Elevated atmospheric CO2 and drought alter carbon allocation above but not belowground in *Eucalyptus saligna*

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# Abstract

# Key Words

# Introduction

Carbon (C) allocation in trees encompasses investment into biomass production above and belowground as well as fluxes including tissue respiration and exudation (Litton et al. 2007). Trees must allocate C to maximize competitive fitness, reproduction and growth across their life cycle (Dickson 1989). In resource saturated environments plant should maximizes growth by allocating new C to leaves to increase C acquisition (Monsi and Saeki 2005). Environmental stresses such as water, nutrient and light availability, however, may cause plants to invest in roots for belowground resources or stem elongation for increased light harvesting (Friedlingstein et al. 1999). These potential changes in C investment are part of a dynamic system: as the tree grows or sink activities are altered, the fate of C assimilate can shift through time. Understanding allocation is vital, as partitioning among plant organs and their feedback processes profoundly impacts plant growth (Friedlingstein et al. 1999, Lacointe 2000, Shipley and Meziane 2002).

This distribution of photosynthetic C above and belowground is an important factor in terrestrial C cycling yet our knowledge of how global change impacts this distribution is incomplete (Litton et al. 2007, Warren et al. 2012). With rising atmospheric [CO2] (Ca), forest C allocation has drawn particular interest due to its potential effect on C sequestration and the global C balance (Franklin et al. 2012). A meta-analysis by Porter et al (2000) concluded that on average C allocation in plants grown under elevated CO2 (eCa) did not change. Alternatively, total bewloground C allocation (TBCA) was found to be enhanced across four forested free-air Ca enrichment experiments (Palmroth et al. 2006). Understanding the impacts of global climate change on forests also requires investigation of interacting factors in order to tease apart multifaceted relationships (Rustad 2008). For example, how limitations imposed by drought interact with the growth-stimulating effects of increasing Ca requires further attention (Duursma et al. 2011). As a result, there is continued need to empirically measure patterns of tree C allocation under multi-factor global change manipulations to better understand shifts in future forest C balance.

Carbon allocation is best understood by examining all facets of allocation, however, data on TBCA remain sparse and reliable estimates of root biomass in field conditions are difficult to obtain (Litton et al. 2007, Poorter et al. 2012). In forest ecosystems, TCBA has been shown to be equal or greater than aboveground production (Law et al. 1999), yet the controls of this belowground flux are poorly understood (Raich and Nadelhoffer 1989, Giardina et al. 2005).Total belowground carbon allocation is often conceptualized by subtracting the changes in carbon pools of litter, soil and roots from soil CO2 efflux (Raich and Nadelhoffer 1989, Davidson et al. 2002, Giardina and Ryan 2002, Palmroth et al. 2006). A key assumption of this approach is that the changes among the carbon pools are in steady-state conditions (Raich and Nadelhoffer 1989), which is seldom true. Additionally, the reliance on soil respiration in this approach is problematic as studies are often forced to scale up short-term measurements (often monthly) to yearly fluxes while also using a variety of measurement techniques. As allocation of C belowground remains one of the most difficult components of tree C budgets to calculate, new approaches are needed to in order accurately track and account for the investment of carbon belowground.

Consequently, the representation of C allocation is rudimentary compared to A in applied forest models (Friedlingstein et al. 1999, Franklin et al. 2012) and predictions of C allocation is a weak link in current models (McMurtrie and Dewar 2013). The deficiency of large-scale models to allocate C is due to the difficulty in defining principles that are valid under a wide range of conditions (Franklin et al. 2012). As a result, partitioning coefficients or fixed fractions of assimilation, representing the flux of carbon to a particular component, are often used in process-based models of forest carbon cycling (Litton et al. 2007, Franklin et al. 2012). Unfortunately, any use of inappropriate or over simplified allocation schemes can lead to models producing unintended responses (De Kauwe et al. 2014). Additionally, modelling efforts predicting responses of belowground C allocation to global change often assume that responses of aboveground tissues represent those of belowground tissues (Giardina et al. 2005). Generalizations of relationships between aboveground and belowground factors should be made with caution as substantial variation has been reported across forest types (Giardina et al. 2005 and references therein).Currently, the large variation in observed C allocation in response to environmental change combined with a lack of understanding of the mechanisms driving C allocation hinders accurate modelling of global change on terrestrial C cycling (Friedlingstein et al. 1999, Landsberg 2003, Litton et al. 2007, Epron et al. 2012, McMurtrie and Dewar 2013).

The whole-tree chambers (WTC), located at the Hawkesbury Forest Experiment, were designed to allow continuous measurement of whole-tree net CO2 and water fluxes, allowing A, respiration and transpiration to be calculated using a mass balance approach (Medhurst et al. 2006, Barton et al. 2010). Generally, measuring canopy A is difficult as variation in photosynthetic capacity exists within the canopy in response to the environment, requiring leaf measurements and models to upscale to the canopy (Ryan et al. 2010). The WTC, however, can resolve net aboveground C gain (canopy A minus respiration of foliage and aboveground woody components), at high temporal resolution, while controlling temperature and air humidity at ambient conditions. Combining the high resolution carbon flux measurements with an evergreen *Eucalpytus* species that provides near constant annual production enables carbon allocation above and belowground to be tracked over long periods of time. This experimental system can then be used to validate models that scale leaf gas exchange to whole canopies with empirical measurements of the response of whole-tree CO2 fluxes and biomass production to global change manipulations (Barton et al. 2010).

Previous findings in this experiment have shown that trees grown under elevated CO2 were smaller than ambient trees and that larger trees had a smaller reduction in canopy transpiration in drought conditions via deeper access to water resources (Duursma et al. 2011). Therefore, the specific objectives of this study were to determine the response of C allocation among foliage, aboveground woody components and roots of a native Australian tree species to changes in atmospheric CO2 and altered water availability. Utilizing the unique WTC design we then aimed to test how cumulative net aboveground C gain correlates to whole tree carbon mass increment, as a function of tree size. We then applied a mass balance approach to to track the distribution of carbon above and belowground over a one year period.

(1) Overall, the effects of drought and elevated CO2 were expected to alter partitioning of C among biomass components from ambient conditions.

(2) As productivity and growth must be coordinated over long time periods we expected the harvested carbon mass tissue pools to correlate with cumulative total aboveground net canopy carbon uptake.

(3) High resolution data of whole-tree net CO2 flux, provided by the WTC design, were expected to provide empirical evidence of canopy carbon uptake not affected by soil CO2. This canopy flux could then be combined with estimates of aboveground carbon mass to provide a novel framework in which to investigate total belowground carbon allocation

# Methods

## Whole tree chamber experimental design

From April 2007 *Eucalyptus saligna* Sm. seedlings were grown in 12 WTC at the Hawkesbury Forest Experiment in Richmond, Australia. One seedling per WTC (9 m high) was grown for 18 months and chamber conditions tracked outside air temperature and humidity. Each WTC was fitted with a root enclosure barrier that extended to the soil hard layer (1 m depth), separating WTC tree roots from neighboring trees. Roots were allowed to freely grow below 1 m. Full descriptions of the chamber design and operation are provided in Barton el al. (2010). This multifactor experimental design included Ca × drought treatments with three replicates in each of four treatments. Six chambers were kept at ambient Ca of 380 ppm (aCa) and six were maintained at eCa of +240 ppm above ambient. Through October 27th, 2008 all trees were kept well-watered, with 10 mm of water every 3 days. Half of the chambers were then subjected to a drought treatment by completely withholding water (dry) and the remaining six chambers were kept well-watered as an irrigated control (wet). The drought treatment lasted through mid-February 2009 when heavy rainfall ended the drought effect, despite the presence of a root enclosure.

## Above ground chamber CO2 flux

Floors installed above the soil surface, enclosing the main bole, permitted the chambers to functions as cuvettes and allowed for whole tree fluxes of CO2 to be monitored once trees were ca. 3.5 m in height. This allowed high resolution CO2 flux data at 14 min intervals to be collected over the final year of the experiment. Chamber flux measurements were calculated as an hourly time step generated from the average of the raw 14 min (mol hour-1) from each chamber. Missing CO2 flux data were gap filled with SOLO (self-organizing linear output map) (see Abramowitz 2005). This self-fitting model predicted the flux as a function of photosynthetically active radiation, air temperature, vapor pressure deficit and day of year. For this analysis, diurnal CO2 chamber fluxes were converted to grams of C per chamber flux area (10 m2). Cumulative daily carbon fluxes (, g C d-1) were then generated over the last year of the experiment to compare with C allocation above and belowground.

## Harvested tree carbon mass

A final destructive harvest was completed in mid-March 2009. Each tree was harvested across 5 canopy layers, set from the floor height and extended through the top of the canopy. Dry biomass of leaves, branches and boles were measured for each layer and summed for each WTC. Root mass was obtained by excavating and seiving all soil inside each root exclusion barrier to the hard layer. Five roots cores (10 mm diameter) where collected from 0-70 cm in each chamber and biomass from cores was added back to the standing crop total.

Carbon mass was assumed to be 50% of dry biomass for all non-leaf tissue components and this conversion was performed for all harvest and survey (below) data. Leaf and litter carbon mass was calculated by multiplying harvested or estimated biomass by the WTC specific mean leaf carbon content (%). Leaf carbon content was determined from a subsample of final harvest dried and milled leaves analyzed using a Leco TruSpec Micro elemental analyzer (LECO corporation, MI, USA). Mass fractions of leaves, boles+branches and roots were calculated by dividing their respective carbon mass by total carbon mass for each tree.

Additionally, prior to the initiation of the experiment a subset of potted plants of *Eucalyptus saligna* (n=17) were harvested to develop relationships between above and belowground biomass. These seedlings were grown in 25 l pots inside each WTC, while chamber conditions were maintained, until the experiment was started.

## Tree Allometric Surverys

Tree height was measured bi-weekly and stem diameters were recorded monthly at regular intervals (30 cm) along the main bole and split stems. Tree diameters at 65 cm height were used as the standard diameter because none of the trees had split stems at this height. Diameter and length for every branch, including forked branches, were surveyed across seven dates over the final year of the experiment. Branch diameter measurements were recorded at 5 cm from their individual insertion points. Leaf litter was collected from the chambers bi-weekly, oven-dried and weighed.

## Bole Carbon

During the final harvest diameter measurements were recoreded as described above and 1 cm sections were removed from the bole at regular intervals between these measurements. Wood density for each section were calculated by dividing the dry mass by the fresh volume seperately for bark and wood. The mean total bole density for each tree () was then calculated as the total density of bark and wood, weighted by the total diameter of each section.

For boles, individual volume units were constructed as concentric cylinders between diameter intervals from base to tip for each monthly survey. This approach assumed any bole taper was accounted for in the difference in volume between bole sections. The last section including the top of the tree was calculated as a cone with a tip radius of .001 cm. The volume below the standard diameter (65 cm) was calculated separately in order to interpolate taper into this section. Using the height of the tree and the standard diameter, the diameters at 30cm and base were estimated by extending the length of the pre-existing cone. This resulted in two additional stem sections with taper assumed as previously stated. All volume units were then summed, including split stems, to calculate total tree volume. Bole mass was calculated as total volume multiplied by WTC specific .

## Branch Carbon

Additionally, final harvest basal area and length of each branch were measured and used to calculate the total branch volume. A volume shape factor, from Makela et al. (1997), was applied to each branch volume to designate each branch as an intermediate shape between a volumetric cone and a cylinder (, 0.75). A wood density parameter for branches () in each WTC was calculated as the total branch dry mass divided by the cumulative branch volume. Due to a thin bark layer on branches a separate bark density parameter was not created.

To obtain branch mass during each survey period, volume of all individual branches were calculated as outlined above. As diameters were not recorded at branch insertion points, 5 cm were added back to each branch length in order to represent the entire branch volume. Branch mass, at any time point, was the individual branch volume multiplied by WTC specific . We assumed that neither nor calculated from the final harvest changed through time.

## Leaf area and carbon

Final harvest total leaf area and dry mass were measured for each of the five canopy layers. Specific leaf area (SLA, cm2 g-1) was calculated by dividing cumulative tree leaf area by leaf mass for each canopy layer. Mean SLA for each chamber was obtained by weighting SLA of each of the 5 layers by their foliage mass fraction. Estimates of standing leaf area were also obtained in April 2008 from leaf counts for each tree, multiplied by tree-specific mean leaf size (based on a sub-sample).

Canopy leaf area was modeled on daily times steps using the leaf count census and harvest leaf area estimates, along with height growth and litter fall rates. Leaf growth was assumed to coincide with height growth, so that no leaf growth occurred when height growth had ceased. This method assumes that total cumulative leaf area (i.e. standing leaf area plus that produced by litter fall) followed and allometric relationship with tree height (Barton et al. 2010) such that:

(1)

where is the total 'potential' leaf area (m2), a and b are tree specific coefficients and H is tree height (m). Then standing leaf area at time t are obtained from tree height at time t and cumulative litterfall:

(2)

where is the litterfall (m2 t-1) rate at time t. Litter was assumed to be produced by all canopy layers. The daily leaf area contribution of litterfall is the difference between and . The mean SLA for each harvested tree was multiplied by daily estimates leaf and litterfall area to calculate biomass. Specific leaf area was assumed to be constant over the final year of the experiment.

## Total Belowground Carbon Allocation

As the installation of chamber floors into each WTC separated the aboveground carbon uptake from the soil carbon efflux, total belowground carbon allocation (TBCA) at any time point was able to be calculated as:

(3)

where is the gross primary productivity (g C) of the each tree aboveground minus respiration of leaves, stems and branches and is the total standing crop carbon mass (g C) of stems, branches, leaves and cumulative leaf litterfall . As the final standing crop of root biomass was known, TBCA could be further broken down into the total carbon mass of roots () and the residual belowground carbon flux (). The residual belowground carbon flux includes; root and soil respiration, root turnover, root exudation and any unaccounted for root carbon mass. The use of aboveground allometry to interpolate through time combined with Fc allowed TBCA to be estimated on daily time steps over the final year of the experiment while was calculated at the final harvest.

## Visualizing carbon allocation via mass balance

The contributions of aboveground tissue components and TBCA to carbon mass balance were visualized by combining estimates of bole, branch, leaf and litterfall carbon with over the final 11 months of the experiment. The cumulative sum of , at any given time point, represented the net carbon uptake for each WTC. The allocation of carbon to boles and branches were seen by linear interpolation between survey measurements and the final harvest. Daily modeled estimates of leaf and litter carbon were then added to bole and branch carbon mass to estimate on any given day. Importantly, the initial estimated carbon mass of each aboveground component and on the first day were subtracted from all respective daily values so mass balance could be tracked with a 0 starting value. The significant log-linear relationship between aboveground mass of harvested trees and potted seedlings (R2 = 0.98) was used to predict using on the final date.

## Data analysis

Differences in experimental parameters to the interaction of CO2 and drought treatments at the final harvest where analysed using two-way ANOVA in R (R Development Core Team 2011). If interactions were present, planned pairwise comparisons were analyzed using one-way ANOVA and p-values were adjusted as in Benjamini & Hochberg (1995). Results were considered significant at P ≤ 0.05.

# Results

## Total canopy carbon flux, leaf area and whole tree carbon

There was a positive linear relationship between and both whole tree carbon (R2 = 0.86, Figure 1,a) and (R2 = 0.78, Figure 1,b). was significantly reduced by 30.5 % under elevated CO2 (P = 0.043), while no effects of the drought treatment were detected. Similarly, both whole tree carbon and were reduced under elevated CO2 by ca. 32 % (both P < 0.03). Leaf area at the final harvest was significantly reduced by by 31.3% under elevated CO2 (p < 0.001), which was also evident across the final year of the experiment (Figure 2). Overall, was positively correlated with mean daily leaf area (P < 0.001, R2 = 0.77, Figure 3).

## Tree carbon allocation

Carbon allocation to individual tissue components were affected differentially by CO2 and drought treatments (Table 1). There was a marginal interaction of elevated CO2 and drought on harvested bole carbon mass (p = 0.075). Elevated CO2 reduced bole carbon mass only in wet treatments (P = 0.041), while drought was found to reduce bole carbon mass in ambient CO2 treatments only (P = 0.051). Total branch carbon mass was marginally reduced under elevated CO2 (P = 0.086) but was not affected by drought. Neither leaf or litter carbon mass were affected by elevated CO2 and drought treatments. Total root carbon mass was marginally reduced under elevated CO2 (P = 0.091) but not affected by drought.

Final LMF was increased by 15.2% under elevated CO2 (P = 0.031) but not affected by the drought treatment. Final LMF was negatively correlated with (R2 = -0.62, Figure 4a). Final SMF was reduced by 8% under elevated CO2 (P = 0.014), with no effect of the drought treatment detected. Final SMF was positively correlated with F[c,t] (R2 = 0.37, Figure 4b). Final RMF was not affected by either treatment nor related to (Figure 4c).

## Total belowground carbon allocation

Within each treatment combination the cumulative carbon mass of each tree component (boles, branches, leaves and roots) did not achieve mass balance with (Figure 5). Across a large range in tree size, similar patterns were detected in each individual WTC (Figure S1). It was therefore necessary to account for allocation to both TBCA and . Neither TBCA nor were affected by CO2 or drought treatments (Figure 6). Thus, even though F[c,t] and allocation to aboveground tissue components were affected by the treatments the allocation of of carbon belowground was relatively constant at the final harvest. Total belowground carbon allocation and were positively correlated at the final harvest (R2 = 0.65, P < 0.001) and the proportion of C allocated belowground was relatively constant through time and between treatments (Figure 7). TBCA had a weak positive correlation with mean daily leaf area (R2 = 0.26, P = 0.093), while F[s,r] and leaf area were not related.

# Discussion

# List of Tables

# Tables

**Table 1**.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Treatment** | **Bole** | **Branch** | **Leaf** | **Litter** | **Root** | **Tree C flux** |
| aCO2-dry | 5449.8 (715.6) b | 2915.9 (654.4) a | 2642.8 (370.7) a | 1129.8 (336.0) a | 3180.1 (521.0) a | 19394.2 (2169.5) a |
| aCO2-wet | 4250.6 (710.9) ab | 2006.3 (384.8) a | 2232.1 (235.4) a | 889.4 (82.6) a | 2623.6 (501.7) a | 14620.7 (3456.2) a |
| eCO2-dry | 8109.4 (278.2) a | 3286.0 (715.7) a | 3254.2 (393.5) a | 1043.1 (47.3) a | 3830.6 (330.1) a | 23556.5 (1689.0) a |
| eCO2-wet | 4194.1 (816.0) a | 1934.2 (494.3) a | 2358.3 (473.6) a | 919.0 (244.3) a | 2306.1 (735.2) a | 15197.9 (3253.5) a |

# List of Figures

**Figure 1**. Treatment means of harvested whole tree carbon mass (a) and aboveground carbon mass (b) as a function of cumulative canopy carbon flux over the final year of the experiment. The dotted line is the 1:1 relationship and the solid lines represent the significant linear model fit for whole tree carbon (R2 = 0.86) and aboveground carbon mass (R^2 = 0.78).

**Figure 2**. Estimated tree leaf area for each chamber trees between 2008-4-15 and 2009-3-16. Estimates are based on height growth, litterfall rates, and leaf area estimates at two dates. Color and and line type distinguish the treatment combination for each individual chamber.

**Figure 3**. Treatment means of cumulative canopy carbon flux as a function on mean daily leaf area over the final year of the experiment. The solid line represents the significant linear model fit (R2 = 0.77).

**Figure 4**. Treatment means of carbon mass partitioning to leaves (a), boles + branches (b) and roots (c) at final harvest as a function of tree size (total tree carbon). Solid lines represent model fit for either LMF, SMF or RMF (R2 = -0.55, 0.55 and 0.01, respectively).

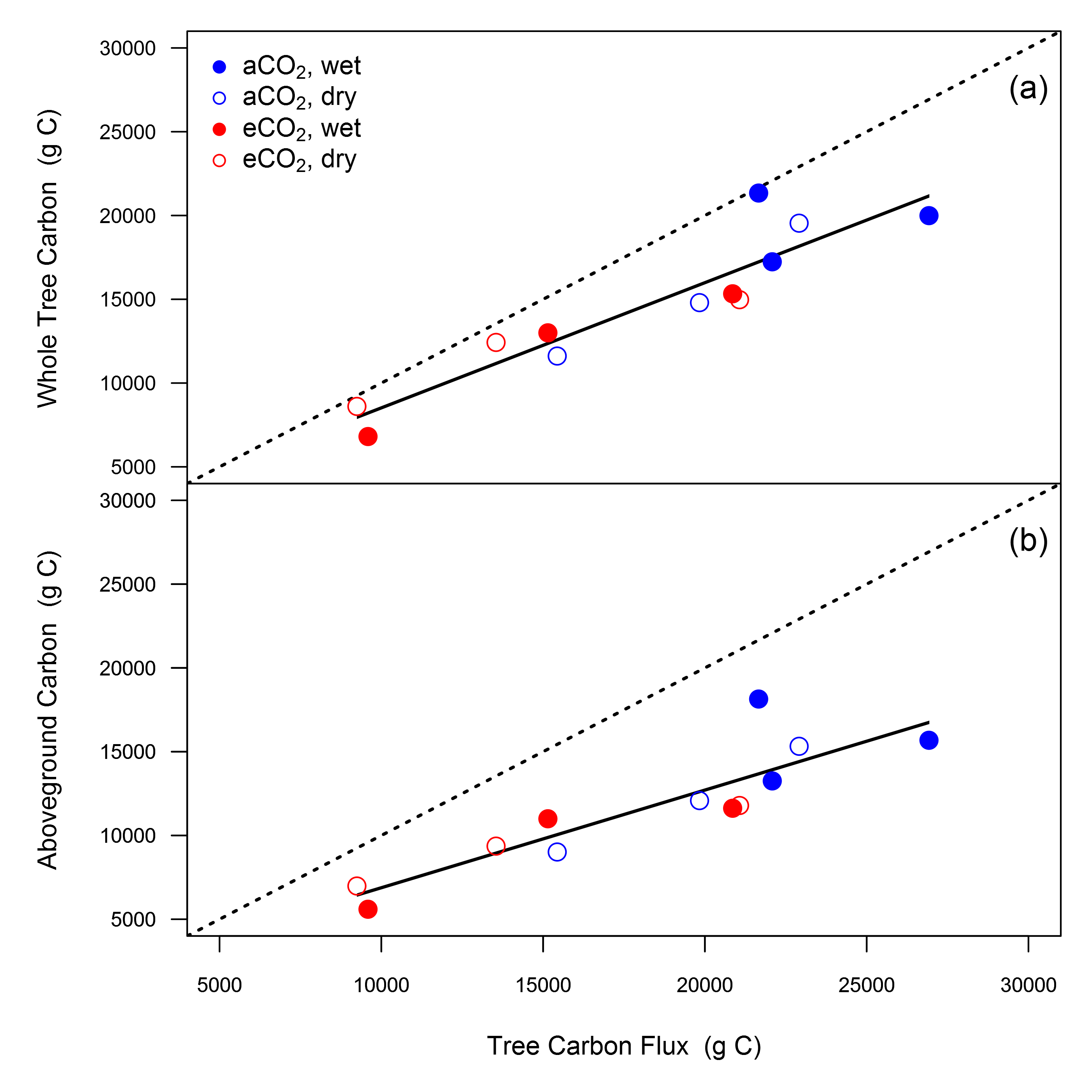
**Figure 5**. Cumulative canopy carbon flux and additive carbon mass partitioning of individual tree components from 2008-4-15 and 2009-3-16 for each treatment combination. Both carbon flux and tissue carbon partitioning where set to 0 on 2008-4-15 in order to track allocation of new C uptake on a daily time scale. Total root carbon mass, predicted from the log relationship between above and belowground mass partitioning of pre-planting seedlings and harvested trees, is shown on the last date.

**Figure 6**. Treatment means ± 1 standard error of cumulative canopy carbon flux, total belowground carbon allocation, and the residual belowground C flux at the final harvest.

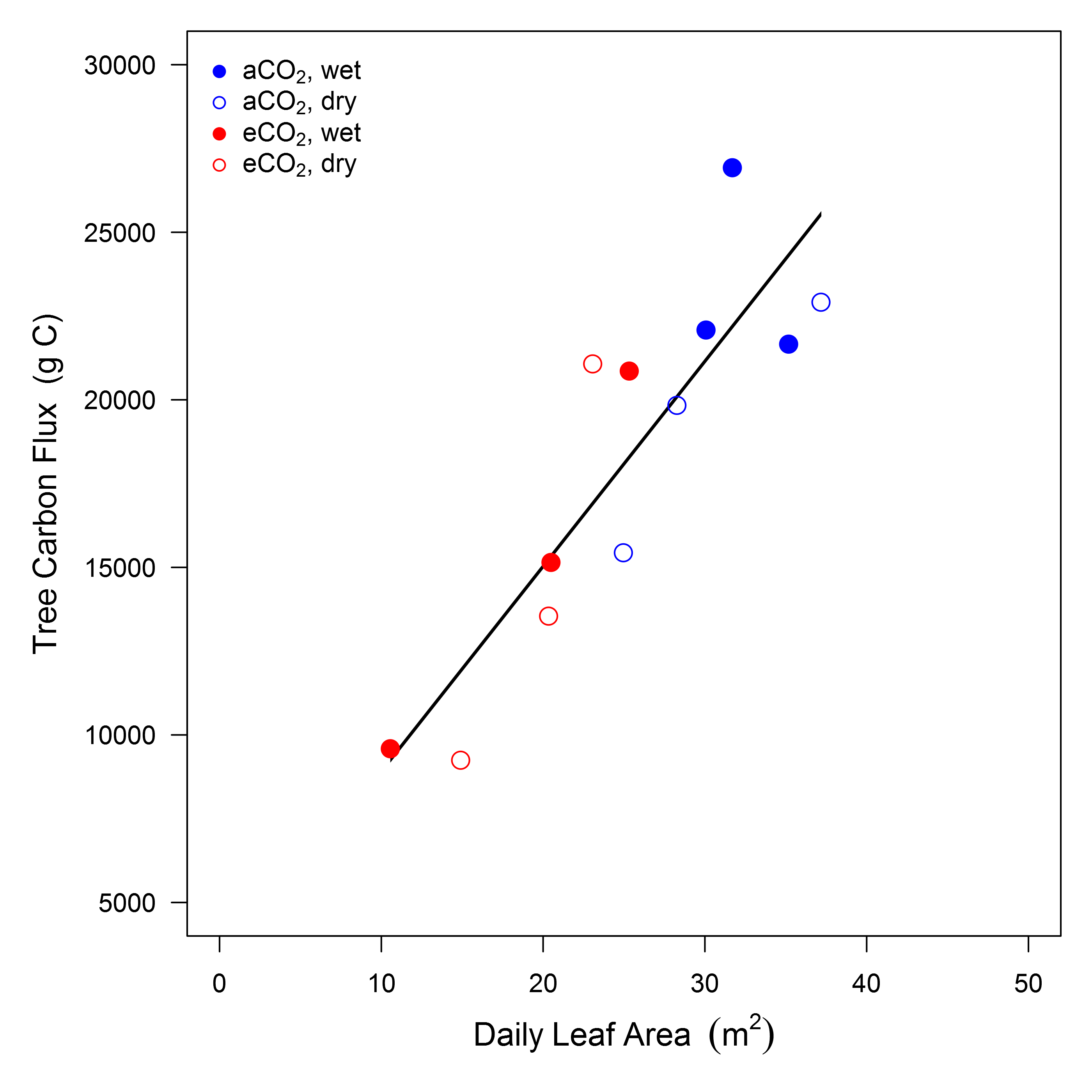
**Figure 7**. Total belowground carbon allocation as a function of cumulative canopy carbon flux across the final year of the experiment. Carbon allocation aboveground was estimated from allometric surveys, interpolated on a daily time scale and then removed from the cumulative canopy carbon flux to then quantify TBCA. Individual lines represent treatment means and the dotted line is the 1:1 relationship.

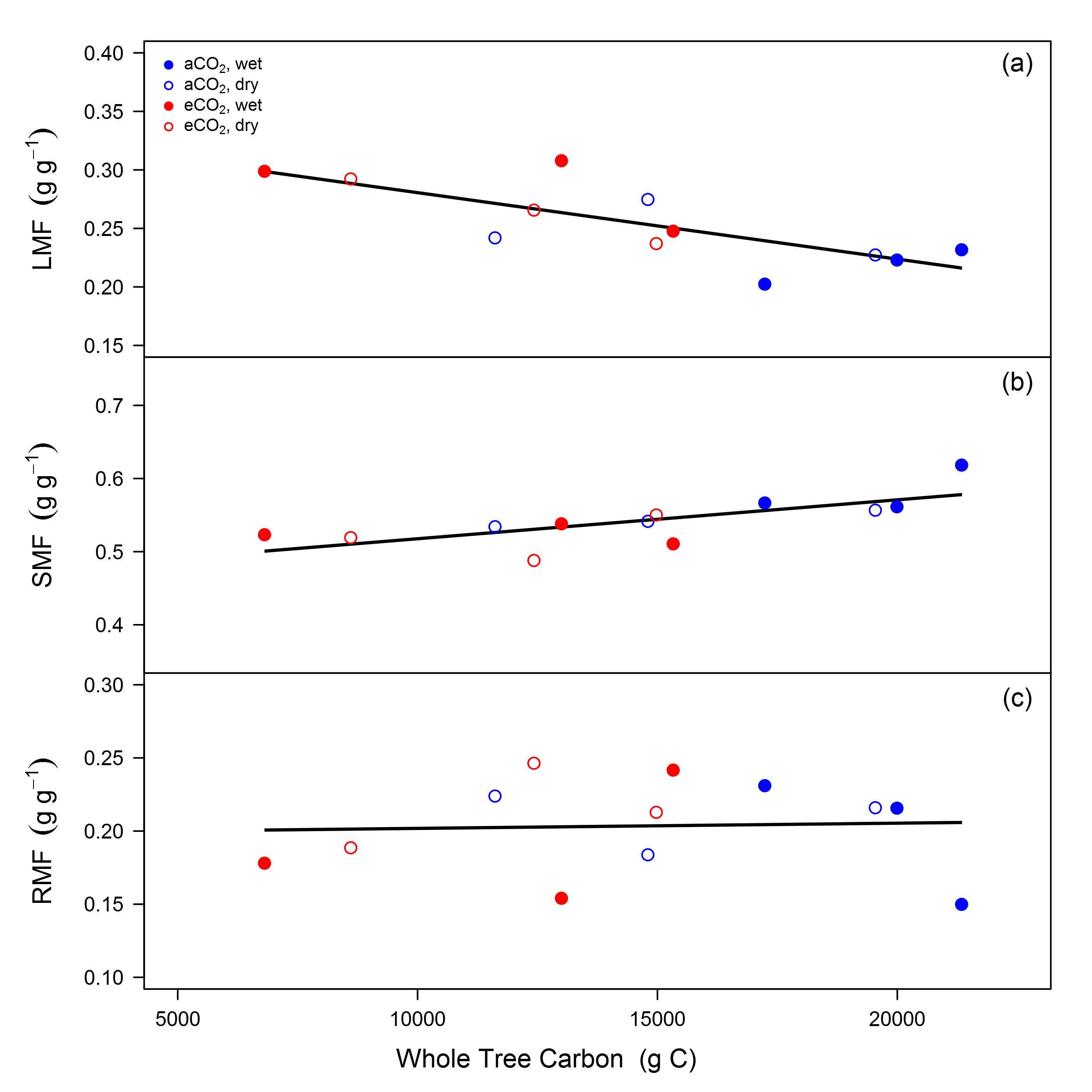
**Figure S1**. Cumulative canopy carbon flux and additive carbon mass partitioning of individual tree components from 2008-4-15 and 2009-3-16 for each individual WTC. Both carbon flux and tissue carbon partitioning where set to 0 on 2008-4-15 in order to track allocation of new C uptake on a daily time scale. Total root carbon mass, predicted from the log relationship between above and belowground mass partitioning of pre-planting seedlings and harvested trees, is shown on the last date.

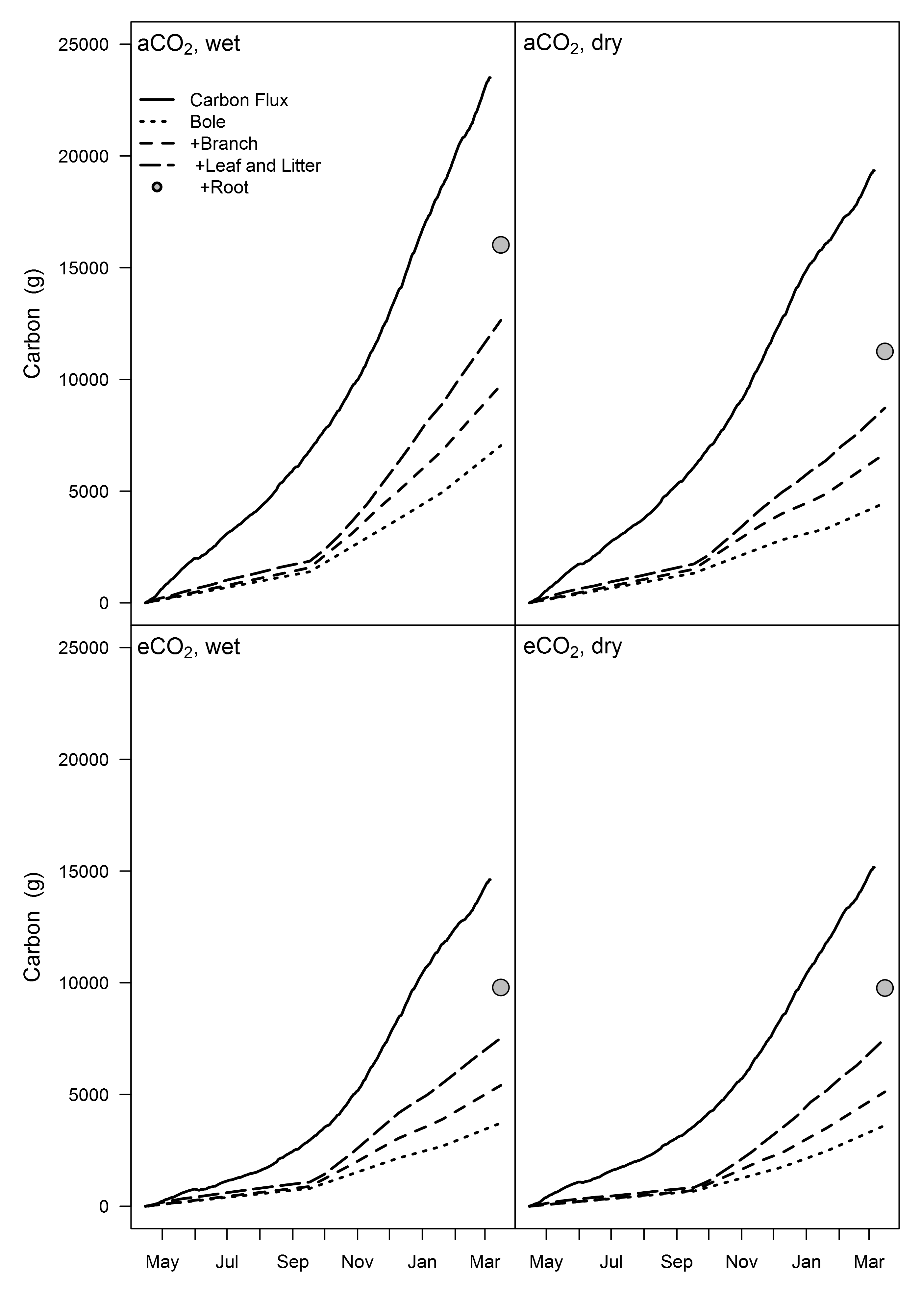
# Figures

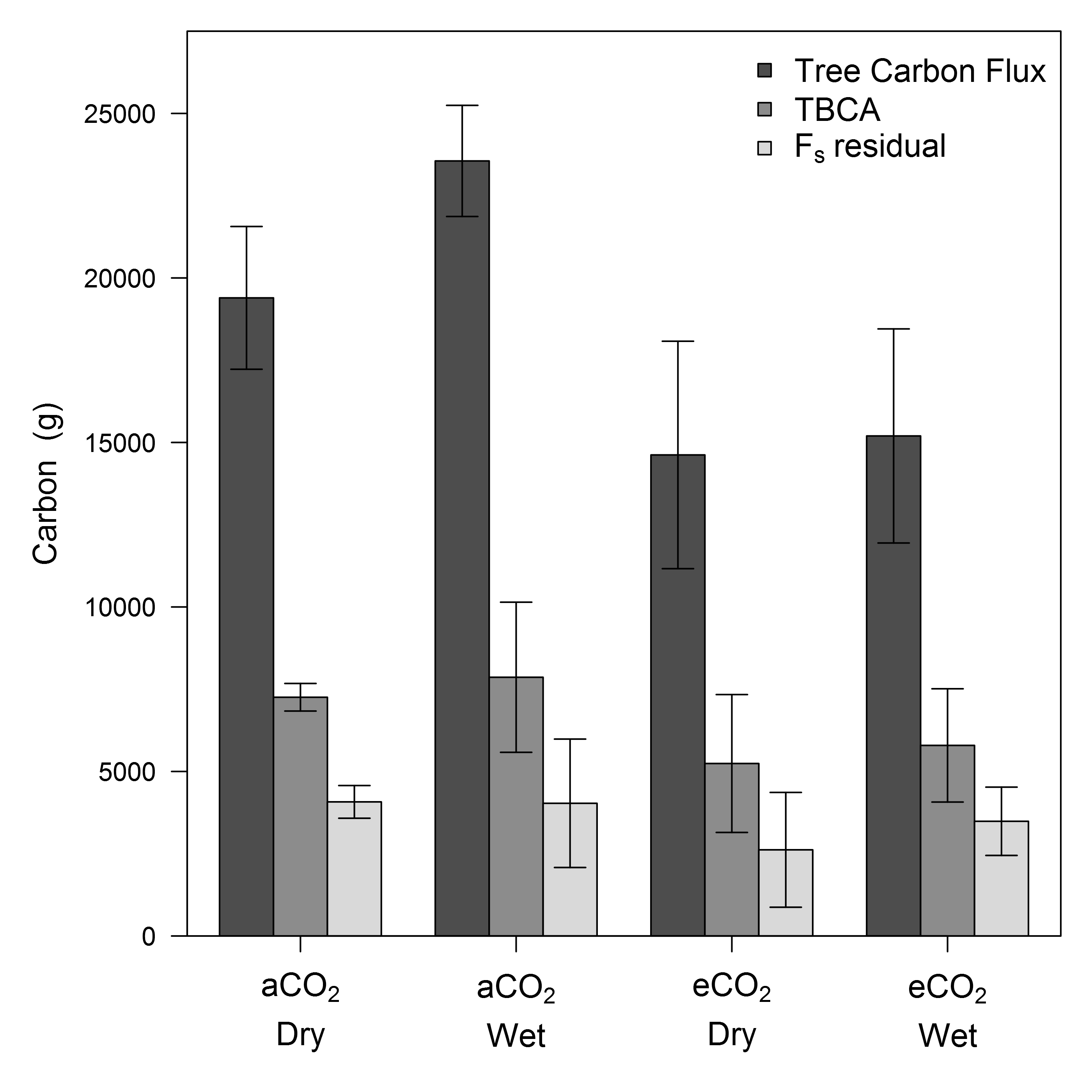
  
**Figure 1**.

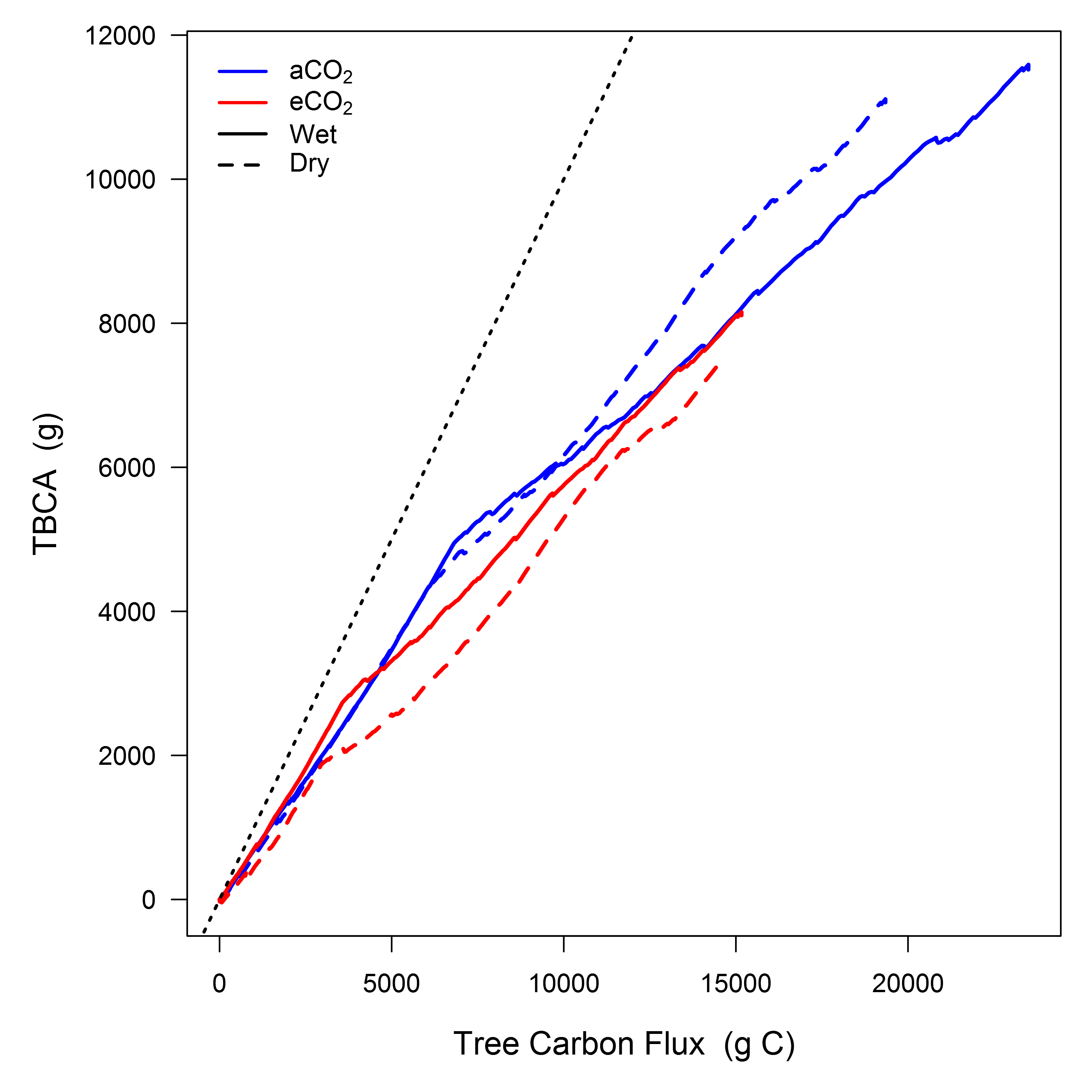
  
**Figure 2**.

  
**Figure 3**.

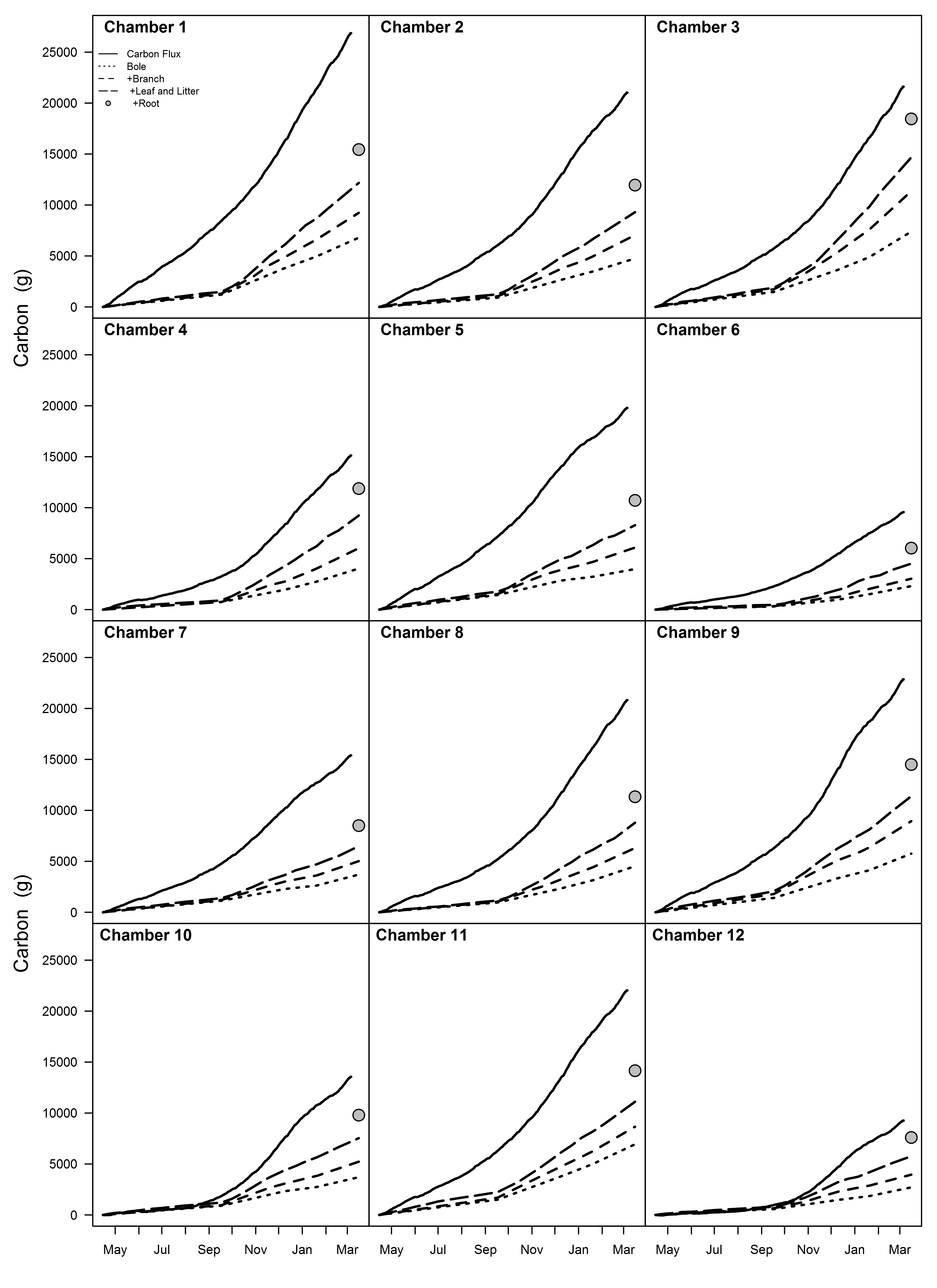
  
**Figure 4**.

  
**Figure 5**.

  
**Figure 6**.

  
**Figure 7**.

# Supporting Information

  
**Figure S1**.

# References

Abramowitz G (2005) Towards a benchmark for land surface models. Geophysical Research Letters 32

Barton CVM, Ellsworth DS, Medlyn BE, Duursma RA, Tissue DT, Adams MA, Eamus D, Conroy JP, McMurtrie RE, Parsby J, Others (2010) Whole-tree chambers for elevated atmospheric CO 2 experimentation and tree scale flux measurements in south-eastern Australia: The Hawkesbury Forest Experiment. Agricultural and Forest Meteorology 150:941–951.

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society Series B (Methodological):289–300.

Davidson EA, Savage K, Bolstad P, Clark DA, Curtis PS, Ellsworth DS, Hanson PJ, Law BE, Luo Y, Pregitzer KS, Others (2002) Belowground carbon allocation in forests estimated from litterfall and IRGA-based soil respiration measurements. Agricultural and Forest Meteorology 113:39–51.

De Kauwe MG, Medlyn BE, Zaehle S, Walker AP, Dietze MC, Wang Y-P, Luo Y, Jain AK, El-Masri B, Hickler T, Others (2014) Where does the carbon go? A model–data intercomparison of vegetation carbon allocation and turnover processes at two temperate forest free-air CO2 enrichment sites. New Phytologist 203:883–899.

Dickson RE (1989) Carbon and nitrogen allocation in trees. In: Annales des sciences foresti{è}res. EDP Sciences, pp 631s—–647s.

Duursma RA, Barton CVM, Eamus D, Medlyn BE, Ellsworth DS, Forster MA, Tissue DT, Linder S, McMurtrie RE (2011) Rooting depth explains [CO2]times drought interaction in Eucalyptus saligna. Tree physiology:tpr030.

Epron D, Nouvellon Y, Ryan MG (2012) Introduction to the invited issue on carbon allocation of trees and forests. Tree physiology 32:639–643.

Franklin O, Johansson J, Dewar RC, Dieckmann U, McMurtrie RE, Brännström Å, Dybzinski R (2012) Modeling carbon allocation in trees: a search for principles. Tree Physiology:tpr138.

Friedlingstein P, Joel G, Field CB, Fung IY (1999) Toward an allocation scheme for global terrestrial carbon models. Global Change Biology 5:755–770.

Giardina CP, Ryan MG (2002) Total belowground carbon allocation in a fast-growing Eucalyptus plantation estimated using a carbon balance approach. Ecosystems 5:487–499.

Giardina CP, Coleman MD, Hancock JE, King JS, Lilleskov EA, Loya WM, Pregitzer KS, Ryan MG, Trettin CC (2005) The response of belowground carbon allocation in forests to global change. In: Tree species effects on soils: Implications for global change. Springer, pp 119–154.

Lacointe A (2000) Carbon allocation among tree organs: a review of basic processes and representation in functional-structural tree models. Annals of Forest Science 57:521–533.

Landsberg J (2003) Modelling forest ecosystems: state of the art, challenges, and future directions. Canadian Journal of Forest Research 33:385–397.

Law BE, Ryan MG, Anthoni PM (1999) Seasonal and annual respiration of a ponderosa pine ecosystem. Global Change Biology 5:169–182.

Litton CM, Raich JW, Ryan MG (2007) Carbon allocation in forest ecosystems. Global Change Biology 13:2089–2109.

Mäkelä A (1997) A carbon balance model of growth and self-pruning in trees based on structural relationships. Forest Science 43:7–24.

McMurtrie RE, Dewar RC (2013) New insights into carbon allocation by trees from the hypothesis that annual wood production is maximized. New Phytologist 199:981–990.

Medhurst J, Parsby J, Linder S, Wallin G, Ceschia E, Slaney M (2006) A whole-tree chamber system for examining tree-level physiological responses of field-grown trees to environmental variation and climate change. Plant, cell & environment 29:1853–1869.

Monsi M, Saeki T (2005) On the factor light in plant communities and its importance for matter production. Annals of Botany 95:549–567.

Palmroth S, Oren R, McCarthy HR, Johnsen KH, Finzi AC, Butnor JR, Ryan MG, Schlesinger WH (2006) Aboveground sink strength in forests controls the allocation of carbon below ground and its [CO2]-induced enhancement. Proceedings of the National Academy of Sciences 103:19362–19367.

Poorter H, Nagel O (2000) The role of biomass allocation in the growth response of plants to different levels of light, CO2, nutrients and water: a quantitative review. Functional Plant Biology 27:1191.

Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytologist 193:30–50.

R Development Core Team R (2011) R: A Language and Environment for Statistical Computing Team RDC (ed). R foundation for statistical computing 1:409. <http://www.r-project.org>

Raich JW, Nadelhoffer KJ (1989) Belowground carbon allocation in forest ecosystems: global trends. Ecology 70:1346–1354.

Rustad LE (2008) The response of terrestrial ecosystems to global climate change: towards an integrated approach. Science of the Total Environment 404:222–235.

Ryan MG, Stape JL, Binkley D, Fonseca S, Loos RA, Takahashi EN, Silva CR, Silva SR, Hakamada RE, Ferreira JM, Others (2010) Factors controlling Eucalyptus productivity: How water availability and stand structure alter production and carbon allocation. Forest ecology and management 259:1695–1703.

Shipley B, Meziane D (2002) The balanced-growth hypothesis and the allometry of leaf and root biomass allocation. Functional Ecology 16:326–331.

Warren JM, Iversen CM, Garten CT, Norby RJ, Childs J, Brice D, Evans RM, Gu L, Thornton P, Weston DJ (2012) Timing and magnitude of C partitioning through a young loblolly pine (Pinus taeda L.) stand using 13C labeling and shade treatments. Tree physiology 32:799–813.