SHORT-TERM CARBON PARTITIONING FERTILIZER RESPONSES VARY AMONG TWO FULL-SIB LOBLOLLY PINE CLONES

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ABSTRACT

We investigated the effects of fertilizer application on the partitioning of gross primary productivity (GPP) between contrasting full-sib clones of *Pinus taeda* (L.). Our objective was to determine if fertilizer growth responses resulted from similar short-term changes to partitioning. A modeling approach incorporating respiratory carbon (C) fluxes, soil CO2 efflux (FS), and biomass was applied to a factorial design with two clones, fertilizer and control treatments, and four sequential monthly harvests of seedlings planted in a greenhouse. Partitioning was integrated over 121 days to above, belowground, and total net primary production (ANPP + BNPP = NPP), total belowground C flux (TBCF), aboveground plant respiration (APR), and FS. While both clones showed similar GPP and responses to fertilizer application, they did so by partitioning GPP in different ways. Fertilizer application increased GPP and resulted in corresponding increases in ANPP, BNPP, and TBCF ($p < 0.01$). When considered as a fraction of GPP partitioned, differences between clones emerged. Clone-by-fertilizer interactions for carbon use efficiency (i.e. NPP / GPP), ANPP / GPP, and APR / GPP were all observed ($p < 0.10$). TBCF was significantly greater in one clone, indicating that plant-soil interactions could be affected by clone-specific partitioning. The other clone had greater growth efficiency (ANPP / GPP) without fertilizer, but with fertilizer application the clones were similar. Our results suggest multiple possible short-term ecophysiological mechanisms are responsible for fertilizer growth response in different yet closely related clones.

INTRODUCTION

Pinus taeda (L.) and less commonly *Pinus elliottii* (Engelm.) plantations are widespread across the Southeast, currently covering more than 13 million hectares, or approximately 75 percent of the 17 million total hectares of plantation forestland in the United States (Wear and Greiss 2002; FAO 2007). High productivity is achieved not only through improved genetics, but also through intensive silvicultural practices including site preparation, competition control, and fertilizer application, which combined are estimated to have increased productivity per land area by approximately 40 percent over natural stands (Fox, Jokela and others 2007). Since the early 1990's millions of hectares of plantations have been fertilized, at an annual rate of 0.5 million hectares as of 2004 (Fox, Allen and others 2007). Fertilizer growth responses vary across sites, but average 25 percent in response to mid-rotation application of nitrogen and phosphorous (Fox, Allen et al. 2007). Tree improvement has also resulted in significant gains in productivity. While open-pollinated seedlings still represent the vast majority of those planted in the Southeast, a number of methods for the production of elite genotypes have been developed in the last two decades (McKeand, Mullin and others 2003). Somatic embryogenesis is utilized to produce millions of genetically identical clonal seedlings from a single seed (Merkle and Dean 2000). More than 20 million clonal *P. taeda* seedlings have been planted as of 2010, and production and planting of clones is only expected to increase as production capabilities of the companies producing clonal seedlings increases (McKeand, Zobel and others 2007; Bettinger, Clutter and others 2009).

Clonal variability in a number of different tree species has been shown for survival (Bitoki 2008), growth and phenology (Paul, Foster and others 1997), soil CO2 efflux (Kasurinen, Kokko-Gonzales and others 2004), light-saturated net-photosynthetic rates (King, Seiler and others 2008), crown structure and radiation interception (Emhart, Martin and others 2007), biomass partitioning (Scarascia-Mugnozza, Ceulemans and others 1997), and partitioning of gross primary production (Bown, Watt and others 2009). As many of these processes affect fertilizer growth response, this suggests the possibility that clone-by-fertilizer interactions may be widespread. However, genotype-by-environment interactions are not problematic in open-pollinated *P. taeda*: high-performing families surpass low-performing families across a range of sites (McKeand, Jokela and others 2006; Roth, Jokela and others 2007). Further, research suggests that across a large number of clones, clone-by-site interactions may not be any more common than G x E interactions in open-pollinated families (McKeand, Jokela et al. 2006). By contrast, some studies among dissimilar sites have observed notable clone-by-site interactions that were more prevalent than interactions observed among half-sib families (Isik, Li and others 2003; McKeand, Jokela et al. 2006). However, it remains uncertain the extent to which clone-by-silviculture interactions may play a role in clonal plantations comprised of a small number of individual genotypes.

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To better understand the ecophysiological mechanisms that may cause different fertilizer growth responses in different clones we examined the C budget of a simplified model system (seedlings in pots). We developed a time-integrated C budget for a four month greenhouse experiment with a factorial design of two full-sibling *P. taeda* clones and two levels of fertilizer application. Quantifying C allocated to biomass and comparing individual fluxes does not accurately assess the full partitioning of gross primary productivity (GPP) to various plant organs and processes (Litton, Raich and others 2007). Modeling of GPP partitioning integrated over time is possible by scaling measurements of biomass, aboveground respiratory C fluxes, and soil CO2 efflux (Ryan 1991; Ryan 1991; Ryan, Hubbard and others 1996; Giardina and Ryan 2002; Giardina, Ryan and others 2003). To develop a more comprehensive representation of the C budget in our model system, we used this modeling approach as adapted to container-based seedlings by Bown et al. (2009).

METHODS

STUDY DESIGN

Clones GE034 and GE769 (ArborGen LLC, Summerville, South Carolina, USA) were planted in this study. These two clones, produced from a single full-sib cross, were among the first selected by ArborGen in 2005 (Bitoki 2008), and have contrasting crown ideotypes. Clone 34 is the faster growing of the two, has a narrower crown than clone 769, and allocates less to branches (Bitoki 2008). Trees were removed from the cooler (4° C) where they had been for two months and were potted on April 30, 2009 in their plugs. Plug media was comprised of a mixture of peat moss and vermiculite and contained an undisclosed quantity of fertilizer. They were left in plugs to minimize reductions in growth rates or survival due to excessive root mortality that would have resulted from removing the trees from the densely rooted plugs. Trees were potted in homogenized A-horizon soil from the USDA Forest Service's Southeastern Tree Research and Education Site (SETRES). The soil is a Wakulla series (siliceous, thermic Psammentic Hapludult), and was selected to minimize native nutrition to allow for as complete nutrient control as is possible in a natural soil. Soil was sieved through a 1-cm mesh to remove any coarse roots, was homogenized, and was placed into 15-by-15-by-38 cm pots (8,550 cm3) that were sufficiently large to limit extensive root binding during this four month experiment.

Trees were in the greenhouse in Blacksburg, Virginia, USA, (37.24°N 80.43°W) from April 30 to October 15, 2009. Watering was conducted daily in an attempt to prevent drought stress while also minimizing leaching from the bottom of the pots. Nighttime minimum temperature was set to 18° C in the greenhouse, and while the vents were set to open during the day at 25° C daytime temperatures did exceed this frequently. Relative humidity was allowed to fluctuate with the ambient air. High-pressure sodium lights were turned on daily for several hours pre-dawn from September 15 to October 15 to augment photoperiod, which averaged 12.9 hours throughout the experiment. Environmental conditions were recorded by a single HOBO datalogger (Onset Computer Corp., Bourne, Massachusetts, USA) placed in the center of the experiment.

The ramets were randomly assigned to fertilizer and control treatments, and fertilizer was applied to the selected ramets on June 16, 2009. This date will be referred to as day 0 throughout the remainder of this chapter. Fertilizer was applied at an operational rate with DAP and ammonium nitrate at 225 kg N per hectare and 56 kg elemental P per hectare. Control trees received no fertilizer. Following fertilizer application, ramets from each treatment combination were harvested monthly on July 16, August 16, September 15, and October 15, 2009 (30, 61, 91, and 121 days after fertilizer application). Thus the experiment was a two-by-two-by-four factorial randomized complete block design replicated eight times (128 trees total), with treatments consisting of clone, fertilizer, and sequential harvest, respectively. Some measurements were only made on the final harvest group (day 121 harvest) throughout the experiment. These variables are described below, and may be considered a two-by-two randomized complete block design with repeated measures. Other variables were measured on each tree at harvest and thus reflect a tree-for-time-substitution assumption.

DATA COLLECTION

At each of the four destructive harvests the entire tree was partitioned into components. Fine roots were considered those < 2 mm diameter, with coarse roots being any root > 2 mm diameter. All biomass components were oven-dried at 65° C for > 10 days, and weighed. Throughout the experiment ground-line diameter and total height were measured weekly on the final harvest group. Prior to each destructive harvest heights and basal diameters of all trees were measured to ensure that no significant growth differences existed between harvest groups, and that tree-for-time-substitution assumptions were valid.

Total soil CO2 efflux (FS) was assessed in the morning between 10:00 and 12:00 EDT using a small dynamic closed (231 cm3 volume, 55 cm2 area) cuvette with no fan. A LI-6200 infrared gas analyzer (IRGA) was used for all respiratory C flux measurements (LiCor Biosciences Inc., Lincoln, Nebraska, USA). The IRGA was zeroed daily immediately prior to the first FS measurement and a blank reading on a sealed cuvette with no soil was taken to ensure the apparatus was operating correctly. Soil temperature (thermocouple) and volumetric moisture content (TDR) were measured concurrently with efflux for use as covariates

in statistical analyses. These measurements were made on 22 separate dates. Procedures were based on those described in Gough and Seiler (2004).

Aboveground dark respiration rates were measured at night between 23:00 and 5:00 EDT within two days prior to the day 30 and day 91 harvests. A large inverted trash-can (volume = 120,000 cm3) was used as a cuvette. An incision was made along a radius of the lid, so that it could be sealed with weather-stripping around the base of the stem of the seedling being measured without damaging the seedling. A small fan was installed in the cuvette to mix the air volume inside. Ambient temperature inside the cuvette was measured with a thermocouple during each measurement so that respiration rates could be standardized to 20° C assuming a Q10 of 2.0 (Ryan 1991). Rates were calculated using subsequent harvest data on a plant dry mass basis in order to account for varying tree sizes.

DATA MODELING

The C budget model is shown in equations 1 through 7, and each variable is described in Table 1. Equation 1 partitions GPP into aboveground net primary productivity (ANPP), aboveground plant respiration (APR), and total belowground C flux (TBCF).

$$GPP = ANPP + APR + TBCF \quad \text{[Equation 1]}$$

Partitioning to ANPP is the sum of litter-fall production, mortality, and changes in woody and foliar biomass C storage (Equation 2). Because litter-fall and mortality were not observed in our four month greenhouse study, we set these fluxes equal to zero, yielding Equation 3 for ANPP.

$$ANPP = FA + FW + \Delta CF + \Delta Cw \quad \text{[Equation 2]}$$

$$ANPP = \Delta CF + \Delta Cw \quad \text{[Equation 3]}$$

Partitioning to TBCF is the sum of soil CO2 efflux, C lost through erosion or leaching, changes in soil C, changes in root biomass C, and changes in litter layer C less new litterfall that was previously quantified as part of ANPP (Equation 4). We were again able to eliminate some of these variables, resulting in the Equation 5. We assumed that there was no erosion or leaching, and we observed no litter layer or litter-fall in this study. Analysis of soil data between days 30 and 121 showed no significant changes in soil C, so this flux was also set equal to zero.

$$TBCF = FS + FE + \Delta CS + \Delta CR + \Delta CL - FA \quad \text{[Equation 4]}$$

$$TBCF = FS + \Delta CR \quad \text{[Equation 5]}$$

Two further terms are defined in Equation 6 and Equation 7. Net primary productivity (NPP) is the sum of ANPP and the change in root biomass C, or total aboveground and belowground change in biomass C. Carbon use efficiency (CUE) is defined as the proportion of GPP partitioned to NPP, or biomass.

$$NPP = ANPP + \Delta CR \quad \text{[Equation 6]}$$

$$CUE = NPP / GPP \quad \text{[Equation 7]}$$

In the greenhouse study various C fluxes were quantified with a variety of different cuvettes of different sizes and shapes. As a result, the individual fluxes measured represent an accurate comparison of treatments, but likely did not reflect the magnitude of the absolute fluxes (Norman, Kucharik and others 1997). Further, we did not apply multiple measurement techniques to each flux to determine the accuracy of our methods in assessing the actual rates. Thus, while this modeling approach likely did not reflect the absolute magnitude of GPP partitioned to each component assessed, it remained an accurate treatment index that allowed us to compare the effects of fertilizer application on the C budget of both clones (Bown, Watt et al. 2009).

The model was applied to only the day 121 harvest group of trees and represents data integrated over the duration of the experiment (i.e. days 0 through 121). Thus, all values reflect the change in biomass C pools or the integrated total of respiratory C fluxes from the time of fertilizer application through the final destructive harvest four months later. Data from all trees was utilized in order to estimate parameters for the day 121 harvest group trees.

ANPP was calculated as the change in aboveground biomass from day 0 to day 121, assuming that 50 percent of biomass was carbon. Aboveground biomass was the sum of foliar, branch, and stem mass. Treatment specific non-linear regressions on all trees were applied to determine the relationship between stem dimensions and aboveground biomass. Regressions were of the form shown in Equation 8, and were estimated using PROC NLIN in SAS software version 9.2. (SAS Institute Inc., Cary, North Carolina, USA). Coefficients and statistics for each regression are shown in Table 2. Regressions were then applied to stem dimension measurements taken on each tree from the day 121 harvest group on day 0. Difference between actual aboveground biomass from the day 121 harvest, and estimated aboveground biomass at day 0 was then calculated for each tree.

Aboveground biomass = a (basal diameter)b (height)c
[Equation 8]

Modeling efforts found in the literature typically calculate APR by including maintenance respiration rates separately for foliage and wood, and then assume construction respiration as a uniform fraction of biomass (Ryan 1991; Maier, Albaugh and others 2004; Bown, Watt et al. 2009). This was unnecessary in our experiment, as we directly measured APR by placing the entire aboveground portion of the tree in a cuvette. The flux we measured included maintenance respiration of both foliage and wood as well as construction respiration due to elongating shoots and fascicles or secondary woody growth.

APR was measured on days 30 and 91 on those respective harvest groups, and was converted to 20° C using ambient air temperature measured concurrently by assuming a Q10 of 2.0 (Ryan 1991). APR was expressed per plant mass based on harvest data to account for variability in tree size. The average mass-specific APR rates for each treatment group were calculated, and the day 30 rates were applied to days 0 through 59 (inclusive), while the day 91 rates were applied to days 60 through 121. Rates were back-corrected to the temperature measured at the single data logger in the center of the experiment at two minute intervals, again assuming a Q10 of 2.0. Total daily mean mass-specific APR CO2 flux was calculated for each treatment group based on this data. Stem dimension measurements made weekly throughout the trial were linearly interpolated for each tree in the final harvest group between measurement dates at a daily resolution. The regression in Equation 8 was then applied to calculate estimated daily aboveground biomass for each tree in the day 121 harvest group on each day. Mass was then multiplied by the daily mean mass-specific APR CO2 flux for the corresponding treatment group. Daily CO2 yields attributable to APR for each tree were summed from days 0 to 121, and converted from a CO2 basis to a C basis to give APR used in the model.

TBCF was calculated as shown in Equation 5. Change in root biomass C (ΔCR) was calculated in the same manner as ANPP was calculated above. The non-linear regression relating stem dimensions to belowground mass is shown in Equation 9, and coefficients and statistics are shown in Table 2.

Belowground biomass = a (basal diameter)b (height)c
[Equation 9]

FS had been measured on all trees from the day 121 harvest group throughout the trial. FS data was scaled to the soil surface area of each pot and was converted to C mass basis. Rates were then scaled up to a daily flux. Daily fluxes were linearly interpolated between measurement dates for each tree, and all daily values were summed for each tree to yield the integrated FS flux over 121 days. Using midmorning rates to reflect daily fluxes required the assumption that midmorning rates represented the average daily rate, which was unlikely. In order to adjust for the close coupling of photosynthetic and respiratory fluxes (i.e. respiration also declines at night) observed in similar sized trees in other studies (Wertin and Teskey 2008), daily fluxes were multiplied by 0.5. This further reflected that rates likely declined at night due to lower temperatures, and likely declined later in the day due to lower soil moisture availability, as watering was done each morning (Fang and Moncrieff 2001; Qi and Xu 2001; Dilustro, Collins and others 2005). The exact magnitude of this adjustment was arbitrary, but it does not alter the validity of modeling efforts as a treatment index.

Various ratios (e.g. CUE) were calculated from the fluxes and biomass pools described above. Data was transformed as necessary to meet statistical assumptions, although all reported values are untransformed. All variables were analyzed in PROC MIXED with block as a random effect, and comparisons were made in PROC GLM with Tukey's HSD test at a significance level of $\alpha = 0.10$.

RESULTS AND DISCUSSION

Fertilizer application increased GPP and resulted in corresponding increases in the absolute magnitudes of NPP, ANPP, and ΔCR (Figure 1; Table 3; $p < 0.01$). A clone-by-fertilizer interaction occurred for APR, whereby both clones showed increases with fertilizer application, but clone 34 increased more ($p < 0.05$). Partitioning to TBCF and FS also showed clone-by-fertilizer interactions ($p < 0.01$). TBCF was not different between fertilizer treatments in clone 34 due to a reduction in FS coupled with an increase in ΔCR as a result of fertilizer application. By contrast clone 769 showed a significant increase in TBCF with fertilizer application that was the result of increased ΔCR but no significant FS response to fertilizer application.

When considered on the basis of percentage of GPP partitioned, rather than on terms of absolute fluxes and pools, similar trends emerged. Fertilizer application resulted in increased CUE in both clones (Table 3; $p < 0.01$). Overall clone 769 had slightly greater CUE ($p < 0.10$). Greater proportional allocation to ANPP was observed in fertilized ramets of both clones ($p < 0.01$), although the clones were not different in this regard ($p > 0.10$). For APR clone 34 showed no effect of fertilizer application, while clone 769 decreased partitioning from 50.9 percent to 41.5 percent of GPP ($p < 0.10$). Conversely, for TBCF clone 769 showed no effect of fertilizer application, while clone 34 decreased partitioning from 36.2 percent to 27.3 percent of GPP ($p < 0.10$). These results contrasted with those based on absolute fluxes, and were driven by both clones reducing partitioning

to FS as a portion of TBCF when fertilized, but clone 34 doing so to a greater extent than clone 769 ($p < 0.10$).

Interpretation of these results indicated that while both clones showed remarkably similar absolute values of GPP, and GPP responses to fertilizer application, they did so by partitioning GPP in different ways in response to fertilizer application. Clone 769 partitioned less of GPP belowground in controls but more in the fertilizer treatment, indicating that plant-soil interactions could be affected by clone-specific GPP partitioning patterns in response to fertilizer application. Differences CUE showed that the clones were similar without fertilizer application, but with fertilizer application clone 769 had greater growth efficiency. Thus while the clones may perform similarly on a nutrient deficient site, with fertilizer application clone 769 would likely be the best performer based on this data. This conclusion pertains to total biomass, not only to stem mass or volume, the trait of primary economic concern.

Limited inferences may be drawn from comparisons of our results with ecosystem-level studies in older stands due to differences in processes between tree ages and between single-tree and stand scales. Nonetheless, previous research in older stands has found that fertilizer amendment typically does not result in large changes in CUE, contrary to our results (Lai, Katul and others 2002; Giardina, Ryan et al. 2003; Maier, Albaugh et al. 2004). While we found that even control treatments represented a net C sink (GPP was positive), results from a 12-year-old stand with the same soil indicate control treatments may not be an atmospheric C sink, with GPP values of approximately zero (Maier, Albaugh et al. 2004). The proportion of GPP partitioned to respiration has also been found to vary little across treatments, again conflicting with our results (Litton, Raich et al. 2007). However, in the one study did show an effect on APR / GPP, an increase was observed (Giardina, Ryan et al. 2003), contrary to the reduction observed in our study for clone 769. However, when our results are compared with the only study we are aware of comparing GPP partitioning among clonal seedlings under different levels of fertilizer application (Bown, Watt et al. 2009), our results were surprisingly consistent. Bown et al. observed clone-by-fertilizer interactions for CUE and APR / GPP, fertilizer effects for FS / TBCF and ANPP / GPP, and clonal effects for ANPP / GPP and TBCF / GPP. This further supports that while pot-based seedling studies may produce similar results, these results should not be inferentially scaled to the ecosystem level for older plantations.

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Table 1—Description of all variables utilized in the C budget modeling of the greenhouse clone-by-fertilizer-by-sequential-harvest study. Variables assumed to equal zero in this simplified greenhouse pot study are noted in the description

Acronym		Variable	Description
GPP		Gross Primary Productivity	All C fixed through photosynthesis
ANPP		Aboveground Net Primary Productivity	C stored in aboveground biomass
	F_A	Sum of litterfall C production	Assumed equal to 0 (no litterfall)
	F_W	Sum of mortality C production	Assumed equal to 0 (no mortality)
	ΔC_F	C content change of live foliage	C stored in foliar biomass
	ΔC_w	C content change of aboveground woody tissue	C stored in branch and stem biomass
APR		Aboveground Plant Respiration	Sum of construction and maintenance
TBCF		Total Belowground Carbon Flux	All C allocated belowground
	F_S	Sum of soil respiration	C lost from the soil surface
	F_E	C lost from system through erosion or leaching	Assumed to equal 0 (no leaching)
	ΔC_S	C content change of soil	Assumed equal to 0 (no change)
	ΔC_R	C content change of root biomass	C stored in tap and lateral root biomass
	ΔC_L	C content change of litter layer	Assumed to equal 0 (no litter layer)
NPP		Net Primary Productivity	All C stored in biomass
CUE		Carbon Use Efficiency	Portion of GPP allocated to NPP

Table 2—Non-linear regressions of above and belowground biomass based on stem dimensions at harvest for all 128 trees from the greenhouse clone-by-fertilizer-by-sequential-harvest study. Equations were of the form: biomass = a (basal diameter)^b (height)^c. Regressions were implemented in PROC NLIN in SAS software version 9.2.

Aboveground Biomass

Treatments		Coefficients			Statistics			
Clone	Fert	a	b	c	F	p-value	R^2	N
34	0	0.2920	1.1369	0.3848	476.51	<0.0001	0.980	32
34	1	0.1231	1.2144	0.5794	622.51	<0.0001	0.985	32
769	0	0.4868	1.2454	0.1919	856.21	<0.0001	0.989	32
769	1	0.0362	1.6936	0.6130	575.99	< 0.0001	0.983	32

Belowground Biomass

Treatments		Coefficients			Statistics			
Clone	Fert	a	b	c	F	p-value	R^2	N
34	0	0.3013	1.1540	0.1640	307.11	<0.0001	0.969	32
34	1	0.0434	2.1348	0.0833	254.35	<0.0001	0.963	32
769	0	0.0734	1.2373	0.5320	355.50	<0.0001	0.974	32
769	1	0.1332	2.2059	-0.1686	295.06	<0.0001	0.968	32

Table 3—Treatment means and statistics for C allocation in a four month greenhouse experiment with two clones under two fertilizer treatments. Means are shown with standard errors in parentheses. Different letters denote significant differences ($p < 0.10$) based on Tukey's HSD test. P-values are shown in the rightmost three columns. Acronyms are defined in Table 1.

Variable	C34 Control	C34 Fert	C769 Control	C769 Fert	Overall Mean	Clone	Fert	C X F
GPP (g C)	28.7 (1.4) A	39.5 (1.5) B	27.1 (0.9) A	40.1 (2.7) B	33.9 (1.4)	0.60	<0.01	0.51
NPP (g C)	6.7 (0.6) A	14.2 (0.5) B	6.3 (0.4) A	16.2 (1.0) B	10.8 (0.9)	0.48	<0.01	0.19
ANPP (g C)	4.9 (0.5) A	9.4 (0.5) B	3.9 (0.3) A	10.0 (0.9) B	7.0 (0.6)	0.72	<0.01	0.16
APR (g C)	13.4 (0.5) A	19.3 (0.9) B	13.7 (0.3) AB	16.8 (1.6) BC	15.8 (0.6)	0.27	< 0.01	0.05
TBCF (g C)	10.4 (0.6) A	10.8 (0.7) A	9.5 (0.5) A	13.3 (0.5) B	11.0 (0.4)	0.18	<0.01	<0.01
F_S (g C)	8.7 (0.6) A	5.9 (0.5) B	7.1 (0.4) AB	7.1 (0.4) AB	7.2 (0.3)	0.68	<0.01	<0.01
ΔC_R (g C)	1.8 (0.2) A	4.9 (0.4) B	2.4 (0.3) A	6.2 (0.4) C	3.8 (0.4)	< 0.01	< 0.01	0.85
CUE (%)	22.9 (1.4) A	36.2 (1.0) B	23.0 (1.0) A	40.6 (1.4) C	30.7 (1.5)	0.09	<0.01	0.11
ANPP/GPP (%)	16.8 (1.0) A	23.8 (1.1) B	14.2 (1.0) A	24.7 (1.2) B	19.9 (1.0)	0.42	<0.01	0.10
APR / GPP (%)	47.0 (1.5) A	48.9 (0.9) A	50.9 (1.1) A	41.5 (1.3) B	47.1 (0.9)	0.15	<0.01	<0.01
TBCF / GPP (%)	36.2 (0.8) A	27.3 (1.4) B	35.0 (1.1) A	33.7 (1.7) A	33.1 (0.9)	0.02	<0.01	<0.01
F_S / TBCF (%)	83.2 (1.9) A	54.6 (2.5) B	74.9 (1.9) C	53.2 (2.2) B	66.5 (2.5)	0.03	<0.01	0.13

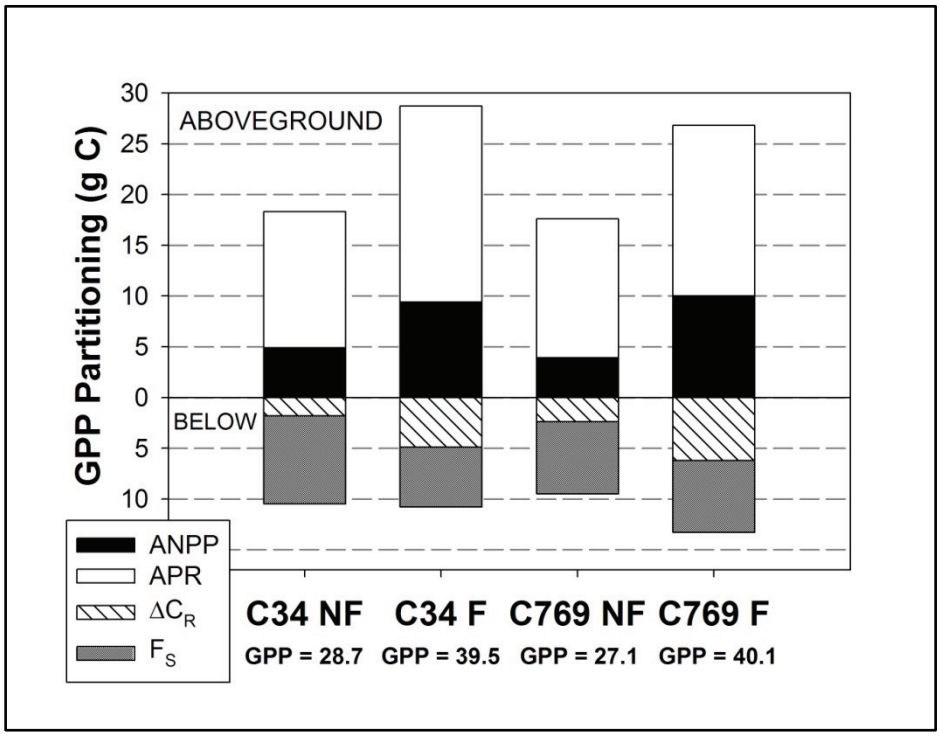

Figure 1—Carbon budget for two clones (C34 and C769) under two fertilizer regimes (F = fertilizer, NF = no fertilizer) over 121 days. GPP = gross primary productivity, ANPP = aboveground net primary productivity, APR = aboveground plant respiration, F_S = soil CO_2 efflux, and ΔC_R = C accumulation in roots, or belowground net primary productivity. Statistics are shown in Table 3.