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The influence of N and P supply and genotype on carbon flux and partitioning in potted *Pinus radiata* plants

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Summary Carbon (C) flux and partitioning responses of *Pinus radiata* (D. Don) clones to a factorial combination of nitrogen (N) and phosphorus (P) supply were estimated in small trees growing in a greenhouse over 44 weeks. Our objective was to use a C budget approach at the plant level to examine how a factorial combination of N and P additions and genotype modify gross primary production (GPP), net primary production (NPP), absolute C fluxes apportioned to aboveground net primary production (ANPP), aboveground plant respiration (APR), total belowground carbon flux (TBCF) and the partitioning of GPP to ANPP, APR and TBCF. Single N or P additions increased plant NPP and GPP similarly, but their combined effects exceeded those of their individual contributions. Nitrogen and to a lesser extent P additions enhanced carbon-use efficiency (CUE, NPP:GPP) and C partitioning to ANPP at the expense of TBCF. The fraction of GPP partitioned to APR was invariant to N or P additions. The ratio of soil respiration (F_S) to TBCF was significantly greater in the low-N low-P addition treatment (61%) than in those treatments with single or combined N and P additions (49%). The slowest growing clone partitioned a significantly smaller fraction of GPP to ANPP (29%) than one of the faster-growing genotypes (33%). This research provides insight into how N and P regulate the C fluxes and partitioning in individual plants. Our results contribute to explaining clonal variation in aboveground growth rates and suggest that greater gains in CUE and partitioning to ANPP occur with addition of N rather than P supply.

Keywords: carbon budgets, carbon-use efficiency, clones, nitrogen, phosphorus.

Introduction

Nitrogen (N) and phosphorus (P) are the nutrients most frequently limiting primary productivity in all ecosystems in the biosphere (Aerts and Chapin 2000, Hall et al. 2005, Elser et al. 2007). This is not surprising as N is a vital constituent of proteins playing an essential role in all enzymatic activities, while P is involved in energy transfer in the cell, and both are important structural elements in nucleic acids (Marschner 1995). Aerts and Chapin (2000) suggested that imbalances between these two elements may be more important than absolute amounts of either element in the plant, and therefore such imbalances may lead to nitrogen or phosphorus deficiencies (Reich and Schoettle 1988, Marschner 1995, Aerts and Chapin 2000). An improved understanding of plant growth sensitivity to N and P deficiencies and imbalances may enhance our ability to predict patterns of productivity and partitioning across environments that differ widely both in fertility and in the ratios of these two important elements.

Most studies in forests have shown that improved N and P nutrition increases the proportion of dry-matter partitioned to aboveground at the expense of belowground components (e.g., Haynes and Gower 1995, Albaugh et al. 1998), whereas a few have found that this proportion does not change with nutrient availability (e.g., Nadelhoffer et al. 1985). The reason for this disparity may be due to the poor understanding of how fertility influences total carbon (C) budgets, and the large proportion of carbon that is respired, partitioned to mycorrhizae, exuded by roots or released as above- and belowground litter (Ryan 1991*a*, Ryan et al. 1996, Giardina et al. 2003). As these components are typically not included in biomass studies, there may in fact be a

nutrition effect on carbon partitioning that is not evident from studying biomass alone. The inherent difficulties in measuring various C fluxes in forests have deterred the determination of whole C budgets and therefore our understanding of the mechanisms regulating these fluxes remain limited (Cannell and Dewar 1994, Giardina et al. 2003).

A relatively new carbon balance method has emerged for forests (Raich and Nadelhoffer 1989), which includes improvements for scaling plant respiration (Ryan 1991*a*, 1991*b*, Ryan et al. 1996) and carbon flux to roots (Giardina and Ryan 2002, Giardina et al. 2003). Using these methods, gross primary production (GPP) can be partitioned into aboveground net primary production (ANPP), aboveground plant respiration (APR) and total belowground carbon flux (TBCF) as

$$\mathrm{GPP} = \mathrm{ANPP} + \mathrm{APR} + \mathrm{TBCF}. \quad (1)$$

The carbon balance approach has provided new insight into the distribution of C to different plant and soil processes. For instance, Giardina et al. (2003) found that GPP and the fraction of GPP partitioned to ANPP increased after the addition of fertilizer to *Eucalyptus saligna* Smith plantations. Shifts in carbon flux were at the expense of belowground processes. Similar results have been reported by other whole-carbon budget studies (e.g., Keith et al. 1997, Ryan et al. 2004).

Although fertilization has been found to influence component C fluxes in forests, the response of the carbon balance to a factorial combination of the two most important elements, N and P, is lacking. Given the sensitivity of growth to nutrient imbalances, this sort of information is likely to be of considerable value in providing insight into how different elements regulate partitioning. This type of information would also greatly enhance our ability to predict patterns of productivity and partitioning across environments that differ widely both in fertility and in the ratios of these two important elements. Given that clonal growth variation is wide, it would also be of interest to determine whether variation in component C fluxes accounts for observed clonal variation in growth.

Using large container-grown *Pinus radiata* (D. Don) clones, the aim of our study was to use a C budget approach to examine the response of GPP, net primary production (NPP), absolute C fluxes to ANPP, APR and TBCF, and the partitioning of GPP to ANPP, APR and TBCF to a factorial combination of N and P additions (N_0P_0, N_0P_1, N_1P_0 and N_1P_1) and genotype. The use of a C budget approach at the plant level, to the best of our understanding, has been not attempted before, and it may provide means to test hypotheses that might otherwise prove difficult to investigate in the field. Consequently our hypotheses were that:

(i) GPP, NPP and absolute C fluxes to ANPP, APR and TBCF increase with single or combined N and P additions (a rising tide lifts all boats; Litton et al. 2007).
(ii) Single or combined N and P additions do not alter the fraction of GPP partitioned to NPP (Ryan et al. 1996, Waring et al. 1998).
(iii) Partitioning to TBCF declines with single or combined N and P additions and the decline in TBCF is matched by a relative increase in ANPP (Ryan et al. 1996, Keith et al. 1997, Giardina et al. 2003).
(iv) Partitioning to APR increases with single or combined N and P additions (Ryan et al. 1996, Giardina et al. 2003).
(v) Faster-growing genotypes exhibit greater C partitioning to ANPP and APR at the expense of TBCF.

Materials and methods

Carbon balance method

The carbon balance method used in this study is the same as described by Giardina et al. (2003) and uses the terminology suggested by Litton et al. (2007) for all carbon balance studies. Briefly, GPP can be determined as the sum of ANPP, APR and TBCF (Eq. (1)). The ANPP can be estimated as the sum of litterfall C production (F_A), C content associated with tree mortality (F_W), C content change of live foliage (ΔC_C) and C content change in live branches, bark and wood (ΔC_w):

$$\mathrm{ANPP} = F_A + F_W + \Delta C_C + \Delta C_W. \quad (2)$$

The APR can be estimated as a sum of foliage construction (L_{RC}), foliage maintenance (L_{RM}) and wood construction and maintenance respiration (W_R):

$$\mathrm{APR} = L_{RC} + L_{RM} + W_R. \quad (3)$$

The TBCF can be estimated as the sum of soil respiration (F_S), carbon loss from the system by leaching or erosion (F_E), change in C content in the mineral soil (ΔC_S), change in C content of root biomass (ΔC_R), and change in C content in the litter layer (ΔC_L), less litterfall C production (F_A):

$$\mathrm{TBCF} = F_S + F_E - F_A + \Delta C_S + \Delta C_R + \Delta C_L. \quad (4)$$

Because of the experimental setup, we were able to ignore several of the components in Eq. (4) (see section Materials and methods for measuring the components of the carbon balance for justification), which simplified to:

$$\mathrm{TBCF} = F_S + \Delta C_R. \quad (5)$$

Plant material

Plant material was selected from a greenhouse experiment laid out in a factorial design with four clones: two nitrogen supply regimes (N_0 = 1.43 mM and N_1 = 7.14 mM) and two phosphorus supply regimes (P_0 = 0.084 mM and P_1 = 0.420 mM). Ingestad (1979) suggested that N should be provided at concentrations of 100 ppm (7.14 mM) and P at 13 ppm (0.420 mM) for optimum growth of *Pinus pinaster* Ait. These concentrations were chosen as the high-N and high-P supply regimes. The low-N (1.43 mM) and low-P (0.084 mM) supply regimes were chosen as one-fifth of the high-N and high-P concentrations, respectively. Nitrogen was provided as NH_4NO_3 and phosphorus as KH_2PO_4. There were six replicates per clone per treatment (96 plants) grouped into three blocks representing locations within the greenhouse. Clones were selected to represent a gradient in growth performance within a set of 400 genotypes planted in the Purokohukohu Experimental Basin within the central North Island of New Zealand (Beets et al. 2004).

One-year-old *P. radiata* cuttings from four clones (clones A, B, C and D) were raised at a nursery in Rotorua and transplanted to 42-l pots containing about 55 kg of air-dry silica sand (< 0.1% organic matter). Nutrient treatments were randomly allocated to the plants and applied for 44 weeks from early spring (September) 2004 until the plants were destructively harvested in the middle of winter (July) 2005. Plant roots were not strongly bounded by the 42-l pots as visually checked at the time of harvesting. Plants were watered twice daily to ensure that they were only limited by nutrients and not by water.

Plants received 1 l of nutrient solution per week over 44 weeks according to the nutrient treatments randomly assigned to the plants at the start of the experiment. Nitrogen additions in the low-N (1.43 mM) and high-N (7.14 mM) treatments to each plant over the entire experiment were 62.8 and 314.1 mmol N, respectively. Phosphorus additions in the low-P (0.084 mM) and high-P (0.420 mM) treatments applied to each plant over the entire experiment were 3.69 and 18.47 mmol P, respectively. Nutrients other than N and P were provided at concentrations of: 0.51 mol m^{-3} K (22.5 mmol total over 44 weeks), 0.25 mol m^{-3} Ca (11.0 mmol total), 0.41 mol m^{-3} Mg (18.1 mmol total), 0.28 mol m^{-3} S (12.4 mmol total), 12.53 mmol m^{-3} Fe (551.6 μmol total), 0.45 mmol m^{-3} Zn (20.2 μmol total), 0.47 mmol m^{-3} Cu (20.8 μmol total), 7.28 mmol m^{-3} Mn (320.3 μmol total), 0.073 mmol m^{-3} Mo (3.2 μmol total), 18.50 mmol m^{-3} B (814.1 μmol total), 0.85 mmol m^{-3} Cl (37.2 μmol total) and 0.13 mmol m^{-3} Na (5.7 μmol total), following Ingestad (1979). Plants were grown in a thermostatically controlled greenhouse where temperature was on average (±1 SD) 20 ± 4 °C during the day and 15 ± 3 °C during the night. Roots of all plants were artificially inoculated with spores of *Rhizopogon rubescens* Tul. and confirmed as mycorrhizal either by visual inspection of roots or by the presence of fruiting bodies.

Measurements of the components of the carbon balance

The ANPP was estimated from Eq. (2). Litterfall was collected monthly, dried and aggregated to yield F_A for each plant. As there was no mortality over the course of the experiment, F_W was set to zero. Initial and final dry masses by plant component (foliage, stems, branches and roots) were used to calculate ΔC_C and ΔC_w. For all calculations, C content was assumed to be 50% of plant dry mass. Initial dry mass (W_T, g) was determined using allometric equations based on plant collar diameter (d, mm) and plant height (h, cm) developed with 10 plants per clone from unplanted stock ($W_T = 0.007252\ d^{1.0611}\ h^{1.5129}$, $n = 40$, $r^2 = 0.90$, $P < 0.001$). Final total and component plant biomasses were determined by harvesting all plants at the end of the experiment. The bulk root system was collected and sand sieved to recover all visible roots. Sieved sand was thoroughly mixed, weighed and a 2.5 kg subsample was taken to recover the remaining roots by flotation. All tree components were oven-dried at 70 °C to constant mass and weighed.

The APR was determined from Eq. (3). Construction respiration costs for leaves (L_{RC}) and wood were assumed to be 25% of leaf NPP and wood NPP, respectively (Penning de Vries 1972, 1975, Ryan 1991*a*, 1991*b*). Wood maintenance respiration was assumed to be 7% of wood NPP based on the data from Giardina et al. (2003). Wood construction plus maintenance respiration yielded W_R. Maintenance respiration for leaves (L_{RM}) was measured as CO_2 efflux at night in all six replicates, four nutrient treatments and four clones. Maintenance respiration was scaled for each plant over the length of the experiment using an exponential response of night respiration to temperature (Q_{10} = 2, Ryan 1991*a*), estimates of leaf area and hourly measurements of air temperature.

The rate of foliage maintenance respiration at night (R_d) was measured on fully expanded foliage of every plant at a time when active growth had ceased. All gas exchange measurements were carried out at night in late autumn. Values of R_d were measured using a portable photosynthesis system (Li-6400, Li-Cor, Lincoln, NE). For each plant, three to six fascicles were arranged in a 6-cm^2 cuvette avoiding overlapping between needles. Temperature in the cuvette was maintained at 20 °C while leaf-to-air vapour pressure deficit was always < 1 kPa. External CO_2 concentration was maintained at 360 μmol mol^{-1} using a CO_2 mixer. Gas exchange measurements were left to stabilize for at least 10 min until measurements of respiration and stomatal conductance were relatively constant, and then values were recorded every 20 s for 2 min.

Following the completion of dark-respiration measurements, foliage samples were carefully removed from the cuvette and were cut to match the leaf area exposed to gas exchange. Half-total surface area of needles was determined based on water volume displacement as described by Johnson (1984). Foliage samples were dried at 70 °C to

constant mass and the dry mass was recorded. For foliar chemical analysis, leaf samples were finely ground and acid-digested by a Kjeldahl method (Blakemore et al. 1987). Nitrogen and phosphorus concentrations in the digests were determined colorimetrically by the Landcare Research Laboratories, Palmerston North, New Zealand. Nitrogen and phosphorus concentrations were expressed on a hemi-surface area basis.

The TBCF was determined from Eq. (5). Soil surface respiration rate (F_S) was measured using a soil respiration chamber (100 mm diameter, Model SRC-1, PP Systems, Herts, UK) and an infrared gas analyser (Model EGM-4, PP Systems, Herts, UK). Soil temperature was measured using a portable thermometer with a sensor plugged to 5 cm depth. All measurements were done within the same day once a month. Values of F_S for each tree were calculated as the sum of the product of actual soil surface respiration rate and the number of hours between intervening monthly measurements. This approach was used because sand surface CO_2 efflux positively scaled with tree size, but was not significantly affected by soil temperature (data not shown). Values of ΔC_R were determined as the difference between initial and final root mass multiplied by 0.5.

Additional to the 96 experimental units, four pots filled with silica sand without trees were set aside as controls for soil respiration and sand carbon. Controls were subject to the same regimes of nutrition and irrigation as those applied in the experimental pots carrying trees (one pot per nutrient treatment). Soil respiration measurements in control pots throughout the experiment were very small or negative (-5 to 5 mg C m^{-2} h^{-1}), suggesting that the measurements made when trees were present reflected true root and mycorrhizal respiration. We are not able to provide analysis to support our absolute values of respiration rate because we did not make measurements using independent instrumentation (e.g., Li-Cor 6400, Lincoln, NE). However, all our measurements are on a comparative basis. If the PP Systems instrument did lead to overestimations in rates of soil respiration, then this would be a systematic error across all our treatments.

Because of our experimental design, we were able to ignore several of the components in Eq. (4); i.e., C leaching (F_E), change in C in the litter layer C (ΔC_L), litterfall available to be decomposed (F_A) and C change in mineral sand substrate (ΔC_S). Carbon lost by leaching (F_E) was assumed to be zero, as irrigation was applied daily but in small amounts ($<$ 0.6 l for each 42-l of sand volume within each pot), so that drainage of C dissolved in water from pot bases would be minimal. Initial and final C content in the silica sand was determined by loss on ignition to yield ΔC_S. Mineral sand C concentration at the end of the experiment did not differ significantly between nutrient treatments and clones (Overall, $F_{47,48} = 1.16$, $P = 0.30$) being on average 0.60 $\pm$ 0.01 mg g^{-1}($\pm$1 SE, $n = 96$), and this value was not significantly higher than that observed at the beginning of the experiment (0.58 $\pm$ 0.02 mg g^{-1}, $n = 20$). Therefore, ΔC_S was considered to be zero. As the litter layer was nonexistent at the start of the experiment and litterfall was collected monthly, values of ΔC_L were set to zero. Litterfall (F_A) was included in the calculation of ANPP but not of TBCF, as litterfall was not available to be decomposed in the sand media.

The NPP was calculated to determine carbon-use efficiency (CUE, NPP:GPP). The NPP was determined as the sum of belowground NPP, estimated above as ΔC_R, and ANPP. Given the short duration of this study, we assumed that there was little significant root mortality between initial and final estimates of belowground biomass.

Fungal biomass in fine roots was estimated using the intersection method in three subsamples of oven-dried fine roots per tree. Basically, small randomly selected fine-root samples were placed on a petri dish over a 5 $\times$ 5 mm grid under a magnifying microscope, and intersections with either mycorrhizae or roots were recorded using a tally-counter. Mycorrhizae infection was then recorded as a percentage of total counts. Coarse roots ($>$ 2 mm) did not exhibit visual signs of mycorrhizal infection.

Data analyses

All analyses were carried out using SAS software (1996; SAS Institute, Cary, NC). Variables were tested for normality and homogeneity of variance, and transformations were made as necessary to meet the underlying statistical assumptions of the models used. Main and interactive effects of nitrogen and phosphorus supply and genotype on carbon flux patterns were examined using analysis of variance. Tukey's least significant difference test was used, where applicable, to distinguish among individual mean values with a confidence level of $P \leq 0.05$.

The block effect was marginally significant for GPP ($F_{2,30} = 4.1$, $P = 0.03$) and nonsignificant for all main C-partitioning variables; i.e., ANPP:GPP, APR:GPP and TBCA:GPP ($F_{2,30} < 2.35$, $P > 0.11$). There seemed to be a slight gradient in GPP from block 1 (66 $\pm$ 7 g C) to block 2 (64 $\pm$ 5 g C) to block 3 (55 $\pm$ 6 g C), but this gradient was not detected using Tukey's test. As the block effect was insignificant to marginally significant on C fluxes and partitioning, it is omitted from the Results section.

Results

Treatment influences on plant growth

Plants exhibited a large range in size by the end of the experiment (4–17 mm in stem diameter, 124–954 mm in tree height and 5–217 g oven-dry mass per tree), with all tree growth variables being strongly influenced by single or combined N and P additions ($F_{3,30} > 74$, $P < 0.001$), by genotype ($F_{3,30} > 6.4$, $P < 0.002$), and in some cases,

Table 1. Relevant tree measurements at the end of the experiment, and treatment differences for components of ANPP, APR and TBCF. Terms are defined in the Materials and methods and in the Appendix. Nutrient treatments comprised two nitrogen supply regimes (N_0 = 1.43 mM and N_1 = 7.14 mM) and two phosphorus supply regimes (P_0 = 0.084 mM and P_1 = 0.420 mM). Values are presented as mean (±1 SE) for each treatment; n = 24. Significance of main effects of clones (C) and nutrient treatments (T) or the interaction between clones and treatments (C × T) is shown as: ns, nonsignificant; *significant at $P < 0.05$; **significant at $P < 0.01$; ***significant at $P < 0.001$. Separation of mean values was determined using a Tukey test where applicable. Different letters between treatments indicate that means were significantly different at $P < 0.05$. Clonal differences are not shown in this table, but shown for main components (ANPP, APR and TBCF) in Table 2.

Measurements	Nutrient treatments				ANOVA		
	N_0P_0	N_0P_1	N_1P_0	N_1P_1	C	T	C × T
Basal diameter (mm)	6.7 ± 0.3 a	9.0 ± 0.2 b	9.4 ± 0.4 b	12.4 ± 0.4 c	***	***	ns
Tree height (mm)	367 ± 25 a	507 ± 14 b	533 ± 27 b	724 ± 31 c	***	***	***
Crown diameter (mm)	267 ± 13 a	346 ± 11 b	382 ± 11 b	518 ± 16 c	***	***	**
Tree dry mass (g)	26 ± 3 a	51 ± 2 b	57 ± 5 b	113 ± 8 c	***	***	**
Leaf area (m^2)	0.11 ± 0.01 a	0.22 ± 0.01 b	0.27 ± 0.02 b	0.54 ± 0.03 c	***	***	ns
Leaf area to mass ratio (m^2 kg^{-1})	10.1 ± 0.2 a	10.8 ± 0.2 a	10.4 ± 0.2 a	10.4 ± 0.2 a	ns	ns	ns
Leaf respiration at night (μmol m^{-2} s^{-1})	0.51 ± 0.03 a	0.53 ± 0.03 a	0.58 ± 0.03 a	0.58 ± 0.04 a	ns	ns	ns
Foliage nitrogen (%)	1.52 ± 0.07 a	1.76 ± 0.05 ab	1.96 ± 0.06 bc	2.16 ± 0.11 c	ns	***	ns
Foliage phosphorus (%)	0.21 ± 0.01 a	0.27 ± 0.01 b	0.21 ± 0.01 a	0.28 ± 0.02 b	ns	***	ns
Mycorrhizal infection (fraction of 1)	0.13 ± 0.02 a	0.10 ± 0.01 a	0.12 ± 0.01 a	0.08 ± 0.01 a	ns	ns	ns
ANPP (g C)	7.9 ± 0.8 a	15 ± 0.7 b	18.2 ± 1.5 b	38.5 ± 2.5 c	***	***	**
F_A	0.4 ± 0.1 a	0.5 ± 0.1 a	0.4 ± 0.1 a	0.7 ± 0.1 b	***	*	ns
Wood NPP	2.0 ± 0.2 a	4.4 ± 0.2 b	4.9 ± 0.5 b	11.5 ± 0.9 c	***	***	***
Leaf NPP	5.9 ± 0.6 a	10.6 ± 0.5 b	13.2 ± 1.0 b	27 ± 1.7 c	***	***	*
APR (g C)	8.8 ± 0.7 a	17.2 ± 1.0 b	16.9 ± 1.5 b	35.9 ± 2.9 c	*	***	ns
L_{RC}	1.5 ± 0.1 a	2.7 ± 0.1 b	3.3 ± 0.3 b	6.7 ± 0.4 c	***	***	*
L_{RM}	6.7 ± 0.5 a	13.2 ± 0.9 b	12 ± 1.2 b	25.5 ± 2.6 c	ns	***	ns
W_R	0.6 ± 0.1 a	1.4 ± 0.1 b	1.6 ± 0.2 b	3.7 ± 0.3 c	***	***	***
TBCF (g C)	13.4 ± 1.2 a	21.1 ± 1.1 b	18.9 ± 1.7 b	34.7 ± 2.6 c	*	***	*
F_S	8.2 ± 0.7 a	10.7 ± 0.6 a	8.8 ± 0.8 a	16.5 ± 1.2 b	ns	***	ns
C_R	5.2 ± 0.5 a	10.5 ± 0.6 b	10.2 ± 1.1 b	18.2 ± 1.6 c	**	***	**
GPP (g C)	30.1 ± 2.5 a	53.4 ± 2.3 b	54.0 ± 4.3 b	109.2 ± 6.7 c	***	***	*

by their interaction ($F_{9,30} > 3.4$, $P < 0.005$) (Table 1). Foliage N and P concentrations conformed and were significantly affected by the nutrient treatments ($F_{3,30} > 9.4$, $P < 0.01$), but not by genotype ($F_{3,30} < 2.67$, $P > 0.05$) or their interaction ($F_{9,30} < 1.47$, $P > 0.17$) (Table 1). The leaf area to mass ratio was independent of the main or interactive effects of nutrient treatments or genotypes (overall, $F_{47,48} = 1.13$, $P = 0.34$) being on average 10.40 ± 0.21 m^2 kg^{-1}. The rate of leaf respiration at night tended to increase mainly with N additions, but such changes were not significantly influenced by nutrient treatment or genotype (overall, $F_{47,48} = 1.58$, $P = 0.06$).

Mycorrhizal infection of fine roots at the plant level varied considerably from 1.3% to 40.3% (average 10.7 ± 0.6%), although such variation was not significantly explained by nutrient treatment or genotype (Table 1). However, mycorrhizal infection tended on average to decrease from 13% in the low-N low-P supply regime to 8% in the high-N high-P supply regime. Mycorrhizal infection also declined more with single P than with single N additions (Table 1).

Treatment influences on GPP

Tree GPP throughout increased with single or combined N and P additions ($F_{3,30} = 71.5$, $P < 0.001$), from an average of 30 g C $plant^{-1}$ in the low-N low-P supply regime to 109 g C $plant^{-1}$ in the high-N high-P supply regime (Table 1). Single N- (53 g $plant^{-1}$) and P additions (54 g $plant^{-1}$) similarly increased tree GPP compared to the low-N low-P supply regime (Table 1; Figure 1). Patterns of GPP changes with N and P additions were closely followed by ANPP, APR and TBCF. Remarkably, similar patterns were also observed for all subcomponents of ANPP, APR and GPP despite varying considerably in scale (Table 1).

The main effect of genotype on GPP was highly significant, but relatively minor compared to the main effect of

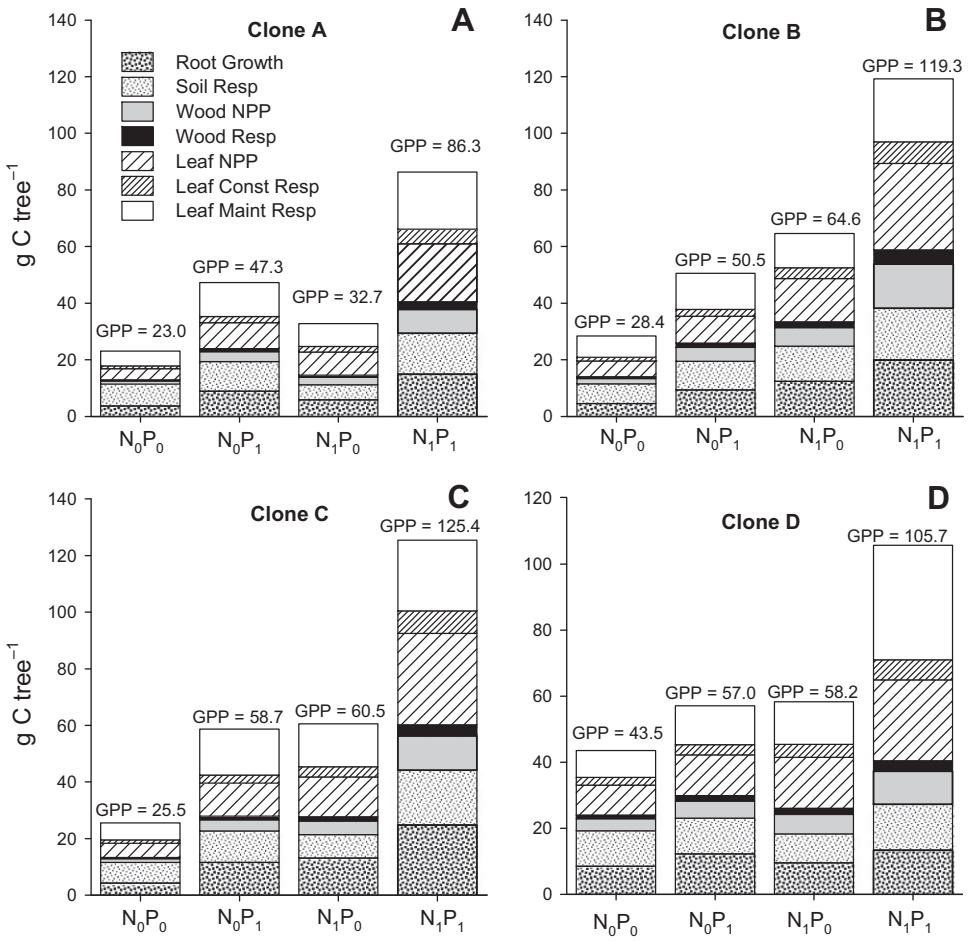

Figure 1. Nutrient treatment influences on average plant GPP and the constituent above- and belowground components for each clone. Nutrient treatments comprised two nitrogen supply regimes (N_0 = 1.43 mM and N_1 = 7.14 mM) and two phosphorus supply regimes (P_0 = 0.084 mM and P_1 = 0.420 mM).

nutrient treatments (F values 7.6 versus 71.5). The interaction between genotype and nutrient treatment was marginally insignificant ($F_{9,30}$ = 2.3, P = 0.05) as clone D developed faster in the low-N low-P supply regime and slower in the high-N high-P supply regime than clones B and C (Table 2). Tukey's test on GPP significantly separated clones into two groups: a slower-growing clone A and faster-growing clones B, C and D (Table 2).

Treatment influences on CUE

Nitrogen and to a lesser extent P additions increased the fraction of GPP allocated to NPP (CUE). The NPP:GPP ratio was significantly smaller in the low-N low-P supply regime (0.43) than in the high-N low-P and high-N high-P supply regimes (0.52). The CUE in the low-N high-P supply regime had an intermediate value (0.47) between these extremes. Overall, this ranking was relatively consistent across clones. The marginally significant interaction between clone and treatment on the NPP:GPP ratio ($F_{9,30}$ = 2.48, P = 0.03) was attributable to the relatively low CUE of N_1P_1 for clone D. Although the influence of clone on NPP:GPP ratio was marginally nonsignificant ($F_{3,30}$ = 2.56, P = 0.07), it is worth noting that the slowest growing clone also displayed the lowest CUE (0.46).

Treatment influences on aboveground NPP

Nitrogen additions, and to a lesser degree genotype, significantly influenced C partitioning to aboveground components. The fraction of GPP partitioned to ANPP was significantly greater in high-N supply regimes (35%) than in low-N supply regimes (27%) (Table 2). Although P-supply did not significantly alter the fraction of GPP partitioned to ANPP, P additions tended to increase the ANPP:GPP fraction above that of the low-N low-P control treatment. The ANPP:GPP fraction differed significantly between genotypes. The slowest-growing clone (A) partitioned overall a significantly smaller proportion of C to ANPP (29%) compared to clone D (33%). Clones B and C had generally greater ANPP:GPP values than clone A, but they did not differ significantly (Table 2).

The fraction of GPP partitioned to foliage ANPP significantly increased with N additions ($F_{3,30}$ = 30.5, P < 0.001). Low-N treatments partitioned on average 19.5 ± 0.5% of GPP to leaf ANPP (19.0% for N_0P_0 and 20.0% for N_0P_1). High-N treatments partitioned 24.8 ± 0.6% of GPP to leaf ANPP (24.8% for N_1P_0 and 24.7% for N_1P_1). Phosphorus additions did not change the leaf ANPP:GPP ratio (Figure 2). Neither the clone ($F_{3,30}$ = 2.34, P = 0.09) nor the interaction between

Table 2. Partitioning GPP into ANPP, APR and TBCF for all combinations of nutrient treatments and clones (GPP = ANPP + APR + TBCF). Components of TBCF are soil respiration C efflux (F_S) and change in C content of root biomass (ΔC_R). The F_S/TBCF ratio represents the amount of C efflux respired by roots and mycorrhizae and root turnover compared to the whole belowground C budget. Nutrient treatments comprised two nitrogen supply regimes (N_0 = 1.43 mM and N_1 = 7.14 mM) and two phosphorus supply regimes (P_0 = 0.084 mM and P_1 = 0.420 mM). Values are presented as means (±1 SE) for each treatment and clone; n = 6. Significance of main effects of clones (C) and nutrient treatments (T) or the interaction between clones and treatments (C × T) is shown as ns, nonsignificant; *significant at $P < 0.05$; **significant at $P < 0.01$; ***significant at $P < 0.001$. Separation of mean values was determined using a Tukey test where applicable. Different letters between treatments or clones indicate that mean values were significantly different at $P < 0.05$. Bold values are significant at $P < 0.05$.

Clone	Treatment	ANPP/GPP (%)	APR/GPP (%)	TBCF/GPP (%)	GPP (g C)	NPP (g C)	NPP/GPP (%)	F_S/TBCF (%)
A	N_0P_0	21.8 ± 1.7 a	30.9 ± 3.5 a	47.3 ± 3.0 a	23.0 ± 3.4 a	8.8 ± 1.6 a	37.6 ± 2.2 a	66.0 ± 2.6 b
	N_0P_1	26.7 ± 1.0 ab	32.3 ± 1.8 a	41.0 ± 2.2 ab	47.3 ± 2.6 b	21.5 ± 0.9 b	45.6 ± 1.1ab	54.1 ± 0.7 ab
	N_1P_0	32.8 ± 1.3 b	30.9 ± 2.5 a	36.2 ± 2.6 ab	32.7 ± 6.4 a	16.5 ± 3.0 b	50.8 ± 1.0 b	49.6 ± 2.8 a
	N_1P_1	33.3 ± 1.5 b	32.7 ± 1.6 a	34.0 ± 1.6 b	86.3 ± 7.0 c	43.8 ± 5.0 c	50.2 ± 2.7 b	50.2 ± 4.6 a
	Mean	**28.7 ± 1.2 a**	**31.7 ± 1.2 a**	**39.6 ± 1.5 b**	**47.3 ± 5.6 a**	**22.6 ± 3.1 a**	**46.0 ± 1.4 a**	**55 ± 2.0 a**
B	N_0P_0	25.8 ± 1.7 a	33.5 ± 1.4 a	40.6 ± 2.5 a	28.4 ± 1.7 a	12.0 ± 1.2 a	41.9 ± 2.3 a	59.7 ± 3.0 a
	N_0P_1	28.6 ± 1.4 ab	32.8 ± 1.2 a	38.7 ± 1.5 a	50.5 ± 3.5 b	23.6 ± 1.6 b	47.0 ± 2.0 ab	51.8 ± 4.0 a
	N_1P_0	34.1 ± 1.5 bc	28.1 ± 1.7 a	37.7 ± 2.5 a	64.6 ± 6.8 b	34.1 ± 4.0 b	52.5 ± 0.9 b	51.6 ± 3.2 a
	N_1P_1	38.4 ± 1.2 c	30.0 ± 2.7 a	31.6 ± 1.8 a	119.3 ± 9.6 c	66.0 ± 6.9 c	54.7 ± 2.3 b	48.5 ± 2.3 a
	Mean	**31.7 ± 1.2 ab**	**31.1 ± 1 a**	**37.2 ± 1.2 ab**	**65.7 ± 7.6 b**	**33.9 ± 4.6 b**	**49.0 ± 1.4 a**	**52.9 ± 1.7 a**
C	N_0P_0	25.1 ± 1.5 a	26.8 ± 3.5 a	48.1 ± 2.7 a	25.5 ± 5.4 a	10.5 ± 2.2 a	41.8 ± 1.2 a	64.8 ± 2.4 b
	N_0P_1	26.8 ± 0.7 ab	35.0 ± 2.6 a	38.2 ± 3.2 ab	58.7 ± 6.8 b	27.2 ± 2.8 b	46.7 ± 1.2 ab	47.1 ± 3.3 a
	N_1P_0	31.5 ± 1.7 bc	33.5 ± 1.3 a	35.0 ± 2.2 b	60.5 ± 8.8 b	31.9 ± 4.8 b	52.5 ± 1.6 b	39.6 ± 3.0 a
	N_1P_1	35.4 ± 1.2 c	29.7 ± 1.0 a	34.8 ± 1.6 b	125.4 ± 16.8 c	69.2 ± 9.3 c	55.1 ± 1.2 b	43.4 ± 1.8 a
	Mean	**29.7 ± 1 ab**	**31.3 ± 1.3 a**	**39 ± 1.6 ab**	**67.5 ± 9 b**	**34.7 ± 5.2 b**	**49.0 ± 1.2** a	**48.7 ± 2.4 a**
D	N_0P_0	29.2 ± 0.8 a	27.2 ± 1.2 a	43.6 ± 1.4 a	43.5 ± 5.0 a	21.1 ± 2.4 a	48.6 ± 1.4 a	55.3 ± 2.2 a
	N_0P_1	30.9 ± 0.8 a	29.3 ± 1.9 a	39.8 ± 2.3 ab	57.0 ± 4.4 a	29.7 ± 2.7 a	51.8 ± 1.4 a	47.9 ± 1.6 a
	N_1P_0	36.4 ± 1.2 a	32.1 ± 1.8 a	31.5 ± 1.0 b	58.2 ± 7.6 a	30.8 ± 4.7 a	52.4 ± 1.6 a	49.0 ± 2.7 a
	N_1P_1	34.0 ± 3.4 a	39.7 ± 3.5 a	26.3 ± 1.8 b	105.7 ± 15.1 b	47.7 ± 5.2 b	46.8 ± 4.4 a	50.5 ± 4.9 a
	Mean	**32.6 ± 1.1 b**	**32.1 ± 1.4 a**	**35.3 ± 1.6 a**	**66.1 ± 6.5 b**	**32.3 ± 2.7 b**	**49.9 ± 1.3 a**	**50.6 ± 1.6 a**
All clones	N_0P_0	25.5 ± 0.9 a	29.6 ± 1.4 a	44.9 ± 1.3 c	30.1 ± 2.5 a	13.1 ± 1.3 a	42.5 ± 1.2 a	61.5 ± 1.5 b
	N_0P_1	28.2 ± 0.6 a	32.3 ± 1.0 a	39.4 ± 1.1 b	53.4 ± 2.3 b	25.5 ± 1.2 b	47.8 ± 0.8 b	50.2 ± 1.4 a
	N_1P_0	33.7 ± 0.8 b	31.2 ± 1.0 a	35.1 ± 1.1 a	54.0 ± 4.3 b	28.3 ± 2.4 b	52.1 ± 0.6 c	47.4 ± 1.7 a
	N_1P_1	35.3 ± 1.0 b	33.0 ± 1.4 a	31.7 ± 1.1 a	109.2 ± 6.7 c	56.7 ± 3.9 c	51.7 ± 1.5 c	48.2 ± 1.8 a
Overall	**Mean**	**30.7 ± 0.6**	**31.5 ± 0.6**	**37.8 ± 0.8**	**61.7 ± 3.7**	**30.9 ± 2.0**	**48.5 ± 0.7**	**51.8 ± 1.0**
ANOVA statistics								
C		**	ns	*	***	***	ns	ns
T		***	ns	***	***	***	***	***
C × T		ns	*	ns	*	**	*	ns

nutrient treatments and clones ($F_{9,30}$ = 1.14, P = 0.37) had an influence on the foliage ANPP:GPP fraction. Although absolute litterfall significantly increased with combined N and P additions (Table 1), the ratio of litterfall to GPP was significantly higher in the low-N low-P (1.3 ± 0.1%) than in the high-N high-P (0.6 ± 0.1%) supply regime ($F_{3,30}$ = 5.44, P = 0.004). Single N and P additions similarly and significantly reduce the ratio of litterfall to GPP, from the low-N low-P addition treatment, to 0.8 ± 0.1%.

The fraction of GPP partitioned to wood ANPP significantly increased with single or combined N and P additions ($F_{3,30}$ = 39.5, $P < 0.001$), from an average of 6.4 ± 0.3% in the low-N low-P supply regime to 10.5 ± 0.4% in the high-N high-P supply regime (Figure 2). Single N- (8.2 ± 0.3%) and P additions (8.9 ± 0.3%) similarly increased the wood ANPP:GPP ratio compared to the low-N low-P supply regime. This trend was observed consistently across all clones, although clone D was less sensitive to nutrient treatments than other clones (Figure 2), as evidenced by a marginally significant interaction between nutrient treatment and clone ($F_{9,30}$ = 2.6, P = 0.03). There was a strong influence of clones on the wood ANPP:GPP ratio ($F_{3,30}$ = 19.3, $P < 0.001$) dividing clones into two groups: a low wood ANPP:GPP ratio, clone A (7.6 ± 0.3%) and clone C (7.4 ± 0.4%); and a high wood ANPP:GPP ratio, clone B (9.8 ± 0.5%) and clone D (9.3 ± 0.3).

Treatment influences on APR

Neither nutrient addition (N and P) nor genotype significantly altered the fraction of GPP partitioned to APR

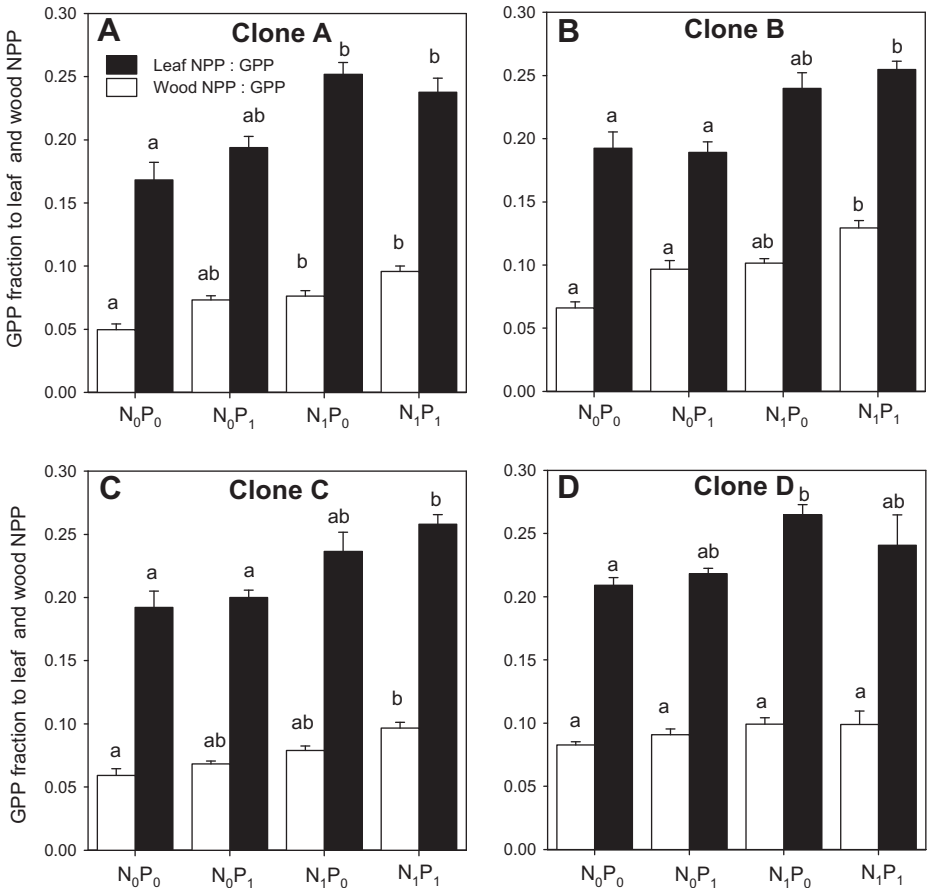

Figure 2. Partitioning of GPP to leaf NPP and wood NPP across nutrient treatments and clones. Nutrient treatments comprised two nitrogen supply regimes (N_0 = 1.43 mM and N_1 = 7.14 mM) and two phosphorus supply regimes (P_0 = 0.084 mM and P_1 = 0.420 mM). Values are presented as mean (±1 SE) for each treatment and clone. Different letters indicate significant differences among treatments at $P < 0.05$. Open bars represent the wood ANPP:GPP fraction and closed bars represent the leaf ANPP:GPP fraction. The leaf ANPP:GPP fraction was only influenced by nutrient treatments ($P < 0.001$). The wood ANPP:GPP fraction was influenced by nutrient treatments ($P < 0.001$), clones ($P < 0.001$) and marginally by their interaction ($P = 0.03$).

(32%, Table 2). Among the components of APR (Table 1), foliar maintenance respiration (L_{RM}) was dominant (73%) over foliage construction respiration (18%, L_{RC}) and wood construction and maintenance respiration (9%, W_R). Foliage dark respiration (R_d), used to scale foliage maintenance respiration (L_{RM}) over the duration of the experiment, ranged from 0.22 to 1.10 μmol m^{-2} s^{-1} (average 0.56 ± 0.02 SE, n = 96). Values of R_d were independent of single or combined N and P additions or genotype (overall, $F_{47,48}$ = 1.58, P = 0.06). Nevertheless, values of R_d showed weak positive correlations ($r^2 < 0.07$) with foliage nitrogen (P = 0.05) and phosphorus (P = 0.01) concentrations (Figure 3), and the slowest-growing clone D had a slightly higher but insignificantly different R_d than the other clones.

Treatment influences on TBCF

Nitrogen and to a lesser extent P additions decreased the fraction of GPP partitioned belowground. The fraction of GPP partitioned to TBCF was significantly greater in the low-N low-P supply regime (45%) than in the high-N high-P addition treatment (32%). Compared to the high-N high-P addition treatment, single N and P additions, respectively, resulted in a 3% and 7% increase in the TBCF:GPP fraction, which was only significant for the single P addition (Table 2). There were significant differences in the TBCF:GPP ratio among genotypes. The slowest growing clone (A) partitioned overall a significantly greater proportion of GPP to TBCF (40%) than clone D (35%). Clones B and C had generally smaller TBCF:GPP fractions than clone A but they did not differ significantly (Table 2).

The partitioning of TBCF between soil respiration (F_S) and the increment in root C content (ΔC_R) varied with nutrient treatment. The ratio of F_S/TBCF did not differ significantly for treatments with single or combined N and P additions (N_1P_0, N_0P_1 and N_1P_1), at an average of 49%, but significantly increased to 61% for the low-N low-P treatment, N_0P_0 (Table 2). Genotype did not change the partitioning of TBCF between F_S and ΔC_R ($F_{3,30}$ = 2.87, P = 0.053). However, the slowest growing clone (A) had an insignificantly higher F_S/TBCF ratio than the other clones (Table 2).

Discussion

Our data support our first hypothesis that GPP, NPP and absolute C fluxes to ANPP, APR and TBCF would increase with single or combined N and P additions (Litton et al. 2007). Values of GPP and NPP and absolute C fluxes

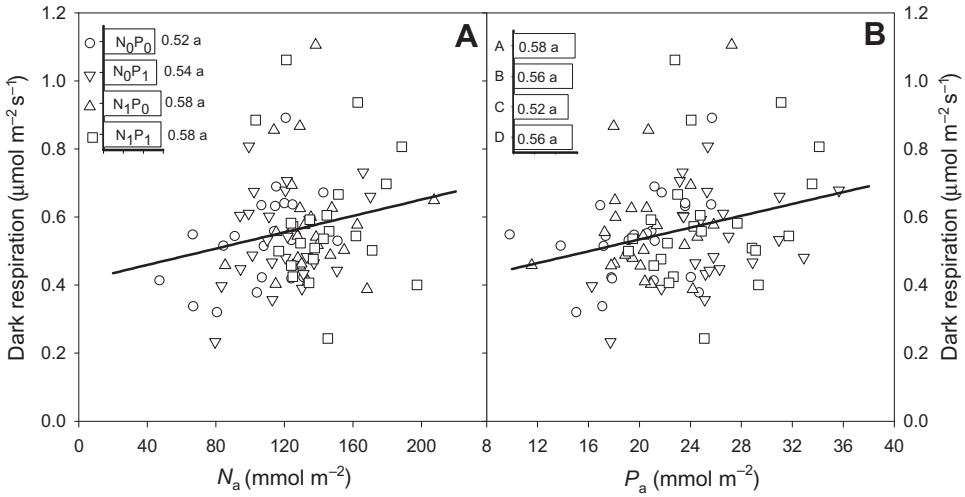

Figure 3. The relationship between the rate of foliage respiration at night (R_d) and (A) foliage nitrogen (N_a) and (B) phosphorus concentration (P_a) on a hemi-surface leaf area basis. Slopes ($F_{3,86} < 0.73$, $P > 0.53$) and intercepts ($F_{3,86} < 0.78$, $P > 0.51$) of these linear relationships were not influenced by nutrient treatment or clone: $R_d = 0.4112 + 0.0012\ N_a$, $r^2 = 0.04$, $P = 0.05$, $n = 94$; $R_d = 0.3600 + 0.0087\ P_a$, $r^2 = 0.07$, $P = 0.01$, $n = 94$. Horizontal bar graph inserts show nonsignificant main effects of nutrient treatment (A) and clone (B) on foliage respiration.

to ANPP, APR and TBCF of our potted plants were enhanced by single or combined N and P additions (Table 1). Single N or P additions similarly increased all C fluxes, but their combined effects exceeded those of their individual contributions. Synergism was previously observed with N and P additions specifically on biomass production of *P. radiata* trees (Sheriff et al. 1986) and potted plants (Davis 1997) and globally for major habitats of the biosphere (Elser et al. 2007). Nitrogen and phosphorus are identified as the nutrients most frequently limiting primary productivity in terrestrial (Aerts and Chapin 2000) and aquatic ecosystems (Hall et al. 2005). However, there is a certain inclination to think that N limitations are more common or more important than P limitations (e.g., Vitousek and Howarth 1991), whereas others tend to believe that N and P limitations are equivalent (Elser et al. 2007). Although our potted plants are arguably different to field-grown trees or entire ecosystems, we found equivalent effects of N and P on overall productivity, but interestingly not on C partitioning.

We also found our second hypothesis that partitioning to TBCF would decline with single or combined N and P additions, and the decline in TBCF is matched by a relative increase in ANPP to be true in a broad sense, but also noted significant differences between how N and P modify partitioning. Nitrogen and to a lesser extent P additions increased the fraction of GPP partitioned to ANPP at the expense of TBCF in our small *P. radiata* trees. Compared with the unfertilized treatment, our data clearly show that single additions of N significantly increased partitioning of GPP to ANPP by fourfold more than single additions of P (N_0P_0 = 26%, and it increased by 2% for N_0P_1 and 8% for N_1P_0). Similarly, compared to the unfertilized control, reductions in partitioning of GPP to TBCF resulting from a single addition of N were twofold higher than those resulting from a single addition of P (N_0P_0 = 45%, and it reduced by 6% for N_0P_1 and 11% for N_1P_0). While fertilization has been reported to bring about such changes in C partitioning in large field-grown trees (Keith et al. 1997, Giardina et al. 2003, Ryan et al. 2004, Litton et al. 2007), we are not aware of any study analysing single or combined effects of N and P additions on individual plant C budgets. However, our results are consistent with generally observed declines in the root-to-shoot ratios in response to single N (e.g., Murray et al. 2000), single P (Topa and Cheeseman 1992) and combined N and P additions (Warren and Adams 2002). Although we might expect that our observed trends in C partitioning in small trees conform with trends observed with field-grown trees, we are cautious about extrapolation of our results. For instance, Ryan et al. (2004) found that the fraction of GPP partitioned to TBCF increased with stand age and contributed to the decline in aboveground wood production of *Eucalyptus saligna* plantations. In contrast, Litton et al. (2007) found that GPP partitioning to TBCF generally decreased with age in a meta-analysis conducted with a large number of forest C budgets from around the globe.

Mycorrhizal infection of fine roots for our potted plants was found to be independent of nutrient treatments or genotypes, although the degree of infection tended to decrease mainly with P rather than N additions. Similarly, fertilization has been shown to reduce mycorrhizal infection and activity in field-grown trees (Ryan et al. 1996, Giardina et al. 2003). This may suggest that a larger fraction of C is partitioned to mycorrhizae in low P conditions. We found that our mycorrhizal infection rates in fine roots ranged

from 1% to 40% with average 11%. Overall, these values are relatively low compared to the conservative estimate for ectomycorrhizal carbon demand of 15% of NPP (range 0–22%) suggested by Söderström (1991). We speculate that our low mycorrhizal infection rate was probably attributable to use of the artificial growth medium.

We found our third hypothesis that partitioning to APR increases with single or combined N and P additions to be false. The fraction of tree GPP partitioned to APR was independent of single or combined N and P additions (0.31) in contrast to other studies where this proportion increased with fertilization in forest ecosystems (Ryan et al. 1996, Giardina et al. 2003). However, in all these cases, relative increases in APR have been far less than the relative increases in GPP, indicating that growth and maintenance respiration are only slightly enhanced by nutrient additions. Supporting evidence for this slight enhancement was found in our weak positive correlations between foliage maintenance respiration rates and foliage N and P concentrations.

Similarly, the data showed our fourth hypothesis that single or combined N and P additions do not alter the fraction of GPP partitioned to NPP to be false. Nitrogen and to a lesser extent P additions reduced the fraction of GPP allocated to respiration. The NPP:GPP fraction is widely used to model the carbon cycle at a range of spatial scales (Ichii et al. 2005, Turner et al. 2006) and it has been found to be relatively invariant for a wide range of forest ecosystems (e.g., 0.45 ± 0.05 SD, Landsberg and Waring 1997; 0.47 ± 0.04 SD, Waring et al. 1998). Although our values of CUE fall within reported ranges, they significantly increased with N and to a lesser extent with P additions. Although Giardina et al. (2003) suggested that CUE of *E. saligna* plantations increases with fertilization, our study showed that N additions exert a greater influence than P additions in minimizing respiratory losses and in enhancing CUE.

A consequence of rejecting our fourth hypothesis is that respiratory losses were reduced mainly with N and to a lesser extent with P additions. However, partitioning to APR was independent of nutrient addition whereas CUE varied with N and P additions. This means that differences in partitioning of GPP to NPP (i.e., CUE) were driven exclusively by changes in partitioning to production versus respiration belowground. This was verified in that the ratio of F_S/TBCF in our study was significantly higher for the low-N low-P addition treatments (61%) compared to those with single or combined N and P additions (49%).

Many ecosystem-process-based carbon budget models assume that TBCF is evenly partitioned between root production and respiration (Ryan 1991*a*, Landsberg and Waring 1997, Waring et al. 1998, McDowell et al. 2001). However, Giardina and Ryan (2002) found that annual soil respiration (F_S) was lower in fertilized than in control plots of *E. saligna* plantations, suggesting a decrease in the F_S/TBCF ratio with nutrient availability. Although we worked with small plants growing in pots where heterotrophic respiration could be neglected, this study extends previous research by demonstrating the interactive effect of N and P on the F_S/TBCF ratio. Both the imbalanced and the high nutrient supply regimes exhibited very similar values for this ratio, which were significantly lower than in the low-N low-P supply regime. This suggests that as nutrient supply declines, our plant roots and mycorrhizae respired proportionally more than when N and P were well supplied. Further research should investigate the regulation of TBCF partitioning to belowground NPP, auto- and heterotrophic respiration by plant and soil nutrition to derive relationships that can be incorporated into ecosystem models.

Litterfall was omitted from the mass balance TBCF equation since it was collected regularly. Litterfall removal would arguably change the rates of F_S and therefore the calculation of the F_S:TBCF ratio. However, litterfall from the young trees over the experiment was very low and varied from only 0.1% to 3.1% of GPP (average 0.9%), whereas F_S ranged from 7.5% to 43.3% of GPP (average 20%). Given that litterfall was a small fraction of F_S and GPP, it is unlikely that litterfall removal greatly impacted F_S or the interpretation of the F_S:TBCF ratios in this study.

We found our last hypothesis that faster-growing genotypes exhibit greater C partitioning to ANPP at the expense of TBCF to be true. Carbon partitioning explained differences in growth performance among genotypes. The slowest growing clone partitioned a significant 4% less of GPP to ANPP and 4% more to TBCF than one of the faster-growing genotypes (clone D). This marginal change in C partitioning may compound over time and account for relatively large differences between genotypes. Fischer et al. (2007) observed substantial changes in fine-root production, soil CO_2 efflux and TBCF along an elevation and hybridization gradient between two *Populus* species, suggesting strong genetic controls over these variables. Similarly, Raison and Myers (1992) argued that genotype, in addition to fertility and silviculture, may influence carbon partitioning in *P. radiata*. Also, Miller and Hawkins (2003, 2007) found that fast-growing families of interior spruce exhibited a greater plasticity in dry mass partitioning between shoots and roots than slow-growing families, suggesting that carbon partitioning might be partially controlled by genotype. Such differences in C partitioning plasticity among genotypes may account for the enhanced ANPP with increased plant genotypic diversity of *Solidago altissima* L. observed by Crutsinger et al. (2006). We also found that the clone × nutrient treatments interactions were minor compared to the main effects of nutrient treatments and clones. This suggests that faster-growing genotypes would have greater C assimilation and C partitioning aboveground, irrespective of nutrient availability as suggested by Carson et al. (2004).

In conclusion, we investigated the effects of N and P supply on carbon flux and partitioning of *P. radiata* clones.

Nitrogen and to a lesser extent phosphorus additions enhanced CUE and aboveground NPP while reducing total belowground C partitioning. Carbon partitioning to APR was invariant to N or P additions, whereas C partitioning to belowground plant respiration decreased similarly and significantly with single or combined N and P additions. The slowest growing clone partitioned a significantly lower fraction of GPP to aboveground NPP, than one of the faster-growing genotypes, which may contribute to explain clonal differences in growth performance.

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References

Aerts, R. and F.S. Chapin. 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Adv. Ecol. Res. 30:1–67.

Albaugh, T.J., L. Allen, P.M. Dougherty, L.W. Kress and J.S. King. 1998. Leaf area and above- and belowground growth responses of Loblolly Pine to nutrient and water limitations. For. Sci. 44:317–328.

Beets, P.N., G.R. Oliver, M.O. Kimberley, S.H. Pearce and B. Rodgers. 2004. Genetic and soil factors associated with variation in visual magnesium deficiency symptoms in *Pinus radiata*. For. Ecol. Manag. 189:263–279.

Blakemore, L.C., P.L. Searl and B.K. Daly. 1987. Methods for chemical analysis of soils. NZ Soil Bureau Sci. Rep. 80:21–45.

Cannell, M.G.R. and R.C. Dewar. 1994. Carbon allocation in trees: a review of concepts for modeling. Adv. Ecol. Res. 25:59–104.

Carson, S.D., M.F. Skinner, A.T. Lowe and M.O. Kimberley. 2004. Performance differences in *Pinus radiata* progeny with differing site nutrient availability. Can. J. For. Res. 34: 2410–2423.

Crutsinger, G.M., M.D. Collins, J.A. Fordyce, Z. Gompert, C.C. Nice and N.J. Sanders. 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. Science 313:966–968.

Davis, M. 1997. Comparative nutrient responses by *Pinus radiata*, *Trifolium repens*, *Dactylis glomerata* and *Hieracium pilosella* on a Mackenzie basin outwash plain soil. New Zealand. J. Agric. Res. 40:9–16.

Elser, J.J., M.E.S. Bracken, E.E. Cleland, D.S. Gruner, S.W. Harpole, H. Hillebrand, J.T. Ngai, E.W. Seabloom, J.B. Shurin and J.E. Smith. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol. Lett. 10:1135–1142.

Fischer, D.G., S.C. Hart, C.J. LeRoy and T.G. Whitham. 2007. Variation in below-ground carbon fluxes along a *Populus* hybridization gradient. New Phytol. 176:415–425.

Giardina, C.P. and M.G. Ryan. 2002. Total belowground carbon allocation in a fast-growing *Eucalyptus* plantation estimated using a carbon balance approach. Ecosystems 5:487–499.

Giardina, C.P., M.G. Ryan, D. Binkley and J.H. Fownes. 2003. Primary production and carbon allocation in relation to nutrient supply in a tropical experimental forest. Glob. Change Biol. 9:1438–1450.

Hall, S.R., V.H. Smith, D.A. Lytle and M.A. Leibold. 2005. Constraints on primary producer N:P stoichiometry along N:P supply ratio gradients. Ecology 86:1894–1904.

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.

Ichii, K., H. Hashimoto, R. Nemani and M. White. 2005. Modelling the interannual variability and trends in gross and net primary productivity of tropical forests from 1982 to 1999. Glob. Planet. Change 48:274–286.

Ingestad, T. 1979. Mineral nutrient requirements of *Pinus silvestris* and *Picea abies* seedlings. Physiol. Plant. 45:373–380.

Johnson, J.D. 1984. A rapid technique for estimating total surface area of pine needles. For. Sci. 30:913–921.

Keith, H., R.J. Raison and K.L. Jacobsen. 1997. Allocation of carbon in a mature eucalypt forest and some effects of soil phosphorus availability. Plant Soil 196:81–99.

Landsberg, J.J. and R.H. Waring. 1997. A generalized model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. For. Ecol. Manag. 95:209–228.

Litton, C.M., J.W. Raich and M.G. Ryan. 2007. Carbon allocation in forest ecosystems. Glob. Change Biol. 13: 2089–2109.

Marschner, H. 1995. Mineral nutrition of higher plants. Academic Press, London, 889 p.

McDowell, N.G., N.J. Balster and J.D. Marshall. 2001. Belowground carbon allocation of rocky mountain Douglas-fir. Can. J. For. Res. 31:1425–1436.

Miller, B.D. and B.J. Hawkins. 2003. Nitrogen uptake and utilization by slow- and fast-growing families of interior spruce under contrasting fertility regimes. Can. J. For. Res. 33:959–966.

Miller, B.D. and B.J. Hawkins. 2007. Ammonium and nitrate uptake, nitrogen productivity and biomass allocation in interior spruce families with contrasting growth rates and mineral nutrient preconditioning. Tree Physiol. 27:901–909.

Murray, M.B., R.I. Smith, A. Friend and P.G. Jarvis. 2000. Effect of elevated [CO_2] and varying nutrient application rates on physiology and biomass accumulation of Sitka spruce (*Picea sitchensis*). Tree Physiol. 20:421–434.

Nadelhoffer, K.J., J.D. Aber and J.M. Melillo. 1985. Fine roots, net primary production, and soil nitrogen availability: a new hypothesis. Ecology 66:1377–1390.

Penning de Vries, F.W.T. 1972. Respiration and growth. *In* Crop Processes in Controlled Environments. Eds. K.E.C.A.R. Rees, D.W. Hand and R.G. Hurd. Acedemic Press, London, pp 327–347.

Penning de Vries, F.W.T. 1975. Use of assimilates in higher plants. *In* Photosynthesis and Productivity in Different Environments. Ed. J.P. Cooper. Cambridge University Press, Cambridge, pp 459–480.

Raich, J.W. and K.J. Nadelhoffer. 1989. Belowground carbon allocation in forest ecosystems: global trends. Ecology 70:1346–1354.

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.

Reich, P.B. and A.W. Schoettle. 1988. Role of phosphorus and nitrogen in photosynthetic and whole plant carbon gain and nutrient use efficiency in eastern white pine. Oecologia 77: 25–33.

Ryan, M.G. 1991*a*. Effects of climate change on plant respiration. Ecol. Appl. 1:157–167.

Ryan, M.G. 1991*b*. A simple method for estimating gross carbon budgets for vegetation in forest ecosystems. Tree Physiol. 9:255–266.

Ryan, M.G., R.M. Hubbard, S. Pongracic, R.J. Raison and R.E. McMurtrie. 1996. Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status. Tree Physiol. 16:333–343.

Ryan, M.G., D. Binkley, J.H. Fownes, C.P. Giardina and R.S. Senock. 2004. An experimental test of the causes of forest growth decline with stand age. Ecol. Monogr. 74: 393–414.

Sheriff, D., E.K.S. Nambiar and D. Fife. 1986. Relationship between nutrient status, carbon assimilation and water use efficiency in *Pinus radiata* (D. Don) needles. Tree Physiol. 2:73–88.

Söderström, B. 1991. The fungal partner in the mycorrhizal symbiosis. *In* Ecophysiology of Ectomycorrhizae of Forest Trees. Ed. T.M.W. Foundation. Marcus Wallenberg Foundation, Falun, Sweden, pp 5–26.

Topa, M.A. and J.M. Cheeseman. 1992. Carbon and phosphorus partitioning in *Pinus serotina* seedlings growing under hypoxic and low-phosphorus conditions. Tree Physiol. 10:195–207.

Turner, D.P., W.D. Ritts, W.B. Cohen et al. 2006. Evaluation of MODIS NPP and GPP products across multiple biomes. Remote Sens. Environ. 102:282–292.

Vitousek, P.M. and R.W. Howarth. 1991. Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry 13:87–115.

Waring, R.H., J.J. Landsberg and J. Williams. 1998. Net primary production of forests: a constant fraction of gross primary production? Tree Physiol. 1998:129–134.

Warren, C.R. and M.A. Adams. 2002. Phosphorus affects growth and partitioning of nitrogen to Rubisco in *Pinus pinaster*. Tree Physiol. 22:11–19.

Appendix

Abbreviations

GPP gross primary production
NPP net primary production
CUE carbon-use efficiency
ANPP aboveground net primary production
APR aboveground plant respiration
TBCF total belowground carbon flux
F_A aboveground twig, bark and leaf litterfall
C_W carbon content of aboveground wood
C_C carbon content of live leaves in the canopy
L_{RC} leaf construction respiration
L_{RM} leaf maintenance respiration
W_R wood construction respiration
F_S soil surface CO_2 efflux
C_R carbon content of root biomass (coarse + fine)