. Dynamics for *Pinus radiata* foliage in relation to water and nitrogen stress: II. Needle loss and temporal changes in total foliage mass. *For. Ecol. Manag.* 52:159–178.
- Santantonio, D. and E. Santantonio. 1987. Effect of thinning on production and mortality of fine roots in a *Pinus radiata* plantation on a fertile site in New Zealand. *Can. J. For. Res.* 17:919–928.
- Schimel, D.S. 1995. Terrestrial ecosystems and the carbon cycle. *Global Change Biol.* 1:77–91.
- Shvidenko, A. and S. Nilsson. 1994. What do we know about the Siberian forests? *Ambio* 23:396–404.
- Snowdon, P. and M.L. Benson. 1992. Effects of combinations of irrigation and fertilisation on the growth and above-ground biomass production of *Pinus radiata*. *For. Ecol. Manag.* 52:87–116.
- Tans, P.P., I.Y. Fung and T. Takahashi. 1990. Observational constraints on the global atmospheric CO₂ budget. *Science* 247:1431–1438.
- Vitousek, P.M. 1991. Can planted forests counteract increasing atmospheric carbon dioxide? *J. Env. Qual.* 20:348–354.
- Vogt, K.A., D.J. Vogt, P.A. Palmiotto, P. Boon, J. O'Hara and H. Asbjornsen. 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. *Plant Soil* 187:159–219.
- Waring, R.H., P.E. Schroeder and R. Oren. 1982. Application of the pipe model theory to predict canopy leaf area. *Can. J. For. Res.* 12:556–560.
- Watson, A.J. and C.L. O'Loughlin. 1990. Structural root morphology and biomass of three age classes of *Pinus radiata*. *N.Z. J. For. Sci.* 20:97–110.
- Williams, M., E.B. Rastetter, D.N. Fernandes, M.L. Goulden, G.R. Shaver and L.C. Johnson. 1997. Predicting gross primary productivity in terrestrial ecosystems. *Ecol. Appl.* 7:882–894.
- Wofsy, S.C., M.L. Goulden, J.W. Munger, S.-M. Fan, P.S. Bakwin, B.C. Daube, S.L. Bassow and F.A. Bazzaz. 1993. Net exchange of CO₂ in a mid-latitude forest. *Science* 260:1314–1317.